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Accounting for food webs to conserve biodiversity and nature's contributions to people in the context of global changes

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THÈSE

Pour obtenir le grade de

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Spécialité : Biodiversité-Ecologie-Environnement

Unité de recherche : Laboratoire d'ECologie Alpine

La pertinence des réseaux écologiques pour la conservation de la biodiversité et des services écosystémiques face aux changements environnementaux

Accounting for food webs to conserve biodiversity and nature's contributions to people in the context of global changes

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Abstract

The erosion of biodiversity is likely to cause a profound reorganisation of the living world, as species are connected through their interactions (e.g. between predators and prey species), and they underpin many nature's contributions to people (NCP). However, species interactions are typically not considered in biodiversity scenarios or in systematic conservation planning. Accounting for species interactions has been hampered by i) the unavailability of large scale datasets on species interactions, ii) a poor understanding of the way species assemble in interacting communities across space and iii) a lack of analytical tools and metrics to analyse them and integrate them in conservation biogeography. The objectives of my thesis are to develop a conceptual and analytical framework to understand the spatial distribution of food webs and their vulnerability to anthropogenic threats, and how best to integrate this new paradigm in conservation. This thesis is structured in three parts. First, I characterise the structure of food webs across Europe, and their contribution to species-based NCP. Second, I investigate how interactions can improve our understanding of the impact of human activities on species and nature's contributions to people. Third, I explore priority areas for the conservation of species and NCP, and I propose and apply a framework to use food web data in systematic conservation planning. This work is based on the development of datasets on the 1,152 terrestrial vertebrates known to occur in Europe: trophic interactions, ecological traits, geographical ranges, and habitat requirements. By combining food web ecology with biogeography and conservation biology, my work offers new perspectives on our understanding of how biodiversity is responding to anthropogenic pressures, and what we can do to conserve life on Earth.

List of Papers

This thesis is based on the following papers:

1. **O'Connor, L.**, Pollock, L.J., Braga, J., Ficetola, G.F., Maiorano, L., Martinez-Almoyna, C., Montemaggiore, A., Ohlmann, M. and Thuiller, W. (2020). Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche. *Journal of Biogeography*, 47(1), 181-192.
2. **O'Connor, L.**, Demarquet, S., Maiorano, L., Verburg, P. H., and Thuiller, W. Terrestrial vertebrates and their interactions underpin essential nature's contributions to people. (To be submitted to *Global Ecology and Biogeography* as a Data article)
3. **O'Connor, L.**, Harfoot, M., Maiorano, L. Pollock, L. J., and Thuiller, W. Vulnerability of terrestrial vertebrate food webs to anthropogenic threats in Europe. (To be submitted to *Diversity and Distributions* as a Perspective paper)
4. **O'Connor, L.**, Dou, Y., Karger, D., Maiorano, L., Renaud, J., Verburg, P. H., Zagaria, C., Pollock, L. J., and Thuiller, W. Implications of the Nature Futures Framework for species and Nature's Contributions to People in Europe. (To be submitted to *Nature Sustainability*)
5. **O'Connor, L.**, Pollock, L.J., Renaud, J., Verhagen, W., Verburg, P.H., Lavorel, S., Maiorano, L., and Thuiller, W. (2021). Balancing conservation priorities for nature and for people in Europe. *Science*, 372(6544), 856-860.
6. **O'Connor, L.**, Brose, U., Gauzens, B., Gaiuzere, P., Graham, C., Harfoot, M., Hirt, M., Lavergne, S., Maiorano, L., Moilanen, A., Verburg, P. H., Thuiller, W., and Pollock, L. J. The untapped potential of food webs for systematic conservation planning. (In revision with *Conservation Letters*)
7. **O'Connor, L.**, Chenevois, E., Moilanen, A., Ohlmann, M., Maiorano, L., Thuiller, W., and Pollock, L. J. Spatial conservation of European vertebrate food webs. (To be submitted to *Conservation Biology*)

The following papers were written during the course of my PhD but are not part of the present dissertation.

1. Botella, C., Gaüzère, P., **O'Connor, L.**, Ohlmann, M., Renaud, J., Dou, Y., Graham, C. H., Verburg, P. H., Maiorano, L., and Thuiller, W. Land-use intensity influences European tetrapod food-webs. (Under review in *Ecology Letters*)
2. Gaüzere, P., **O'Connor, L.**, Botella, C., Poggiato, G., Münkemüller, T., Pollock, L. J., Brose, U., Maiorano, M., and Thuiller, W. (2022). The diversity of interactions complements functional and phylogenetic facets of biodiversity. *Current Biology*, 32(9), 2093-2100.
3. Pollock, L. J., **O'Connor, L.**, Mokany, K., Rosauer, D. F., Talluto, M. V., and Thuiller, W. (2020). Protecting Biodiversity (in All Its Complexity): New Models and Methods. *Trends in Ecology & Evolution*, 35(12), 1119-1128.
4. **O'Connor, L.**, Fugère, V. and Gonzalez, A. (2020). Evolutionary rescue is mediated by the history of selection and dispersal in diversifying metacommunities. *Frontiers in Ecology and Evolution*, 8, 517434.
5. Maiorano, L., Montemaggiore, A., Ficetola, G.F., **O'Connor, L.**, and Thuiller, W. (2020). TETRA-EU 1.0: A species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography*, 29(9), 1452-1457.
6. Marshall, E., Valavi, R., **O'Connor, L.**, Cadenhead, N., Southwell, D., Wintle, B.A., and Kujala, H. (2020). Quantifying the impact of vegetation-based metrics on species persistence when choosing offsets for habitat destruction. *Conservation Biology*, 35(2):567-577
7. Ohlmann, M., Miele V., Dray S., Chalmandrier L., **O'Connor L.**, and Thuiller W. (2019). Diversity indices for ecological networks: a unifying framework using Hill numbers. *Ecology letters*, 22, 737-747.

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“Rachel Carson brought us back to a fundamental idea lost to an amazing degree in modern civilization: the interconnection of human beings and the natural environment.”

Al Gore

“What escapes the eye is a much more insidious kind of extinction: the extinction of ecological interactions”

Daniel H. Janzen (1974)

“Everything in the natural world is connected in networks that support the whole of life on Earth, including us, and we are losing many of the benefits that nature provides to us.”

David Attenborough

“Biodiversity loss is not only an environment or moral issue, it’s a social, economic, and health issue.”

Robert Watson (2019)

“When we rely deeply on other lives, there is urgency to protect them.”

Robin Wall Kimmerer. *Braiding Sweetgrass*

Introduction

The age of the Anthropocene

Biodiversity is declining

Biodiversity is defined as the variety of all life forms that inhabit planet Earth, at all levels of ecological organisations: genes, populations, species, communities, and ecosystems. There is overwhelming evidence that biodiversity is declining at rates unprecedented in human history. Many natural habitats are being lost, fragmented or degraded to make place for artificialized landscapes, inducing population declines and shifts in species ranges, and potentially driving many others towards extinction. Since 1500, over 300 species of terrestrial vertebrates are suspected to have gone extinct, including at least 187 birds [1, 2] - and many more extinctions are likely to have gone unnoticed. In September 2021, 22 species that used to live in the USA were declared extinct [3]. While extinction is a natural process, it is the current rate of extinction that is worrying. Background extinction rates are estimated to be between 1 and 2 extinctions per million species years: for 1 million species on the planet, one or two would go extinct each year. Depending on the taxonomic group, the current extinction rate is 8 to 100 times higher than the normal background rate [4]. Even under the most conservative estimates of background extinction rate, the vertebrate species that were lost during the 20th century would normally have taken between 800 and 10,000 years to disappear.

The global extinction of a species is only the tip of the iceberg, because it is the final outcome of a series of processes that play out across space and time. For example, many mammal species have recently lost over 80% of their geographic ranges, and experienced drastic population declines in the past 40 years [5, 6]. Environmental changes, such as the loss or degradation of habitats, affect the viability of populations, and the ability of individuals to nest, breed or forage for food. These environmental changes affect populations heterogeneously across space and time. Thus, before a species becomes globally extinct, populations can decline or become locally extinct.

The International Union for the Conservation of Nature (IUCN) introduced the Red List of threatened species as a tool to measure the extinction risk of species, in terms of rate of population loss and decline in geographic range size [7]. There are 5 main categories for non-extinct species (Figure 2.2): Critically endangered (CR) (in an extremely critical state); Endangered (EN) (very high risk of extinction); Vulnerable (VU) (high risk of extinction); Near Threatened (NT) (likely to become endangered in the near future); Least Concern (LC) (unlikely to become endangered or extinct in the near future) [8]. For species that lack scientific evidence to attribute a conservation status, two other categories exist: Data Deficient (DD) and Not Evaluated (NE). Findings from a recent study suggest that more than half of Data Deficient species are likely to be threatened with extinction [9].

Today, scientists have quantified that out of 8 million species estimated to exist on the planet, 1 million are threatened with extinction [10]. While the global extinction of a species is irreversible, there are many steps in the trajectory to extinction which can be averted. For example, protection schemes can allow populations to recover or to recolonize lost parts of the species' range.

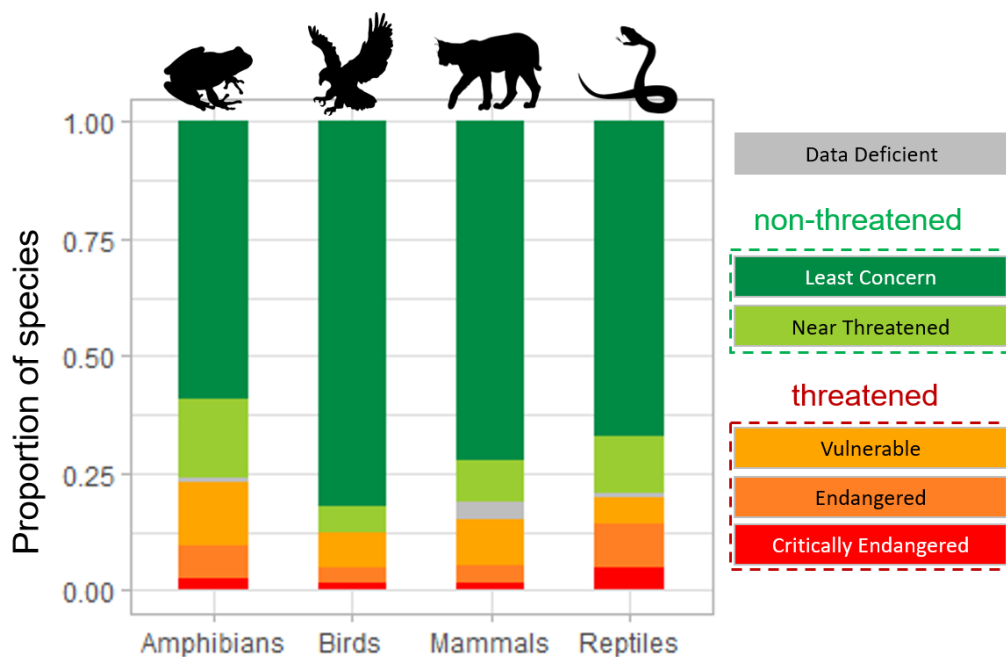


Figure 1: Conservation status of European terrestrial vertebrate species

Drivers of biodiversity loss

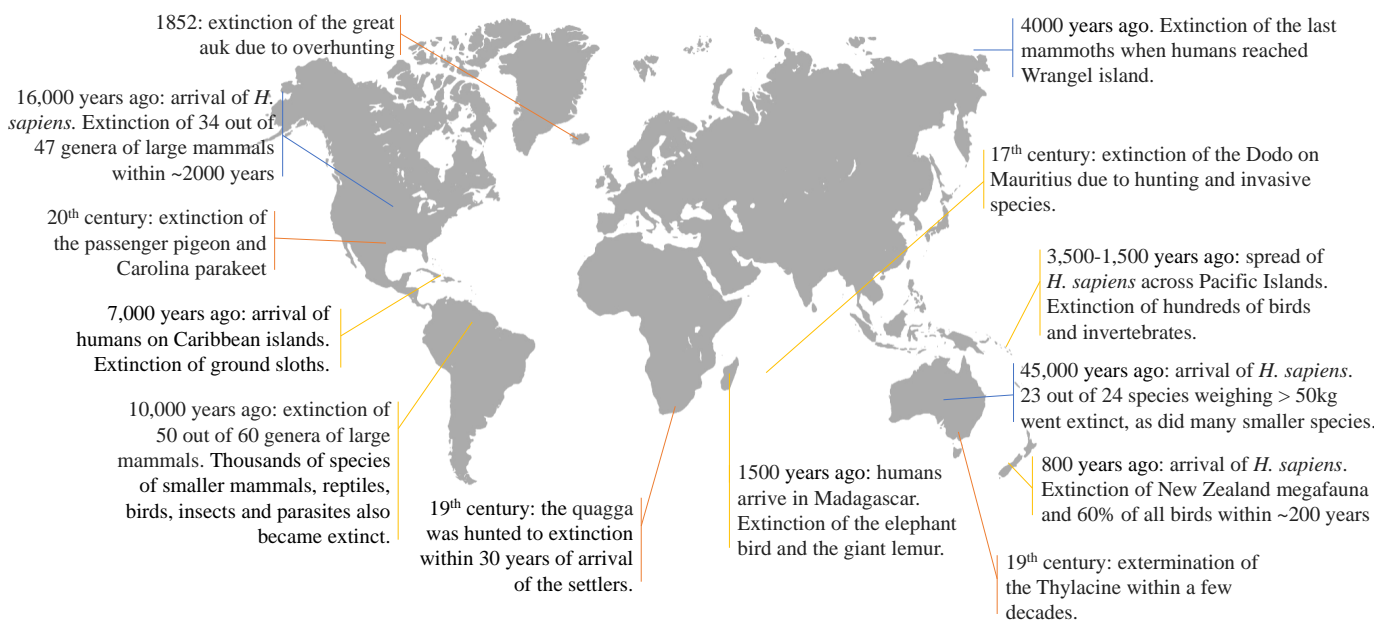
The drivers of biodiversity loss are relatively well understood. As early as the 1960s, the IUCN warned of the negative impacts of pesticides on the environment, and about the effects of climate change on nature. Human activities (such as agriculture, deforestation, urbanisation, trade) have increased in intensity and scale, accelerating the erosion of biodiversity. Five major drivers of biodiversity loss are currently recognized: land and sea use change, over-exploitation (*e.g.* fishing and hunting), pollution, invasive species, and climate change [10].

Direct exploitation. Hunting has been a major driver of species extinctions, and is a major threat for 300 mammal species [11]. In many cases, since the Industrial Revolution, it took only a few decades for human settlers to hunt species to extinction (Box 1). In a few instances, protection measures saved some species from extinction due to unrestricted hunting. Before European settlers arrived, at least 30 million American bison roamed across North America. The native Americans relied on the bison for food, materials and shelter, and they respected the bison as a god.

Around 1830, the settlers exterminated the bison, mostly leaving the corpses to rot, as a strategy to make room for croplands, to build railways, and to displace the indigenous communities which depended on them. At the end of the 19th century, when less than 600 bison were left in the whole of North America, conservation action was finally taken to protect the species. Other examples of last-minute actions to prevent extinction include the pronghorn in North America; the bouquetin in the Alps; the Saïga antelope in Central Asia, which have now recovered from critically low population levels.

Box 1. The toll of overhunting throughout human history.

150,000 years ago, *Homo sapiens* walked the plains of Africa alongside other human species. Around 70,000 years ago, they colonised the entire Eurasian landmass. As *Homo sapiens* progressed, other *Homo* sp. went extinct. 70,000 years ago, the planet was home to about 200 genera of large terrestrial mammals weighing over 50kg. 45,000 years ago, *Homo sapiens* colonised Australia. Within a few thousand years, the Australian megafauna was exterminated. This marked the beginning of the first wave of extinction. By 10,000 years BC, only about 100 genera of large terrestrial mammals remained.



“If we knew how many species we’ve already eradicated, we might be more motivated to protect those that still survive”
Yuval Noah Harari. *Sapiens*

— Extinctions in the Pleistocene following the spread of hunter-gatherers
 — Extinctions in the Holocene following the spread of farmers
 — Extinctions since the Industrial Revolution
 Sources: *Sapiens* (Y. N. Harari); *Living Planet* (D. Attenborough); *Collapse* (J. Diamond); Fricke et al. (2022). World map Image by Layerace on Freepik

Land and sea use change. Land and sea uses are considered to be the greatest threat to nature and are responsible for the loss and degradation of natural ecosystems and suitable habitats for species [12, 13]. Vast land and sea use changes have occurred across the globe, due to the conversion of natural habitats into human land uses, and the intensification of agriculture, urban areas, and forestry. As human land uses become more widespread and intensive, many natural ecosystems, and the species that depend on them, are lost (Figure 2). Natural ecosystems, once destroyed, are replaced by artificial landscapes, where some adapted species are able to thrive. The number of species present may not have changed, but the community has changed completely. As habitats are becoming more and more similar, so are the life forms that inhabit them - a process known as biotic homogenization.

Climate change. The consequences of climate change for biodiversity are projected to increase in coming decades [14]. Not all species are necessarily adapted to rapid climate change and may have to move to track favourable climatic conditions. If they are unable to adapt or disperse, they may become extinct. Consequently, some species will likely move into environments where they were not present before. For example, these shifts in species geographic ranges are already being observed for mosquitoes, golden jackal, and the pine processionary moth. This summer, extreme drought in the south of France have led to a decline in the European roller's food supply (*e.g.* grasshoppers). Because of intraspecific competition over dwindling food resources, some birds moved northward in search of food, several hundred kilometres to the north of their normal breeding range.

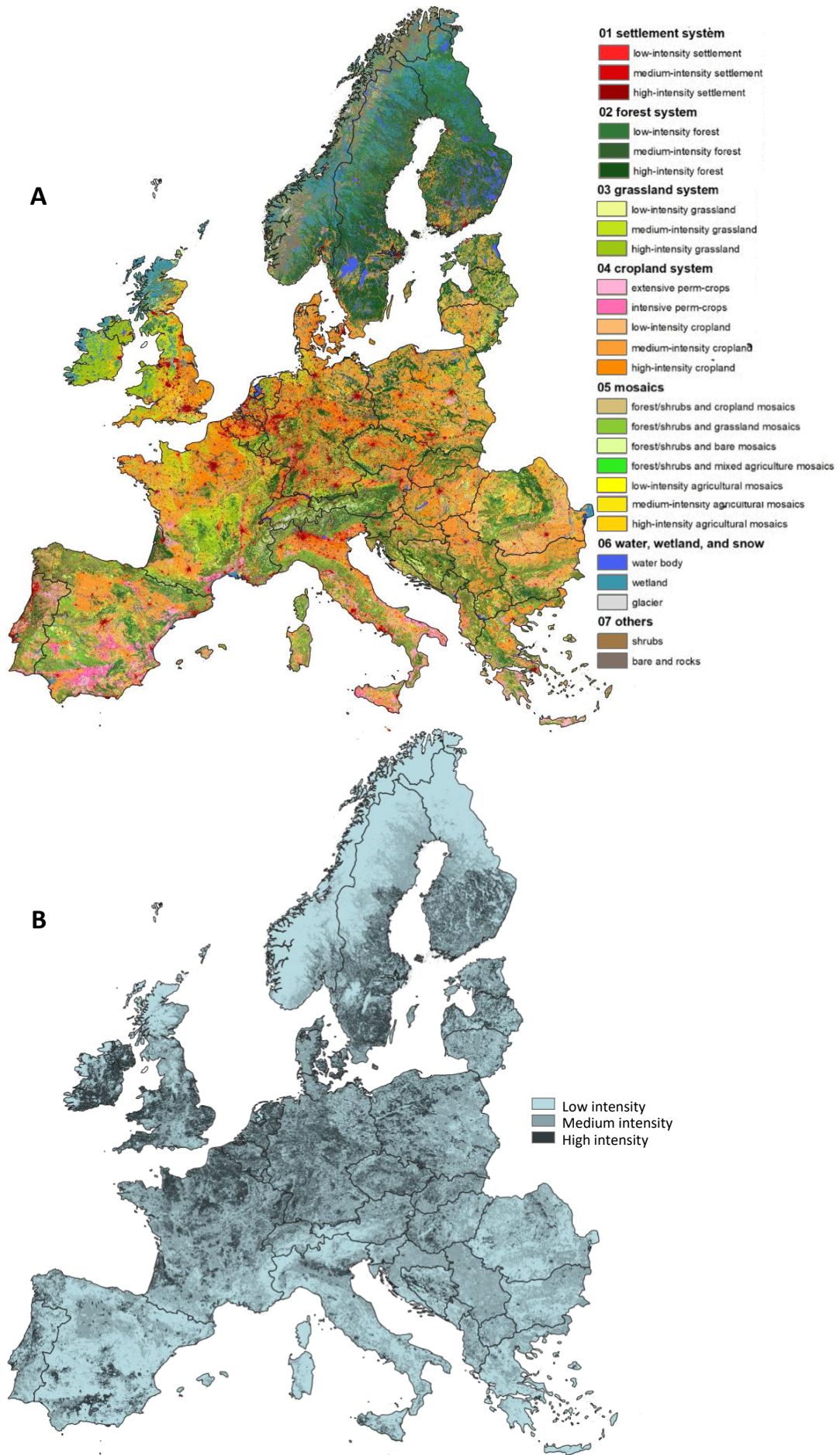


Figure 2: An overview of land systems (A) and land use intensity levels (B) in Europe.

Pollution. The material and chemical waste of our consumerist society accumulate in the environment: in water, in the soil, and in living organisms. Pollution can affect organisms at different stages of their life history. For example, plastic pollution can lead to the starvation of marine animals; chemical pollution in water can lead to poisoning or affect breeding success. Chemical compounds accumulate in the food chain and tend to be found in extremely high concentrations in top predators. In Europe, a variety of chemicals (mercury, Perfluoroalkyl substances (PFASs), Novel Flame Retardants, UV-filters, neonicotinoids, chlorinated paraffins, parabens and bisphenols) were found in European birds of prey, including the Eagle owl (*Bubo bubo*), the White-tailed Eagle (*Haliaeetus albicilla*), Peregrine falcon (*Falco peregrinus*) and Northern goshawk (*Accipiter gentilis*) [15, 16, 17]. Marine pollution is threatening the viability of over half the global populations of orca [18]. Many chemical compounds build up in living organisms: for example, polychlorinated biphenyls and DDT were both banned 40 years ago, but continue to be found in wild animals, and to have an impact on their fitness (e.g., causing infertility). Pollution is not only chemical, but also in the sheer accumulation of human-made things, which now outweigh the mass of living organisms [19].

Invasive Alien Species (IAS). Globalisation has facilitated dispersal for some species. Invasive alien species (e.g. rats and cats on islands) and pathogens are now able to disperse over longer distances and become established in places distant to their original ranges. Invasive alien species and pathogens are causing the decline of a number of native species. For example, a number of amphibian species are severely threatened by chytridiomycosis - the Panamanian golden frog for example is thought to have gone extinct because of this disease.

It is important to understand that these threats may act in synergy, simultaneously affecting a population or a species. It is the combination of these threats that is particularly worrying because one threat can exacerbate the impacts of another, and species may not be able to adapt simultaneously to several threats at the same time.

For example, population declines of the Saïga antelope due to unregulated hunting have decreased genetic diversity, which in turn has increased the vulnerability of the animals to diseases. Similarly, seabird populations, already heavily impacted by industrial fisheries and marine pollution, have recently experienced major declines due to avian flu. Populations that are small and isolated (*i.e.* as the result of previous pressures) are less likely to recover from perturbations (such as epidemics) than large and spatially connected populations (Appendix E). Yet, we tend to investigate the risks posed by one threat at a time, even though species are exposed to multiple threats in combination, not one by one.

The far-reaching consequences of biodiversity loss

It is tragic to witness the extinction of so many species - the outcome of millions of years of evolution - in such a short period of time. These losses highlight both the fragility of the natural world, and the destructive power of modern civilization. When we lose a species, we lose a unique part of nature forever. The loss of species as the side-product of an economic system poses a moral issue, because all species have an intrinsic value and they are irreplaceable [20].

Fraying the fabric of life

The consequences of losing any species are profound, because all species are involved in interactions with other species. Species interactions are decisive in the decline of species following changes in their environment. Predators, particularly those that are specialised on a particular type of prey, are more vulnerable to secondary extinctions driven by the loss of their food resource. For example, four million years ago, the Megalodon dominated the seas. A top predator in the marine food web, it fed on large prey such as whales. Around 3.6 million years ago, its main source of prey shifted in distribution due to a cooling climate, and became scarcer in the habitat of the Megalodon. It started to compete with the white shark for the same prey. The white shark was more agile, and a better competitor. The Megalodon was driven to extinction, not because it was directly affected by the climate, but because of a shift in the distribution of its prey. Following environmental changes

such as climate change, the loss of an interaction can happen due to the geographical mismatch between two interacting species ranges, or through phenological mismatch. For example, insectivorous birds require an abundance of insects at the right time of year in order to be able to feed their offspring. Evidence shows that due to rising temperatures in recent decades, insects have shifted their phenology by several weeks in advance, thus disrupting the synchrony between bird offspring and insect biomass [21]. This illustrates the fact that the functional extinction of biotic interactions often occurs well before the extinction of species themselves [22, 23].

Food webs - the network of trophic interactions between species in a community - can become drastically reorganised because of human-induced environmental changes [24, 25]. The species that have gone extinct in the Anthropocene are not just any species: many of them are large bodied species, with a high trophic level and slow population growth, which makes them particularly vulnerable to environmental pressures [26]. What cascading consequences will the decline of one species have on the rest of the communities? In 1962, Rachel Carson published *Silent Spring*, where she described how pesticides on any species can indirectly impact other species via biotic interactions. In 1966, Robert T. Paine showed that removing a top predator from coastal ecosystems affected the entire food web, with secondary extinctions of many other species due to the loss of top-down control from the predator [27]. Since then, ecologists have made considerable progress in understanding how the structure of food webs can accelerate biodiversity erosion through trophic cascades and secondary extinctions [28, 29, 30]. In general, the extinction of large carnivores can have a big impact on ecosystem processes [31]. In seed dispersal networks, even small amounts of habitat loss can cause up to 10% of species to lose all their interaction partners, leading to secondary extinctions [32]. Because species interactions are essential to the maintenance of biodiversity, the loss of a strongly interactive species can lead to profound changes in the structure and functioning of the community [22]. A recent study investigated the relationship between the loss of species and trophic interactions in regions across the world in the

last 130,000 years. The authors revealed that following the arrival of human settlers, food webs have lost 57% more interactions and 60% more species than would be expected by chance, because highly interactive and functionally unique species had been disproportionately extirpated, ultimately leading to food web collapse [24].

Human activities impact nature across vast spatial scales. Yet, we still lack an understanding of how anthropogenic threats affect food webs at large spatial and taxonomic scales [33]. As both land use and climate changes are projected to intensify, there is a pressing need to better understand how human-induced disturbances affect biodiversity and ecosystem functioning from a macroecological perspective.

Consequences for people

The consequences of biodiversity decline for society are far reaching and profound [34]. We tend to think that we are outside of the natural system, but we are not: we fully depend on species and ecosystems for our well being. The intensification of land use has increased our ability to extract large quantities of natural resources (such as food, timber, fibre and energy), but has also led to a reduction in biodiversity and ecosystems that provide cultural and regulating benefit to people [34, 10]. Ecosystem services [35], or Nature's Contributions to People (NCP) [36], are the structures, functions and processes in the natural world that make life possible. The notion of Nature's Contributions to People, introduced by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), builds on the ecosystem services concept, but it encompasses a wider set of benefits from nature (*e.g.* learning from nature, traditional knowledge) that are not easily quantified or valued in monetary terms [37]. The term itself, "Nature's Contributions to People", is also more inclusive because it is easier to translate in many languages. Most languages have a word for nature, but many languages do not have a word for biodiversity or for ecosystems: these terms only appeared in the English language in the 1970s. Internationally coordinated action for conservation requires terms that make sense in as many languages and cultures as possible around the world.

The IPBES framework recognizes three broad categories of NCP: regulating, material

and non-material NCP [37]. Material contributions are components of nature that are physically consumed, such as food, timber, or medicinal resources. Biodiversity is essential for the high and stable supply of material NCP. Evidence shows that genetic diversity increases crop yield; tree species diversity increases the supply of timber; fish diversity leads to greater stability of yield in fisheries [34]. Non-material (or cultural) contributions are the ways in which species and ecosystems benefit quality of life at the individual and collective level, and include culturally valued landscapes (*e.g.* heritage forests) or species (*e.g.* charismatic species), traditional practices within nature, learning and inspiration from nature. Regulating contributions are the ecosystem processes that underpin favourable environmental conditions, such as pollination, seed dispersal, flood control, regulation of air and water quality, regulation of climate. Note that regulating contributions also sustain material or non-material NCP (*e.g.* people consume foods which rely pollination and seed dispersal) [37]. Again, higher biodiversity leads to higher supply of regulating NCP: higher plant diversity increases the regulation of plant pathogens; biodiversity generally reduces the transmission of diseases and protects human health [38, 39, 40]; carbon sequestration is greater in diverse plant communities; and higher diversity of plants and algae increases the removal of nutrient pollutants from soil and water [41]. Yet, several knowledge gaps remain:

- NCP research is rooted in plant functional ecology (Diaz *et al.* 2007) while the NCP provided by other groups of species (*e.g.* vertebrates) are less known.
- The role of trophic interactions in maintaining nature's contributions to people is poorly understood [42, 43]. We need to identify not the direct providers of NCP, but also better understand the species that indirectly support NCP via their interactions, and the sub-components of food webs that underpin NCP [44, 45, 46, 43].

In sum, the erosion of biodiversity is threatening food supply, water quality, climate, and is increasing the likelihood of the emergence of pandemics [47]. The question we must ask now is: how to prevent further decline in biodiversity?

Conservation: a goal-oriented science

Conservation science emerged in response to the biodiversity crisis. As a discipline, its overarching objective is to find solutions to avoid species extinctions and maintain the ecosystems that our societies depend on [20].

Conservation objectives have evolved over time

Long standing questions in conservation are: What to prioritise? What should protected areas actually protect? There have been different motivations to protect nature in different contexts and time periods (Figure 3).

In Europe, protected areas originated in hunting reserves that both regulated hunting pressure on wild populations of game species and protected the hunting rights of nobility. Following the industrial revolution, as cities became increasingly polluted, natural and wild areas became increasingly attractive and idealised during Romanticism. There was a push towards leaving vast expanses of land “untouched” by humans. Created in 1872, Yellowstone in the USA was the first of many national parks designated worldwide. Their focus was to preserve beautiful wild areas.

In the mid-twentieth century, as we started to document species extinctions, there was growing concern to preserve species themselves. In September 1948, Charles Bernard of the Swiss League for the Protection of Nature, in Fontainebleau, spoke about the creation of the IUCN: ‘An international union where governments would be represented and which could coordinate the measures taken in many countries to protect sites of animals and plants, threatened with extinction because of the expansion of cities, the clearing of forests, the cultivation of new land, the exaggerated industrialization [...] There is a need for nature reserves, where hunting is forbidden and where animals can thrive again [...] In most cases international action between governments is absolutely necessary’. The Birds and Habitats Directives in the EU were adopted in 1979 and 1992, respectively, with the aim to protect rare, threatened or endemic species and ecosystems. And these conservation efforts have been vital: according to a recent report on the State of the world’s birds [2], between 21 and 32 bird species would have gone extinct without conservation action. By the end of

the 20th century, four distinct objectives of conservation were recognized: 1) protect all types of ecosystems, 2) maintain viable populations, 3) maintain the full suite of ecological and evolutionary processes, and 4) foster adaptability to changing environmental conditions [48]. At this stage, the focus was still very much about protecting species and ecosystems for their own sake.

Following the Earth Summit in Rio in 1992, considerable progress was made to investigate how the loss of biodiversity impacted ecosystem functions and their benefits to society, and the concept of ecosystem services was born [34]. The Millenium Ecosystem Assessment [35] concluded that most ecosystem services were declining, which prompted calls to protect species and ecosystems not only for their intrinsic value, but also for their benefits they provide to society (*e.g.* for air quality, pollination, climate regulation).

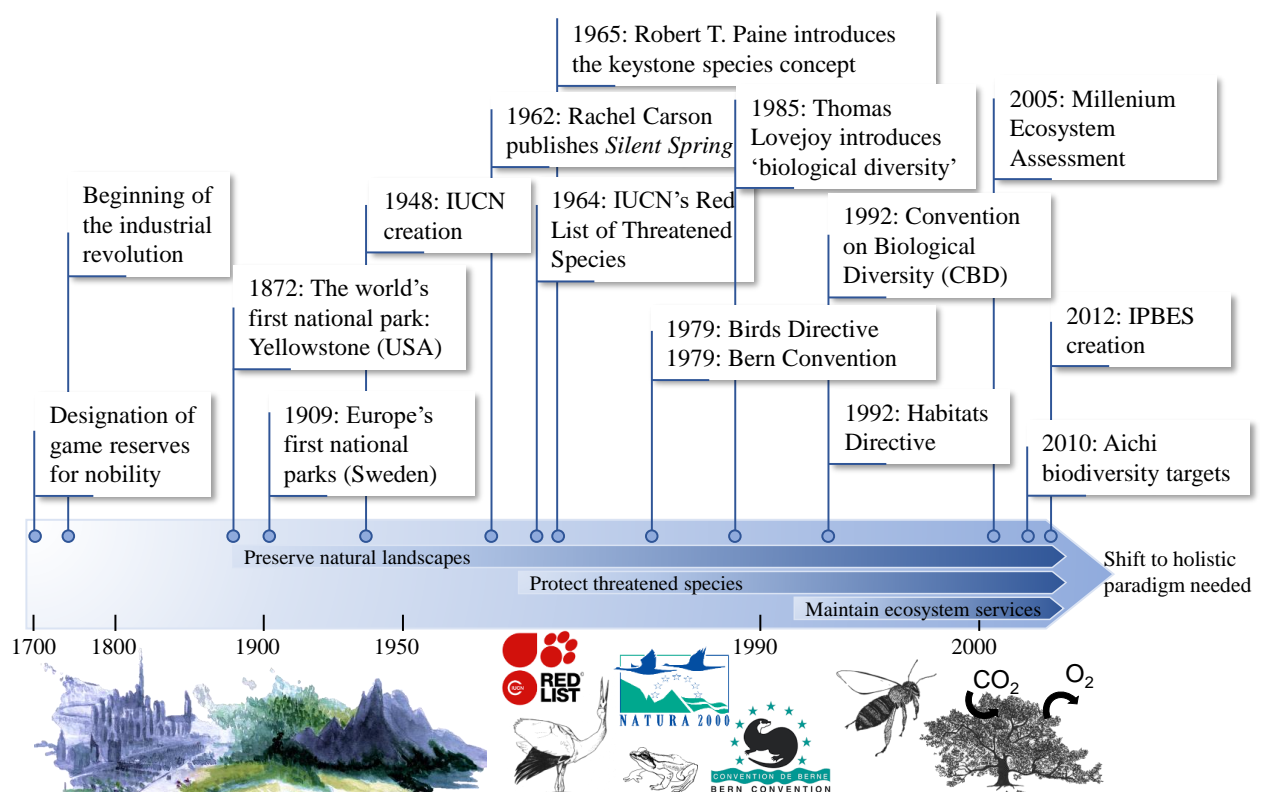


Figure 3: A brief history of biodiversity conservation.

In sum, multiple facets of nature motivate its protection, and these are now superimposed in global biodiversity policy [20, 49]. The dual objectives of preserving biodiversity for its intrinsic value and meeting people's needs in terms of nature's contributions to people are central to the post 2020 global biodiversity framework of the Convention on Biological Diversity [50, 51]. The IPBES recently introduced the Nature Futures Framework [52] which highlights desirable future pathways for people living in harmony with nature, while distinguishing three values of nature that motivate its conservation: Nature for Nature (*e.g.* the intrinsic value of species, ecosystems), Nature for Culture (*e.g.* cultural or non-material NCP), Nature for Society (*e.g.* regulating and material NCP).

Systematic conservation planning

Protected areas are one of the most effective means of halting the decline of biodiversity [53, 54]. Yet, their full potential is far from being reached. This is because protected areas have mostly been established in places that are remote, and where human activities are difficult to establish (*e.g.* in mountainous areas), rather than in locations that are important for biodiversity. Given that an increasingly limited amount of area is available for conservation, there is an urgent need to prioritize areas that maximise conservation gains for biodiversity [55, 56, 57].

Systematic conservation planning (SCP) is a common approach to identify priority areas for conservation at a regional or global level [58] for biodiversity features of interest (species or NCP). Systematic conservation planning can inform decision-making by investigating where and how to efficiently achieve conservation goals. SCP identifies top priority areas for conservation that are of regional or global importance for multiple biodiversity features (*e.g.* species, ecosystems, or NCP). Top priorities can be areas that are locally highly diverse and that provide multiple benefits locally, as well as areas that are globally important for biodiversity in that they capture rare or endemic biodiversity. Priority areas are representative, complementary and irreplaceable for the set of features considered [59]. SCP can integrate many components of biodiversity, such as evolutionary distinctiveness, functional diversity and habitat connectivity [60]. Assessing the conservation status or the ecological

importance of species has mostly been achieved by using species-specific knowledge (*e.g.* population densities, geographic range sizes, functional traits, genetic diversity, provisioning of ecosystem services) or models (*e.g.* metapopulation viability analysis, species distribution models [61], evolutionary distinctiveness [62]). Spatial conservation planning for multiple biodiversity facets has then relied on harnessing these different types of biodiversity data across space [56, 63].

Current challenges in conservation science

Today, the challenge is to adequately preserve biodiversity and NCP in the context of climate and land use changes. Ideally, we would want to simultaneously protect all nature's values (intrinsic, regulating, cultural). Incorporating multiple values of nature in conservation planning is challenging, because of the trade-offs between different objectives [64, 65]. But it is not clear to what extent prioritising the intrinsic value of nature may overlap with the objectives of protecting nature for its cultural and regulating benefits [20, 49]. Recent studies have combined the dual aims of minimising species extinctions and maximising the supply of essential NCP such as carbon sequestration and water quality regulation [66, 67], but research in this direction is still in its infancy.

Incorporating species interactions in conservation might actually help to combine the dual aims of protecting rare species and maintaining NCP. Trophic interactions are crucial for species survival, and for maintaining ecosystem functions and NCP [42]. For example, the seed dispersal function provided by frugivores is essential for forest regeneration and for carbon storage [68]. In particular, rare species underpin NCP through species interactions [69]. Yet, so far, systematic conservation planning has typically not accounted for species interactions, instead maximising the representation of biodiversity features independently of their interactions. Going forward, we need a paradigm shift towards holistic vision for conservation [45]. Conservation needs to consider more than species rarity and threat status [56, 63]: species interactions, and the linkages between biodiversity and NCP are equally important factors to consider to protect biodiversity and NCP.

Interactions: the missing link in biogeography and conservation

Food webs: structure and functioning of biodiversity

Life is interconnected in many ways: species are connected to each other via their interactions; the movement of individuals connects populations and communities across space; species and their interactions underpin diverse and functioning ecosystems that provide nature's contributions to people (NCP). Networks that represent the interconnections between different entities in natural systems have gained traction in ecology and evolution, to understand the structure and functioning of these systems [70]. Interaction networks are a representation of the interactions (mutualistic, competition, predation) between all the species in a community. Food webs are a type of interaction network which represent the trophic interactions between species, *i.e.* between preys and predators.

Food webs emerged nearly a century ago, to describe the structural organisation of an ecosystem and the flow of energy, nutrients and biomass. In 1927, Charles Elton represented the first food webs as the structural organisation of an ecosystem through the interactions between preys and predators [71]. Elton introduced the concept of the Eltonian niche, defined as the position of a species in the food web in relation to all the other species. In 1942, Lindeman highlighted the functional aspect of food webs which represent the dynamic flows of energy and biomass between components of an ecosystem [72, 42].

Species and their interactions are the building blocks of the structure and functioning of ecosystems. Food webs can help improve our understanding of the structure of biodiversity, and to characterise the functional role of a species in the community [73, 74]. The importance of trophic interactions for the structure and functioning of an ecosystem was demonstrated empirically by Robert T. Paine in 1966 [27]. The top-down control of the top predator maintained diversity among prey species by maintaining lower population levels of the more competitive species. In the absence of the predator, a few dominant prey species drove other prey species to extinction

through competitive exclusion. In general, predators can maintain local biodiversity by reducing competition between prey species, allowing multiple species to coexist [31, 75, 76], including rare and endangered species [22]. In prairies for example, plant diversity tends to be higher in the presence of grazers (unless there is overgrazing). Top-down control can also indirectly impact species on lower trophic levels. For example, sea otters feed on urchins, which in turn feed on kelp. The extermination of sea otters in the 20th century led to a massive increase in urchin populations which overgrazed kelp, indirectly impacting the fish species that depended on kelp forests for habitat. The legal protection of the sea otter has since promoted both the recovery of the sea otter and of kelp forests in areas where they were previously present. But now, in some areas, due to the decline of seals and sea lions (killer whales' favourite source of food), killer whales have switched to eating sea otters [77], which indirectly threatens kelp forests. In terrestrial ecosystems, unchecked populations of large ungulates can lead to overgrazing, with the subsequent decline of other species that depend on the vegetation [31]. The reintroduction of wolves in Yellowstone in the mid 1990s is a striking example of how trophic interactions can shape an ecosystem. Wolves were extirpated from the Yellowstone national park at the beginning of the 20th century. As a consequence, the elks had no top predator, so their numbers rose exponentially, and they overgrazed the vegetation across the landscape. The decline of woody plants impacted many other species that depended on shrubs and trees for food and habitat. Vegetation also influences water quality - so following the decline in vegetation, the rivers became filled with sediments and fish populations declined. In 1995, wolves were reintroduced, in addition to other conservation measures in Yellowstone. The wolves controlled the elk population, so the vegetation recovered, followed by the recovery and comeback of many other species that had regionally disappeared [31]. Note that the wolf is probably not the only reason for the ecological recovery in Yellowstone, but it certainly is a part of the picture.

Challenges and avenues for using food webs in biogeography and conservation

Interactions are essential for the survival of species, and for the structure, stability, and functioning of communities. Food webs provide an opportunity to revisit our understanding of the distribution of biodiversity; to better assess threats to biodiversity; to disentangle the direct and indirect drivers of biodiversity erosion; and to improve the conservation of species and NCP. Species interactions shape the biogeography of species and should be considered when designing plans to protect species. Yet, they are not considered in biogeography or scenarios of biodiversity change and in conservation planning. Several challenges have hindered progress in this direction.

Addressing the Eltonian shortfall

Due to the inherent difficulty of sampling interaction networks [78], information on interactions are scarce, and geographically and taxonomically biased - this problem is known as the Eltonian shortfall [79]. Fortunately, there has recently been considerable progress on addressing the Eltonian shortfall. Information on species interactions is becoming increasingly available. Databases such as GloBI [80] or Mangal [81] have grown thanks to the enormous efforts to document ecological interactions globally. But interaction data are fragmented and sampled interaction networks usually provide only local snapshots at a given time period. Spatializing food webs across large spatial extents can be tricky due to this data paucity [82].

The metaweb concept. One way to overcome this problem is to infer or predict species interactions where information on species interaction is limited, based on species functional traits or phylogenies [83, 84, 85]. Another solution is to use metawebs [86]. Metawebs are a particular kind of food web, that comprise the species and all their known interactions across a study region, including potential interactions between species that do not co-occur [87]. Metawebs can be combined with species distributions data to reconstruct local food webs at large taxonomic and spatial scales. Thus, two species that are known to interact in the metaweb

are assumed to interact locally where they co-occur. The metaweb concept has the potential to help address questions from fundamental food web ecology to applied conservation problems. For example, combining the metaweb with dispersal abilities, species distribution models and global change scenarios can help project future distribution shifts and reconstruct food webs of the future, and anticipate the potential consequences of global changes on food webs, including interaction rewiring or invasion risk.

Developing theory and methods for using food webs at macroecological scales

The increasing availability of interaction data in recent years has been paralleled with rapidly developing theory and methods to use food web information at macroecological scales [88, 89].

A key challenge in food web ecology is the need to reduce food web complexity while retaining meaningful information on its structure and functioning. Aggregate network metrics (*e.g.* modularity, connectance, link density) can help quantify community stability and functioning [90], and have been used to describe the variation of food web structure across space [91, 92]. However, the aggregation of food web information in a single variable does not provide information on the species that compose the network, their contribution to network structure and functioning, or their vulnerability. Species level attributes (*e.g.* centrality, degree, trophic level) offer valuable insight on species ecological role and contribution to community stability [93, 43].

The intermediate level of the Eltonian niche is a useful concept for food web biogeography because it simplifies the information contained in a food web, while retaining its functional structure. Species belong to the same Eltonian niche (or trophic niche) if they have the same sets of prey and predator species. Recent developments, building on socio-economic network science [94], now enable us to identify trophic niches in food webs. Group models (*e.g.* the stochastic block

model) [95] are one method to define the trophic niche of species based on its preys and predators: Species in a food web are aggregated into trophic groups, within which species have the same probability of interacting with all other trophic groups in the food web [96, 97, 98]. Structural equivalence is another method to identify the position of a node in a network, based not on probabilities but on the node's environment: A node's position in the food web is defined relatively to its neighbours' position, and its neighbours' neighbours, and so on in a recursive manner [94]. The concept of the Eltonian niche can be used to i) identify groups of species that are functionally irreplaceable or that are linked to NCP supply; ii) quantify ecosystem functioning (*e.g.* trophic diversity); iii) quantify the redundancy of a trophic role in the food web [99]. Trophic redundancy is useful for estimating the resilience of a function. In protein-protein networks, nodes that are functionally redundant reflect past selection for the function to be robust in case of mutations, indicating functional importance. Similarly, high trophic redundancy in food webs could help buffer the functional consequences of species losses, and foster resilience of the system, because the loss of a species may have no immediate consequence if that species is functionally redundant with another.

Recent studies have developed theory and testable hypotheses on how food webs may respond to environmental change, and how interactions may shape the distribution of biodiversity. For example, a recent study translated how ecogeographical rules might apply to food webs [100]. Another has applied the species area relationship to food webs to investigate how network metrics scale with area [101]. Pellissier *et al.* (2017) reviewed how to analyse the variation of interaction networks along environmental gradients [102].

Key points to address to understand and protect biodiversity in all its complexity

Taken together, these recent developments in i) addressing the Eltonian shortfall and ii) developing a toolbox to analyse food webs, now make it possible to address knowledge gaps that we could not address before, such as:

- Understand and characterise the spatial structure of interaction networks in order to then predict the effects of global change on species interaction networks. How does food web structure and composition vary across space? Do food web metrics provide complementary, or redundant, information when studying biodiversity patterns?
- Understand how anthropogenic threats impact food webs at a macro-ecological scales for multiple threats and for multiple species. There is a need to disentangle the direct and indirect impacts of threats on biodiversity via trophic interactions. Which components of the food web are the most vulnerable to what threats? What are the consequences for ecosystem services?
- How to use food webs in spatial conservation planning? What are the most appropriate ecological network metrics or data to use for conservation?

Objectives of the thesis

The aim of my PhD is to elucidate the direct and indirect effects of anthropogenic change on food webs and to suggest solutions to design more ecologically relevant protected area networks.

I used databases that survey scientific and naturalistic knowledge of the prey and predator interactions of all vertebrate species that live in Europe [87]; their ecological and morphological characteristics; their geographic ranges, and the habitats on which they depend (Figure 4).

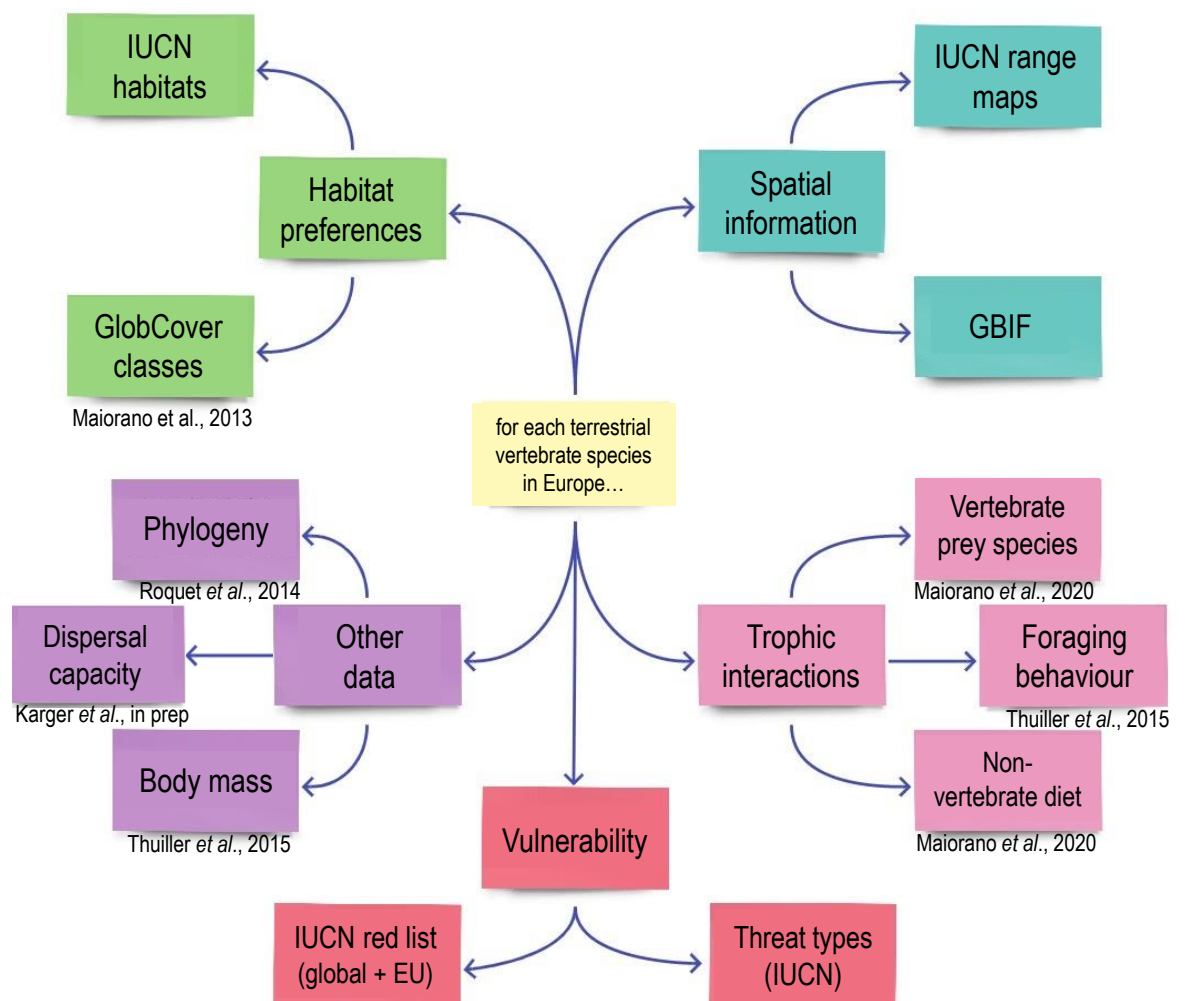


Figure 4: Overview of data types used in the thesis. I explain which datasets are used in each Chapter in the Material and Methods section.

This thesis is structured in 3 parts and 7 chapters (Figure 5):

Part I: The structure and functioning of food webs. The challenge is to aggregate food web data in a meaningful way - how to do so? So far, most studies have looked at the distribution of node-level metrics (e.g. degree distribution) or average values at the level of the food web (e.g. connectance) to describe the variation of interaction network structure across space [91, 92, 103]. But few studies have used the concept of the Eltonian niche. In Chapter 1, I used the concept of the Eltonian niche to explore the functional structure of food web and variation across Europe. I characterised the functional role of the 1,152 vertebrate species based on their interactions [104], in order to study their geographic distribution. This allowed me to address questions like: i) How to synthesise information in food webs while retaining functional structure? ii) How are food webs structured across space at a functional level? A central question in functional ecology is: which components of biodiversity contribute to human well-being? So far, NCP literature has mostly focused on plant functional ecology, and many maps of NCP supply at macroecological scale are based on biophysical models (*i.e.* linked to habitat types and landscapes). By contrast, NCP related to vertebrate species have been poorly documented. In Chapter 2, I created a database of NCP provided by each terrestrial vertebrate species, by using scientific literature as well as the metaweb and trait data for these species. I then mapped the richness of species associated with each NCP across Europe.

Part II: Effects of anthropogenic change on species, their interactions, and NCP. Human-induced changes in the environment can have different impacts on biodiversity: positive (e.g. protection and restoration) or negative (e.g. habitat loss). In Part II, I explore different dimensions of anthropogenic impacts on biodiversity in the context of food webs. The vulnerability of food webs to anthropogenic threats at a large spatial scale, for a large number of species, is not known. In Chapter 3, I assessed the vulnerability of terrestrial vertebrates food webs across Europe to anthropogenic threats, based on the knowledge of threats to each species and

their trophic interactions (Harfoot *et al.*, 2021). This allowed me to quantify the vulnerability of trophic groups, interactions, predators and prey to anthropogenic threats; and to highlight areas that are most vulnerable to different threats across Europe. In Chapter 3.4, I used land use change scenarios that translate alternative desirable pathways based on the Nature Futures Framework [52] in Europe, to predict species ranges under different scenarios and the consequences of these changes on species-based NCP. I asked: does the Nature Futures Framework benefit species and NCP across Europe?

Part III: Conservation scenarios for species and NCP. What is the best strategy for setting conservation priorities over large spatial scales (in terms of data requirements, cost-effectiveness, representation of multiple features of interest)? Spatial conservation planning focuses on species and does not explicitly recognize the multiple values of nature, so the trade-offs and synergies of prioritising species versus NCP are poorly known. In Chapter 4, I identified priority areas for protection in Europe, both for species and for NCP [105]. I then explored the difference between focusing on priority areas for the utilitarian versus the intrinsic value of nature. In Chapter 5, I reviewed the scientific literature at the interface between network ecology and conservation biology and highlighted options to incorporate species interactions in systematic conservation planning. SCP does not incorporate species interactions, in part because of a lack of consensus on how to do so. In Chapter 6, I investigated the difference between a prioritisation that includes trophic information versus one that focuses on species habitats only (*i.e.* the traditional approach). I then explored the costs and benefits of considering trophic interactions in a prioritisation for terrestrial vertebrates in Europe.

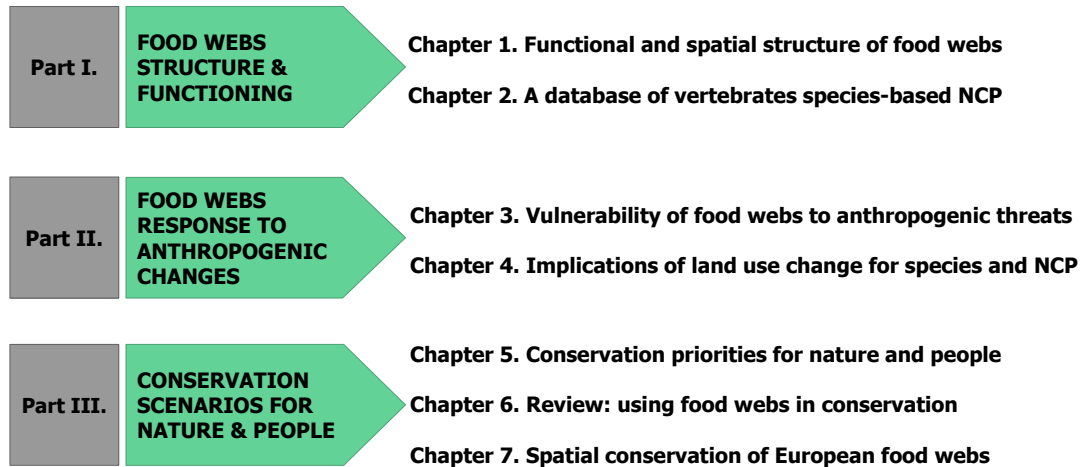


Figure 5: Overview of the thesis.

Other work peripheral to my PhD are included in the Appendices.

In Appendix B, I present three studies on the biogeography of food webs which I contributed to as a co-author. In a study published in *Current Biology* led by Pierre Gaüzère, we investigated whether studying the spatial variation of interaction diversity provided additional insight to functional and phylogenetic diversity. Work by Marc Ohlmann on developing diversity indices for interaction networks led to a publication in *Ecology Letters*, for which I prepared the figures and contributed to writing the manuscript. This framework has implications for the spatial conservation of food webs. In a study led by Christophe Botella, recently submitted to *Ecology Letters*, we investigated how land use intensity (in different land systems, and different bioregions) affect food web structure.

In Appendix C, I included the study led by Yue Dou (in preparation for submission to *Global Environmental Change*), to guide the interpretation of the land use change scenarios and results presented in Chapter 3.4.

Though I did not account for spatial connectivity in my PhD, this is an important aspect to consider in conservation, and which I have worked on in previous projects. In Appendix E, I present two studies where we considered the spatial connectivity between patches of habitat to study population dynamics following a perturbation.

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Part I

The structure and function of the entangled bank

Chapter 1

The biogeography of terrestrial vertebrate food webs in Europe

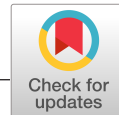
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Despite recent calls for integrating interaction networks into the study of large-scale biodiversity patterns, we still lack a basic understanding of the functional characteristics of large interaction networks and how they are structured across environments. We use a metaweb summarizing trophic interactions between European tetrapods to characterize the trophic groups in terms of functional traits and then map the variation of these trophic groups across Europe. We show that the 1,136 species within the metaweb can be classified into 46 functional trophic groups of species with a similar role in the metaweb. Across space, trophic diversity was driven by both biotic and abiotic factors, and the representation of trophic groups differed among European ecoregions. Our results highlight the need to integrate network science, functional ecology and biogeography in global change research.



Unveiling the food webs of tetrapods across Europe through the prism of the Eltonian niche

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Abstract

Aim: Despite recent calls for integrating interaction networks into the study of large-scale biodiversity patterns, we still lack a basic understanding of the functional characteristics of large interaction networks and how they are structured across environments. Here, building on recent advances in network science around the Eltonian niche concept, we aim to characterize the trophic groups in a large food web, and understand how these trophic groups vary across space.

Location: Europe and Anatolia.

Taxon: Tetrapods (1,136 species).

Methods: We combined an expert-based metaweb of all European tetrapods with their spatial distributions and biological traits. To understand the functional structure of the metaweb, we first used a stochastic block model to group species with similar Eltonian niches, and then analysed these groups with species' functional traits and network metrics. We then combined these groups with species distributions to understand how trophic diversity varies across space, in function of the environment, and between the European ecoregions.

Results: We summarized the 1,136 interacting species within the metaweb into 46 meaningful trophic groups of species with a similar role in the metaweb. Specific aspects of the ecology of species, such as their activity time, nesting habitat and diet explained these trophic groups. Across space, trophic diversity was driven by both biotic and abiotic factors (species richness, climate and primary productivity), and the representation of trophic groups differed among European ecoregions.

Main conclusions: We have characterized the Eltonian niche of species in a large food web, both in terms of species interactions and functional traits, and then used this to understand the spatial variation of food webs at a functional level, thus bringing together network science, functional ecology and biogeography. Our results highlight the need to integrate multiple aspects of species ecology in global change research. Further, our approach is strongly relevant for conservation biology as it could help predict the impact of species translocations on trophic diversity.

KEYWORDS

food webs, functional traits, metaweb, stochastic block model, trophic diversity, trophic groups

1 | INTRODUCTION

Understanding spatial biodiversity patterns and underlying ecological processes is a central research axis of biogeography (Humboldt & Bonpland, 1805). Owing to the historical importance of this issue, its current relevance for conservation, and its revived momentum in the era of big data, recent work has allowed new comprehensive syntheses on the ecological and evolutionary drivers of large-scale diversity patterns (Ficetola, Mazel, & Thuiller, 2017; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Mazel et al., 2017). The majority of these studies have used functional or phylogenetic information to group species or quantify diversity (Davies & Buckley, 2011; Safi et al., 2011). While functional and phylogenetic data have offered many insights into ecological processes (e.g. Sundstrom, Allen, & Barichiev, 2012), they are only indirect proxies for how species interact in communities. Biotic interactions, such as trophic interactions, can shape macroecological patterns of diversity (Gotelli, Graves, & Rahbek, 2010), in addition to the better-known effects of the abiotic environment. Especially in the context of global change, where species interactions are altered (Valiente-Banuet et al., 2015), with cascading effects on the response of multiple species to global change (Bascompte, García, Ortega, Rezende, & Pironon, 2019; Tyljanakis, Didham, Bascompte, & Wardle, 2008; Van der Putten, Macel, & Visser, 2010; Wisz et al., 2013), it is of prime importance to integrate the interaction networks into the study of biodiversity patterns (Baiser et al., 2019; Pellissier et al., 2017; Tyljanakis & Morris, 2017).

Food webs are particular interaction networks that represent both the species composition of a community together with the fluxes of biomass associated with their interactions, thus providing the potential to reconcile the structure and function of biodiversity (Thompson et al., 2012). So far, food webs have been analysed and compared across space through either network-level metrics or species-level metrics (Baiser et al., 2019; Kortsch et al., 2019), but we still lack the capacity to unveil how large food webs are structured in terms of the roles of the species that compose them, and consequently to understand how the structure and function of food webs vary across environmental gradients (Pellissier et al., 2017). Both the complexity of interaction networks and the scarcity of empirical interaction network datasets across large spatial scales have hindered this progress.

One approach to reduce the complexity of large food webs while preserving their structure is to group the species together based on their role in the food web, or their Eltonian niche, defined as the 'place of an animal in a community, its relation to food and enemies' (i.e. to prey and predators; Elton, 1927). There have been two lines of research that seek to understand the role of species in food webs. The first approach focuses on the position of a species within a food web, using methods from network science to aggregate species into a number of trophic groups that contain species with similar sets

of prey and predator species (Cirtwill et al., 2018). The stochastic block model (Allesina & Pascual, 2009; Daudin, Picard, & Robin, 2008; Karrer & Newman, 2011), in particular, provides the opportunity to aggregate the species that have the same probability of interacting with the rest of the species in the network, i.e. similar Eltonian niches (Gauzens, Thébault, Lacroix, & Legendre, 2015). The second approach focuses on the use of functional traits to deduce the role of a species within a food web and infer their interactions (Gravel, Albouy, & Thuiller, 2016). For example, a trophic interaction between two species results from a match between the vulnerability traits of the prey species and the foraging traits of the predator species (Gravel et al., 2016; Rossberg, Brännström, & Dieckmann, 2010). Characterizing a species from its position in the network topology on the one hand, and from its functional traits on the other, have thus been two contrasting approaches to determine a species' Eltonian niche. However, integrating both perspectives to understand how and which biological traits define the role of species in a food web has seldom been investigated (Baskerville et al., 2011; Coux, Rader, Bartomeus, & Tyljanakis, 2016; Kéfi, Miele, Wieters, Navarrete, & Berlow, 2016). Here, we used a novel food web dataset of all European tetrapod species to merge these approaches by first modelling the trophic role (or Eltonian niche) of species in the food web using recently developed methods in network science, and then describing how these trophic roles relate to species' functional traits. We expect the food web to be structured into functionally meaningful trophic groups that aggregate species with overlapping sets of prey and predator species in the food web, due to similarities in their foraging and vulnerability traits (Laigle et al., 2018).

Combined with the species' geographic distributions, the Eltonian niche concept further enables the structure of food webs to be portrayed across space, adding a new dimension to spatial biodiversity patterns. Trophic diversity, defined as the number of trophic roles played by species (Bascompte, 2009), appears as a convenient measure to map food web patterns across macroecological scales. Ecogeographical rules observed for species richness, such as the latitudinal gradient, have not yet been investigated for species roles in food webs (Baiser et al., 2019), and divergences between species richness and trophic diversity patterns have the potential to reveal the underlying ecological processes driving the patterns of biodiversity at macroecological scales. We expect different environments to select the species based on their role in interaction networks (Tyljanakis & Morris, 2017). For instance, in more favourable climatic conditions and more productive ecosystems, high competition for resources should lead to high trophic specialization and trophic complementarity (Poisot, Mouquet, & Gravel, 2013), translating into a more diverse range of trophic roles filled locally, therefore a higher trophic diversity, than in harsher environmental conditions with the same number of species (Gaston, 2000).

Here, following on recent calls to bridge the gap between contrasting views of the niche (Gravel et al., 2018), we built a large food web made up of the 50,408 potential trophic interactions between all the tetrapod species across Europe (i.e. the metaweb of 1,136 species of birds, reptiles, amphibians and mammals). We first inferred trophic groups in the metaweb using the stochastic block model and investigated the functional trait structure of these trophic groups. Second, we combined the metaweb with species distribution data, to explore how these trophic groups vary across space, in quantity and in quality. We hypothesized that: (a) the metaweb of European tetrapods can be simplified into trophic groups which are determined by the functional traits of the species that compose them, and (b) divergences between the patterns of trophic diversity and those of species richness across the European continent should provide insights into the underlying ecological processes that contribute to the food web structure and function at macroecological scales.

2 | MATERIALS AND METHODS

An overview of the material and methods is depicted in Figure S1.

2.1 | Study area, species distributions and biological traits

The study area included Europe (including Macaronesia and Iceland) and Anatolia. We extracted the distributions for all tetrapods naturally occurring within the study area from Maiorano et al. (2013), which were modelled by combining the extent of occurrence for each species with their habitat requirements (see Maiorano et al., 2013 for a full description of species distribution data). In total, our analyses focused on 508 bird, 288 mammal, 237 reptile and 103 amphibian species. Species distributions were mapped in a regular grid of 300 m resolution, where cells had values of zero for unsuitable habitat, one for marginal habitat (habitat where the species can be present, but does not persist in the absence of primary habitat; Maiorano et al., 2013) and two for primary habitat. Here, we treated primary habitat only as 'suitable habitat', which provides a better prediction of the actual species distribution (Ficetola, Rondinini, Bonardi, Baisero, & Padoa-Schioppa, 2015). All range maps were up-scaled to a 10 × 10 km equal-size area grid (ETRS89; total of 78,873 cells). We considered the species potentially present in a 10 × 10 km cell when they had least one 300 m suitable habitat cell within it.

For the same set of species, we gathered biological trait data from Thuiller et al. (2015). We used traits that are linked to trophic interactions (Luck, Lavorel, McIntyre, & Lumb, 2012) and restricted our analyses to comparable traits between the four groups. These consisted of information on:

- diet (17 categories: mushrooms, seeds/nuts, fruits/berries, mosses/lichens, vegetative plant parts, invertebrates, vertebrates, fish, small mammals, large mammals, herptiles, bird eggs, small birds, large birds, bones, carrion, coprophagous)
- nesting habitat (tree hole, ground, rocks, artificial, underground water, cave/burrow, lodge, temporary water, brooks/springs/small rivers, puddles/ponds, brackish waters)
- activity time (diurnal, crepuscular, nocturnal, arrhythmic)
- foraging behaviour (grazer, opportunistic, hunter, browser)
- morphology (body mass for birds and mammals, body length for herptiles).

2.2 | The network of potential trophic interactions

The network of potential trophic interactions between all European tetrapod species (hereafter, the metaweb) was built using a combination of expert knowledge, published information and field guides (a list of references is found in Appendix 1). Trophic interactions between a predator and its prey were identified from published accounts of their observation, morphological similarities between potential prey and literature-referenced prey and, in the absence of this information, the diet of the predator's sister species. The full dataset and methods description is available in the Dryad data repository. The metaweb contained 1,136 tetrapod species and a total of 50,408 potential trophic interactions. In this metaweb, 883 basal species did not prey on European tetrapod species (i.e. basal species here could feed on plants, detritus, invertebrates, fish, domestic animals or were coprophagous), 213 intermediate consumer species had both prey and predator species among European tetrapods and 40 top predator species had no predator species. The metaweb had a connectance of 0.0385.

2.3 | Trophic groups definition

To build trophic groups, we used a stochastic block model (SBM) on the metaweb of potential trophic interactions (R-package *mixeR* version 1.8 Daudin et al., 2008; Miele, 2006), following previous studies (Baskerville et al., 2011; Gauzens et al., 2015; Kéfi et al., 2016; Mariadassou, Robin, & Vacher, 2010). The SBM is a random graph model with several groups of nodes (also known as 'group model' in Allesina and Pascual (2009) or 'block model' in Newman and Leicht (2007)). A parameter of this model is an aggregated graph with groups of nodes, linked to one another through edges that represent the probability of connection between any two nodes in the corresponding groups. Consequently, two nodes belonging to the same group have the same probability of connection with all other nodes in the graph. Given a network, the statistical machinery of the SBM aims to recover the groups defining similar groups of species in terms of the interactions they have with each other (Gauzens et al., 2015). The goodness of fit of the model is assessed using the integrated classification likelihood (ICL) information criterion. Applied to the metaweb, the SBM inferred groups of species such that two species belonged to the same group if they had the same probability of interacting with all other species in the metaweb - in other words, they potentially preyed on similar sets of species, and were potentially

preyed upon by similar sets of species. Using the SBM, we partitioned the species in the metaweb along a range of 10–60 groups, hereafter referred to as trophic groups. We defined the optimal number of groups based on the partitioning of the metaweb that maximized the ICL criterion (Figure S2). We then computed the average trophic level of each trophic group (R-package NetIndices (version 1.4.4; Soetaert, Kipyegon Kones, & van Oevelen, 2015)). We also computed the in- and out-degree of the species (defined as the number of predator and prey links of a species respectively) in the potential metaweb (R-package igraph (version 1.2.4; Csárdi, 2019)) and expressed the distribution of in- and out-degree within each trophic group (Figure S3).

2.4 | Functional composition of trophic groups

To visualize the metaweb, we removed the links between species that never co-occurred in space (in terms of range and habitat co-occurrence) and used the software Gephi (version 0.9.2, Bastian, Heymann, & Jacomy, 2009; Figure 1). We then described the composition of the groups in terms of the taxonomy (at the class level) and generalism of the species (Figure S3).

We then performed a multivariate analysis to understand the composition of trophic groups in terms of the biological traits of the species they contained. We did so using a co-inertia approach called

the Outlying Mean Index (Dolédec, Chessel, & Gimaret-Carpentier, 2000) that is usually meant to identify the ecological niche of species as a function of the environment (function *niche* in package *ade4* (version 1.7-13) in R (Dray, Dufour, & Thioulouse, 2018)). Here, we took advantage of this approach to characterize the different trophic groups (species x trophic groups matrix) as a function of the biological traits (species x traits matrix). In other words, we mapped the trophic groups in the space of the functional traits of the species they contained.

2.5 | Quantifying and mapping trophic diversity across Europe

To characterize how trophic diversity varied across space, we first mapped trophic diversity (as the number of trophic groups found in each grid cell) with species richness (the number of species in each grid cell). Then, we tested the response of trophic diversity to species richness, environmental variables and the interactions between these drivers using a linear model. Bioclimatic data at 10 km resolution and net primary productivity (NPP) were downloaded from Worldclim v2 (<http://www.worldclim.org>) and SEDAC (<https://sedac.ciesin.columbia.edu/data/collection/hanpp/sets/browse>) respectively. We tested the pairwise correlations between all environmental variables and selected those that were not correlated (Figure S4). We then ran linear models

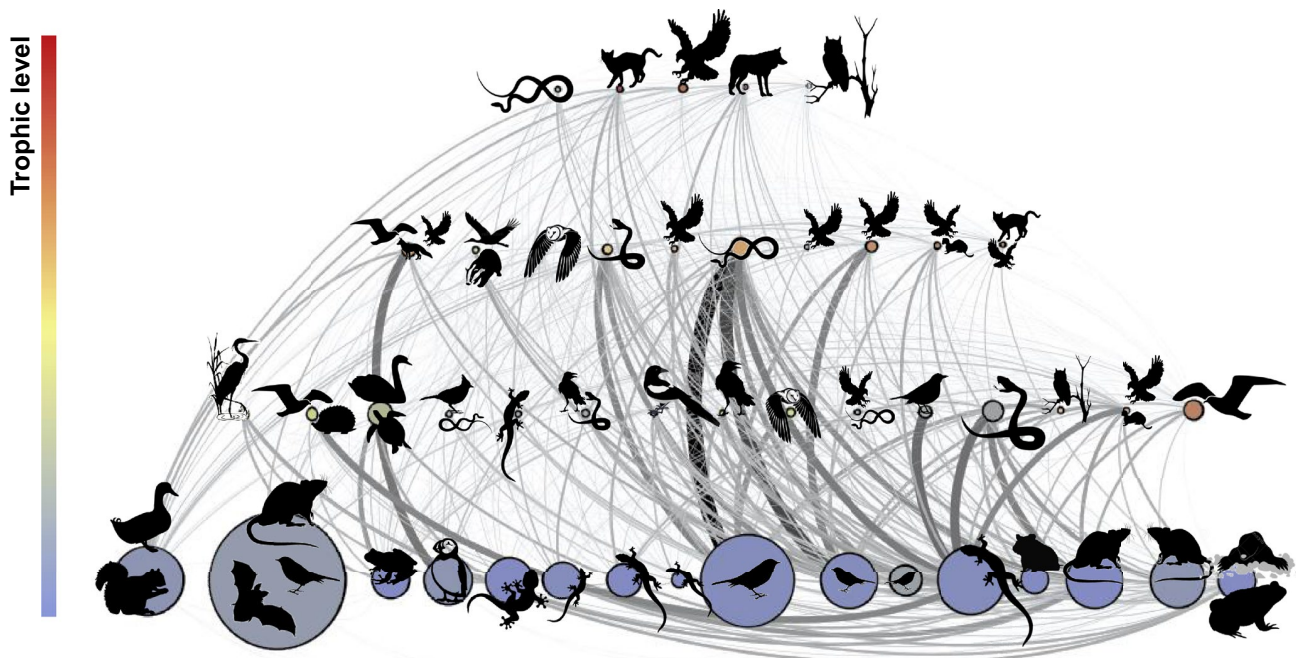


FIGURE 1 Trophic groups as a function of trophic level. The nodes of this network represent the trophic groups, with their size proportional to the number of species in the group. Groups are positioned according to the average trophic level of the species they contain, from the bottom of the metaweb (basal preys) to the top (top predators), and coloured according to in-degree (i.e. predatory generalism). Silhouettes represent the characteristic species found in each trophic group and reflect the taxonomic coherence of these groups. The width and intensity of the links between two given groups represent the number of realized links between them - that is, the number of species pairs belonging to both groups and that co-occur at least once in Europe [Colour figure can be viewed at wileyonlinelibrary.com]

accordingly with different combinations of explanatory variables and selected the model with the smallest AIC. We mapped the residuals of the linear model including species richness alone and compared it with the residuals of the full model (that included average annual temperature, net primary productivity and temperature seasonality in addition to species richness; Figure S5). Finally, to understand how each environmental variable influenced the relationship between species richness and trophic diversity, we computed the predictions of the linear model for the first, second and third quartile of each environmental variable to plot their statistical interaction with species richness.

We then investigated how the trophic groups and types of interactions in the tetrapods' food web varied across the different European ecoregions, defined by the European Environment Agency (EEA, 2019) to represent 'extents of areas in Europe with relatively homogeneous ecological conditions, on the basis of climatic, topographic and geobotanical data, within which comparisons and assessments of different expressions of biodiversity are expected to be meaningful'. We compared ecoregional metawebs across 11 ecoregions: alpine, Anatolian, arctic, atlantic, boreal, Black Sea, continental, Macaronesia, Mediterranean, Pannonian and steppic. We built each ecoregional metaweb by sampling the species occurring in the ecoregion and the interactions between co-occurring species within the ecoregion from the European metaweb. We then aggregated each ecoregional metaweb using the 46 trophic groups defined in the European metaweb. The links between two given groups represented the sum of interactions realized in the ecoregion (i.e. the number of pairs of species belonging to these groups that co-occurred and interacted in the ecoregion). We also computed the geographic specialization of species to each European ecoregion (computed as the ratio between a species' ecoregional range and its European range), then computed the median value of specialization for each group.

All analyses were conducted in R version 3.4.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Defining trophic groups in the European metaweb of tetrapods' trophic interactions

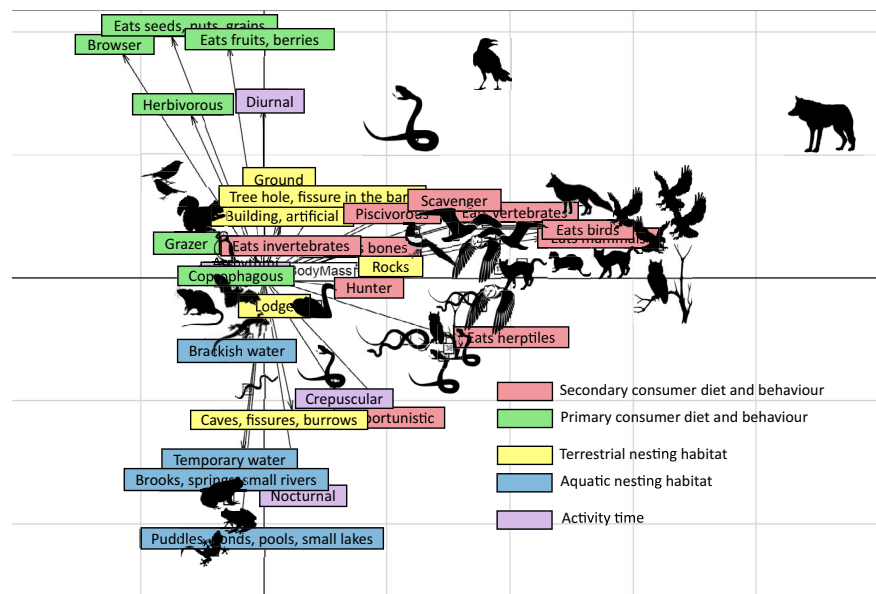
Based on the ICL criterion, the SBM partitioned the European metaweb into 46 groups (Figure S2). A qualitative examination of the partitioning suggested that groups were homogenous in terms of taxonomy, trophic level and the degree of generalism of the species within them (Figure 1; Figure S2). We organized the 46 trophic groups within four trophic levels to visualize the flow of biomass, from herbivores to intermediate consumers, mesopredators and finally top predators.

The outlying mean index revealed that specific traits strongly explained the trophic groups (Figure 2). The first component was primarily driven by the feeding behaviour and the diet of species, with secondary consumers and carnivores (e.g. hunters) belonging to different trophic groups than herbivore species (e.g. grazers and browsers), consistent with the organization of the trophic groups into the aforementioned trophic levels. The second component was driven by the activity time and the nesting habitat of species, with diurnal species separated from nocturnal species in these trophic groups, meaning that the time of activity determines the types of prey or predator of a species, and species nesting in aquatic habitat belonging to different trophic groups than species nesting in terrestrial habitat. This second component especially structured the trophic groups within intermediate and basal trophic levels.

3.2 | Mapping trophic diversity across Europe

Trophic diversity generally decreased with latitude in a similar manner to species richness - that is, there was a latitudinal gradient for trophic diversity as well for species richness (Figure 3A,B). Species richness and trophic diversity were both at their lowest in northern latitudes. Several trophic groups (e.g. groups composed by herptiles)

FIGURE 2 Trait niche of trophic groups. This bi-plot characterizes the mean position of each trophic group along the two-dimensional space represented by the species biological traits. Traits are coloured according to their category (activity time, secondary consumer characteristics, primary consumer characteristics, aquatic or terrestrial nesting habitat type). The length and orientation of each arrow reflects the relative importance of a given trait in explaining the variation between the groups. Groups are positioned in this multivariate space and represented by the same silhouettes as in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]



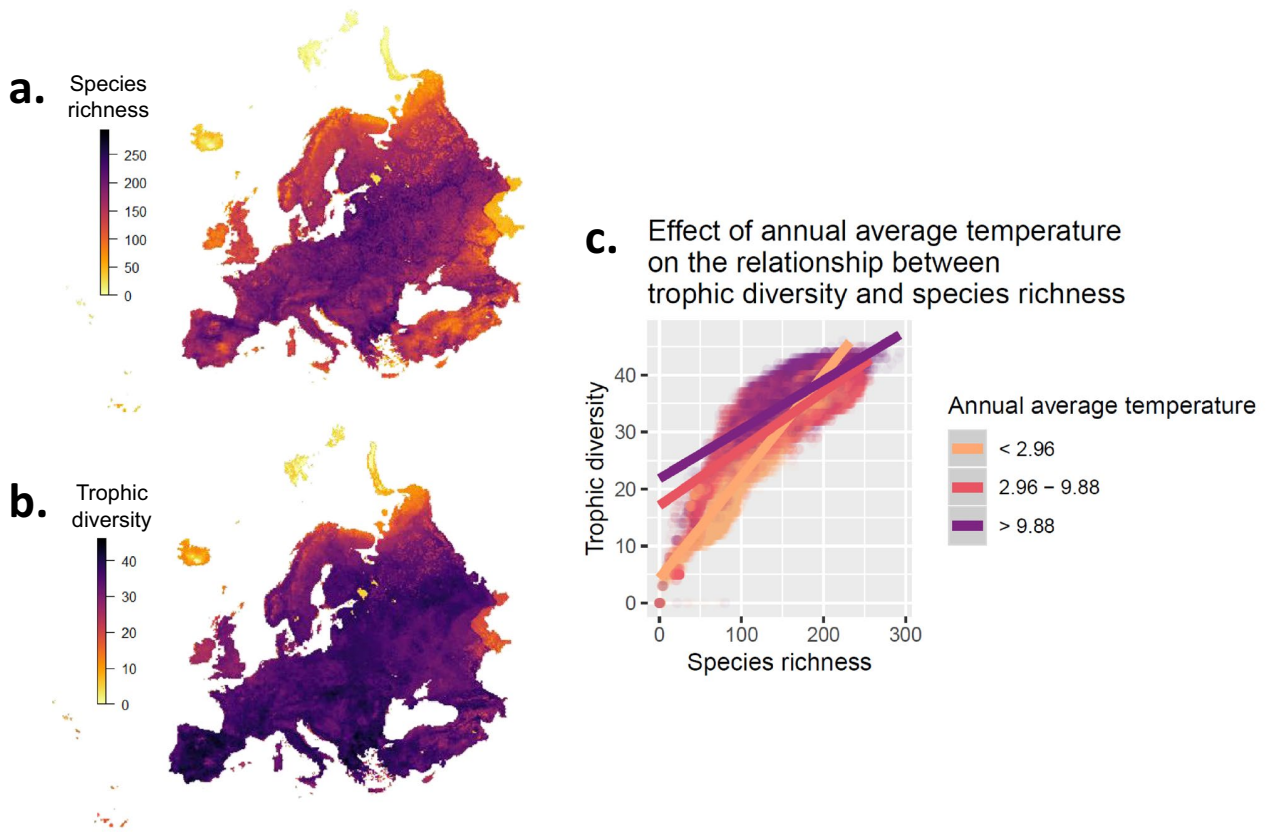


FIGURE 3 Species richness and trophic diversity across Europe. a, b: Maps representing species richness and trophic group richness across Europe. c: Interaction plot between annual mean temperature and species richness in driving trophic diversity. The scatterplot of trophic diversity as a function of species richness is overlaid with the interaction plot between the annual average temperature and species richness effects on trophic diversity, based on predictions from the linear model. The three categories of annual average temperature represent the first, second (median) and third quartiles. The lines and the data points in the scatterplot are coloured accordingly to these three categories [Colour figure can be viewed at wileyonlinelibrary.com]

were completely absent from both the arctic and boreal ecoregions, reducing the complexity of these regional metawebs (Figure 4), parallel to a regional decrease in trophic diversity. Because of these low diversities, a single type of interaction was strongly represented in the Arctic metaweb, involving a group of mesopredators (e.g. predatory seabird species and the arctic fox) preying on a group of basal species in the Arctic (mainly small birds and rodents). Then, trophic diversity and species richness both peaked at intermediate latitudes (Figure 3A,B): species richness peaked at around 600 species/100 km² and trophic group diversity peaked at 46 groups/100 km², frequently reaching these highest values in mountainous areas. To illustrate, the alpine metaweb displayed the highest species richness, trophic diversity and link density of all ecoregional metawebs (Figure 4). However, in southern Europe, trophic diversity patterns diverged from species richness patterns (Figure 3A,B) – trophic diversity remained close to its maximum, while species richness was lower in southern Europe than in intermediate latitudes. This was exemplified with the Mediterranean and Anatolian metawebs in southern Europe (Figure 4), where all trophic groups of the European metaweb were represented by at least one species, but with fewer species representing them overall, than in the alpine metaweb for instance.

Modelling for latitude and species richness alone showed that trophic diversity declined significantly towards northern latitudes and increased significantly with species richness, as expected ($R^2 = 0.89$). Further, the latitudinal gradient of trophic diversity was fully accounted for when including environmental variables in the linear model (annual mean temperature, temperature seasonality and net primary productivity) in addition to species richness (Figure S5). More precisely, trophic diversity increased significantly with annual mean temperature and NPP, and displayed a quadratic response to temperature seasonality (i.e. mild seasonality was linked to higher trophic diversity while extreme seasonality, both high and low, was detrimental to trophic diversity; Table S1). Furthermore, results show that the environmental variables significantly affected the linear relationship between trophic diversity and species richness (Figure 3C; Figure S6, Table S1). For instance, trophic diversity was generally higher where annual mean temperatures were warmer in Europe, while holding species richness constant (Figure 3C). Conversely, in colder environments, trophic diversity was lower than explained by species richness alone. Interestingly, in colder environments, trophic diversity was also gained more quickly as species were added to the local assemblage.

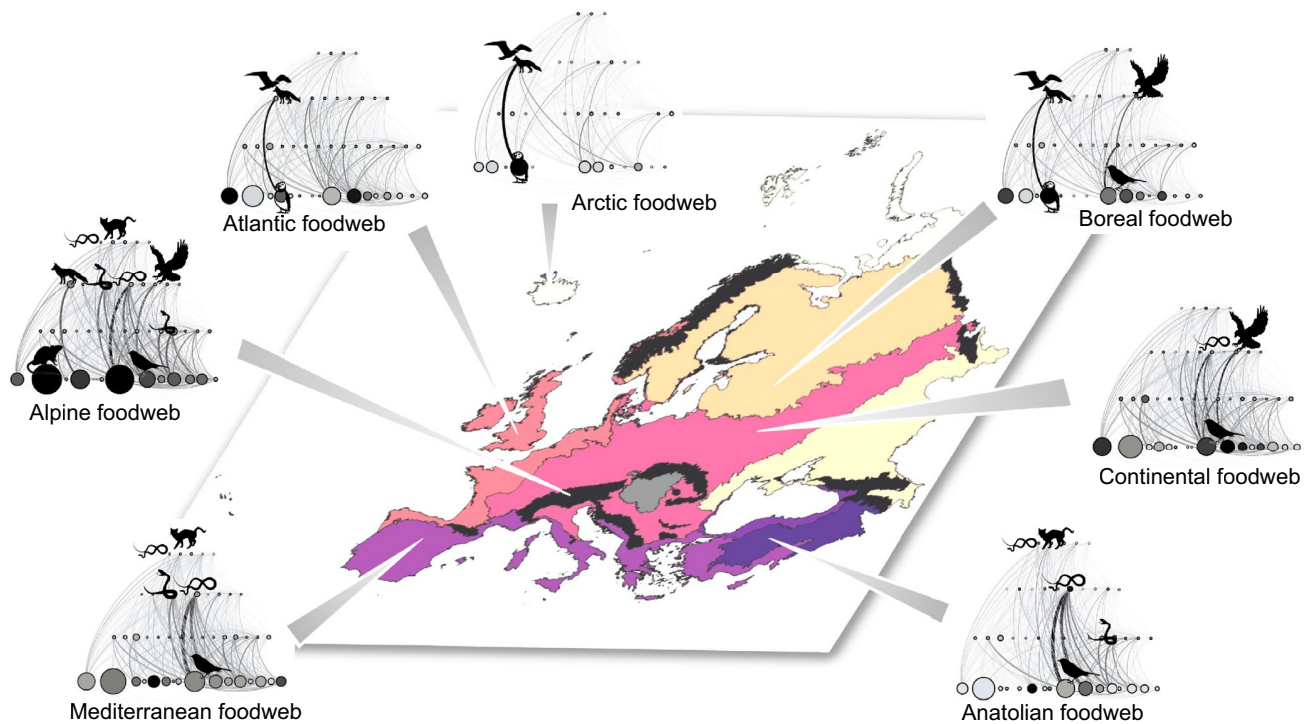


FIGURE 4 Regional metawebs of European tetrapods. The size of the nodes correspond to the number of species representing a given trophic group in the ecoregion; the width and intensity of the links represent the number of interactions that exist between two given groups in this ecoregion. Nodes are coloured according to the median specialization of the species to the ecoregion within each trophic group: the darker the node, the higher the specialization of the trophic group to the ecoregion [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

In this paper, we investigated the spatial structure of food webs from a functional perspective. Building on the Eltonian niche concept, we showed that species interacting in a large food web can be aggregated into a few dozen trophic groups of species with the same role in the food web using a novel network science approach, the stochastic block model. We then showed that trophic groups were coherent with the trophic level, trophic specialization, functional traits and taxonomy of species within them. Second, our analysis revealed a latitudinal gradient in trophic diversity (richness of trophic groups) that varied with the well-known species richness gradient, but was also additionally explained by environmental conditions (e.g. warmer temperatures, mild seasonality) and net primary productivity. Taken together, these results show that the Eltonian niche provides an unmatched opportunity to unveil the structure and function of large food webs at a continental scale.

4.1 | Recovering species' Eltonian niche from large food webs with the stochastic block model

The stochastic block model goes further in capturing the different dimensions of a species' role in the food web than the trophic level concept, which overlooks important aspects of species' ecological role such as their taxonomy, trophic specialization and biological traits (Cirtwill et al., 2018). In addition, the trophic level is a concept that

implies a hierarchy in the food web that is not always relevant (Cousins, 1987; Polis & Strong, 1996). This is especially important for other types of networks (e.g. multiple interaction types (Pilosof, Porter, Pascual, & Kéfi, 2017)) where there are many loops and no clear trophic levels. Conceptually, the trophic groups resulting from the stochastic block model are linked to trophic guilds since they represent a group of species that exploit the same resources, that is that have a similar role in a food web (Simberloff & Dayan, 1991). However, the two approaches differ in methodology: while guilds are usually based on expert opinion, the stochastic block model explicitly uses the interaction network. Such a data-driven approach to identify species roles has the potential to bring to light some similarities between pairs of species that otherwise might have been ignored. In other words, the stochastic block model enables to bridge the gap between network theory and functional ecology (Gravel et al., 2016).

Furthermore, we showed that trophic groups were driven by species functional traits. The metaweb studied here included tetrapod species exclusively, therefore basal trophic groups sometimes contained secondary consumers such as piscivorous and insectivorous species, and basal groups were not always as homogenous in terms of taxonomy as trophic groups further up the trophic levels. Nonetheless, biological traits associated to species foraging and vulnerability traits explained trophic groups across all trophic levels. Unsurprisingly, diet categories and feeding behaviour strongly determined species' trophic role. Then, activity time and nesting habitat also structured the trophic groups, particularly within lower

trophic levels. Interestingly, activity times of predators did not necessarily coincide with the activity time of their prey: indeed, nocturnal predators may preferentially feed on diurnal prey, provided that their foraging habitat coincides with their prey's nesting habitat. Overall, these results exemplify that a species' Eltonian niche (i.e. the potential occurrence of a trophic interaction), as recovered with the stochastic block model, is determined by the temporal, spatial and functional aspects of a species' ecology.

4.2 | From Eltonian niches to food web structure at macroecological scales

In our study, we have not addressed the intraspecific variability in species interactions (Poisot, Stouffer, & Gravel, 2014) nor the realized Eltonian niche of species, which can only be deduced from empirical food web datasets that are unavailable at macroecological scales. Besides, comparison of empirical food webs between several locations is impossible to date unless only one dimension is considered (e.g. along a linear gradient, or time: Matias & Miele, 2017; Miele & Matias, 2017). Instead, we have used the potential interactions that are either known or expected to occur between all tetrapod species in Europe (i.e. the metaweb, *sensu* Dunne, 2006), thus recovering the potential Eltonian niche of species. Indeed, if the potential niche of a species represents the set of abiotic environmental conditions in which it could thrive without accounting for its biotic interactions (Hutchinson, 1957), then the potential Eltonian niche of a species should represent the set of species that it could interact with if they coexisted.

Our results showed that trophic diversity, defined as trophic group richness or the range of Eltonian niches in an area, increased linearly with species richness across Europe, but also reveal interesting deviations from this linear relationship. We found that generally, trophic diversity was higher in southern Europe than would be explained from species richness alone, reflecting a higher niche differentiation in more favourable environments, where the climate is milder and ecosystems are more productive. Conversely, in northern Europe, in the Arctic or Boreal ecoregions for example, where climatic conditions are harsher and ecosystems less productive, trophic diversity was lower than that would be explained by species richness alone. This could be due to the absence of some trophic groups (mostly those represented by herptiles) in northern latitudes, due to their physiology (Snyder & Weathers, 1975). In addition, in northern Europe, trophic diversity was more sensitive to species richness; as species are added to the community, they tend to fill different Eltonian niches, maximizing the trophic complementarity (Poisot et al., 2013) in these simple food webs. Our results further support earlier findings suggesting that niche breadth increases with latitude, leading to fewer niches overall in northern latitudes (Baiser et al., 2019; Cirtwill, Stouffer, & Romanuk, 2015).

The particular case of the alpine metaweb suggests environmental heterogeneity is an additional driver of trophic diversity. The alpine metaweb contained the highest diversity in terms of species, trophic groups and types of interactions. It is well established that in the Alps, the elevational gradient combined with spatial heterogeneity naturally

provide a diversity of habitats which results in a higher diversity of niches available in the Alps (Kadmon & Allouche, 2007; Tylianakis & Morris, 2017). Furthermore, the alpine ecoregion is a highly fragmented ecoregion, widespread across Europe, with isolated inlets in Scandinavia, the Alps, the Balkans and the Pyrenees, therefore comprising a wide variety of climatic and land cover conditions (Figure 4), which can explain high trophic diversity in the alpine metaweb.

In addition to driving regional differences in trophic diversity, different types of environments were composed of different trophic groups: some trophic groups and their interactions were specialized to certain ecoregions, supporting the well-established principle in biogeography that different environments select for different functions (Buffon, 1761), in particular different trophic roles (Tylianakis & Morris, 2017). For example, top predator feline species and snakes preying upon smaller reptiles and rodents is a type of interaction that is particularly well-represented in the Mediterranean metaweb. On the other hand, despite regional differences in environmental conditions, some trophic groups were common to all ecoregional metawebs, which could be represented by wide-ranging, generalist species (Devictor, Julliard, & Jiguet, 2008). More fundamentally, such similarities in the trophic composition between different ecoregions echo with Elton's conception of the niche: different communities can display convergence in ecological roles and function, even when species composition differ (Simberloff & Dayan, 1991). Overall, our results suggest that trophic diversity is driven by the interplay between the functional traits, Eltonian niche, and geographic distribution of species and environmental conditions. Our study does not disentangle the factors upon which the environment selects species, and in fact, it would be vain to attempt to tease apart these drivers. In addition, there is a need to integrate the aspects of history together with the current biotic and abiotic conditions across space to understand diversity patterns in all of their complexity. The history of land use in particular has been shown to be a major driver of diversity patterns (Niedrist, Tasser, Lüth, Dalla Via, & Tappeiner, 2009; Pimm & Raven, 2000), especially in Europe where a complex history of local extinctions, species reintroductions and translocations has unfolded over the past centuries, particularly for large tetrapods such as the wolf or the bear (Chapron et al., 2014). Ultimately, our study has illustrated how the environment can filter species assembly, based on the interplay between their trophic role, biological traits and taxonomy, and further supports the relevance of using trophic diversity as a new dimension of functional diversity in an area.

4.3 | Perspectives

In the era of big data, there is an ever-increasing availability of information on potential interactions, together with high-resolution distribution data and life-history traits. Harnessing these data with novel developments in network science while relying on fundamental niche concepts should lead to a new approach for addressing pressing topics, such as the potential effects of environmental changes on biodiversity and ecosystem functioning, or identifying

conservation priorities to sustain multi-trophic communities. Here, we have shown that the trophic groups inferred using the stochastic block model encompass multiple dimensions of the role of species in a community. As global change triggers communities to be disrupted and interactions to be broken, understanding the Eltonian niche of species has the potential to inform conservation planning. For example, trophic groups can help predict the impacts of species translocation as populations go locally extinct, or the invasive potential of species as their distributions shift. Overall, this study calls for the integration of multiple aspects of species' ecology to understand how they assemble across space; ecologists need to account not only for species' response to environmental gradients (i.e. their Hutchinsonian niche; Guisan & Thuiller, 2005), but also for their biological traits, their biotic interactions and their Eltonian niche, to understand the biodiversity patterns across space and time.

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DATA AVAILABILITY STATEMENT

We used the data on species trophic interactions, species distributions and biological traits built by LM, GFF, WT and AM. The full dataset of trophic interactions analysed in this article, as well as the output of the stochastic block model, is archived in the Dryad data repository at <https://doi.org/10.5061/dryad.bcc2fqz79>.

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BIOSKETCH

Louise O'Connor recently started a PhD aiming to understand the influence of interaction networks on predictions of biodiversity patterns in the context of global change, in order to better inform conservation planning.

Author contributions: WT, LJP and LOC conceptualized and wrote the paper. LM, GFF, WT and AM built the trophic and trait data. LOC carried out the analyses with the help of JB, LJP, WT and MO. CMA and MO gave additional perspectives to the paper. All authors contributed significantly to the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX 1

LIST OF REFERENCES USED TO BUILD THE METAWEB OF TROPHIC INTERACTIONS BETWEEN EUROPEAN TETRAPOD SPECIES

The trophic links for mammals were compiled from the Handbook of the Mammals of the World composed of nine volumes (Wilson and Mittermeier 2009–2019). Furthermore, we considered multiple books on the mammalian fauna of the single countries and all volumes of Mammalian Species (published by the American Society of Mammalogists) available for species included in the database. The trophic links for breeding birds were compiled from the Handbook of the Birds of Europe, the Middle East and North Africa (9 volumes; Cramp et al. 1977–1994), the Handbook of the Birds of the World (16 volumes; del Hoyo et al 1992–2013), and the Handbook of the Birds of the World Alive website (del Hoyo et al. 2014). The trophic links for amphibians and reptiles were compiled from the Handbuch der Reptilien und Amphibien Europas (Arntzen et al. 1999; Bohme 1984; Fritz 2001; Grossenbacher and Thiesmeier 2003; Thiesmeier et al. 2004) plus multiple books and papers on the herpetofauna of the single countries. Trophic links for each species were compiled by the authors using a standardized data input protocol in MS Excel. For each species, we included in the database all trophic links reported in the publications using the highest possible taxonomic detail. Most of the time the information was available at the level of family or

higher; for instance, the food habits of *Falco tinnunculus* (the common kestrel) are described as: “in Europe up to 90% voles, with some mice and shrews; open area passerines normally less important [...]”; also lizards and insects [...]”, therefore we included as potential prey species all mammals of the families Arvicolinae, Muridae, and Soricidae, all birds of the family Alaudidae, and all reptiles of the family Lacertidae.

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Refining trophic groups using non-vertebrate diets

During my PhD, I developed several versions of the stochastic block model. One of the main limitations of the original (published) trophic groups was the fact that basal groups were poorly defined. Therefore, I developed a second version of the trophic groups, using diets, which allowed us to better differentiate basal species based on their non-vertebrate food requirements. To do so, I included non-vertebrate food resources as additional interactions in the input the stochastic block model refined the trophic group definition, particularly for basal species that feed on non-vertebrate food items (unpublished). A third version of the stochastic block model included only obligate interactions, based on a new version of the metaweb, developed by Luigi Maiorano and colleagues in 2022. Importantly, I distinguished 4 diet classes of invertebrates (ground invertebrates, aerial invertebrates, aquatic invertebrates, and vegetation invertebrates) using the foraging space of insectivorous species, because invertebrates are a major source of food for a majority of terrestrial vertebrates. I used this refined version of the SBM in Chapter 3.

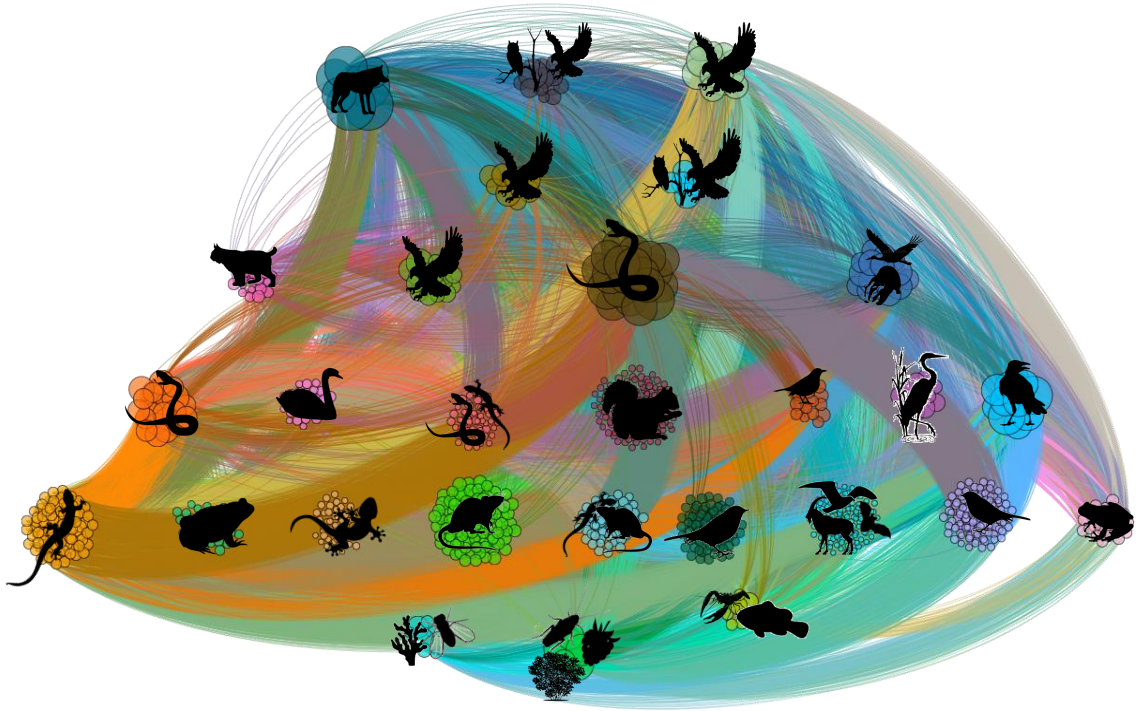


Figure 1.1: Representation of the metaweb of terrestrial vertebrate species, aggregated into 28 trophic groups, using non-vertebrate diet items and obligate interactions only. Each node is a species, coloured and positioned by trophic groups. The size of the nodes represents the degree (number of preys and predators) of each species. This version of the metaweb and trophic groups was used in Chapter 3.

Chapter 2

Terrestrial vertebrates and their interactions underpin nature's contributions to people

In preparation for submission to *Global Ecology and Biogeography* as a Data article.

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Species and their interactions underpin essential NCP, but a trophic perspective on NCP has been lacking. We created a database of NCP provided by each terrestrial vertebrate species and their trophic interactions in Europe based on existing literature and ecological databases. This dataset is based on a literature review by Servane Demarquet, whom I supervised together with Wilfried Thuiller for her MSc internship in 2021.

Abstract

Knowledge on the functional linkages between species and nature's contributions to people (NCP) can shed light on the synergies between biodiversity patterns and the supply of NCP, with important implications for conservation decisions. So far, the majority of NCP models have been derived from land cover and plant ecology, while NCP provided by vertebrate species have been poorly documented. Here, we present the first spatial database of 12 NCP provided by terrestrial vertebrates in Europe. We document the contribution of each species (including 292 mammals, 528 birds, 247 reptiles and 101 amphibians) to a set of 8 regulating NCP and 4 cultural NCP, based on the literature and on existing datasets on species' ecological traits and their diets. We then mapped species-based NCP, by combining species extent of occurrence, habitat preferences, and land use intensity. This database can then be used to understand the variation in species-based NCP diversity across space, to assess threats to species-based NCP, and for systematic conservation planning.

2.1 Introduction

A long-standing question in functional ecology is: which components of biodiversity contribute to human well-being? The concept of Nature's Contributions to People (NCP) [1] expands on the concept of ecosystem services [2], and describes how certain components of ecosystems can sustain human life as we know it, including benefits that are material (food, energy, timber), non-material (recreation, inspiration) and regulating (climate regulation, pollination, erosion control). The ecosystem services literature originated in plant functional ecology, and plants and soil have thus been the subject of numerous ecosystem services studies [3, 4]. There is now increasing evidence that terrestrial vertebrate species underpin nature's contributions to people (NCP) [5, 6]. For vertebrates, studies have emerged more recently but have been restricted to specific taxonomic groups such as amphibians [7] or birds [8] or specific ecosystems [6, 9, 10]. However, a comprehensive study integrating the knowledge of the multiple NCP provided by all terrestrial vertebrates at a macroecological scale is lacking. There is a need to better understand species that provide

NCP in order to improve estimates of NCP across space and subsequent conservation decisions [5].

Species richness underpins NCP supply in the long term [3]. Higher redundancy (i.e. multiple species that provide the same NCP in the same community) leads to increased resilience of provisioning of the NCP in the case of fluctuations in species presence or abundance over time. In particular, a high diversity of species that provide the NCP locally is essential for high regulating NCP capacity in the long term. For instance, predators can regulate zoonotic disease reservoirs (e.g. rodent-borne diseases, or mosquito-borne diseases) [11]. On the one hand, specialist predators have a strong effect on reservoir populations, but they are also known to drive prey populations through boom and bust cycles. Generalist predators, on the other hand, regulate prey populations at more consistently low levels. Consequently, the highest level of disease control occurs when many different predator species can simultaneously control reservoir populations in order to stabilise the local NCP capacity [11]. More generally, NCP capacity in a local ecosystem is stronger, and more stable, when there is a diversity of species that provide it.

Here, we synthesise the literature on species based NCP in the case of terrestrial vertebrates in Europe, and use datasets on ecological traits and feeding information of each species to build a database linking European vertebrate species to NCP. We then map species-based NCP capacity across Europe, using a novel habitat suitability model [12] that accounts for land use intensity [13].

2.2 Materials and Methods

2.2.1 Building the database of species-based NCP

We considered all terrestrial vertebrate species that are known to be native to Europe and for which we had spatial distribution data and trophic interactions data [14]. The species-based NCP database includes 1169 terrestrial vertebrate species in total: 292 mammals, 528 birds, 247 reptiles and 101 amphibians.

We reviewed the literature on NCP provided by terrestrial vertebrates, specifically in the context of Europe. We selected species-based NCP that were likely to

be delivered across a wide range of contexts with widespread societal demand for the service across Europe. Furthermore, we selected only positive NCP and ignored negative NCP (i.e. ecosystem disservices). We built a binary matrix summarising the NCP provided by terrestrial vertebrates in Europe, by combining existing lists of species that provide NCP and data on their trophic interactions where relevant.

Our final selection of NCP contained 8 regulating NCP (agricultural pest control, mosquito control, tick host control, pine moth control, invasive hornet control, carrion elimination, seed dispersal, pollination) and 4 cultural NCP (species of community interest, evolutionary heritage, nature tourism, wild food foraging) (Figures 2.1 & 2.2).

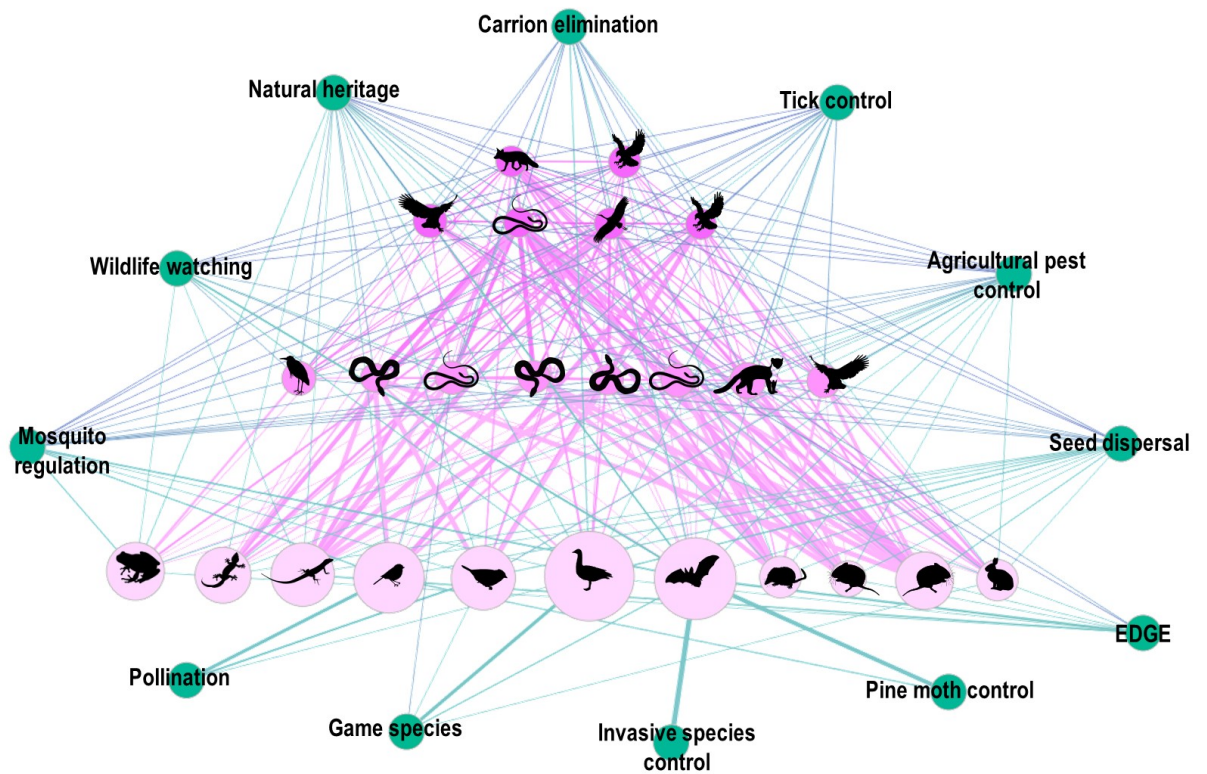


Figure 2.1: Representation of the metaweb of species interactions at the trophic group level and species-based NCP. The colour distinguishes trophic groups (pink) and NCP (green). Node labels in black are the name of the NCP. Node size of trophic groups is proportional to the number of species within the trophic group.

2.2.1.1 Regulating NCP

The majority of regulating NCP rely on trophic interactions data. We used an updated version of the Tetra-EU metaweb of the trophic interactions between all vertebrate species in Europe (Maiorano et al. 2020) and other diet items: Mushrooms, Mosses and Lichens, Algae, Detritus, Sees and Grains, Nuts, fruits, Berries, Bark, Woody vegetation, Leaves, Flowers, Nectar, Bulbs, Aquatic vegetation, Other plant parts, cultivated planted, Invertebrates (4 categories: aerial/vegetation/ground/aquatic), Fishes, Carrion, Coprophagous, Garbage. This metaweb distinguishes obligate or frequent interactions from occasional feeding interactions. Here, we only considered the obligate feeding interactions, because these represent significant and frequent energy flow, and are likely to underpin NCP. We thus assumed that occasional interactions are not representative of a species' feeding ecology, and therefore only make marginal contributions to NCP supply.

Agricultural pest biocontrol. We extracted the species in the dataset built by Civantos *et al.* [10], which provides the list of species that feed on rodent and/or invertebrate species that are considered pests for agriculture in Europe. In total, there were 110 species that provide agricultural pest control.

Mosquito biocontrol. Mosquitoes are a threat to human health since they are vectors for diseases which may become widespread in Europe due to climate change. Using data on the diet and foraging space of species, we identified species that can regulate populations of mosquitoes: insectivorous bats and birds with aerial foraging space (predators of the adult life stage of mosquitoes) [15], and amphibians that feed primarily on aquatic invertebrates [7]. In total, we identified 202 species that can regulate mosquito populations in Europe.

Invasive Asian hornet biocontrol. The Honey buzzard (*Pernis apivorus*) is a proven predator of the invasive Asian hornet nests [16]. While other birds such as the Red-backed Shrike (*Lanius collurio*) or the European Bee-eater (*Merops apiaster*) are also active predators of the European hornet and may attack the yellow-legged hornet, we assume *Pernis apivorus* to be the single most effective terrestrial vertebrate species in Europe for the Asian hornet biocontrol because of its behaviour

of destroying the nests.

Pine processionary moth control. The pine processionary moth has been listed as a species of concern to human health [17]. One of the most effective means to control their spread is biocontrol by predators. Cuckoos (*Clamator glandarius* and *Cuculus canorus*), Eurasian hoopoe (*Upupa epops*), and birds of the tit family (*Paridae*), are predators of the caterpillar life stage [18]. Insectivorous bats are predators of the adult lifestage. In total, we identified 55 species that can provide biocontrol of the pine processionary moth.

Regulation of tick-borne diseases. Ticks are widespread across Europe and pose a risk to human health via tick-borne diseases (e.g. Lyme disease). Large, unchecked populations of tick hosts, especially ungulates and rodents, are important reservoirs for tick borne pathogens. Predators of rodents and of ungulates can help control the spread of tick-borne disease and protect human health [19, 20]. In total, we identified 128 species that are obligate predators of rodents and/or ungulates at any life stage, and therefore that are able to provide tick host biocontrol.

Carrion elimination. The removal of carcasses by scavengers reduces the risk of disease transmission and contributes to nutrient cycling in the ecosystem [21, 22, 23]. In total, we identified 52 species that feed frequently on carrion or are obligate scavengers and therefore provide carrion elimination

Seed dispersal. Vertebrate seed dispersers are essential for plant populations' long term survival [24, 25], since seed dispersal is key to the regeneration of vegetation (especially shrubs and forests), and is therefore indirectly linked to carbon sequestration. We consider all obligate frugivore species to provide this NCP by endozoochory. We also considered species with a scatter-hoarding behaviour (e.g. the European jay) to be highly effective seed dispersers. We extracted the scatter-hoarding species from the dataset built by [26]. In total, we identified 228 vertebrate seed dispersers in Europe.

Pollination. Pollination is linked to both food supply in pollinator-dependent croplands and to the long term survival of flowering plants through reproduction. A few European bird species are occasional pollinators. Even if occasional, their

role as pollinators is complementary to pollinating insects as they can pollinate over larger distances. We extracted 49 species of bird pollinators from the dataset built by da Silva *et al.* in 2014 [27].

2.2.1.2 Cultural NCP

Culturally valued species We extracted terrestrial vertebrate species listed as species of community interest according to the latest European legislation, i.e. the Annexes II and IV of the Habitats Directive and the Annex I of the Birds Directive. We excluded non-breeding birds and non-native species. In total, we identified 438 terrestrial vertebrate species that are culturally valued and protected as part of European natural heritage.

Nature-based tourism and wildlife watching We identified 44 terrestrial vertebrate species frequently mentioned on touristic websites. Species that are important for wildlife watching are those with a very high number of observations given their small range size. To identify them, we computed the ratio between the number of observations per species in GBIF and their European range size (km²). We selected the top 2% species with the highest ratio as the most important for wildlife watching. In total, we identified 55 species of terrestrial vertebrates that are important for nature-based tourism.

Wild food foraging We extracted 35 terrestrial vertebrate game species that are important for hunting in Europe, from the dataset of wild foods built by Schulp *et al.* in 2014 [28].

Evolutionary heritage We extracted the 65 European terrestrial vertebrate species listed as Evolutionarily Distinct and Globally Endangered in the EDGE database [29].

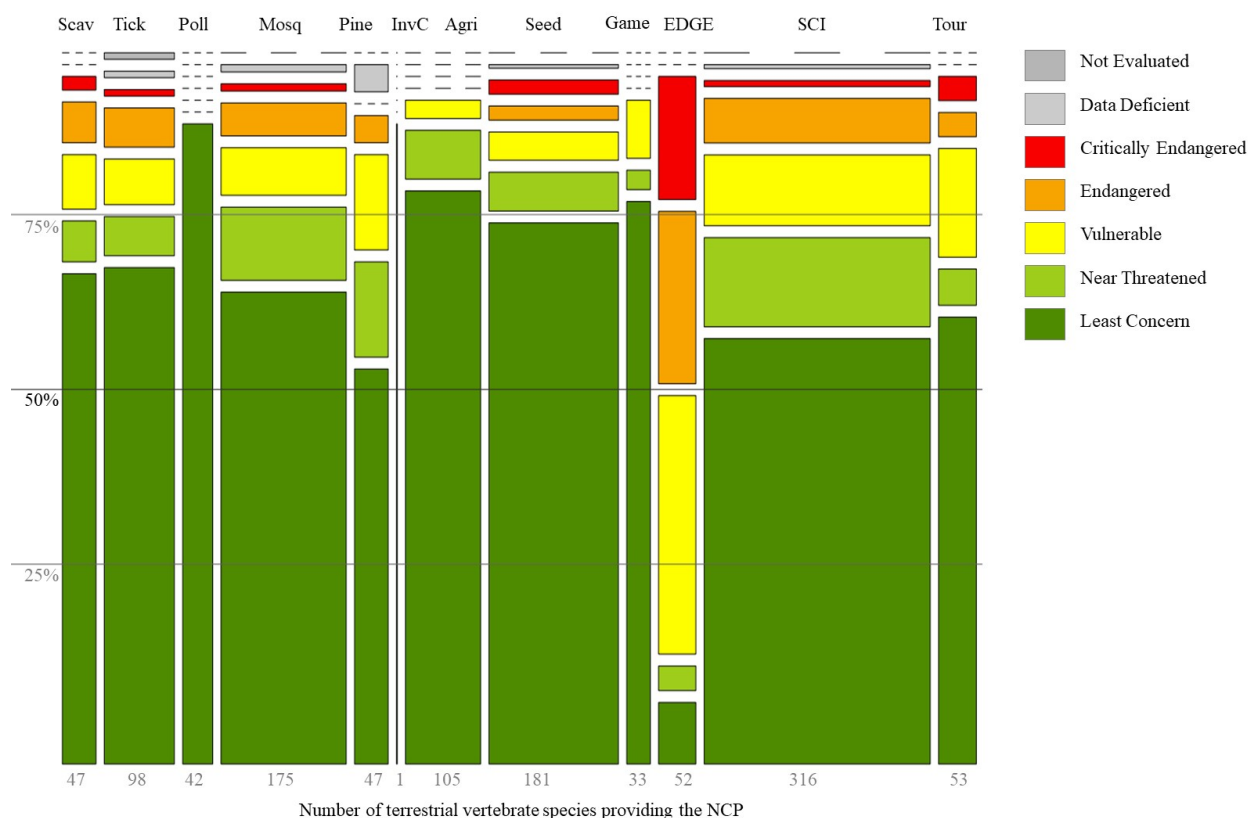


Figure 2.2: Mosaic plot representing the number of species providing each NCP (x axis) and the conservation status of species providing the NCP (y axis). Abbreviations: Scav: carrion elimination; Tick: tick host control; Poll: pollination; Mosq: mosquito control; Pine: pine moth control; InvC: Asian Hornet control; Agri: agricultural pest control; Seed: seed dispersal; Hunt: game species; EDGE: evolutionary heritage; SCI: species or species of community interest ; Tour: Nature tourism and wildlife watching.

2.2.2 Mapping richness of NCP providers across Europe

Study area. The study area covered the spatial extent of the European Union (EU) with the United Kingdom (EU28+), Norway, Switzerland, and the Western Balkans (Serbia, Kosovo, North Macedonia, Montenegro, Albania, and Bosnia and Herzegovina). We excluded Iceland, Cyprus, Turkey and Macaronesia. We considered all native and breeding terrestrial vertebrate species that are known to occur in the study area, and for which data on habitat requirements was available, bringing the total number of species considered to 735.

Species distributions. For mammals, amphibians and reptiles, we downloaded the latest estimates of species extent of occurrence (EOO) from the IUCN red list

website (downloaded in March 2022). For birds, we extracted the EOO from BirdLife (2020), retaining the “extant” and “possibly extant” ranges, for resident and breeding birds.

Habitat suitability model. We used the recently published land system classification [13] which includes 8 land systems and distinguishes low, medium and high intensity land use (for settlements, forests, crops, grasslands, and agricultural mosaics), making 26 land use classes in total. We built a table of species habitat preferences, indicating the suitability of each habitat for each species (0 is unsuitable; 1 suitable habitat). To do so, we combined information from the expert-based table of habitat suitability for vertebrates based on land cover [30] and the IUCN red list data on species geographic ranges, habitat preferences and threat types, using the databases at the global (IUCN Red List) and the European level (EEA, 2020) (see Extended Methods).

NCP capacity maps. We created 1km² species distribution maps by filtering the estimated EOO of all species with the habitat preferences and distance to water requirements of each species, as was previously done [30]. We considered a species to be present in a 1km² grid cell if the cell was within the species EOO **and** consisted of suitable habitat for the species.

To estimate the capacity value for each NCP across space, we built on the methodology used in Ceaușu *et al.* in 2021 [5]. We quantified the capacity of NCP as the provider richness in each grid cell j as:

$$PR_j = \sum_i H_{i,j}$$

where $H_{i,j}$ is the local habitat suitability for species i in grid cell j . We then mapped NCP capacity as provider richness, and NCP diversity as the sum of NCP capacity (scaled between 0 and 1) per broad NCP type (i.e. regulating, and cultural) (Figure 2.3)

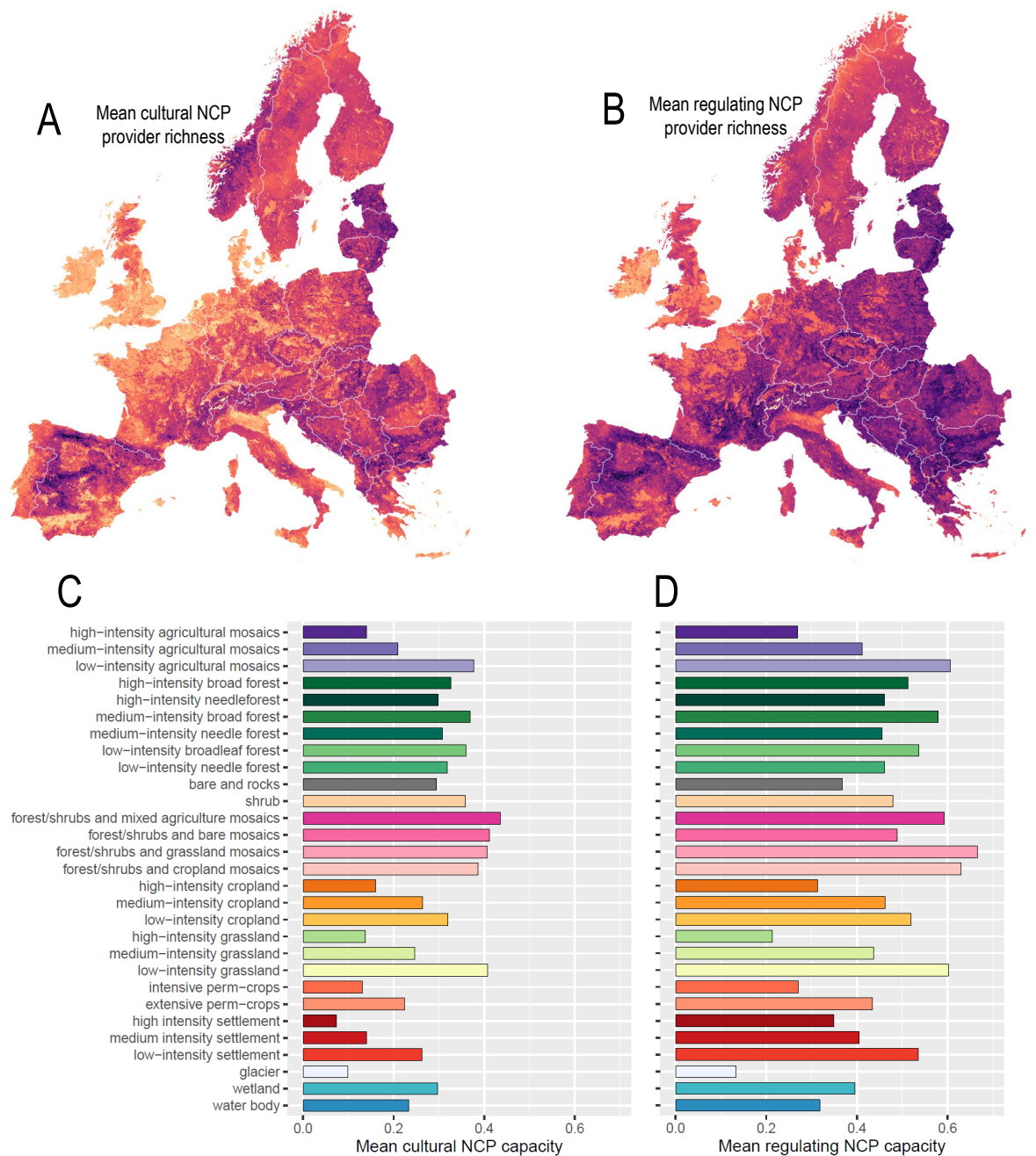


Figure 2.3: NCP diversity is affected by land use intensity across Europe. Regulating and cultural NCP capacity are lower in higher intensity of land use. This is in line with previous studies showing that organic agriculture promotes pest control [31]. Maps show the average value of NCP capacity (i.e. provider richness) of all cultural NCP (A) and regulating NCP (B) in each grid cell, from low (light yellow) to high (dark purple) provider richness. NCP provider richness is scaled between 0 and 1 for each NCP by dividing by the maximum provider richness value for this NCP in Europe. The bar plots show the average value of NCP capacity of all cultural NCP (C) and regulating NCP (D) in each of the land systems. This figure shows that higher land use intensity negatively affects species-based NCP capacity. In all land systems, as intensity level increases, the mean NCP capacity decreases for both regulating and cultural NCP. Cultural NCP is lowest in high intensity urban areas, high intensity agriculture and glaciers. Regulating NCP is lowest in high intensity agriculture (croplands and grasslands) and glaciers.

Combining capacity and societal demand to map NCP supply. Building on previous work, we defined NCP supply as the product between supply and demand layers for each NCP [32]. The demand for many NCP was assumed to be related to land use. We used the European land system classification built by Dou *et al.* [13]. We evaluated whether or not there can be demand for each NCP in each land use class. The result is a binary matrix, where element (i, j) is equal to 1 if there is demand for NCP i in land use class j .

For two NCP, the demand was not related to land use but to other factors: this is the case for Lyme disease regulation and for mosquito control. Demand for Lyme disease regulation was assumed to be higher in areas where ungulates and/or rodents are present. Demand for mosquito control was assumed to be higher where human density is higher.

2.3 Limitations of the database

Here, we highlight a number of limitations to clarify what this database can and cannot do, and discuss options to address these limitations in the future.

First, we assigned equal weight to each species that provided an NCP. Yet, it is possible that not all species are equally efficient in doing so. The functional effectiveness of species in providing an NCP is likely to be related to both intrinsic traits (e.g. body mass, diet specialisation, diet preferences) and local traits (relative abundance or biomass of the species, resource availability).

Second, we assumed NCP capacity increases linearly with the number of species that provide it. Yet, this relationship may be non-linear, so we may overestimate actual NCP capacity [33]. There may be thresholds, where a certain amount of biodiversity is required to have a significant amount of NCP. We assumed that a diversity of predators are more effective in reducing the populations of herbivorous pest species, but a diversity of predators may inhibit biocontrol if predators attack each other through intra-guild predation [34, 33]. Furthermore, a study has suggested that abundance of dominant species that provide NCP, not species richness, drives the

delivery of ecosystem services [35]. 2015). Work by Antunes et al. (in preparation) holds promise to quantify the biomass of NCP providers and energy fluxes that underpin NCP (see Appendix ??). Which NCP are influenced by single species? In which cases do you need a certain specific species or just a group of species? Because this is likely dependent on the NCP and the local context, it is particularly challenging to account for this in the mapping of NCP capacity at a large spatial scale. Further, other diversity metrics than species richness may be relevant for NCP capacity, such as functional diversity [3]. High functional diversity may increase the stability of NCP capacity in different ecological contexts due to niche complementarity. However, the question of which functional traits to include in the functional diversity metric is non-trivial. Besides, functional diversity is tightly linked to species richness.

2.4 Potential applications

Knowledge of species-based NCP can help predict the vulnerability of NCP to anthropogenic pressures, and to guide conservation decisions for both biodiversity and NCP. By combining both food web information and species-based NCP, it is possible to identify terrestrial vertebrate species that are important for the robustness of both food webs and NCP capacity in Europe. Species that are indirectly linked to NCP through species interactions (e.g. important prey) are equally important for NCP supply. By using the PageRank algorithm, we could thus identify species that indirectly support each NCP (i.e., supporting species) [9]. One interesting avenue may be to consider incorporating supporting species in the mapping of NCP capacity, under the assumption that NCP supply is higher where there is a higher richness of species that both directly and indirectly contribute to the NCP. Our database can be useful for identifying gap species that are not currently prioritised in conservation policies (e.g. Birds and Habitats Directives) yet they are important and irreplaceable NCP providers. Across space, it can help prioritise areas and examine the synergies and trade-offs between species and NCP conservation [36]. Areas with high societal demand for an NCP but low richness of NCP providers, could be prioritised to invest

conservation resources in order to increase the diversity and population levels of NCP providers.

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Supplementary Figures

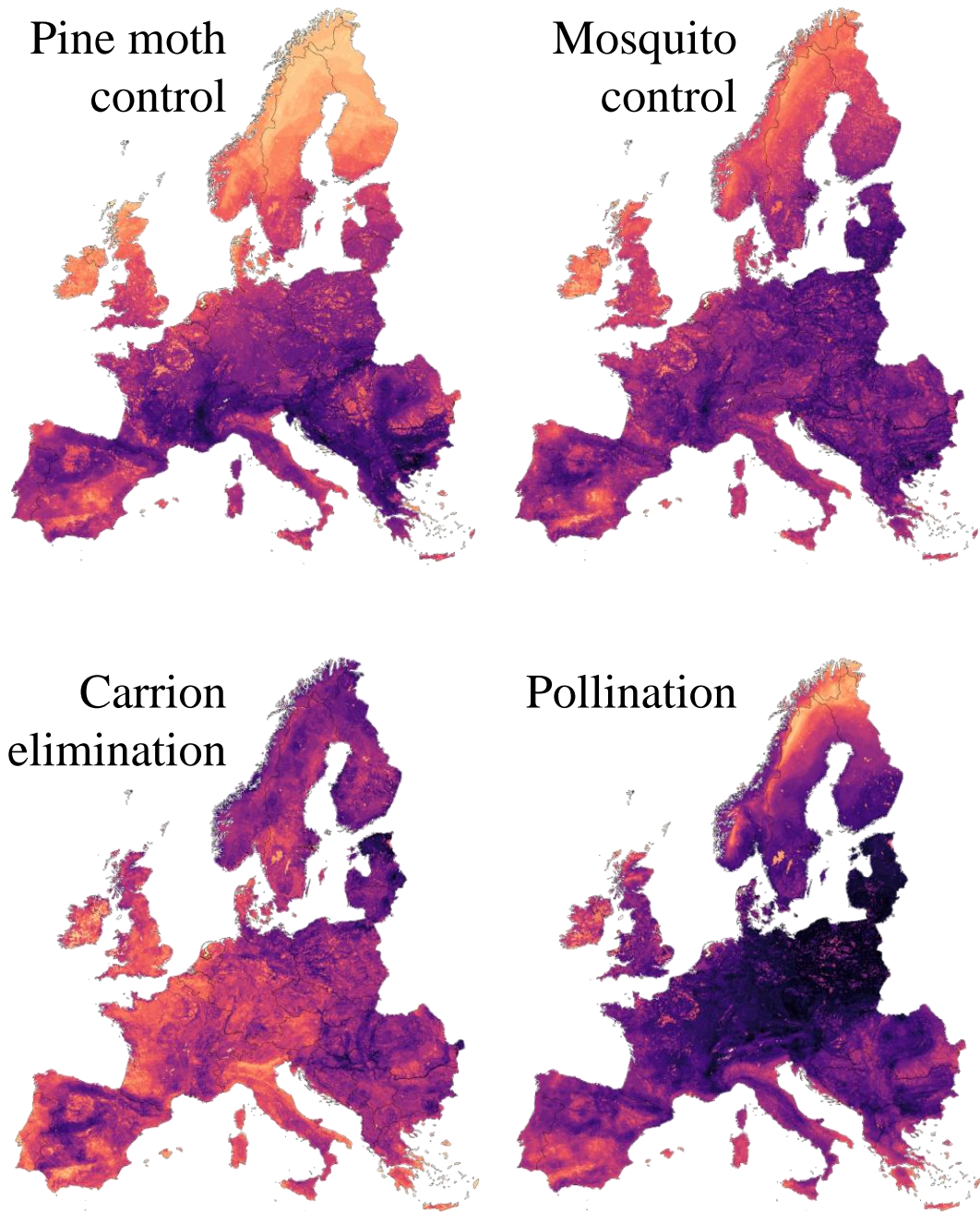


Figure 2.4: (A) Species richness of regulating NCP providers, accounting for land use intensity

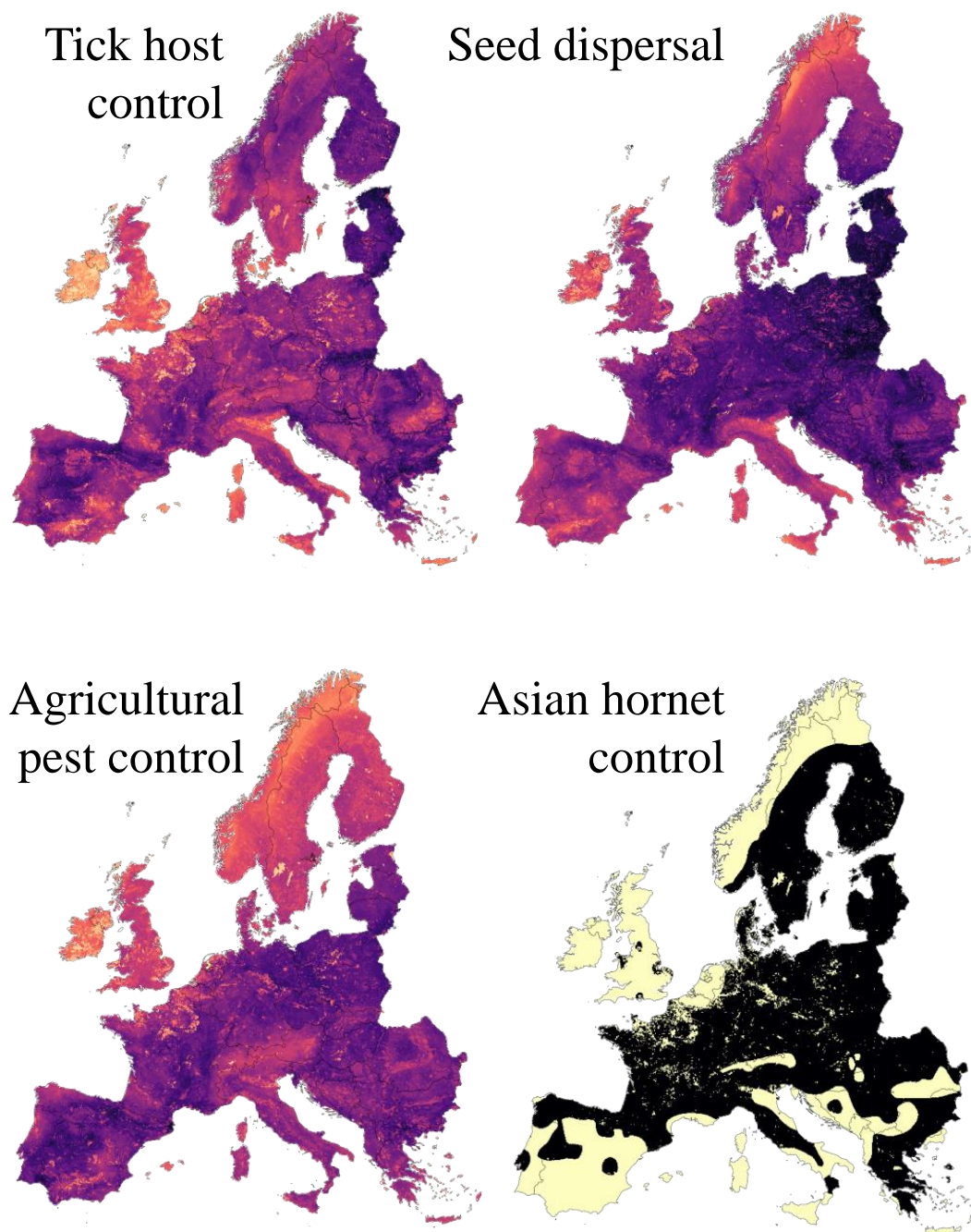


Figure 2.5: (B) Species richness of regulating NCP providers, accounting for land use intensity

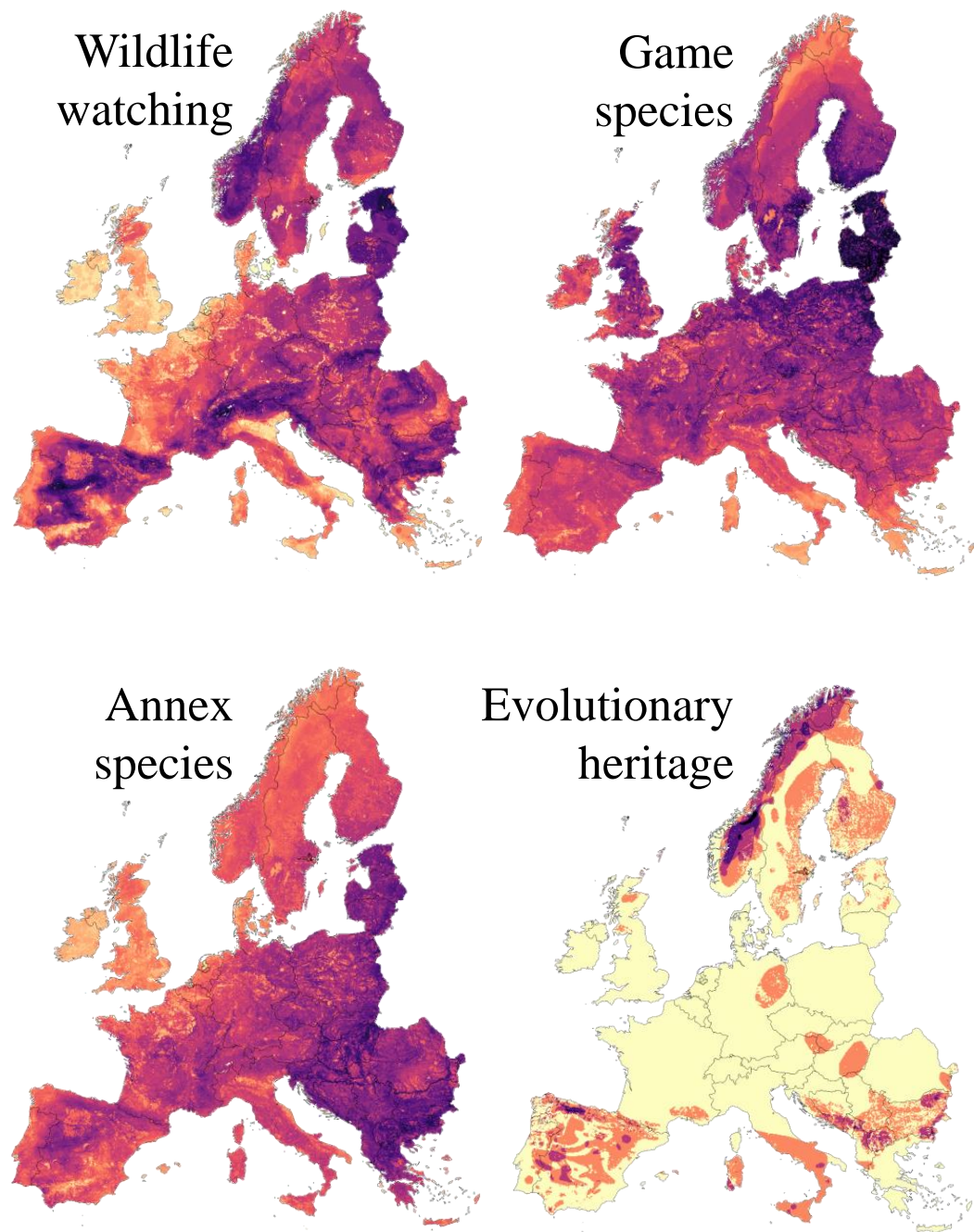


Figure 2.6: Species richness of cultural NCP providers, accounting for land use intensity

Part II

Food web responses to anthropogenic changes

Chapter 3

Vulnerability of terrestrial vertebrate food webs to anthropogenic threats

In preparation for submission to *Diversity and Distributions* as a Perspective paper.

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The direct and indirect impacts of anthropogenic threats in food webs are poorly understood, especially at a macroecological scale. We combined IUCN red list data and food webs to address this gap. We ask: Does considering species interactions improve our understanding of the vulnerability of species and communities? How vulnerable are food webs and species interactions to anthropogenic threats? Where are the most vulnerable areas to different threats?

Abstract

While major direct threats are now well-documented for many species, indirect threats caused by species interactions are much less understood despite their potential importance. Indeed, threats faced by prey species can jeopardise their predator's survival through scarcity of food resources. These indirect threats from species interactions have been poorly investigated so far. Here, we combined the data on trophic interactions between over 800 European terrestrial vertebrates with data on their anthropogenic threats from the IUCN red list. We quantified the vulnerability of different components of the food web (species, species interactions, and trophic groups) and identified the hotspots of food web vulnerability to six major threats (pollution, agricultural intensification, climate change, direct exploitation, artificialization, and invasive alien species). We found that: i) agricultural intensification and direct exploitation are the most impactful threats overall for terrestrial vertebrates and their interactions; ii) pollution and invasive alien species impact the majority of water-dependent trophic groups; iii) trophic interactions reveal a much higher vulnerability to anthropogenic threats than a species-based threat assessment would suggest, in particular in the case of agricultural intensification and direct exploitation. Combining network ecology with threat impact assessments improve our understanding of the scale of the impacts of human activities on biodiversity.

3.1 Introduction

Biodiversity is in decline, and we may be entering the 6th mass extinction [1]. Ecologists now have a good understanding of the major threats that affect different compartments of biodiversity: land use change (e.g. agricultural expansion, deforestation), direct exploitation (hunting and trapping), pollution, climate change and invasive alien species (IAS). These human activities lead to population declines by affecting one or more aspects of species' life history traits (breeding, nesting and feeding) or reducing individuals' fitness. A macroecological perspective has recently emerged to better grasp the scale of the impacts of multiple human-induced threats to biodiversity. In a recent study, Harfoot *et al.* [2] mapped the impacts of several major

threats to a large number of species at a global scale. They showed that different groups of species face different direct threats: pollution was suggested to be the most prevalent threat for amphibians, whereas hunting and persecution was more harmful to mammals and birds. Another recent study [3] showed that some functional groups (carnivores, large endotherms and small ectotherms) are disproportionately impacted in disturbed landscapes compared with other groups of species, which could severely impact the structure of ecological communities. Although particularly insightful to derive specific protection measures, these studies miss the cascading threats that could arise from trophic interactions. In other words, past studies may underestimate the impact of threats to biodiversity.

Species are indeed not independent of each other and are instead interconnected in food webs such that any human activity that threatens one species, or a set of similar species, may indirectly affect another [4]. For example, the loss or decline of a prey is likely to affect a predator's feeding success and, therefore, chances of survival, and in some cases can lead to the extinction of predators [5]. These indirect threats can be particularly strong in the case of trophic specialists (a predator feeding on a specific prey) or when a threat extirpates a set of species that constitute the overall resource required by one or more predators. More generally, trophic interactions can shed light on the cascading impact of threats on interacting communities and ecosystem functioning [6, 7]. However, the impact of multiple threats on food webs is poorly known and there is a need to disentangle the direct and indirect impacts of threats to biodiversity. A recent study [8] used simulations to quantify the loss of biotic interactions in seed dispersal networks following habitat loss and showed that small amounts of habitat loss can cause up to 10% of species to lose their interaction partners. But these questions have not been addressed at a macroecological level and for large trophic networks.

Here we fill this gap by asking: 1) Can considering species interactions improve our understanding of the impact of multiple threats on biodiversity? 2) What species, interactions, and trophic groups are most vulnerable to which threats, and where? To answer these two questions, we quantified and mapped the vulnerability

of all European vertebrate species and their trophic interactions to six major threats: agricultural intensification, direct exploitation, artificialization (e.g. urbanisation, housing development, infrastructure for tourism and leisure), climate change, pollution and invasive alien species. We combined IUCN European regional red list data on threats to species, with trophic interactions [9] and geographic distributions [10]. We first investigated whether species' vulnerability to threats is related to their position in the food web (i.e. trophic role and number of prey and predators), to identify whether certain trophic roles are more vulnerable to specific threats. We then quantified the vulnerability of interactions, with a specific focus on bottom-up risks (i.e. the vulnerability of each predator's prey species). Finally, we investigated the vulnerability of local food webs to the six different threats across Europe.

3.2 Materials and Methods

3.2.1 Anthropogenic threats to species

We used the European Red List of species (downloaded in October 2020 (European Red Lists of Species, 2018)), which describes the types of threats that each species is known to be vulnerable to, anywhere within their range. We extracted the threat data for all 935 terrestrial vertebrate species available in the dataset. Because the data on threats to species is available in the form of sentences, we searched for character strings that correspond to different threats (Table S1). Building on the IUCN red list threat classification scheme (IUCN Red List), we defined 10 primary threat categories and 26 subcategories (Table 1). We then focused on the 6 major threat categories which affect the highest number of terrestrial vertebrate species in Europe (at least 200): residential & commercial development (hereafter Artificialization), direct exploitation, agricultural intensification, pollution, invasive species, and climate change.

3.2.2 Metaweb of trophic interactions

We used an updated version of the Tetra-EU metaweb of the trophic interactions between all vertebrate species in Europe [9]. This version distinguishes obligate interactions (which are essential for predator species survival) from occasional feeding interactions (which are unlikely to play a role in the propagation of threats in the food web). Here, we only considered the obligate feeding interactions on the adult life stage of the prey species. We further removed the interactions between species that never co-occur across Europe. The resulting metaweb contained 1084 species and 12,226 interactions (Figure 3.1).

3.2.3 Species distributions

The study area covered the spatial extent of the European Union (EU) with the United Kingdom (EU28+), Norway, Switzerland, and the Western Balkans (Serbia, Kosovo, North Macedonia, Montenegro, Albania, and Bosnia and Herzegovina). We excluded Iceland, Turkey and Macaronesia to avoid border effects. We considered all species that are included in both in the European red list dataset and in the European Tetra-EU database [9], which includes only native species and resident and breeding birds. We corrected taxonomical mismatches (Supplementary Materials), and removed the species that are disconnected from the metaweb (i.e. that are both not predators in the metaweb and that are not prey in their adult life stage). We extracted the distributions of the species occurring in the study area (804 species in total) from Maiorano *et al.* (2013) [10]. These distributions were obtained by combining the extent of occurrence for each species with their habitat requirements. Species distributions were mapped in a regular grid of 300 m resolution, where cells had values of zero for unsuitable habitat, one for marginal habitat (habitat where the species can be present, but does not persist in the absence of primary habitat) and two for primary habitat. Here, we treated primary habitat only as ‘suitable habitat’, which provides a better prediction of the actual species distribution [11]. Given that a number of vertebrate species have large home ranges (e.g. 100 km²), we upscaled distribution maps to a 10 × 10 km equal-size area grid (ETRS89; total of 49,818 grid cells). We considered the species potentially present in a 10 × 10 km cell if the grid

cell contained at least one suitable habitat.

3.2.4 Quantifying the vulnerability of food webs to multiple threats

We quantified the main threats faced by species and their interactions, as well as particular trophic groups.

First, we investigated whether a species' vulnerability to different threats was related to the trophic role of the species. We used the same methodology as in [12]: we used the stochastic block model (R package `blockmodels`) to group together the species that eat the same food and are eaten by similar sets of predators in the metaweb. To do this, we also included diet categories in the metaweb: algae, aquatic vegetation, fishes, aquatic invertebrates, aerial invertebrates, invertebrates on ground, invertebrates on vegetation, fruits, flowers, nectar, bulbs, berries, leaves, bark, seeds & grains, nuts, woody vegetation, other plant parts, mushrooms, mosses & lichens, cultivated plants, domestic animals, garbage, detritus, dung, carrion. We selected the model with the highest Integrated Classification Likelihood (ICL) information criterion, which partitioned the metaweb into 28 groups (Figure 3.1). We then computed the proportion of species within each group that are vulnerable to each threat.

In addition, we computed the degree (number of prey, number of predators, and total number of neighbours) of species using the R package `igraph::degree`. This allowed us to investigate whether highly connected species are vulnerable to certain threats, which would have a potential higher impact on the rest of the food web.

Second, we quantified the indirect threats to predator species as the number of species' potential prey that are affected by each threat. To do so, we performed a matrix multiplication between:

- the threats matrix M_1 where element (i, j) is equal to 1 if species j is threatened by threat i , and

- the adjacency matrix representing the food web M_2 , where element (i, j) is equal to 1 if species i is eaten by species j

This matrix multiplication results in a third matrix M_3 . Each element (t, p) of this resulting matrix is equal to the number of prey species of predator p (in columns) that are affected by threat t (in rows). Then, we divided each value by the total number of prey species of the predator, to get a proportion of vulnerable prey for each predator, for each threat.

In this matrix multiplication, we assumed that predators are indirectly vulnerable to threats that affect their prey. We only quantified the threats associated with species that are neighbours in the food web, rather than cascading threats across multiple trophic levels.

3.2.5 Quantifying the vulnerability of food webs to anthropogenic threats across Europe

We combined the spatial distributions with the metaweb to build local food webs in each grid cell, by sampling the metaweb with the local community of species. We assumed that if two species interact in the metaweb and they both occur in the grid cell, then the interaction exists in the local food web. We assumed a link is vulnerable if it is associated with a vulnerable prey and/or predator species. In other words, vulnerable interactions can be both top-down (the species may stop functioning as a predator) or bottom-up (the species may stop functioning as a resource). We quantified the proportion of vulnerable species, and vulnerable interactions in the food web that are associated to species that are vulnerable to each threat type. We first compared the proportion of vulnerable species and vulnerable interactions at the level of the metaweb. Then, we quantified these proportions across space: for each pixel p , we quantify the proportion of species, and interactions that are vulnerable to the major threat types. Finally, we identified food web vulnerability hotspots to each major threat, by multiplying the number of vulnerable species and the number of vulnerable interactions in food webs across Europe.

3.3 Results

Different trophic groups face different threats. Hunting and persecution was the most impactful threat for European vertebrates, affecting 34% (319) species, essentially top predators (Figure 3.1) with a high number of prey (Figure 3.2). As a result, 85% interactions in the metaweb were vulnerable to hunting and persecution (Figure 3.3). Agricultural intensification was the second most impactful threat, affecting 31% (285) species and 6% metaweb interactions. Importantly, highly connected species were among the most vulnerable to agricultural intensification (Figure 3.2). In particular, over 70% of birds of prey (groups 2, and 24) and 78% of generalist predator species (group 13) were vulnerable to agricultural intensification, primarily due to the use of pesticides; 42% of insectivorous shrews & moles (group 19) were also affected. Artificialization (i.e. residential and commercial development) were the third most prevalent threat, affecting 255 species and 42% metaweb interactions, across multiple trophic levels: 50% of birds of prey (groups 2 and 24), 50% of macro vipers (group 23), 41% of amphibians (group 1) and 41% wading birds (group 15) were found to be vulnerable to artificialization. Climate change was a threat for 26% (235) species and 41% interactions across different trophic levels: passerines (group 11), birds of prey (group 24), aquatic predators (group 9). Pollution, invasive alien species and wetlands loss were major threats to all the water dependent trophic groups: amphibians (group 1), herbivorous water birds (group 15) and aquatic predators (group 9, including the otter and predatory wading birds). The latter were also highly vulnerable to hunting and persecution (which affects 75% of aquatic predators) and agricultural intensification (56%).

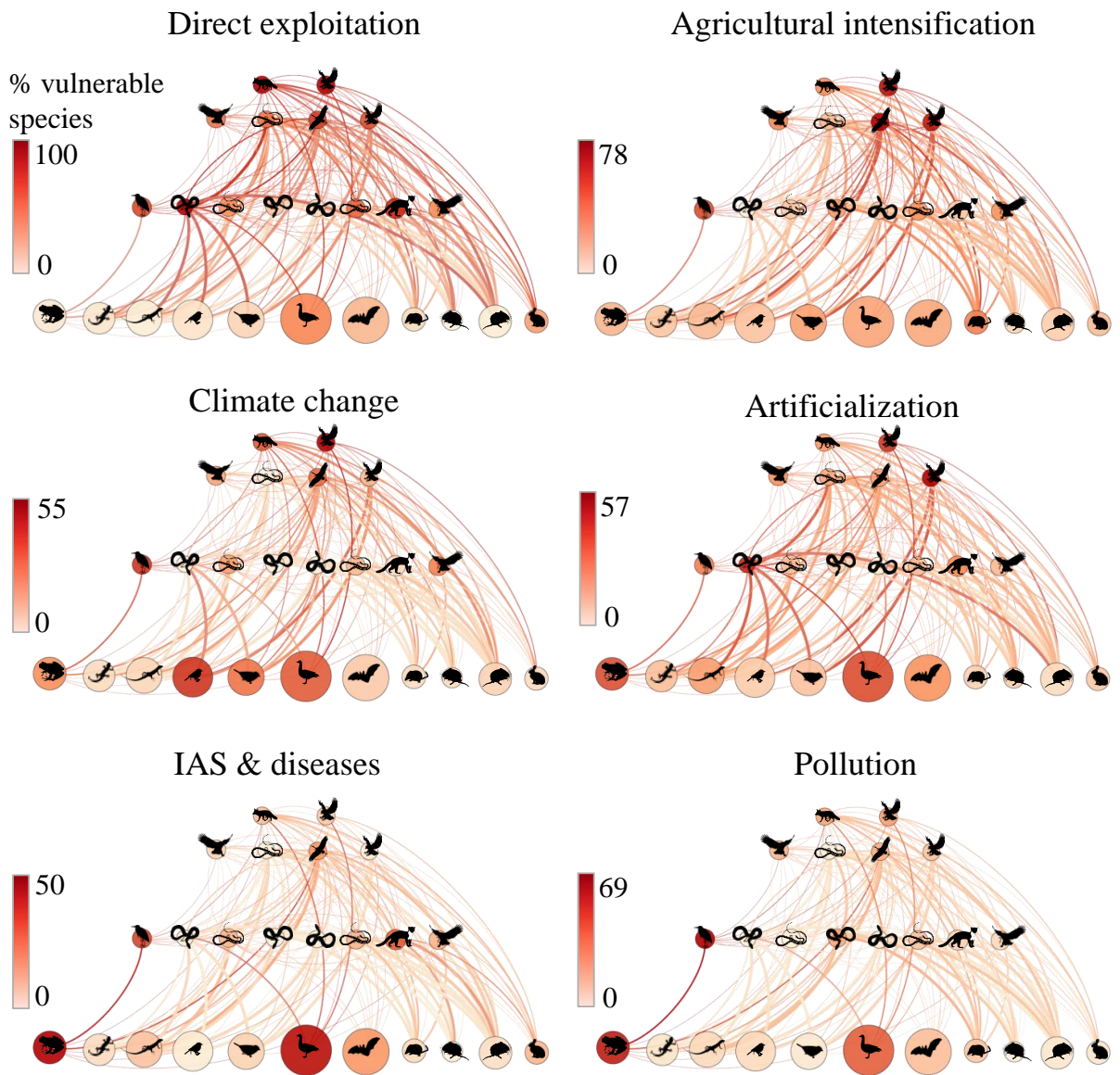


Figure 3.1: Different trophic groups are vulnerable to different threats. Each network represents the metaweb, coloured by the type of threat. Nodes are trophic groups, and links represent feeding interactions between trophic groups. Node size represents the number of species within the group, and link width represents the number of interactions between trophic groups. Colour intensity of the node represents the proportion of species in each group affected by the threat. Link colour is the mixed colour of the two interacting nodes.

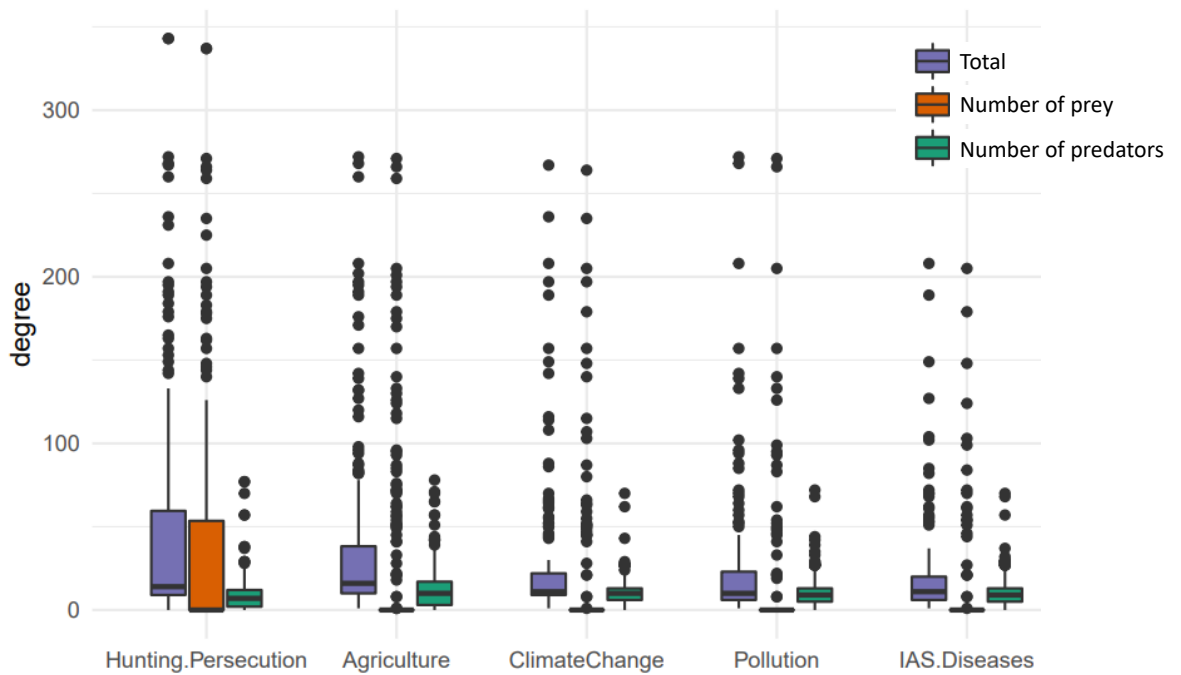


Figure 3.2: Relationship between the degree of species and their vulnerability to each threat. We consider 3 types of degree: number of prey in orange, number of predators in green and total number of neighbours in purple.

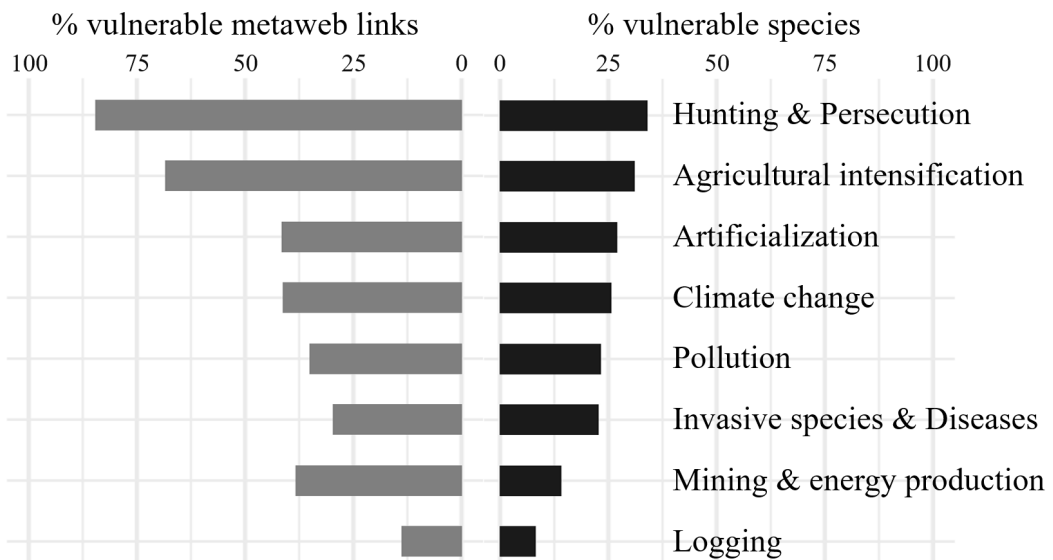


Figure 3.3: Percentage of species vulnerable to each threat and their associated links in the metaweb. Right: percentage species vulnerable to each threat type. Left: percentage of links in the metaweb associated to vulnerable species (both predator and prey). The links considered here are interactions between species that co-occur at least once in Europe.

Most predators are indirectly vulnerable to agricultural intensification. When focusing on the vulnerability of prey for predators, we found that agriculture was the most impactful threat for predator resources overall: on average, 30% of predators' prey species are vulnerable to agricultural intensification (Figure 3.4). *Lynx pardinus*, a specialist predator of the European rabbit, was indirectly highly vulnerable to agricultural intensification, hunting, and diseases that affect its main prey species. Climate change was another major indirect threat for predators (affecting 18% prey per predator on average), as well as artificialization and hunting and persecution (both affecting 22% prey per predator on average).

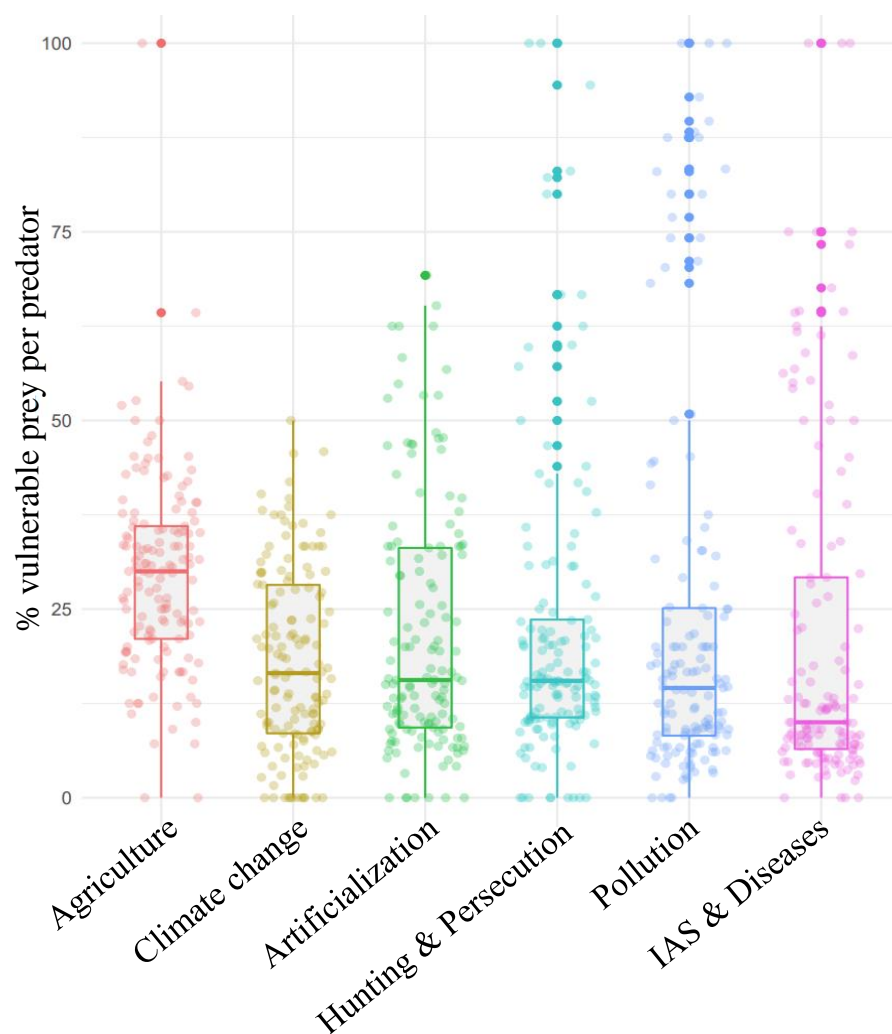


Figure 3.4: Indirect vulnerability of predators in the metaweb to each threat. Each dot corresponds to 1 predator species (i.e. that have at least 1 terrestrial vertebrate prey), y axis= % prey of this predator species that is affected by the threat type on the x axis. Threats are ordered from highest to lowest median value of % prey affected per predator.

Interactions are disproportionately more vulnerable than species. In the metaweb and across space, a higher number of vulnerable species inevitably leads to a higher number of vulnerable interactions, but we found that some threats had a disproportionate impact on interactions relative to the number of vulnerable species (Figures 3.3, 3.5 and 3.6). In the metaweb, we found that for instance, IAS and diseases and pollution both affected 23% species and 30% metaweb interactions, while pesticides affected 15% species and 53% interactions (Figure 3.3). Hunting and persecution affected 34% species but these species were responsible for 85%

interactions in the metaweb, because these species were highly connected (Figure 3.2). Similarly, across Europe, we found that the proportion of vulnerable interactions was consistently higher than the proportion of vulnerable species in food webs (Figures 3.5 and 3.6). In some areas, 100% interactions in the food web were vulnerable to major threats, while only a fraction of the species were vulnerable (Figure 3.6). The difference between species vulnerability and link vulnerability varied with the threat type. In the case of hunting and persecution and agricultural intensification, the proportion of threatened interactions (85% and 79% on average, respectively) was 2 to 3 times higher than the proportion of threatened species (38% affected on average). The difference was lower for other major threats: on average, climate change affected 28% species and 39% interactions; 22% species and 35% interactions were vulnerable to pollution; 21% species and 33% interactions were vulnerable to IAS and diseases. We also found that there was greater variability in the proportion of threatened interactions compared to the proportion of threatened species, across all threat types considered. Combining the number of both vulnerable interactions and species, we highlighted hotspots of food web vulnerability to major threats across Europe, i.e. with a high number of vulnerable species and interactions (Figure 3.7). These were mostly located in species-rich areas, but spatial patterns of vulnerability hotspots differed between threat types.

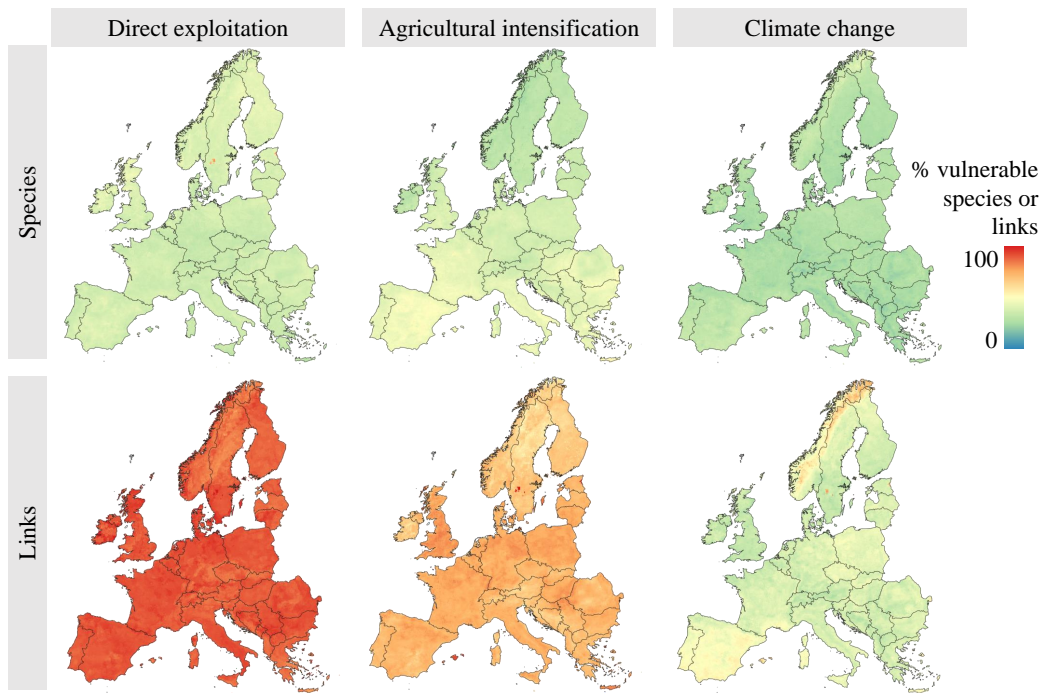


Figure 3.5: Vulnerability of species and links across Europe to 3 major threats: direct exploitation, agricultural intensification and climate change. Top: percentage of species in the grid cell that are vulnerable to each threat. Bottom row: percentage of links in the local food web that the vulnerable species are associated to. The colour gradient used is the same for all maps.

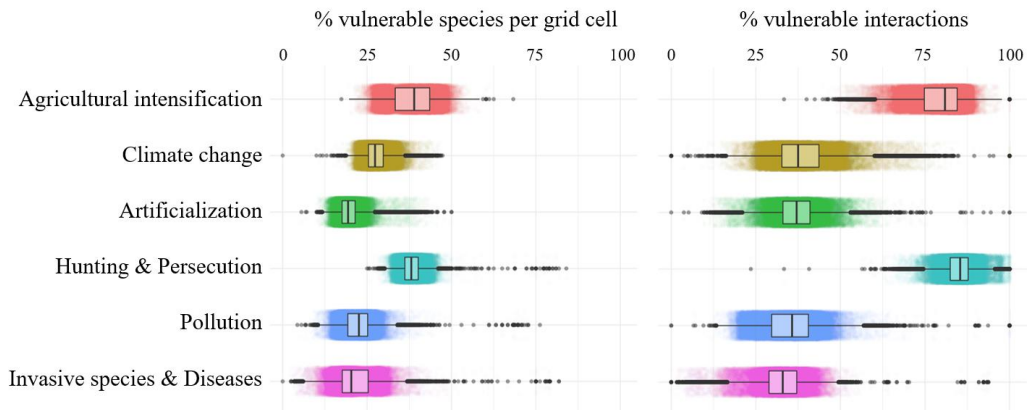


Figure 3.6: Proportion of vulnerable species (left) and links (right) across Europe to different threats. Each dot represents one grid cell, coloured by the threat type.

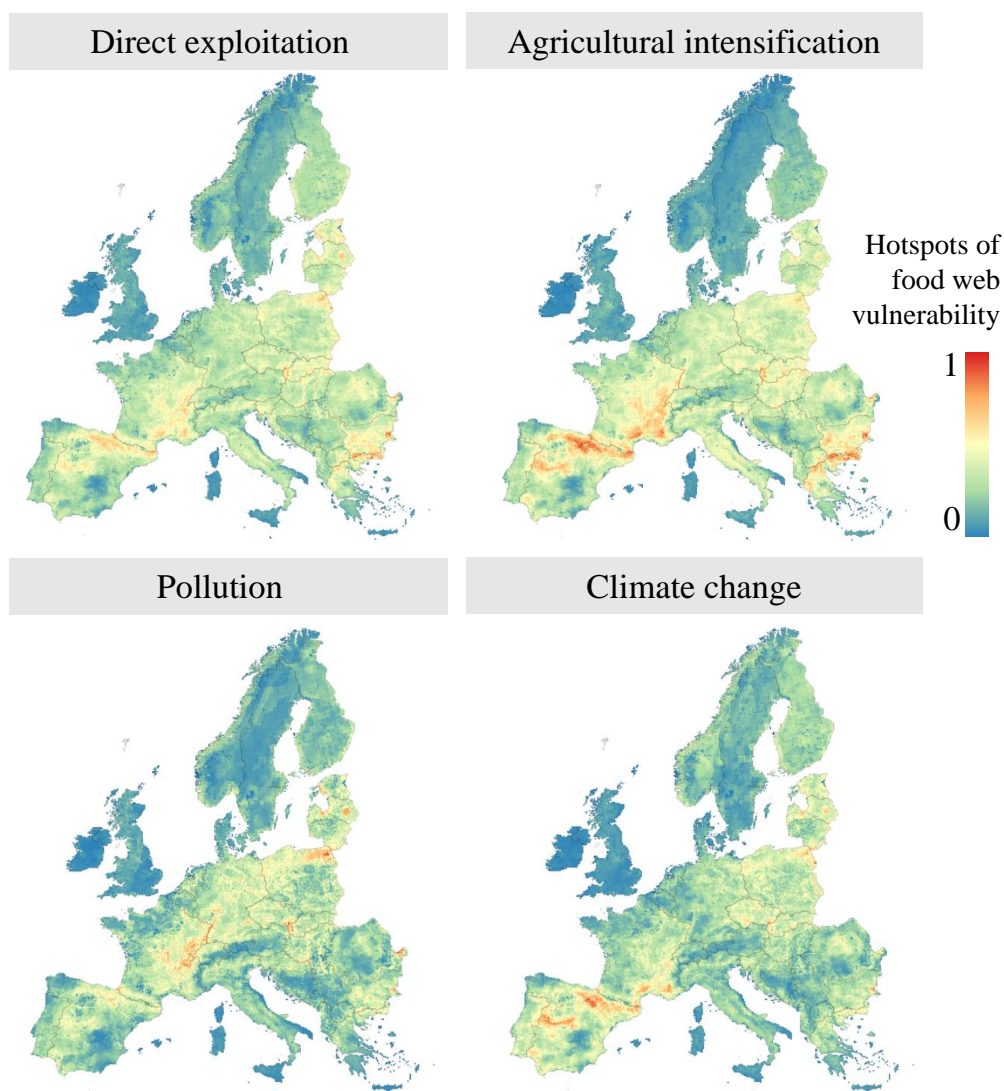


Figure 3.7: Hotspots of food web vulnerability. The value in each cell is the multiplication of the number of vulnerable species (scaled between 0 and 1) and the number of vulnerable links (scaled between 0 and 1) in each grid cell, for each threat. Red colour indicates areas with a high vulnerability of both species and links to each threat. Blue indicates low vulnerability values of species and links.

3.4 Discussion

In 1962, Rachel Carson published *Silent Spring*, describing how impacts from pesticides can spread in the entire food chain. Since then, conservation efforts may have increased globally [13], but remain insufficient compared to the scale and intensity of human impacts on nature. Sixty years later, we are only starting to understand how different types of human activities are impacting interaction networks at a

macroecological scale [14]. Identifying what components of biodiversity are most at risk, and where, can inform threat mitigation strategies and help locate priority areas for conservation [15]. Our results suggest that investigating the vulnerability of interactions in a food web provides novel insight in our understanding of threats to biodiversity. In particular, we showed that interactions tend to be disproportionately more vulnerable to certain threats relative to species, in particular in the cases of direct exploitation and agricultural intensification. Because they both affect highly connected species, these pressures may cause ecosystem disruption and extinction cascades [7]. The impact of direct exploitation on terrestrial vertebrates is unsurprising given the long list of species that have been hunted to extinction in the past [16, 14]. Our results highlight the need for a strict regulation of the direct exploitation of species in Europe in order to avoid large-scale disruption of food webs. Such regulation is fortunately made possible in the European Union through the Annex V of the Habitats Directive (“species whose taking in the wild and exploitation may be subject to management”), but the legislation only includes 19 species, which may be insufficient given the 319 terrestrial vertebrate species that are vulnerable to direct exploitation in Europe. The scale of the impact of agricultural intensification on species and their interactions is also deeply worrying. It is well established that agricultural intensification has a negative impact on many species through multiple processes: the use of pesticides and nitrates leads to a decline of insect prey for insectivores and to the eutrophication of ecosystems; the loss of green linear elements that are essential habitats for many species and their prey; the conversion of natural habitats converted to agricultural lands. But our study is the first, to our knowledge, to describe the staggering impact of direct exploitation and agricultural intensification on terrestrial vertebrate food webs across Europe. Since terrestrial vertebrates underpin essential ecosystem services in agricultural landscapes such as pest control [17], there is a need to better consider biodiversity in agricultural systems [18]. While IAS, diseases and pollution impact relatively less species and interactions overall among terrestrial vertebrates, they affect over half of water-dependent species and trophic groups, meaning that food webs in degraded

wetlands are at serious risk of disruption. There is overwhelming scientific consensus that different drivers of biodiversity loss interact synergistically [19] and one threat exacerbates the effect of another (e.g. climate and agriculture) [20]. Incorporating biotic interactions has the potential to improve our understanding of the scale of impacts of anthropogenic threats on biodiversity and nature's contributions to people [21] and to better inform policy making on threat mitigation.

Here, we only investigated the vulnerability of food webs to threats, and not the impact of threats. To assess the actual impact of threats, there are a number of options. In some instances, the threat data indicates where in the range of the species (e.g. in which country) and in which time period (present, past or future) the threat occurs. It is species-specific and threat specific information. Because it is not consistent across species, we decided to ignore these specifications. Another option would be to use land use maps as a proxy for threats that are related to land use intensification and habitat loss (e.g. agriculture intensification, forest management, urbanisation, wetlands loss, forest loss, grassland loss). We would then combine the spatial risk of threat with the vulnerability of food webs to each threat to estimate threat impact across Europe. This can be applied to the current situation [22], past change (e.g. through CORINE change), or future scenarios of change [23]. This could then allow us for example to i) identify orphaned species that lose all their interactions [8], ii) to locate areas where predators are losing vertebrate prey due to the combined action of multiple threats locally, and iii) to quantify the cascading impact of threats on food webs across space. Food webs offer the opportunity to investigate the synergistic effect between threats on a species or community: a predator can lose part of its prey due to one threat, and the rest of its prey due to a different threat. Quantifying the impact of multiple threats on a food web can give a more realistic view of the risks posed by human activities to biodiversity. We expect that the severity of cascading extinctions will result from the combination of the environmental threats faced by individual species, and the susceptibility of the community itself to propagate perturbations due to food web topology.

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Supplementary Materials

Major threat category	Threat subcategory	Number of vulnerable species	
Residential & commercial development (i.e. Artificialization)	leisure, tourism	146	255
	construction	71	
	human disturbance	48	
	urbanisation	69	
Agriculture	agriculture expansion and intensification	202	285
	pesticides	140	
Aquatic resource	fishing industry, aquaculture	57	
Pollution	including chemical pollution in water & soils	219	
Energy production & mining	mining, quarries	51	136
	oil & gas exploration and extraction	62	
	renewables (wind farms, hydroelectricity, tidal energy plants)	66	
Forestry practices	logging	76	154
	deforestation	28	
	afforestation	60	
Direct exploitation	hunting & exploitation	233	319
	persecution	154	
	collection & pet trade	118	
Invasive species & diseases	invasive alien species	130	212
	diseases & pathogens	123	
Climate change & severe weather	including warming, droughts, severe winters, extreme weather events	235	

Figure 3.8: Threat classification

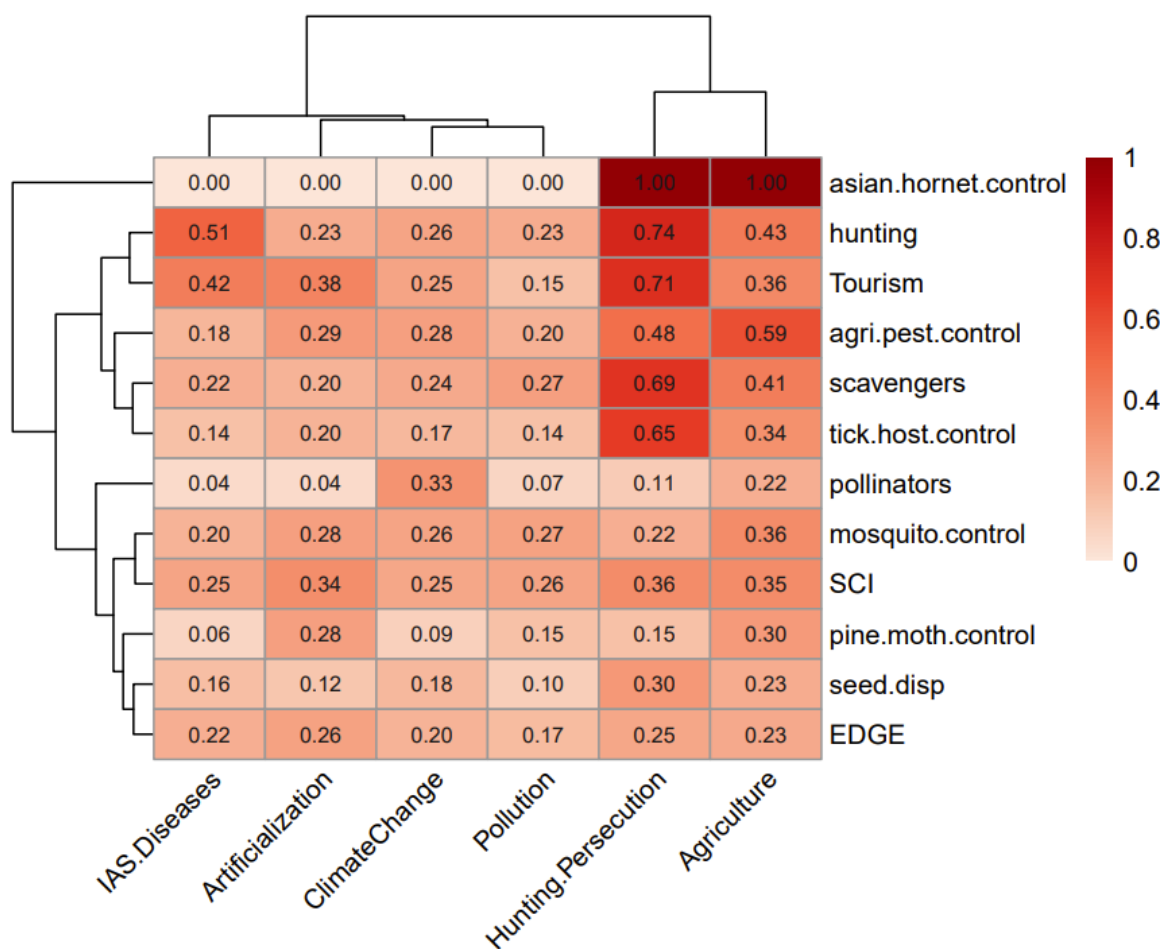


Figure 3.9: Threats to species-based NCP. Values are the proportion of species that provide the NCP that are affected by each threat type (left to right) according to the EEA red list database. Unsurprisingly, hunting affects 74% of game species, but is also a major threat to species that are important for tourism (71%), carrion elimination (scavengers), and that provide tick host control. Agriculture intensification is a threat for 59% of species that provide agricultural pest control.

Implications of the Nature Futures Framework for species and Nature's Contributions to People in Europe

In preparation for submission to *Nature Sustainability*.

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3.5 Abstract

The post-2020 Global Biodiversity Framework under the CBD has set ambitious environmental targets to reduce the impact of humans on the biosphere. The Nature Futures Framework (NFF) is a conceptual tool to envision desirable pathways for both people and nature, which can translate into different trajectories of land use change according to the way stakeholders value and manage nature. Yet, is it unclear to what extent the EU Green Deal targets implemented through the lens of the NFF would actually benefit species and NCP. Here, we test the implications of NFF scenarios for species and the NCP they provide. To do so, we combined species geographic ranges and habitat preferences (accounting for land use intensity levels), a set of land use change scenarios corresponding to desirable futures, and data on species-based NCP. Contrary to previous studies on the effects of land use change scenarios on biodiversity, we consider land use intensity levels and focus on NCP provided by terrestrial vertebrate species and their trophic interactions. We find that all NFF scenarios would benefit species-based NCP across Europe significantly more than the SSP1 scenario. Implementing the NFF scenarios would balance the competing claims on land use in Europe, on the one hand meeting societal demands for food and shelter to ensure high quality of life for people, and on the other hand, achieving overall gains for species and associated NCP via the expansion of protected areas and the de-intensification of agriculture and forestry in key areas.

3.6 Introduction

The intensification of human activities is having far-reaching consequences on biodiversity, including species and the NCP they provide. The Nature Futures Framework (NFF) has highlighted plausible trajectories where the impact of humans on nature is reduced. The NFF recognizes three major pathways, which correspond to different values of nature in society [1]: the intrinsic value of nature (Nature for Nature), its direct benefits to society (Nature for Society), and its cultural value (Nature for Culture). These desirable future pathways require a deep reconfiguration of landscapes at regional, continental and global levels. Dou et al (in prep; see Appendix)

translated the narratives of the different NFF pathways into three alternative land use change scenarios for Europe. These scenarios incorporate both societal demand and environmental policy targets that aim to curb biodiversity loss. It is expected that the Nature for Nature scenario should benefit species, in particular endangered species; that Nature for Culture should benefit cultural NCP; and that Nature for Society should benefit regulating NCP. **However, whether these desirable pathways would deliver what we expect for biodiversity and NCP is unknown.** For species and NCP, what matters is not necessarily the amount of new protected areas, or restored habitats such as forests and grasslands, but where these changes occur. There is a need to test the relevance of these pathways, to investigate whether these changes occur in areas that benefit species and associated NCP.

Estimating and refining species distributions is typically done by combining the geographical ranges and habitat requirements of species, to identify the suitable and unsuitable habitat within species ranges (or extent of occurrence). These data are essential for biogeography, for spatial conservation, but also to explore the consequences of land use change scenarios on species habitat-suitable ranges. In a recent study, Powers and Jetz (2019) [2] used this approach to quantify the impacts of a set of shared socio-economic pathways (SSP) scenarios on global distributions of 19,400 species of mammals, birds, and amphibians and highlighted areas in need of conservation planning. So far, species distributions estimates have incorporated land cover classes as habitat types, without differentiating the level of land use intensity. Yet, it is well established that highly intensive land uses have more negative impacts on biodiversity than low-intensity land uses [3, 4]. The same land cover class can have very different impacts on biodiversity depending on its intensity level: intensively managed forests are ecologically very different from primary forests; and intensive croplands (with large fields, no hedgerows and high pesticides input) have drastically higher impacts on biodiversity compared with extensively managed agriculture. Therefore, it is crucial to integrate land use intensity when estimating suitable habitat for species; but so far no spatial habitat classification has incorporated land use intensity. A novel land system map for Europe [5] has addressed this gap

by including land use intensity levels (low, medium and high) for each land system (e.g. settlements, forests, grasslands, croplands) in Europe.

Here, we investigate the effects of a range of sustainable land use change scenarios on terrestrial vertebrate species distributions and the consequences for the NCP they provide. To do so, we considered four alternative land use change scenarios that were recently developed by colleagues from VUA (Dou et al, in preparation), that considered socio-economic constraints (i.e. human requirements for food and shelter), as well as environmental targets. As a baseline scenario, we considered the land use change scenario that corresponds to the most sustainable Shared Socioeconomic Pathway (SSP1). The three other scenarios translated the targets of the EU Biodiversity Strategy in the light of three different dimensions of the Nature Futures Framework: these are "Nature for Nature" (NFFa); "Nature for Culture" (NFFb); "Nature for Society" (NFFc). We refined estimates of species distributions by including the land use intensity levels of habitats, for all terrestrial vertebrates known to occur in Europe. We estimated species distributions in different scenarios by accounting for land use intensity levels [5] and using the latest estimates of species Extent of Occurrence from the IUCN red list. We considered the NCP directly provided by terrestrial vertebrate species, addressing recent calls [6] to better identify the biodiversity components that are important for NCP supply. We then quantified the amount of suitable habitat lost or gained within the range of NCP providers between the different land use change scenarios and the current land system map. We identified the species, NCP and locations in Europe that are most affected under a set of plausible land use change scenarios that account for land use intensity (Dou et al., in prep; see Appendix).

3.7 Materials and Methods

3.7.1 Including land use intensity when filtering distributions with suitable habitat

3.7.1.1 Study area and species considered

The study area covered the spatial extent of the European Union (EU) with the United Kingdom (EU28+), Norway, Switzerland, and the Western Balkans (Serbia, Kosovo, North Macedonia, Montenegro, Albania, and Bosnia and Herzegovina). We excluded Iceland, Cyprus, Turkey and Macaronesia. We considered all native and breeding terrestrial vertebrate species that are known to occur in the study area, and for which data on habitat requirements was available, bringing the total number of species considered to 735.

3.7.1.2 Land system maps

The land system classification [5] contains 8 land systems (settlements, forests, arable crops, permanent crops, grasslands, shrubs, rocks & bare soil, mosaic systems, freshwater systems). The classification distinguishes low, medium and high intensity land use within all the managed land systems (settlements, forests, crops, grasslands, agricultural mosaics), making 26 land use classes in total. This classification was applied for the current European land system [5] and for 4 land use change scenarios where yearly land use change was modelled until year 2050: three NFF scenarios (NFFa: nature for nature; NFFb: nature for culture; NFFc: nature for society) and the sustainable shared socio-economic pathway (SSP1) (Dou et al., in prep; see Appendix). These land use change scenarios incorporate the competing claims on land use to produce enough materials and provide shelter to human society on the one hand, as well as the implementation of environmental targets, including protection and restoration of natural habitats on the other hand. Note that the SSP1 scenario (and the NFF) are the only scenarios that are compatible with low emissions RCP. All the other SSPs are incompatible with significant reductions in greenhouse gas emissions that would keep average global temperatures below 2°C. In other words: only the SSP1 is comparable with NFF in terms of climate scenarios.

3.7.1.3 Habitat crosswalk and filtering distributions

We produced a table of species habitat preferences, where each habitat is one of the 26 land use classes [5], and where each element indicates the suitability of each habitat for each species (0 is unsuitable; 1 suitable habitat). To do so, we combined information from the expert-based table of habitat suitability for vertebrates based on land cover [7] and the IUCN red list data on species geographic ranges, habitat preferences and threat types. Because each database (GlobCover, IUCN) has its own habitat classification, we had to build a crosswalk between each classification and the land system classification.

We assumed a given land use class was suitable habitat for a species if:

- The corresponding land cover class is noted to be suitable to the species in at least one of the following sources: Maiorano et al., 2013 OR IUCN global data OR IUCN regional European data
- AND the intensity level of the land use class is suitable for the species according to habitats preferences in the IUCN regional European data (EEA) AND/OR this class is not associated with any threats to the species. For instance, if the species is noted to specifically prefer low intensity habitat in the EEA data, then high intensity level is assumed unsuitable habitat.

3.7.1.4 Species habitat-suitable range maps

For mammals, amphibians and reptiles, we downloaded the latest estimates of species extent of occurrence (EOO) from the IUCN red list website (downloaded in March 2022). For birds, we extracted the EOO from BirdLife (2020), retaining the “extant” and “possibly extant” ranges, for resident and breeding birds.

For each of the 5 land system maps considered, we created 1km² species distribution maps by filtering the estimated EOO of all species with the habitat preferences and distance to water requirements of each species, building on the methodology used in Maiorano et al 2013. In the resulting 1km² resolution species distribution maps, the value of a grid cell was equal to 1 only if the cell was within the species EOO and consisted of suitable habitat for the species; otherwise, the

value of the grid cell was equal to zero. Then, we aggregated the distributions to 5x5 km² by counting the number of 1km² cells of suitable habitat within the aggregated cell. To obtain binary presence/absence data, a species was assumed to be present in a 5x5 km² grid cell if at least 50% of the aggregated grid cell contained suitable habitat.

3.7.2 Species-based NCP database

We considered a total of 8 regulating NCP (Table 1) and 4 cultural NCP (Table 2) provided by European terrestrial vertebrate species and their interactions.

Regulating NCP	Provider species	Total number of providers	Reference
Agricultural pest control	Predators of rodent and invertebrate pest species in agriculture.	108	Civantos et al., 2012
Mosquito control	Insectivorous bats and birds with aerial foraging space (predators of the adult lifestage) and amphibians that feed primarily on aquatic invertebrates	162	Hocking and Babbitt, 2014; Puig-Montserrat et al., 2020
Tick host control	Predators of ungulates and rodents, both important reservoirs of tick-borne diseases	85	Černý et al., 2020; Hofmeister et al., 2017
Pine processionary moth control	Cuckoos, Eurasian hoopoe, birds of the tit family are predators of the larval stage. Insectivorous bats are predators of the adult life stage.	44	Barbaro and Battisti, 2011; de Boer and Harvey, 2020
Carrion elimination	Frequent or obligatory scavengers	39	Mateo-Tomás et al., 2017; Probst et al., 2019; Vicente and VerCauteren, 2019
Seed dispersal	Frugivorous species (endozoochory) and scatter-hoarders.	154	Gómez et al., 2019; Maiorano et al., 2020
Pollination (croplands)	Pollinating birds. Note: these bird species are not obligate pollinators and only provide this NCP seasonally, but their role is complementary to that of insect pollinators.	46	da Silva et al., 2014

Table 3.1: Overview of regulating NCP provided by terrestrial vertebrates and associated references.

Cultural NCP	Provider species	Total number of providers	Reference
Species of community interest	Species listed in the Annex I of the Birds Directive, and in the Annexes II and IV of the Habitats directive	281	EU legislation
Game	Species that are commonly hunted for game	35	Schulp et al., 2014
Evolutionary heritage	Species listed as EDGE (Evolutionary Distinct and Globally Endangered)	31	EDGE Lists, 2018
Nature tourism and wildlife watching	Species mentioned on touristic webpages; big 5: lynx, wolf, bison, brown bear, wolverine; and top 2% species with highest number of observations (GBIF) relative to their geographic range	47	O'Connor et al., in prep (Chapter 2)

Table 3.2: Overview of cultural NCP provided by terrestrial vertebrates and associated references.

3.7.3 Assessing effects of land use change scenarios on species-based NCP

3.7.3.1 NCP capacity maps

We mapped each NCP as the sum of the distributions of the providing species in each scenario. Therefore, in each grid cell, the capacity of each NCP was equal to the number of species providing this NCP that occurred in the local grid cell (see Chapter 2 for more details).

3.7.3.2 Species-based indices

We quantified the percentage change in habitat-suitable range (Δ HSR) in future land use scenarios (compared with the current land system) for each species:

$$\Delta HSR = \left(\frac{HSR_{future}}{HSR_{current}} - 1 \right) \times 100$$

We used linear models (ANOVAs) to test the effect of scenarios (four levels) on the change in suitable habitats of different groups of terrestrial vertebrate species and associated NCP, by grouping species that provide regulating and cultural NCP. When main effects were statistically significant, we conducted post hoc pairwise comparisons of factor levels using Tukey’s “Honest Significant Difference” method (function `TukeyHSD` in R).

3.7.3.3 Community-based indices

We quantified the gains and losses for species richness (SR) between the land use change scenarios and the current land system across space (Figure 3.11).

$$\Delta SR = SR_{future} - SR_{current}$$

Then, we quantified the local change in the capacity value of each NCP (defined as the number of species providing the NCP) between the land use change scenarios and the current land system map.

$$\Delta NCP_i = NCP_{i,future} - NCP_{i,current}$$

We then computed the average change in NCP capacity. We first scaled the capacity value of each NCP in each land system map between 0 and 1. Then, we computed the difference between the capacity value of each NCP in the future land use change scenarios and the current land system map. We averaged these differences in each land use change scenario, considering regulating and cultural NCP separately.

Finally, we used RGB plots (R package `terra`) to visualise the areas of overlap between the NFF scenarios in terms of gains and losses of regulating and cultural NCP (Figure 3.12). We attributed a colour channel to each scenario: NFFa in blue, NFFb in green, NFFc in red. All analyses were conducted in R version 4.0.2.

3.8 Results

Compared with SSP1, the NFF scenarios all delivered higher benefits to species and species-based NCP. NFF scenarios were associated with an average increase of 10.5% (NFFa) to 11.4% (NFFc) habitat suitable range for all species, while SSP1 was associated with an average increase of only 0.8% (Figure 3.10). In particular, SSP1 led to a 29% decline in suitable habitats on average for the 8 species in the dataset that are listed as critically endangered.

Increases in suitable habitats for amphibians were significantly higher in NFFb and NFFc scenarios than in SSP1 (ANOVA: $F = 8.296$, $p < 0.01$). Increases in suitable habitats for mammals were significantly higher in NFFa scenarios than in SSP1 (ANOVA: $F = 3.012$, $p < 0.05$). Differences between scenarios were not significant for reptiles and birds.

Gains in suitable habitats for regulating NCP providers were significantly higher in all three NFF scenarios than in SSP1 (ANOVA: $F = 7.87$, $p < 0.01$). In particular, increases in HSR for species providing mosquito control were significantly higher in all three NFF scenarios than in SSP1 (ANOVA: $F = 5.254$, $p < 0.05$). Increases in suitable habitats for species providing agricultural pest control were significantly higher in NFFb and in NFFc than in SSP1 (ANOVA: $F = 4.68$, $p < 0.05$) (the gain was marginally significant for NFFa: $p = 0.053$).

Nature for Society (NFFc) was the most beneficial scenario for cultural NCP providers overall. Gains in suitable habitats for cultural NCP providers were significantly higher in NFFc than in SSP1 (ANOVA: $F = 2.875$, $p < 0.05$), but they were not significantly higher in NFFb ($p = 0.15$) and NFFa ($p = 0.09$) compared with SSP1. Nature for Culture (NFFb) was also the only scenario that led one EDGE (Evolutionarily Distinct and Globally Endangered) species to lose their suitable habitat range entirely (*Iberolacerta aranica*) as well as one Annex I species (*Sitta krueperi*). Gains in suitable habitats for game species, and for species listed in Annex II of the Habitats Directive, were significantly higher in Nature

for Nature (NFFa) than in SSP1 (ANOVA: $F = 3.556$, $p < 0.01$; and $F = 3.08$, $p < 0.05$, respectively), but this was not significant for the other two NFF scenarios. Differences in percentage change in suitable habitats among the three NFF scenarios were non significant. In other words, Nature for Nature did not benefit the intrinsic value of nature significantly more than the other NFF scenarios; Nature for Culture did not lead to significantly higher gains for cultural NCP than the other NFF scenarios; and Nature for Society did not benefit regulating NCP significantly more than the other NFF scenarios.

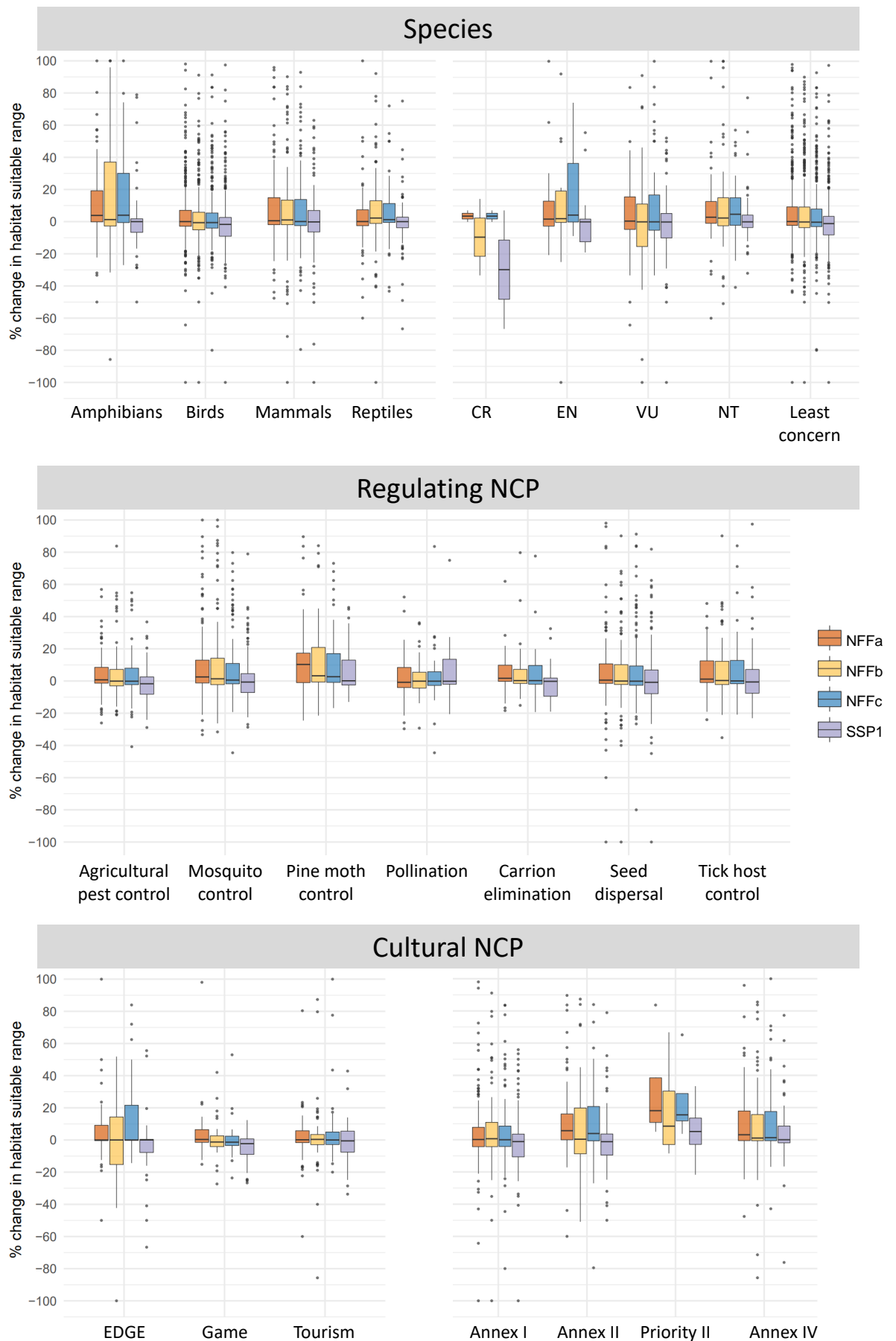


Figure 3.10: Boxplot of percentage change of different groups of species' suitable habitats in the four different land use change scenarios.

Across Europe, the NFF scenarios led to an average increase in local species richness and NCP capacity. By contrast, local species richness declined on average in the SSP1 scenario (Figure 3.11). Patterns of gains and losses for species-based NCP capacity differed between the land use change scenarios across Europe (Figure 3.12). Overall, most changes in species-based NCP occurred in Eastern Europe, which is where the majority of land use changes occur in the NFF scenarios. All three NFF scenarios lead to gains in species-based NCP in central France, in Switzerland, in Wales, in Hungary and the north of the Balkans, and in the Transylvanian plateau in Romania, due to the de-intensification of agriculture and the conversion of intensive agriculture to forest/agriculture mosaics in these areas. By contrast, all NFF scenarios project declines in species-based NCP in south-west France due to the conversion of forest/grassland mosaics to intensive permanent crops; and in the Carpathian mountains in Romania, due to forest intensification. In the Czech Republic, the Nature for Culture scenario leads to gains in species-based NCP, while the other two scenarios are associated with the conversion of forests and mosaics to intensive croplands, which would lead to declines in species-based NCP.

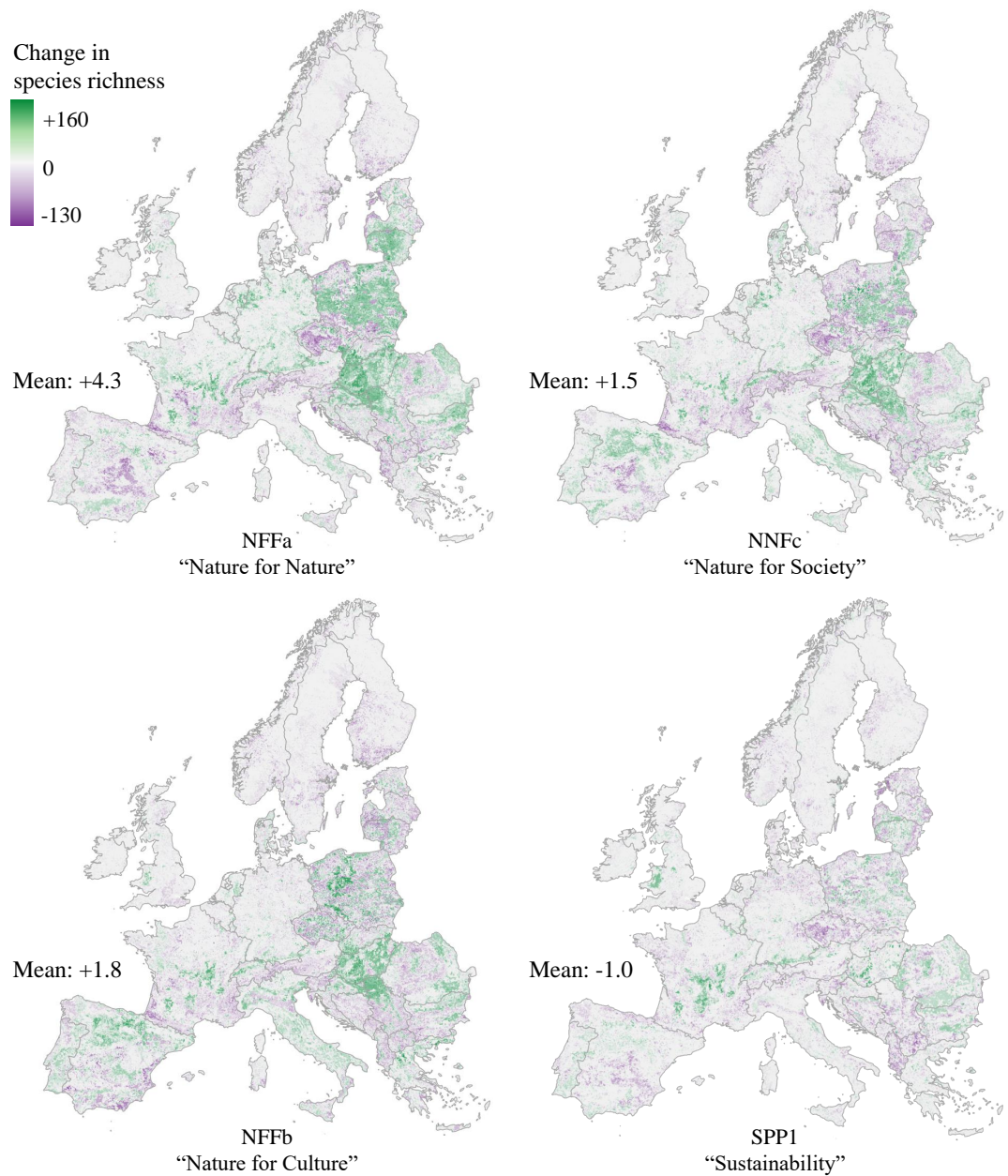


Figure 3.11: Impacts of land use change scenarios for terrestrial vertebrates species richness across Europe. Change in species richness: $SR(\text{scenario X}) - SR(\text{current})$. Same patterns are apparent when looking at change in NCP richness.

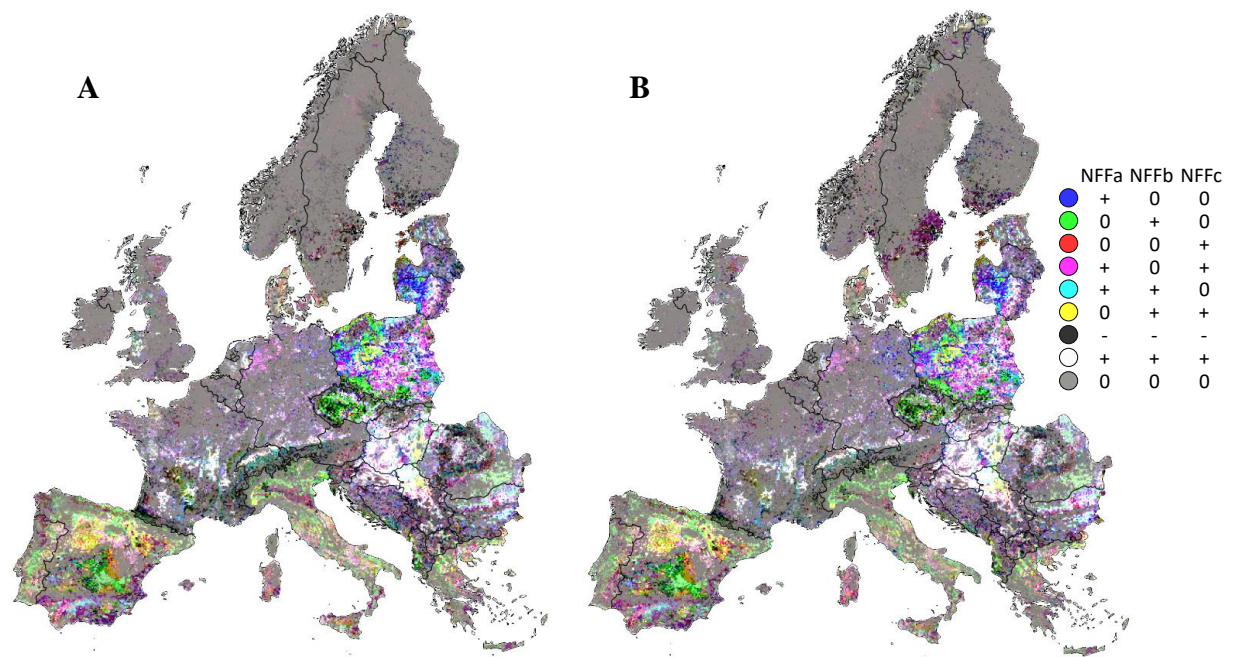


Figure 3.12: Impacts of NFF scenarios for species-based NCP capacity in Europe. The maps show RGB plots of change in regulating (A) and cultural (B) NCP supply in the three NFF scenarios. Each NFF scenario is represented by one RGB colour channel: NFFa in blue, NFFb in green, NFFc in red. The colour legend is shown in (C): “+” represents an increase of NCP supply, “-” represents a decline, and “0” represents no change. For example, white areas are those where average NCP capacity increases in all three scenarios, while dark areas are those where NCP capacity decreases in all three scenarios.

3.9 Discussion

There have been calls to incorporate linkages between biodiversity, nature’s contributions to people and human well-being in future scenarios [8]. Our work is a first step towards testing the implications of desirable future pathways for people and nature at a macro-ecological scale. We showed that land use changes that would implement any of the three NFF scenarios would lead to significantly higher gains for species-based NCP than SSP1. Even though SSP1 is the most sustainable of all SSP scenarios, it would lead to some declines in species-based NCP across Europe, while the NFF scenarios would instead lead to gains in species-based NCP across Europe. Our work shows that the NFF scenarios make it possible to significantly increase diversity and associated NCP [9] via the expansion of protected areas, and

the de-intensification of agriculture and forestry in key areas, while still providing sufficient material resources to ensure high quality of life for people. Our findings are in line with previous work that showed that an international strategy to increase land protection and restoration could reverse trends of biodiversity loss by the mid-century [10]. The implementation of these desirable scenarios would require a deep reconfiguration of the way European land systems are currently used and managed, which implies an integrated strategy at the international level. In the NFF scenarios, most land use changes occur in East Europe while the other regions undergo less change. It is important to test the relevance of these scenarios, and improve them so that efforts towards sustainable trajectories are distributed more equitably between countries.

In this work, we only compared sustainable futures. Desirable futures for people and nature presume a high capacity to mitigate and adapt to climate change, therefore we assumed that these are trajectories where emissions have been cut substantially. However, to truly evaluate the benefits of NFF scenarios for nature and people, we are missing a comparison with “business as usual” trajectories. This would require modelling species distributions with a range of land use change scenarios with corresponding climate change scenarios [11]. We also did not consider trophic interactions for: 1) projecting species distributions (predators need their prey for survival in the long term) and for 2) quantifying secondary extinctions, and associated NCP losses. Accounting for species interactions will provide insight on the robustness of food webs and the supply of NCP in the aftermath of climate and land use changes [12].

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3.10 Extended methods for including land use intensity in species distributions

3.10.1 Building species habitat preferences table, accounting for land cover and land use intensity

We proceeded in two steps.

Suitability of different land cover types for species. First, we determined the suitability of each land system (i.e., habitat type), regardless of land use intensity.

We used different expert sources:

- We use the original species habitat table (based on the GlobCover classification) as a basis for determining species habitat preferences. For this, we build a crosswalk between the GlobCover classification and the land system classification. The previous distributions filtering used GlobCover 2006 as the habitat classification [7]. In this data, there are three measures of habitat suitability: 0: unsuitable; 1: secondary habitat; 2: optimal habitat.
- We add specific information retrieved from the habitat preferences in the European IUCN table. We retained only the habitats that are noted to be suitable (i.e. we exclude marginal and unknown). We used API queries on the global IUCN red list dataset (global) to extract species habitat preferences. We only retained 39 habitat classes that are relevant for terrestrial European ecosystems and we excluded all subantarctic, subtropical, tropical, savanna, and marine habitats. We then performed a crosswalk between the IUCN habitat classification scheme, and the land system classification [5]. In this step, we only retained the habitat classes that have a correspondent land use class: this excludes caves and subterranean habitats as well as several artificial-aquatic habitats.
- We combined this with the global IUCN on species preferences for habitat types (no notion of intensity but it is complementary). At this stage, we still do not account for land use intensity.

Suitability of different intensity classes within each land system. Second, we determined the suitability of different intensity classes within each land system: For this, we used the EEA red list dataset on species habitat requirements and threat types. Because this data is in the form of sentences, we searched for unsuitable land use classes in the form of character strings in the threats column in the EEA red list database. We used the threat data in the following way: if a species is threatened by intensive land use (e.g. "agricultural intensification"), then the intensive land use classes are assumed to be less suitable. For example: intensive forests are associated to: "logging—sylvi—silvi—wood harvesting—forestry—plantation—shortening of rotation time—commercial monocultures—felling—loss of old trees—removal of old tree—ntensive forest—ntense forest—ntensification of forest—fellin—loss of old trees—mature—loss of old mature—loss of old wood—forest management". If any of these are noted to be a threat for the species, then it is assumed that the intensive land use is unsuitable habitat. In addition to using the threat information, we also used the habitats information: when it was specified in the habitat column that the species prefers 'low intensity' habitat, we assume that medium and high intensity are less favourable.

The case of mosaics. One of the specificities of the land system classification is its diversity of mosaics classes [5]. Most of these mosaic classes are not recognized in the other habitat classifications. We assume that a mosaic of habitats combines the characteristics of all the different habitats that compose it - a reasonable assumption given the resolution of 1 km². Consequently, we assume that a mosaic is suitable if at least one of the habitats within the mosaic is suitable for the species.

3.10.2 Filtering distributions with species ecological requirements

Distance to water requirements. For birds, we used the same data as in [7]. For the other species: we attributed a buffer to those that rely on water for food and/or nesting. We attributed a buffer for species that: have aquatic foraging space (meaning they feed in water) and/or that eat aquatic food (i.e. feeds on aquatic invertebrates, algae, aquatic vegetation, fish, amphibians) and/or that nest or breed in aquatic

habitat (temporary water, rivers, lakes, small rivers, small lakes). In total, 258 species (11 reptiles, 19 mammals, 84 amphibians, 144 birds) were dependent on water for feeding, nesting or breeding. The buffer reflected how far the species can disperse away from water, and was equal to the annual maximum dispersal capacity of the species (for species missing data the value was imputed).

For the water layer, we used the water and wetness maps from Copernicus, consistent with Dou et al., 2021 (version of 2018, downloaded from <https://land.copernicus.eu/pan-european/high-resolution-layers/water-wetness/status-maps/water-wetness-2018>). Original data was at a resolution of 100 m, we upscaled it to 1 km grid.

We then used the species habitat table and species distance to water requirements to filter species extent of occurrences (Figure 3.15).

The case of forests. The land system maps (current and future) do not include the type of forest (needle or broad-leaf), yet this is an important distinction for many species of terrestrial vertebrates. For the current land system, we overlaid the current leaf type of forests with the forest systems, resulting in 6 classes for forests: low, medium and high intensity needle or broad-leaf forests.

For future scenarios, there were two types of situations:

- the grid cell contains forest both in future and current maps. In this case, we assigned the leaf type that exists in the current map.
- the grid cell contains forest in the future scenarios but not the current land system. In this case, we assigned the forest type that is most frequent in 10 x 10km around the grid cell. In some instances, a few dozen afforested grid cells were further than 10 km from current forests; for these, we assigned the forest type that is most frequent in 100 x 100 km around the grid cell.

3.10.3 Other limitations of the habitat suitability model

- Forest structure (open, dense), and mixed forests, are not considered in the land system classification.

-
- We assume that water and wetlands are unchanged in the future; yet they may be affected by climate change or drainage of wetlands for agriculture or other land use changes.
 - We do not distinguish secondary vs. primary habitats. We were inclusive here so maybe overestimated the capacity of species to survive in diverse habitats.
 - Caves and subterranean habitats were not considered.
 - We would need to test the validity of the filtered distributions using GBIF data. We could select GBIF observation records that are within the EOO of species and that satisfy a number of constraints to avoid observation bias (see Botella et al.; Appendix B). Then, we could investigate to what extent the filtered distributions we produced overlap with observation records for each species, for example by testing whether observation records fall within the suitable habitats more frequently than random.

3.11 Supplementary Figures

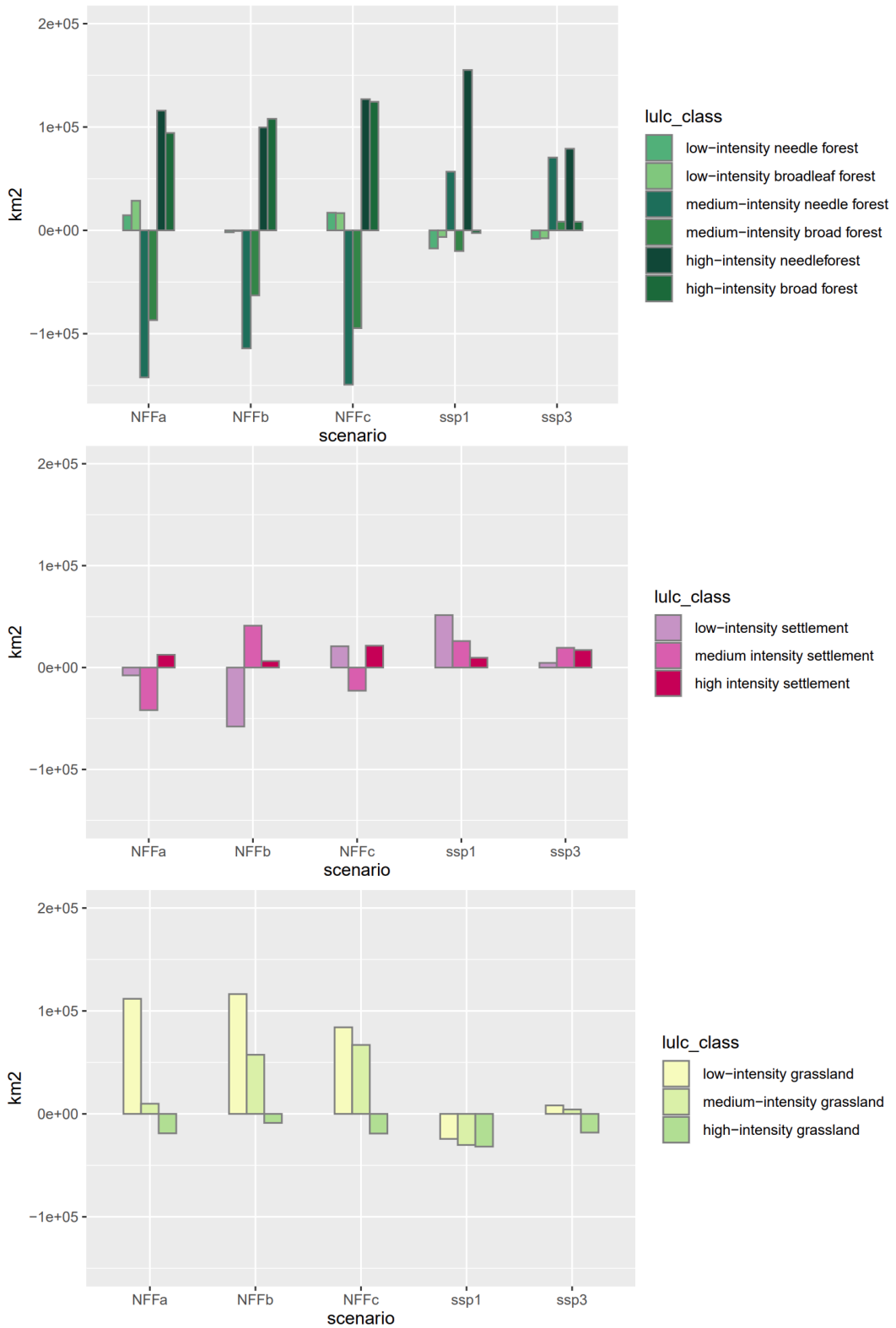


Figure 3.13: Changes in land use classes (in forests, settlements, and grasslands) in each scenario.

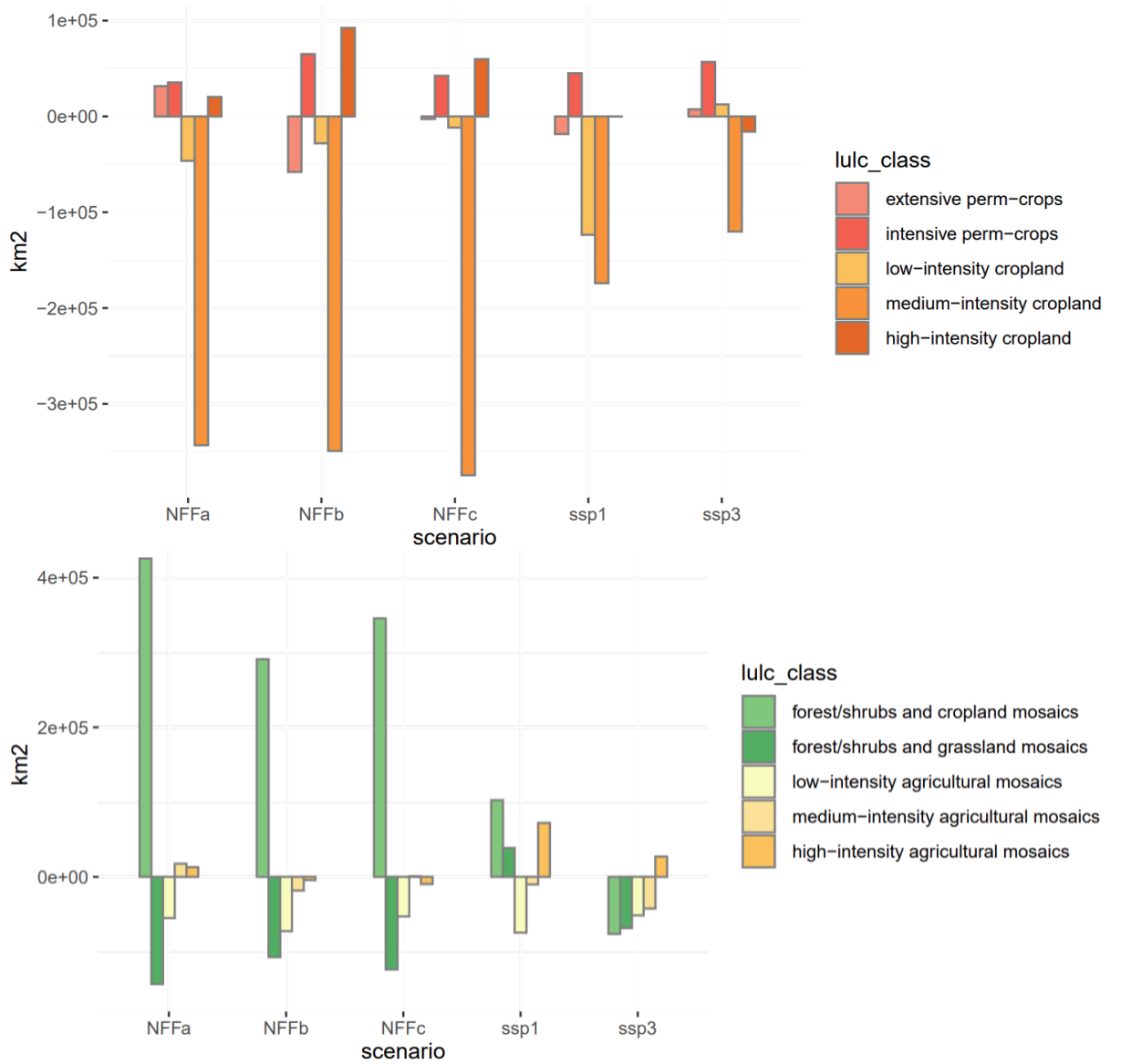


Figure 3.14: Changes in land use classes (in croplands and mosaics) in each scenario

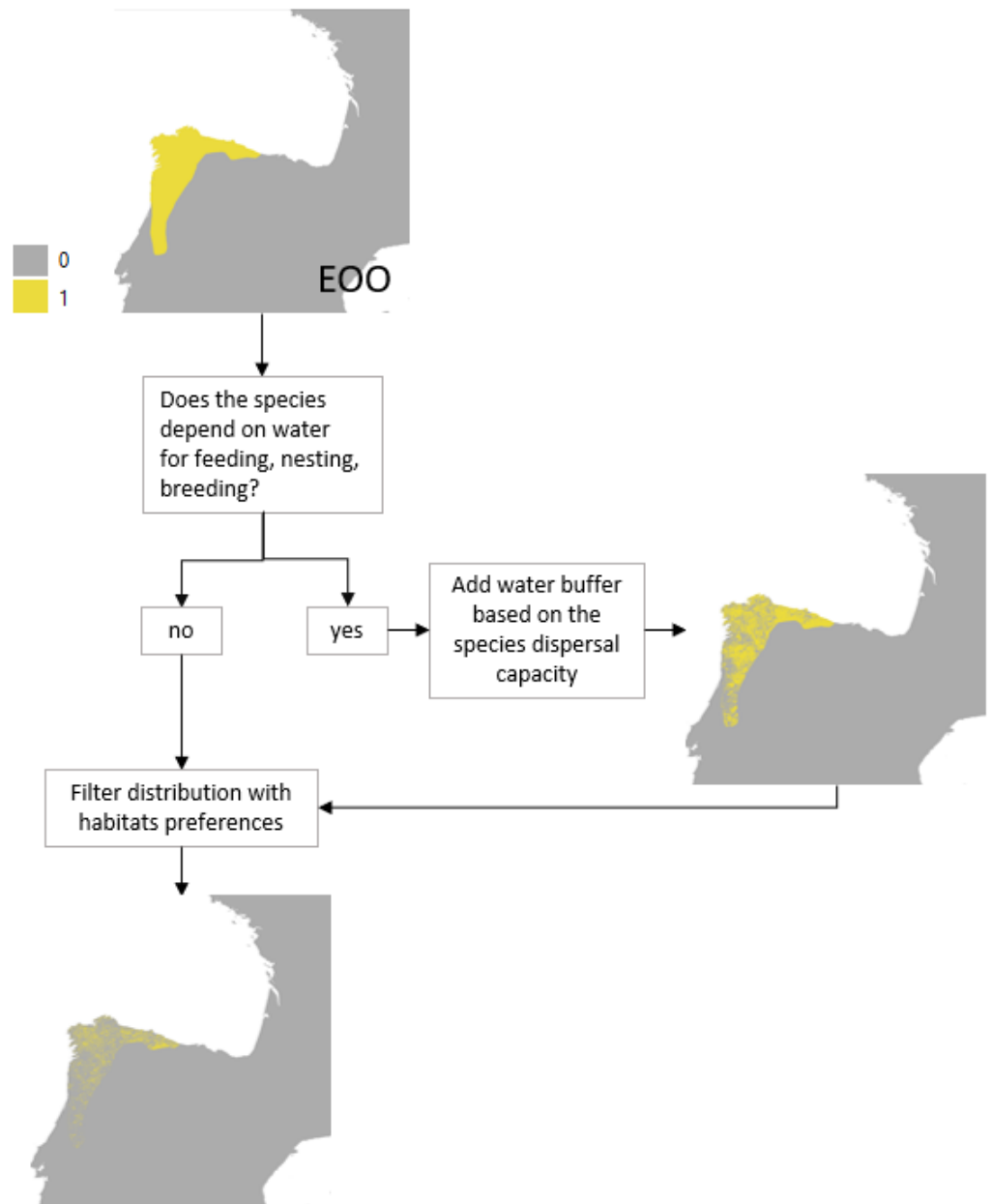


Figure 3.15: Workflow for filtering distributions.

Part III

Identifying priority areas for biodiversity and NCP

Chapter 4

Balancing conservation priorities for nature and for people in Europe

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In this chapter, we explored to what extent spatial priorities defined for preserving the intrinsic value of nature also captures the cultural and regulating values of nature, and vice versa.

CONSERVATION

Balancing conservation priorities for nature and for people in Europe

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There is an urgent need to protect key areas for biodiversity and nature's contributions to people (NCP). However, different values of nature are rarely considered together in conservation planning. Here, we explore potential priority areas in Europe for biodiversity (all terrestrial vertebrates) and a set of cultural and regulating NCP while considering demand for these NCP. We quantify the spatial overlap between these priorities and their performance in representing different values of nature. We show that different priorities rarely coincide, except in certain irreplaceable ecosystems. Notably, priorities for biodiversity better represent NCP than the reverse. Theoretically, protecting an extra 5% of land has the potential to double conservation gains for biodiversity while also maintaining some essential NCP, leading to co-benefits for both nature and people.

There have been recent policy calls to expand protection to at least 30% of the world's area by 2030 to halt the extinction of species and degradation of nature's contributions to people (NCP) (1, 2), but exactly where and how to focus conservation efforts is unclear (3). Biodiversity underpins functioning ecosystems, which sustain NCP essential to human life (4, 5). These include critical regulating NCP, such as pollination, carbon sequestration, flood prevention, and regulation of air quality. Beyond material benefits, ecosystems also contribute to invaluable parts of human culture: Foraging for wild foods, nature-based tourism, and heritage landscapes are examples of cultural NCP (5). Protected areas have been shown to safeguard not only biodiversity (6) but also regulating and cultural NCP (7). However, although they are conceptually linked, different values of nature [intrinsic, cultural, and regulating (fig. S1)] are likely to be tied to different conservation outcomes (8, 9). So, how can we maximize conservation gains across the spectrum of nature's values?

There is a need to conserve key, irreplaceable ecosystems that are not only particularly diverse but that also sustain rare species and provide locally valuable NCP. So far, few studies have combined biodiversity and NCP in spatial conservation planning at large spatial scales (8–10). Many conservation studies place high

value on exceptionally biodiverse locations, which risks overlooking endemic or threatened species (11) and might not lead to the most efficient selection of sites (e.g., if biodiverse sites all contain similar species). Consideration of irreplaceability and complementarity between priority areas is crucial to maximize conservation gains in limited amounts of land (12, 13).

Spatial conservation planning also needs to account for existing protected areas. In Europe, high levels of habitat fragmentation and a long history of human development have shaped the continent's biodiversity. Natura 2000, the densest network of protected areas on the planet (fig. S2), incorporates a diversity of management practices, from strict nature reserves to multiuse areas. This variety of management types is relevant for the conservation of different values of nature, especially in a context where human-induced environmental changes already dominate landscapes. However, the designation and management of Natura 2000 protected areas only consider certain rare species and ecosystem types, do not explicitly consider NCP (14), and have been repeatedly criticized for not integrating local beneficiaries (15).

Here, in line with the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services framework (5, 16) and based on the principles of complementarity and irreplaceability, we contrast conservation priorities at 1-km² resolution for three important values of nature in Europe (fig. S1): (i) biodiversity, represented here by all 785 vertebrate species occurring in the study area, including 124 threatened species (fig. S3); (ii) regulating NCP, represented here by carbon sequestration, air quality regulation, flood control, and pollination (fig. S4); and (iii) cultural NCP, represented here by heritage agriculture, heritage forests, foraging areas for wild foods, and nature tourism (fig. S5 and table S1) (17). We considered the demand for NCP, so that

NCP priorities are ecosystems where a high capacity of providing NCP coincides with a high demand, consistent with the Convention on Biological Diversity targets (18). We first identified spatial priorities separately for each value (species, cultural, and regulating NCP) for the entire European Union (EU) regardless of protection status, and we quantified the incidental gains and losses for different nature values within these top priorities. Second, we assessed how well these values of nature are currently represented in the Natura 2000 network of protected areas. As a preliminary step to integrate multiple values of nature into conservation planning, we identified priorities outside Natura 2000 that would best complement the existing network.

We found that, in an optimal allocation of EU land for conservation, top priorities (the highest-ranked 10% of area) for different values of nature rarely coincide: Areas where top priorities for two values overlap cover 3.2% of EU land, and areas where top priorities for all three values overlap only cover 0.29% of EU land, mostly in Mediterranean woodlands (Fig. 1, A and B; and fig. S9A). Cultural benefits are gained linearly as more area is protected (Fig. 2C and fig. S10A), because of the broad spatial distribution of the cultural NCP considered here. On the contrary, for the vertebrate species and the regulating NCP considered, a few key areas could yield high conservation gains (Fig. 1C and fig. S10A), but not in the same places. Top 10% priorities for species include on average 39% (SE = 1.2%) of all species distributions [including 59% of threatened species distributions but only 10% of regulating NCP (Fig. 1C and fig. S11)], and they are mostly located in Mediterranean countries, Eastern Europe, and Scandinavia (Fig. 1A and fig. S12). By contrast, top priority areas for regulating NCP (Fig. 1C) include on average 42% (SE = 11%) of key ecosystems for the regulating NCP considered (but only 9.5% of all species distributions) and are mostly located in forests of Romania, seminatural habitats of Spain, peri-urban vegetation in Sweden, and riparian ecosystems in central Europe (Fig. 1A and figs. S9A and S12). This analysis shows that simultaneously conserving vertebrate species and regulating NCP can only be achieved through considering them both. Further, species priorities coincide more often with cultural priorities than with regulating priorities (Fig. 1B and figs. S13 and S18) and incidentally represent a much higher proportion of threatened species distributions than priorities for regulating NCP (Fig. 1C and fig. S11). Even though species priorities do not optimally represent regulating NCP, the losses in relation to the optimal representation are smaller when prioritizing species than when prioritizing regulating NCP (Fig. 1C and fig. S19). Our results suggest that focusing on species

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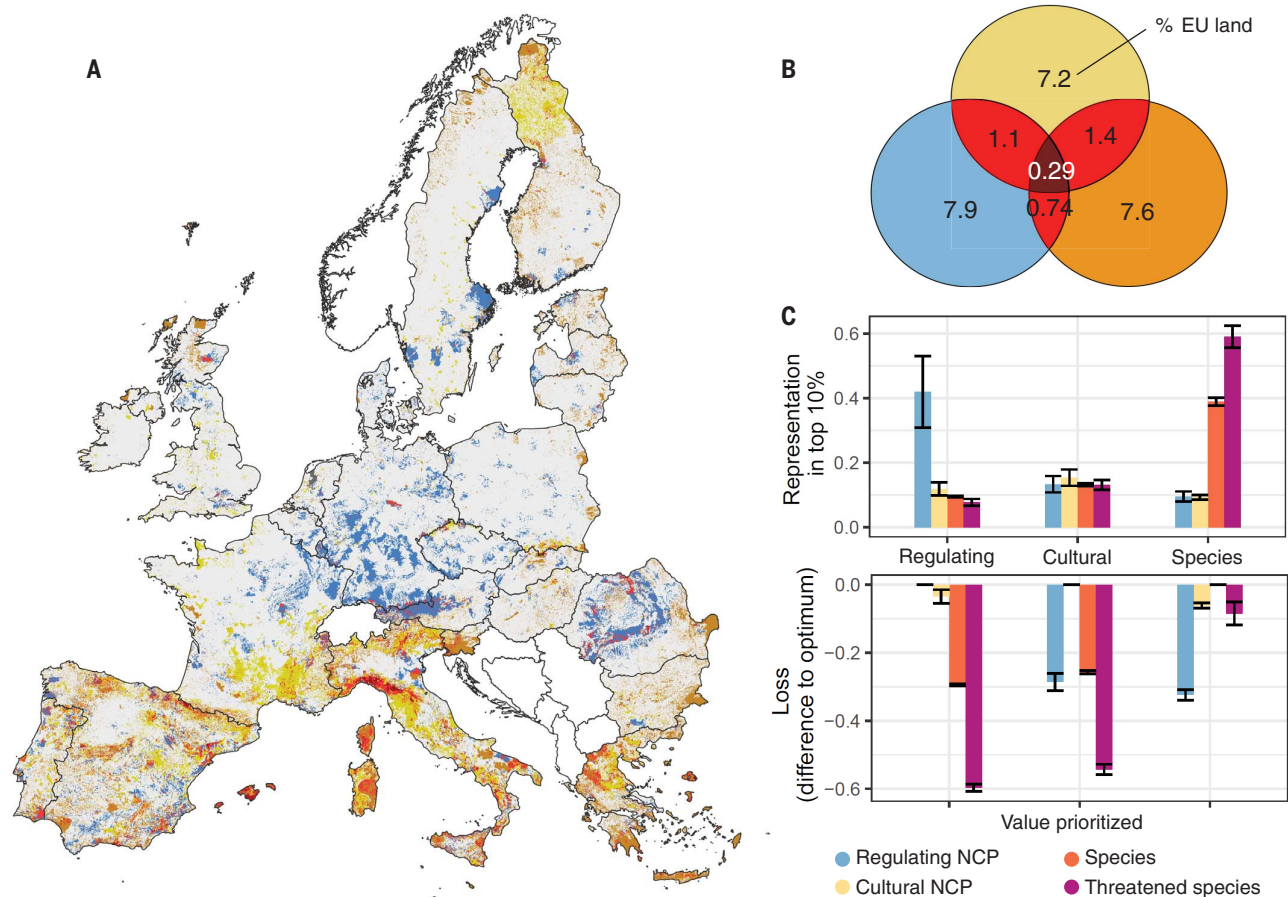


Fig. 1. Spatial coverage and ecological value of top 10% priorities in the optimal scenario. (A) Map locating the top 10% priorities for all three nature's values considered. Top priorities for vertebrate species are shown in orange, cultural NCP are in yellow, and regulating NCP are in blue. Areas of overlap between top priorities for two different values are bright red (3.2% of entire study region); areas of overlap between top priorities for all three values are brown (0.29% of entire study region). (B) Percentages of the study region (EU27)

covered by different priorities and areas of spatial overlap. Color scheme is the same as in (A). (C) Bar plots quantifying the proportion of all distributions represented (y axis) in the top 10% of each prioritization (x axis) on average (error bars represent the SE) and the corresponding loss (i.e., the difference between the incidental representation in the prioritization and the optimal representation of a given value). The colors represent the value: magenta, threatened species; orange, all species; yellow, cultural NCP; blue, regulating NCP.

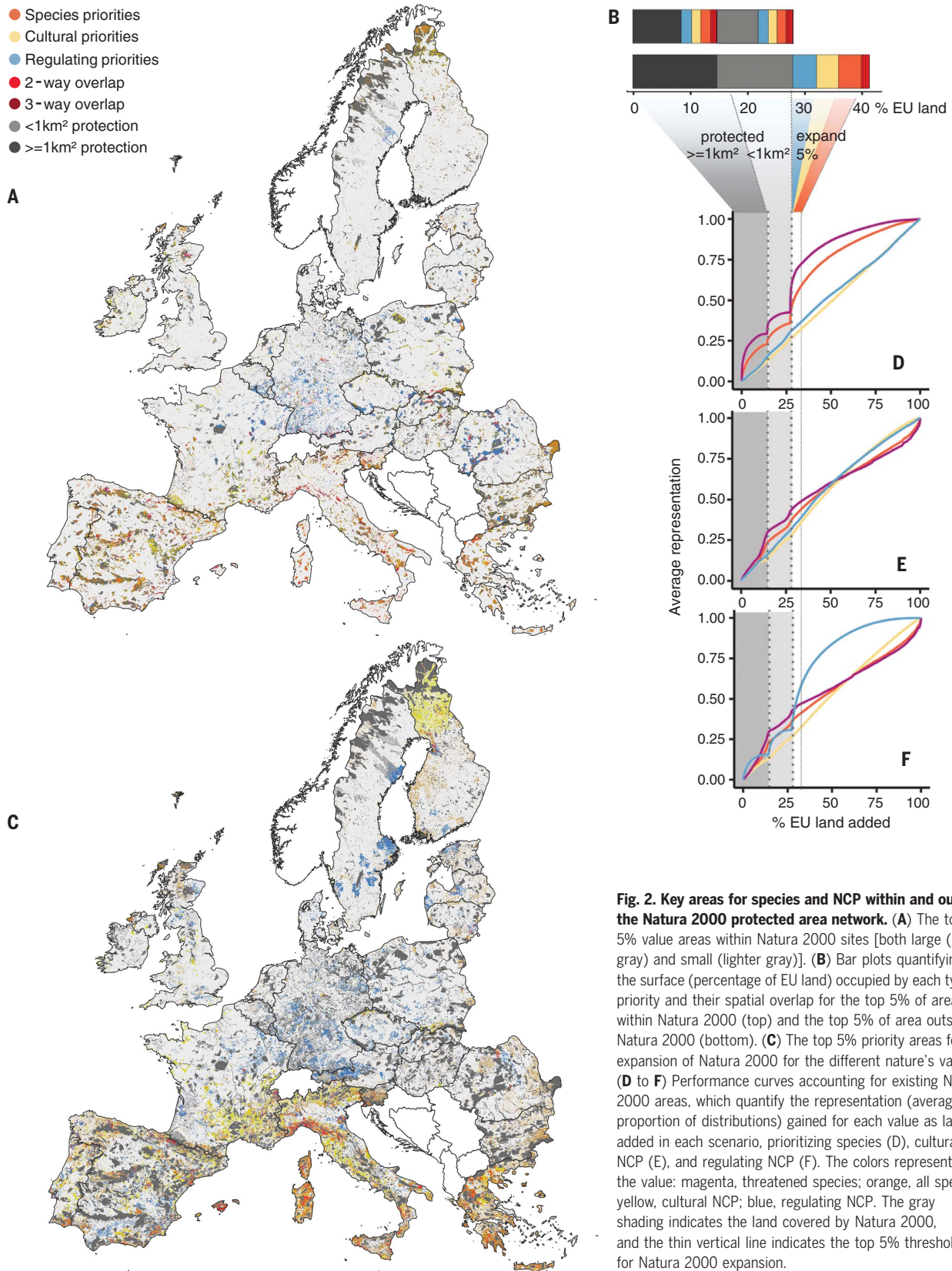
could be more effective to maximize conservation gains across the spectrum of nature's values than any other value considered here (fig. S19). These results are robust to variations in the top priority threshold, input data, and spatial resolution (figs. S13 to S19).

A gap analysis revealed that half of the Natura 2000 sites are of high conservation value (the highest-ranked 5% of area within the network) for species, regulating, and cultural NCP. A quarter of these top priorities overlap for at least two values (Fig. 2, A and B), mostly in Mediterranean countries (fig. S12). Half of these "protected" cells of high conservation value actually contain less than 100 ha of Natura 2000 (Fig. 2B and figs. S10B and S20). However, despite covering one-fifth of EU land, Natura 2000 does not optimally represent any of nature's values considered here. On average, 70% of key ecosystems for regulating NCP and 64% of all vertebrate

species' ranges (and 57% of threatened species' ranges) are not protected (Fig. 2, D to F). Our results suggest that large conservation gains are within reach: If the Natura 2000 network were to be expanded by 5%, the protection of species and key ecosystems for the considered NCP would become equivalent to the optimal scenario (Fig. 2, D to F). If protected, these key areas have the potential to double the current representation of vertebrate species and of regulating NCP in Natura 2000 and also to protect almost 75% of threatened species ranges on average. Locations that complement the existing Natura 2000 areas simultaneously for species and NCP represent 1.38% of EU land, and they are concentrated in Mediterranean woodlands and extensive agricultural areas (Fig. 2C and fig. S9B). This analysis is a preliminary step to integrate different values of nature into conservation planning, but it demonstrates that the protection of small, but

well-selected, areas can yield large benefits to both species and NCP.

Here, we harnessed fundamental principles of spatial conservation planning while recognizing the multiplicity of relationships that link humans to nature (5) at a continental scale. Despite fundamental differences between key ecosystems for species and NCP, our results indicate that top priorities for species incidentally represent NCP better than the reverse (figs. S11 and S19). This is because there are highly irreplaceable areas for species (particularly for rare or endemic species), and vertebrates occur in a diverse set of ecosystems, including those that provide NCP. By contrast, most NCP are more widespread, and priorities for NCP are unlikely to capture the areas crucial for all vertebrates. Most regulating NCP are primarily provided by forests (fig. S9), whereas protecting the full set of European species requires a complementary set of habitats,



of which forests are only one example, alongside grasslands, bare areas, and aquatic ecosystems (fig. S9). Our findings support recent calls that multiple targets are needed to protect the spectrum of nature's values (19), but we also show that larger conservation gains are possible, in more specific and ecologically diverse areas, when species are prioritized rather than NCP. Furthermore, terrestrial vertebrates have been shown to play a key role in the provision of both cultural and regulating NCP (20, 21), including threatened species (22, 23), which are efficiently represented in top priorities for all species.

The full set of vertebrate species considered here (many of which are understudied) represent a much broader diversity of ecological niches and evolutionary histories than most conservation planning studies, but these species are still only a subset of Earth's biodiversity. A variety of other taxa (invertebrates, plants, fungi, bacteria) and other biodiversity facets, such as functional or phylogenetic diversity (24) (figs. S15 and S18), are even less represented in conservation policies (25). Improving knowledge on the spatial distribution of biodiversity and integrating different ecological datasets are paramount to inform conservation (26). There is a discrepancy between the currently moderate quality of biodiversity data at large spatial scales and the limited areas available for conservation in Europe. Here, we used a resolution of 1 km², which is based on the trade-offs between the uncertainty in species distribution data (17), data on locally valuable NCP (e.g., pollination, air quality regulation), and the needed resolution to be sufficiently relevant for conservation planning. Working at a coarser resolution (e.g., 100 km²) would lead to problems when assessing the Natura 2000 areas (many of which are smaller than 100 ha), especially given the mosaic nature of Europe's landscapes.

Most NCP are currently decreasing except those related to the production of material goods (27). Therefore, protecting key ecosystems that provide cultural and regulating NCP is especially urgent. We identified priorities where high NCP capacity overlaps with high demand, but conserving the capacity of ecosystems to provide NCP independently of current demand can be beneficial. Priority areas could shift in future conditions as a result of shifting human demand for NCP [for instance, with increasing population concentration in Europe's more productive regions (28)]. In addition, pressures such as climate change and habitat loss will further threaten biodiversity and NCP. Improved biodiversity models and innovative con-

servation approaches (29) are needed to protect biodiversity and NCP into the future as species ranges shift and ecosystems are modified (30).

The expansion of agriculture and peri-urbanization restricts wilderness to ever smaller areas, jeopardizing both biodiversity and NCP. In this context, protected areas should exist along a continuum of human presence, from untouched wilderness to sustainable use of nature. In Europe, Natura 2000 allows precisely this flexibility in management, and our results indicate where to ideally expand protection, in ecosystems that potentially sustain a majority of European vertebrate species and some essential NCP. Our results also highlight the potential ecological value of certain small Natura 2000 sites and the borders of larger Natura 2000 sites. Ensuring that these sites are sufficiently large and adequately connected across space will be crucial to sustain ecological processes and maintain viable populations for the long term (31). But to make realistic recommendations for the expansion of protected areas, further issues will need to be addressed. First, different stakeholders need to take part in the process, and economic and opportunity costs for varying sectors should be considered alongside potential ecological value (32). Our prioritization does not include spatial costs (e.g., market value, opportunity costs) (12), which would be necessary to designate protected areas but are likely to reduce the ecological value of the conservation solution (33). Second, the designation of protected areas takes place at national or local levels, despite widespread recognition that spatial prioritization across broader spatial scales (e.g., continents, ecoregions) is more efficient to conserve the total biodiversity across a region (13, 34). In our study, conservation priorities defined at the level of the EU optimize the representation of both species and NCP and would ultimately be more efficient at preventing widespread losses at the continental scale. Finally, our results highlight the complementary roles that different countries need to play to conserve ecosystems for nature and for people (fig. S12) (35). Governing conservation in a concerted manner on much broader taxonomical and geographical scales is crucial to meet global conservation needs but will require mechanisms to efficiently share the responsibilities of conservation management (36).

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/372/6544/856/suppl/DC1
Materials and Methods
Appendices S1 to S4
Figs. S1 to S21
Tables S1 to S4
References (38–59)

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Chapter 5

The untapped potential of food webs for conservation planning

Under review in *Conservation Letters*

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Abstract

International conservation policy includes the dual aims of protecting biodiversity and nature's contributions to people (NCP). Food webs are increasingly recognized as a fundamental link between these two aims because ecosystem functioning and NCP depend on a diversity of species and their biotic interactions. However, food webs are rarely used in applied conservation and best practices remain an open question. Here, we review the literature at the interface between food web ecology and conservation, and we synthesize how food webs can inform three major conservation goals: preventing species extinctions, maintaining ecosystem functions and NCP, and fostering ecosystem resilience. While the potential approaches and indicators are vast, we show how specific indicators derived from food webs can provide complementary insights for multiple objectives. We highlight examples and future directions for integrating food web ecology with systematic conservation planning. Incorporating food webs in conservation planning will be necessary to anticipate secondary extinctions, and ultimately, maintain biodiversity and ecosystem functions now and into the future.

Highlights

At the level of species, interactions can be used to protect predators together with their prey, or to identify species that are structurally important for the entire food web.

1) **Protect species of conservation interest** (including species that provide NCP) **together with their prey**. This can be achieved through prioritizing areas of overlap between prey and predators; optimising the representation of trophic interactions themselves as features; or maximising the spatial connectivity between interacting species (e.g. with the interaction connectivity parameter in Zonation 5).

2) **Prioritise keystone species**. A modified version of the google PageRank algorithm has emerged as a useful method to identify species that are structurally important for food webs and associated NCP. The legal protection of such species would incidentally benefit a large number of other species whose persistence depends on the keystone species.

At the community level, the diversity of species within and across trophic groups is essential for maintaining diversity and ecosystem functions.

3) **Prioritise areas with high food web diversity**. Different measures of food web diversity exist. Trophically diverse food webs (i.e. with a high number of trophic niches) are less prone to invasions and reflect higher energy flow. Interaction diversity is linked to robustness to extinctions. Highly distinct food webs are irreplaceable, less degraded, and less prone to extinction cascades.

4) **Prioritise areas with high trophic redundancy**. The local diversity of species with overlapping trophic roles (i.e. trophic redundancy) enhances the robustness of food webs to species extinctions, and ensures a high and stable supply of important ecosystem functions and NCP.

1. Why food webs are relevant to conservation

Global changes are disrupting entire communities, from species to ecosystem functions (Dirzo et al., 2014). Global change, such as climate change or habitat loss, not only influences individual species directly, but also indirectly through the loss of interactions (Valiente-Banuet et al., 2015). As such, individual species responses might ultimately lead to a profound reorganization of food webs, due to mismatches in interacting species ranges or phenology, extinction cascades, and interaction rewiring (Tekwa et al., 2022) (Figure 1). For example, the recent mass die-off events of birds from starvation (New Mexico Department of Game and Fish, 2020) are a testament to the fact that, to survive, species require sustained biotic interactions as much as preserved habitats (Figure 1). Secondary extinctions can increase the total number of extinctions by at least two-fold compared to primary extinctions (Bascompte et al., 2019; Koh et al., 2004), but their effects are typically delayed, resulting in an extinction debt in degraded communities and a high impact on communities in the long-term. Further, some species may be disproportionately important for maintaining the stability of an ecosystem (e.g. keystone species) (Keyes et al., 2021; McDonald-Madden et al., 2016) and their loss can strongly influence the persistence of multiple species in a food web. These losses have potentially far-reaching impacts on ecosystem functioning and nature's contributions to people (NCP) (Pecl et al., 2017).

Despite the clear links between food webs and conservation outcomes, food webs are rarely used to derive indicators that are relevant for conservation planning (Harvey et al., 2017; Heinen et al., 2020; McDonald-Madden et al., 2016). Some exceptions are the consideration of interactions as essential biodiversity variables (Kissling et al., 2015) and in the emerging IUCN Red List of ecosystems (Keith et al., 2020). There are few examples of incorporating species interactions in systematic conservation planning (SCP), which includes the establishment of protected areas—one of the most efficient ways to halt biodiversity decline (Godet & Devictor, 2018). For example, while many top predators are now included in interactional legislation, they are not systematically protected within interaction networks that can sustain them on the long term (e.g. with sufficient prey). While SCP can integrate many components of biodiversity (e.g. evolutionary distinctiveness, functional diversity and habitat connectivity), considering species interactions is particularly challenging (Rayfield et al., 2009).

A key part of this challenge is the lack of large-scale food web data and of clear methods for integrating information from food webs into conservation planning. Fortunately, large-scale food web data are becoming increasingly available (Brose et al., 2019; Maiorano et al., 2020; Middleton et al., 2021), as are methods to predict trophic interactions from limited data (Caron et al., 2022; Strydom et al., 2021), and to describe and analyse food web structure at different levels of organization, from species and their interactions to emerging network properties. For many species and ecosystems, these novel datasets and methods could lead to the first possibility to include food webs in conservation planning.

However, to realize this potential, the complexity of food web data must be distilled into relevant and interpretable metrics and approaches. Many measurable components of food webs

have been identified as being relevant to conservation (Tylianakis et al., 2010), but there is currently no consensus nor a general methodology on how to use them in conservation practices. Here, we address the challenges of this complexity and outline ways to better integrate food webs in conservation. First, we review the food web indicators that are relevant for major conservation goals: 1) prevent species extinctions, 2) maintain ecosystem functions and services and 3) foster ecosystem resilience (Table 1, Figure 2). Second, we discuss desirable outcomes of conservation in the light of food web ecology and outline ways to incorporate food webs in systematic conservation planning.

2. Linking food web properties and conservation goals

2.1. Prevent species extinctions

One overarching aim of conservation is to prevent species extinctions. For example, Goal A of the draft post-2020 global biodiversity framework proposes to reduce the rate of extinctions by tenfold, and to halve the risk of species extinctions (CBD, 2021). Food webs can help identify i) which species are most vulnerable to secondary extinctions, as well as ii) those that are key to preventing the extinction of many others.

2.1.1. Species position in the food web indicate their vulnerability

Both top-down and bottom-up effects act together to determine the vulnerability of species in a food web (Curtsdotter et al., 2011). Interactions can drive species to extinction either through 1) the decline or loss of beneficial interactions (e.g. decline of a prey) or 2) the increase or introduction of antagonistic interactions (e.g. competition and predation).

Top predators are thought to be particularly vulnerable because (1) their energy supply is limited by going through long chains with imperfect assimilation, and (2) they are affected by any disturbances that impact lower trophic levels in the food web. In addition, they typically have few offspring, occur in low densities (Brose, 2011), and many have been (or still are) persecuted by humans. Effective conservation of top predators requires both suitable and large enough habitat (Hirt et al., 2021) as well as abundant and diverse prey populations, to support them on the long term (Thompson et al., 2012).

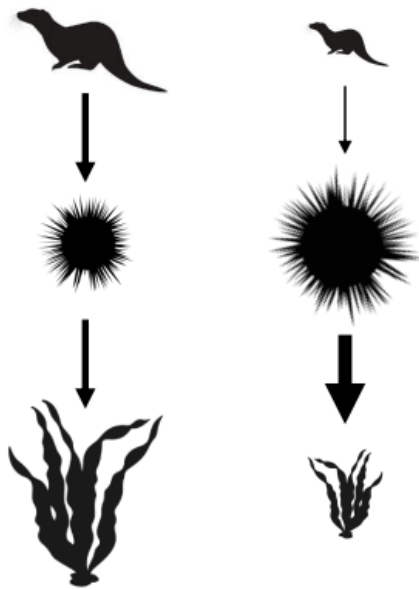
Trophic specialists are species that are specialized to a certain type of food. For example, the main source of food of the Iberian lynx is the European rabbit (Figure 1); the European honey buzzard primarily eats bees and wasps. Specialist predators are particularly vulnerable to the decline in their prey and to secondary extinctions (Fordham et al., 2013; Melián & Bascompte, 2002). For these specialist predators, it is particularly crucial to protect them together with their main source of food, upon which their survival depends.

For lower trophic level **prey species** with limited dispersal capacity and suffering from other environmental threats, predation (especially by introduced predators) can represent an additional threat to already vulnerable populations of prey species. Furthermore, prey species with many different predators are likely to experience sustained predatory pressure and

restricted geographic range due to multiple, spatially variable predator populations (Holt & Barfield, 2009). For such species, refuge from predatory pressure can be crucial to avoid extirpation (Decker et al., 2017). In practice, food web data might indicate where to manage a mosaic of habitats on a very local scale, to simultaneously protect the predator's nesting and foraging habitats, and the prey's nesting habitat that constitutes a refuge from predators (Decker et al., 2017; Rayfield et al., 2009).

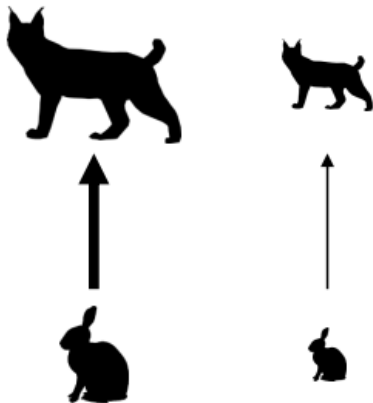
Top predators, trophic specialists and highly vulnerable prey are known to be more vulnerable to extinction than other species due to their trophic position. More generally, nodes (species or trophic groups) in a food web that are highly vulnerable to secondary extinctions can be identified by comparing different demographic and community scenarios of extinction and identifying the nodes that systematically go secondarily extinct. Their effective conservation requires the consideration of species interactions in addition to specific habitat requirements.

A. Loss of top-down control



1. Extermination of sea otters in the 20th century
2. Urchin populations are released from top-down control
3. Kelp disappear due to overgrazing by urchins
4. Benefits provided by kelp (coastal erosion control and habitat to fish species for the fishing industry) are lost

B. Loss of biotic resources



2. Iberian lynx populations decline due to prey scarcity (rabbit makes up >80% of the Iberian lynx diet)
1. European rabbit populations decline due to disease and overhunting (*Fordham et al 2013*)

Figure 1: Importance of top-down and bottom-up control for species and NCP. **A:** On the one hand, predators can maintain local biodiversity by reducing competition between prey species, allowing multiple species to coexist, including rare and endangered species (Soulé et al., 2005). Top-down control can also indirectly impact species on lower trophic levels. For example, through the top-down control of urchins, sea otters help maintain kelp forests, which are important for preventing coastal erosion and also provide habitat for fish species. The extermination of sea otters in the 20th century led to the overgrazing of kelp by urchins. **B:** On the other hand, prey species can sustain entire food webs through bottom-up control, if many other species rely on them for food. In the case of trophic specialists, prey species are essential for the survival of their predators. For example, the Iberian lynx relies on European rabbits as their main source of food, and the overhunting of the European rabbit led to a decrease in populations of Iberian lynx.

2.1.2. Food webs can help identify keystone species and interactions

Keystone species in a community are species that can be vital to many others by playing a disproportionate role (relative to their abundance or biomass) in maintaining the structure and functioning of their community (Cottee-Jones & Whittaker, 2012). Their loss triggers trophic cascades that can affect the entire ecosystem, with secondary extinctions of many other species and the loss of associated ecosystem functions and services (Estes et al., 2011; Keyes et al., 2021). First introduced to explain drastic decline in species richness following the removal of the predator *Pisaster ochraeus* (Paine, 1969), the keystone species concept has intuitive and appealing conservation applications. For example, keystone species can be added to lists of species that require legal protection (e.g. endangered species act in the USA or the EU's Birds and Habitats Directives), and their habitat can be protected to prevent threats to these species. Keystone species are crucial to ecosystems, similarly to ecosystem engineers which create habitats for other species (e.g. prairie dogs, beavers, coral, or kelp). However, the lack of consistency in criteria used to define the keystone status has hampered the systematic use of the concept in conservation (Cottee-Jones & Whittaker, 2012). We suggest that the use of food web metrics will help filling this gap.

A first set of metrics infer the structural importance of a species from its position in the food webs. Networks hubs (highly connected species, that have a high number of predators or prey) (Tylianakis et al., 2010) and central species (those through which most energy paths of a network flow) (Jordán et al., 2007) were previously thought to be keystone. Indeed, the removal of highly connected species can lead to secondary extinctions and drastic food web reorganization (Keyes et al., 2021). However, metrics based on centrality or the number of connections might not be the most effective to identify keystone species, because **indirect effects** (e.g. secondary extinctions reaching beyond the direct interaction partners of an extinct species) and **interaction strength** play an important role in driving extinction cascades (Zhao et al., 2016), more so than the number of predator or prey of a species. A version of the **Google Page Rank algorithm** adapted to food webs has recently been proposed as the most accurate method to identify keystone species to date (McDonald-Madden et al., 2016). Species with a high Page Rank are connected with a large number of other species in the food web, both directly and indirectly. In particular, species that are prey to many different species have been shown to be key for the robustness of entire food webs and for the sustained provision of NCP (Keyes et al., 2021).

A second set of approaches rely on simulations to quantify cascading effects (e.g. number of secondary extinctions) to identify keystone species as the ones triggering the largest number of secondary extinctions when they are removed. The extinction scenario that is linked to the highest rate of secondary extinctions can be used to build an index of structural importance of species (Santos et al., 2021). Other studies based on simulations show that interactions, rather than species, might be the keystone components in communities (Harvey et al., 2017). Conserving **keystone interactions** implies not only protecting both interaction partners together, but also making sure the interaction can take place (e.g. spatial and phenological

overlap, and abundant populations of both species) – this is likely to be extremely challenging in practice.

Both these approaches are complementary, but research is needed to compare the accuracy of different metrics to identify the keystone role, as well as their sensitivity to sparse interactions data. A long-standing question concerns the context-dependency of the keystone role of species, but evidence suggests that trophic roles are inherent to species (Baker et al., 2015; Stouffer et al., 2012), which encourages the generalization of the keystone role of a species across different contexts (Tylianakis & Morris, 2017). Quantifying the intra-specific variation in the Page Rank index in different environments will be a step forward on this question. One important driver of a species' keystone role is related to its abundance or biomass; but data on abundance or interaction strengths are largely lacking. One urgent and critical task for ecologists will be to continue to address the Eltonian shortfall: this includes empirically measuring interactions, or inferring interaction strength from other ecological data (e.g. biomass).

2.2. Maintain ecosystem functioning and NCP

Another major aim of conservation is to maintain ecosystem functions, in particular those that are linked to NCP (O'Connor et al., 2021). Food web ecology helps to identify the functional role of species in a community, *i.e.* the Eltonian niche, that allows simplifying food web information while retaining the functional structure, and sheds lights on ecosystem functioning and stability (Harvey et al., 2017; O'Connor et al., 2019). The Eltonian niche of a species in a food web could be used to prioritize species that fill irreplaceable (rare) trophic roles, maintain high ecosystem functioning, and protect groups of species that are linked to NCP.

2.2.1. Trophic uniqueness

In food webs, species with a unique trophic niche occupy a position in the food web that is shared by no other species. Such species typically interact with specific sets of species, as a result of unique combinations of functional traits (Gravel et al., 2016). Consequently, any ecosystem functions or biomass transfers associated to a unique trophic position would be lost if the species disappeared. For example, the bearded vulture is the only bird in Europe that is able to eat bones, and its presence benefits the decomposition of carcasses and organic matter cycling. Akin to functionally unique species (Violle et al., 2017), species that have a unique trophic position are important contributors of functional diversity, community stability and ecosystem functioning (O'Gorman et al., 2011). Additionally, these unique species are often very sensitive to extinction cascades (Petchey et al., 2017). Trophically unique species should be prioritized, in order to safeguard the irreplaceable functions that they provide, and their benefits for ecosystem processes (Ehrlich & Walker, 1998; Loiseau et al., 2020). A promising research avenue will be to transpose methods from functional ecology to food web ecology to consistently quantify trophic uniqueness (Dehling & Stouffer, 2018; Violle et al., 2017).

2.2.2. Trophic diversity

Trophic diversity is the diversity of trophic niches in a food web and is a facet of functional diversity (O'Connor et al., 2019). Trophic niche diversity can also be derived from the interaction volume of a food web, based on the traits of the prey and predators of each species (this can also be used to calculate trophic uniqueness) (Dehling & Stouffer, 2018). High trophic diversity reflects high trophic uniqueness across species in the community, with high niche complementarity and resource partitioning, which optimizes energy uptake in the community. Explicitly considering trophic diversity in conservation will be a step forward to prevent the simplification and homogenization of communities.

2.2.3. Trophic interactions underpin nature's contributions to people (NCP)

Certain NCP are directly dependent on species interactions. For example, agricultural production depends on pollinator visitation, and on pest regulation by predators that feed on rodents and other agricultural pests (Civantos et al., 2012); and decomposition of organic matter is a regulating NCP that relies on necrophage species. Supporting species (i.e., the prey of NCP-providing species) are equally essential for maintaining NCP (Keyes et al., 2021). Thus, preserving species that are either directly or indirectly involved in the provision of NCP is beneficial for the long-term supply of NCP. Furthermore, some species only indirectly provide NCP through trophic cascades. For example, forest regeneration is essential for carbon sequestration, and depends not only on pollination and seed dispersal (by frugivores and seed hoarders) (Fricke et al., 2022), but also on trophic regulation of large populations of herbivores by their predators (Estes et al., 2011) (Figure 1). Top-down control can also reduce the risk of zoonotic diseases and pandemics, because predators of the vector can reduce the risk of transmission by controlling the population of the vector and killing weaker individuals that have contracted the disease, and by maintaining prey species diversity (i.e. "dilution effect") (IPBES, 2020). To maintain NCP, it is crucial to protect and manage trophic interactions and groups of interacting species that contribute to an identified set of NCP.

2.3. Foster resilience to perturbations

Ultimately, conservation aims not only to prevent species extinctions or maintain ecosystem services, but also to foster ecosystem resilience to future perturbations such as pollution, invasive species or climate change. Food web structure (e.g. modularity, ratio of weak and strong interactions, trophic redundancy) can help anticipate the functional and structural consequences of extinctions in a food web (Binzer et al., 2011). Using food webs to estimate the resilience potential of ecosystem functions and of whole communities can help prioritize ecosystems that are less likely to collapse following environmental changes.

2.3.1. Trophic redundancy

Trophic redundancy is measured by the number of species that occupy the same trophic niche in a community. High trophic redundancy buffers the functional consequences of species losses, and fosters resilience of the system (Sanders et al., 2018), because fluctuations in a species

presence or abundance may have no immediate consequence if that species is functionally redundant with another. High trophic redundancy reflects resilience of a trophic position to species extinctions, while trophic uniqueness reflects the strong dependency of a trophic position to a single species. In particular, the vulnerability of NCP to species extinctions depends on trophic position and redundancy of the species (Keyes et al., 2021): NCP that are provided by species on higher trophic levels or by one trophically unique species are more vulnerable to species extinctions. Note that two species with the same trophic niche in a food web may differ in other aspects of their ecology (e.g. phenology, migration, activity time), which can increase the stability of the functions associated to their trophic niche.

2.3.2. Network metrics linked to food web resilience

The following network metrics can help quantify the extent to which perturbations (e.g. extinctions) can spread in a network (i.e. the risk of secondary extinctions).

Connectance measures the number of interactions within a food web, relative to the number of species. Connectance has been related to food web robustness (Dunne et al., 2002), and to ecosystem functioning (Montoya et al., 2003; Tylianakis et al., 2010). Higher connectance reflects that species are connected to many other species in the food web (on average), which may provide a buffer to fluctuations in prey availability (Tylianakis et al., 2010). However, high connectance can also be driven by one or a few highly connected species, even if the majority of species have few connections. Another limitation is that connectance (and other metrics that summarize community structure in a single value) does not provide information on specific species, their functional importance, or their vulnerability.

Interaction strengths strongly influence food web structure and stability (Curtsdotter et al., 2011). Food webs with many weak interactions are more resilient to perturbations, because weak interactions can become strong if the environment changes or if a resource is lost (Navarrete & Berlow, 2006). Evidence shows that i) functionally unique species tend to have the weakest interactions and that ii) both unique and weakly interacting species contribute to greater stability in food webs (e.g. less fluctuations in overall functioning) (O’Gorman et al., 2011). This suggests that functionally unique and weakly interacting species could be prioritized in conservation. While measuring interaction strengths can be challenging and labour-intensive, it is possible to estimate them (Berlow et al., 2009), for example, by using movement speed of predator and prey to calculate encounter rates (Pawar et al., 2012), or using a combination of local estimates of biomass, primary productivity and feeding interactions to estimate energy fluxes (Gauzens et al., 2019).

Stable **motifs**, such as trophic chains and omnivory motifs can promote food web persistence (Stouffer & Bascompte, 2010). Food webs with a high level of omnivory and trophic chain motifs could be prioritized. Focusing conservation resources on the species that compose stabilizing motifs can also be a cost-efficient strategy with a positive impact on community persistence. But whether motifs still have these positive effects when combined in entire food webs is uncertain.

Modularity in networks measures the extent to which groups of nodes (modules) are more densely connected to each other than to the rest of the network. High modularity can reflect ecological or spatial segregation between different parts of a food web. For instance, food webs that contain both aquatic and terrestrial species would typically have (at least) two modules, as aquatic species are typically more connected to each other than to terrestrial species. High modularity is thought to buffer perturbations between modules (Stouffer & Bascompte, 2011), as modules are mostly independent from each other and are only connected through a limited number of species. These species that connect modules to each other are known as **connector hubs**, and are crucial to the persistence of entire modules. Hub species need to be adequately protected, to prevent their extinction or decline which could have drastic consequences on the different modules the hub species connects. Modules can additionally indicate which species that depend more on each other than on species from other modules, and that should be conserved together as a functional assemblage (i.e. functional subnetworks).

2.3.3. Fostering resilience across habitat networks

The movement of species across landscapes, and predators in particular, has direct implications for biodiversity, including structure of food webs, species viability and ecosystem functioning (Gonzalez et al., 2011; Hirt et al., 2018). Spatial connectivity between habitat patches has been incorporated in prioritization algorithms (Albert et al., 2017; Lehtomäki & Moilanen, 2013), while interactions are not currently considered. This is a major gap because the impact of spatial connectivity on the persistence of local populations depends on the structure and dynamics of trophic interactions (Ryser et al., 2021). Research is needed to investigate how trophic interactions can help optimize the spatial connectivity for multiple species simultaneously, while also making sure vital interactions can occur (e.g. in habitats patches where predators can forage for food (Rayfield et al., 2009). A fascinating research avenue is to combine interaction networks with spatial habitat networks in conservation planning to protect diverse, functioning and resilient trophic metacommunities (Rayfield et al., 2009). The challenge is to integrate species-specific (trait-based) movement capacities into food web models (Boitani et al., 2007; Guzman et al., 2019). Interestingly, both dispersal and trophic interactions have the same currency (biomass flow), a similarity which can be leveraged to use them together in conservation planning.

Overall, the relevant components of the food web are different for each conservation goal (Table 1, Figure 2), but there is some overlap. The question is now: how to bring together these different food web components in conservation planning?

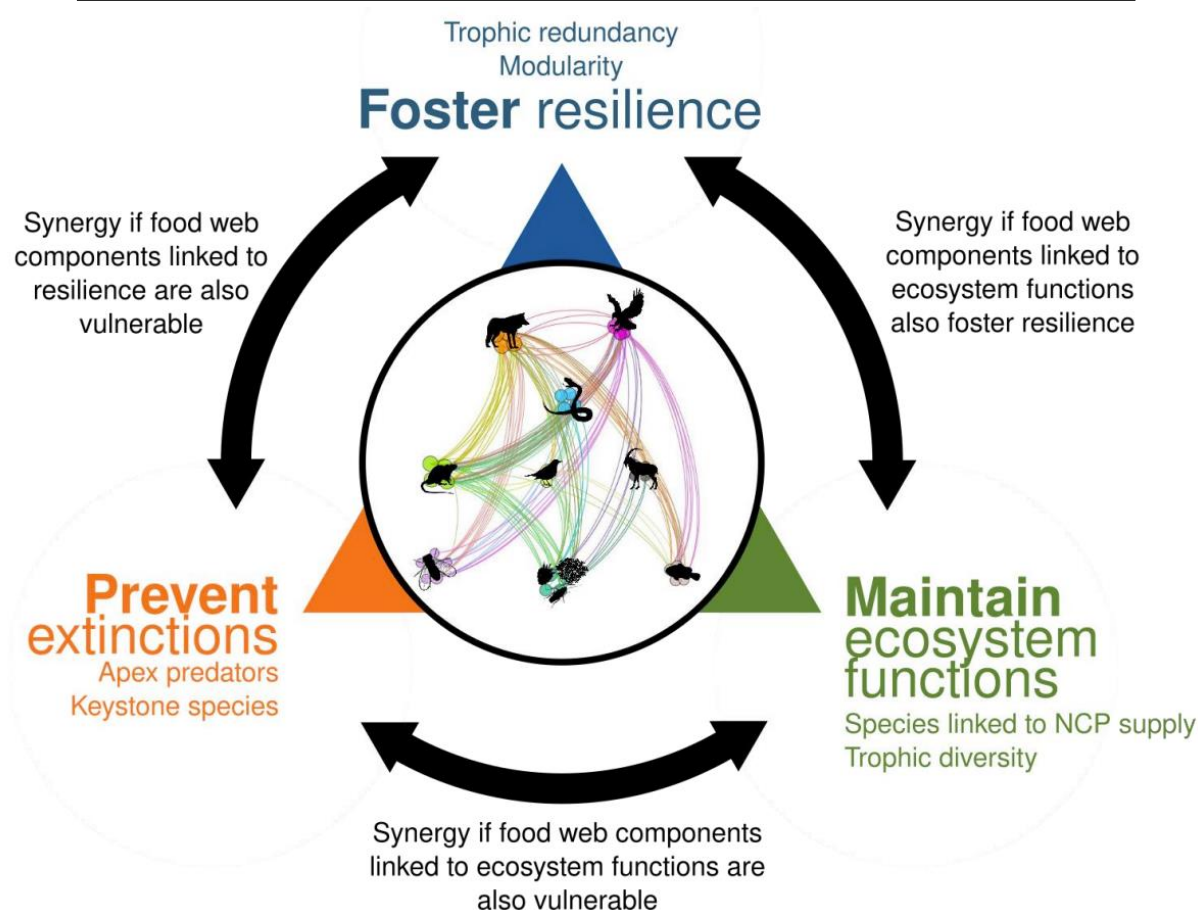


Figure 2: The structure and function of food webs are linked to conservation goals. Food web components, including species, trophic groups and emerging food web properties can be used to address major conservation goals: 1) prevent species extinctions and protect rare and vulnerable biodiversity; 2) maintain ecosystem functions and NCP; and 3) foster ecosystem resilience to environmental change. Synergy here means that a given metric could simultaneously address two conservation goals. For example, keystone species are essential for robustness of food webs and the supply of NCP. Even in the absence of synergy, priorities that optimize different components may coincide across space.

3. Linking food web ecology with systematic conservation planning

Systematic conservation planning (SCP) is a common approach to identify species in need of protection or to establish priority areas at a regional or global level for the conservation of multiple species (Nicholson et al., 2019) or NCP (Jung et al., 2021; O'Connor et al., 2021). SCP optimizes the spatial **representation** of multiple **non-interacting features** (e.g. species, ecosystems, or NCP) (Figure 3), within a set of priority areas that are **complementary** and **irreplaceable** for the set of features considered (Kukkala & Moilanen, 2013). SCP can integrate many components of biodiversity, such as evolutionary distinctiveness, functional diversity and habitat connectivity. Few studies have incorporated trophic information in SCP (Decker et al., 2017) and applications remain embryonic, due to both a lack of food web data, and a lack of methods to use trophic information in SCP. Yet, there are many options to include food web information in conservation planning (Figure 4), which we describe below.

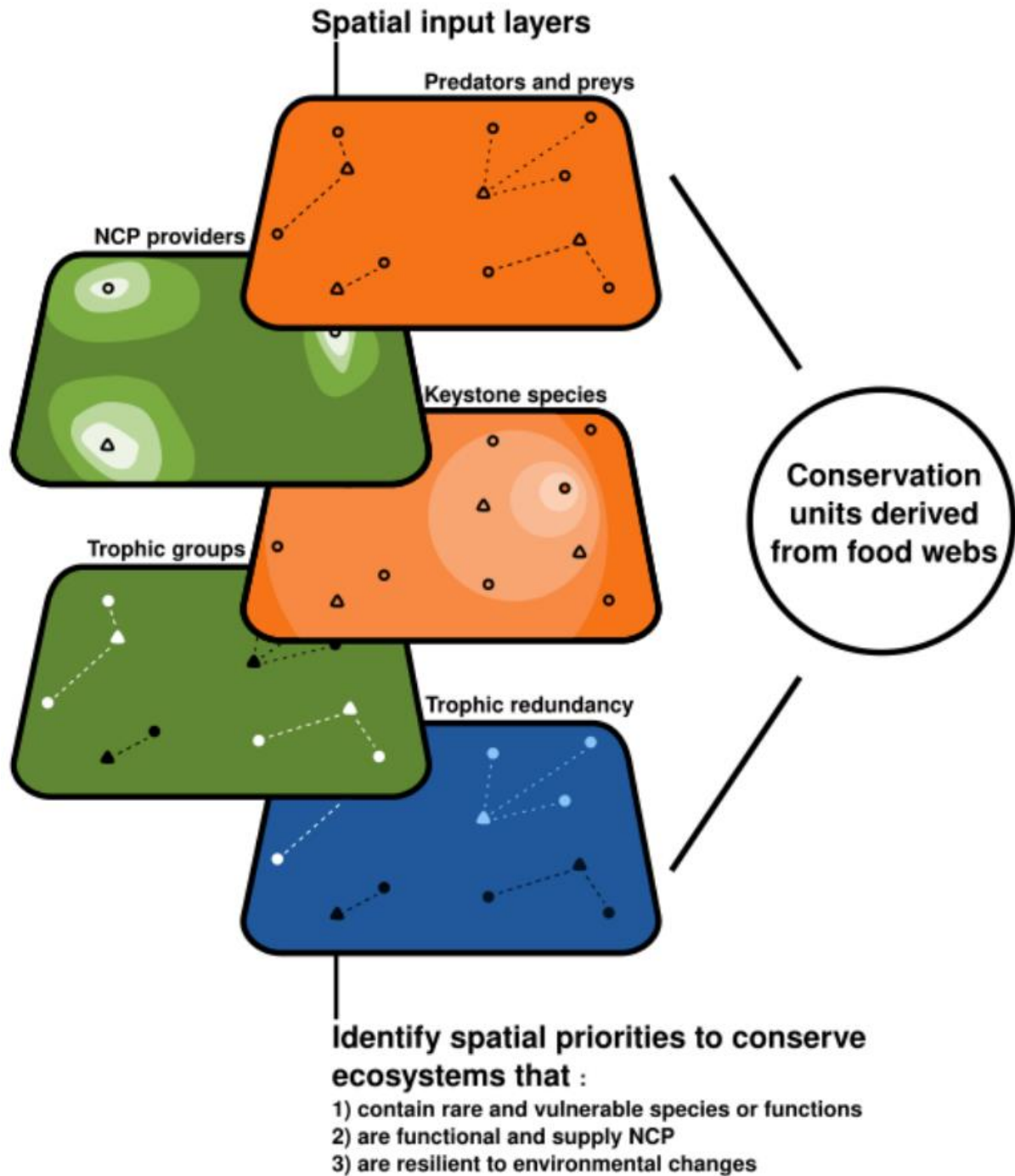


Figure 3: Framework to integrate food web components into spatial conservation prioritization. Spatial input layers are coloured by conservation goal: prevent extinctions in orange, maintain ecosystem functioning and NCP in green, foster ecosystem resilience in blue.

3.1. Using food webs to weight individual features

In SCP algorithms, weights can be assigned to individual features (e.g. species or NCP) to prioritize them over others and to reflect their higher conservation value. In the context of food webs – where features could be either species, trophic groups, or interactions – higher weights could be assigned to features that are: prey to a large number of species; important for food web robustness (e.g. high PageRank index); important for sustaining NCP (e.g. pollination, seed dispersal, pest control), directly or indirectly via their interactions (Keyes et al., 2021); or that are metacommunity hubs (top predators) that stabilize the metacommunity (Moreno-Mateos et al., 2020). However, SCP algorithms do not aim to protect species in the same location but to maximize the representation of each species individually across the region of interest. Therefore, simply adding weights to individual layers may not help achieve the desired outcome of protecting a predator together with its prey.

3.2. Using food web components as conservation units

The outcome of a prioritization is largely shaped by the conservation unit and the corresponding spatial layers used as input (Figure 3) (Lehtomäki & Moilanen, 2013). The following conservation units derived from species interactions data can be used to identify key areas for species and for food web diversity, functioning and resilience:

- i) **Species**—While typically used as the conservation units, here the focus could be on subsets of species (e.g. top predators, threatened species, keystone species, and species that provide NCP). We propose that spatial input layers for these species should include not only habitat suitability, but also food availability (*i.e.* prey diversity or abundance, when available), in order to prioritize areas that can sustain the species (and any NCP it provides) on the long term (Figure 4). This approach could also help identify locations with low abundance of food and where other types of conservation measures may be required to increase food availability locally for the species of interest (e.g. prey reintroduction, or agricultural set-aside). By contrast, input layers for threatened prey species could include a cost (or a lower habitat suitability value) where predators are present, in order to identify refuge from predatory pressure (Decker et al., 2017).
- ii) **Predator-prey interactions**—Focusing on the interactions themselves could protect vital areas where predators co-occur and interact with their prey, and where food webs are densely connected. However, using interactions at the species level will risk skewing the prioritization to interactions with rare species. For instance, insectivorous bats need to co-occur with flying nocturnal insects, rather than with a specific species. One solution would be to prioritize types of predator-prey interactions, by grouping species by genus or family, or considering interactions between trophic groups.
- iii) **Trophic groups**—the focus on trophic groups would prioritize ecosystems with high trophic diversity and with high trophic redundancy (more resilient) and rare trophic groups (functionally irreplaceable) (Figure 4).

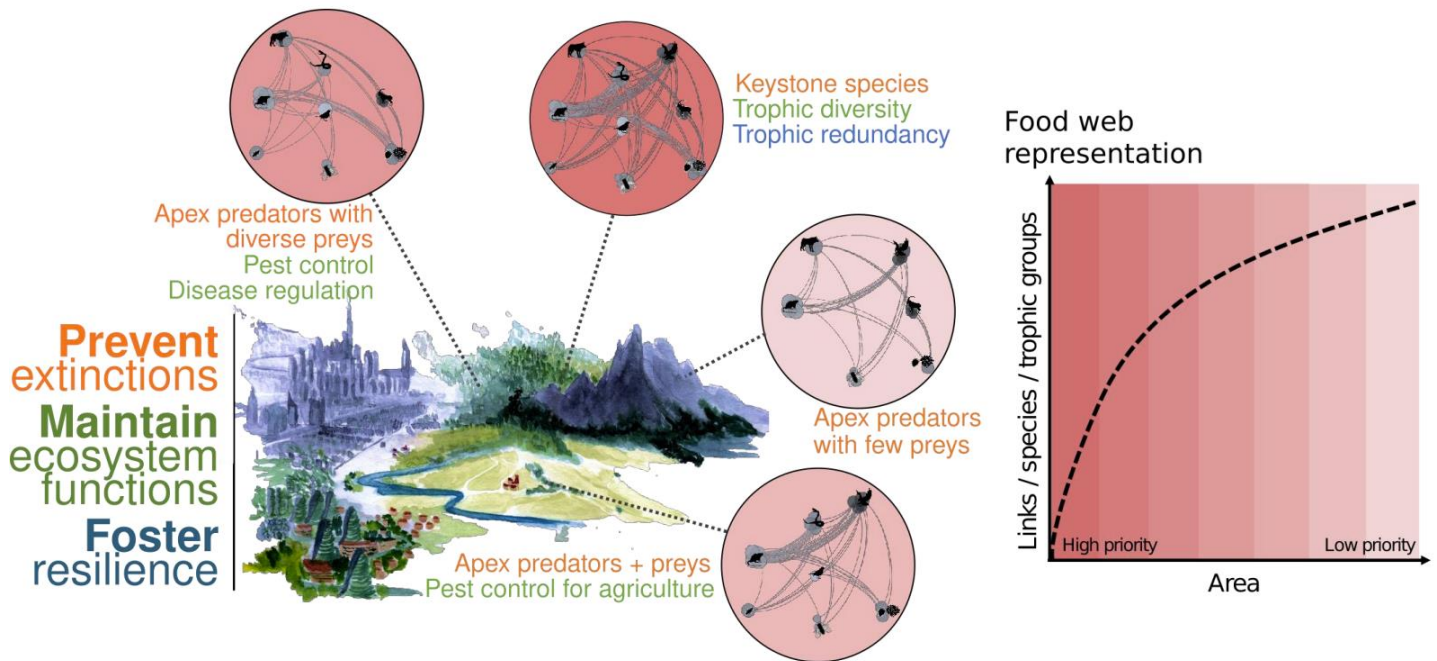


Figure 4: Using food webs to rank priority areas. To improve the conservation of species, priority areas should optimize the protection of species of conservation interest (threatened species; species that provide NCP; keystone species) together with diverse prey. To maintain ecosystem functioning and resilience, priority areas should maximize trophic diversity, interaction diversity, trophic redundancy (functional resilience) and prioritize distinct food webs. Performance curves (on the right) help quantify the biodiversity features contained within a set of areas, ranked from high to low priority.

3.3. Using insights from food web biogeography to identify irreplaceable areas

Recent advances in network ecology have made it possible to quantify the compositional turnover (i.e. the complementarity) between different food webs and their distinctiveness. Food web distinctiveness can be measured through network beta-diversity (Poisot et al., 2012). Distinct food webs (high network beta-diversity) contain assemblages of species and interactions that are not nested in others: they are unique and irreplaceable at a regional level. Furthermore, distinct food webs are thought to be less degraded (Tylianakis & Morris, 2017) and less invadable, and to contribute to the robustness of trophic metacommunities (Santos et al., 2021).

Chapter 6

Food web component	Conservation goal	Desirable outcome of conservation from food web perspective	References	Limitations
Trophic specialists	Protect vulnerable species	Trophic specialists should be protected together with abundant prey, because they are more vulnerable to secondary extinctions	(Fordham et al., 2013)	Not necessarily important for ecosystem functioning or robustness (Keyes et al., 2021)
Top predators	Protect vulnerable species, prey diversity, functioning	Top predators should be protected together with abundant and diverse prey	(Estes et al., 2011)	Causality remains to be demonstrated; bottom-up effects are equally important (Lafferty & Suchanek, 2016)
Endangered prey species	Protect vulnerable species	Endangered prey species require refugia from predatory pressure	(Decker et al., 2017)	Predators can benefit even vulnerable prey through competitor control (Soulé et al 2003).
Trophic redundancy	Resilience (of the given trophic function)	Trophic redundancy should be optimized in priority areas	(Ehrlich & Walker, 1998; Sanders et al., 2018)	Risk of competitive exclusion, if ecological niches of trophically redundant species are fully overlapping
Groups of species linked to NCP	Maintain functions, NCP	NCP providers should be protected together with their prey (supporting species)	(Keyes et al., 2021)	Risk of unanticipated surprise effects
Keystone species or groups of species	Prevent species extinctions	Keystone species or groups should be identified (e.g. high Page Rank) and prioritized	(McDonald-Madden et al., 2016)	No clear definition or metric
Trophic diversity, interaction diversity	Maintain diversity and ecosystem functioning	Food webs that are diverse and distinct (high interaction diversity, trophic diversity, network distinctiveness) should be protected	(Tylianakis & Morris, 2017)	Primary productivity strongly correlated and easier to monitor
Unique trophic groups	Irreplaceable and vulnerable functions	Species with a unique trophic position should be prioritized	(Ehrlich & Walker, 1998)	Not necessarily linked to ecosystem functioning or robustness
Network motifs	Resilience	Food webs with stabilizing motifs should be prioritized	(Stouffer & Bascompte, 2010)	Effects in large food webs or as species disperse are unclear.
Modularity	Resilience (lower risk of extinction cascades)	Connector hubs should be prioritized Food webs with higher modularity could be prioritized	(Moreno-Mateos et al., 2020; Stouffer & Bascompte, 2011)	Strongly dependent on sample size
Connectance	Functioning, resilience	Unclear	(Tylianakis et al., 2010)	Uninformative for species composition and vulnerability

Table 1: Relevance and limitations of different food web components to address different conservation goals.

The implementations outlined above relate to different conservation strategies, and they likely represent very different prioritization outcomes. A key decision is whether to target specific predator-prey pairs or whether to use information derived from the entire food web, which will depend on the conservation goal (Figure 2). A similar dichotomy has been addressed in species versus community-based prioritization (Leathwick et al., 2010). Likewise, prioritizing evolutionarily distinct species (which protects the global tree of life) is not the same as prioritizing local assemblages that have high phylogenetic diversity (Pollock et al., 2017).

Building on the framework to integrate phylogenetic diversity in systematic conservation planning (Faith et al., 2004), we could imagine that a corresponding metric in the context of food webs could correspond to the marginal gain in food web structure, function and resilience by protecting additional species or restoring habitat. Once suitable metrics are determined, then SCP algorithms (e.g. Zonation, Marxan, prioritizR) could be used or adapted, but establishing how the metric relates to conservation target will be critically important (Pollock et al., 2020). Going forward, another task will be to investigate how these strategies perform compared to a traditional approach that ignores species interactions, in terms of species representation (particularly for endemic species), ecosystem functioning and long-term species viability.

Concluding remarks

In this review, we identified a clear set of food web metrics that are linked to major conservation goals, and outlined ways to incorporate them in spatial conservation. We discussed how food webs can be used to 1) identify *species* of conservation concern (that are particularly vulnerable, or species that are particularly important for NCP or ecosystem resilience); and 2) identify key *areas* with functional, diverse and resilient communities. Incorporating information derived from food webs in conservation planning has the potential to lead to more effective and more robust conservation outcomes in the long term, and can complement other biodiversity data (e.g. population sizes, generation times, body mass, genetic diversity) (Pollock et al., 2020). Food webs are a holistic representation of biodiversity that enable the identification of the ecosystem functions or communities that are inherently resilient and those that are inherently vulnerable. Resilient, irreplaceable communities are the least likely to collapse in the context of global changes and are obvious priorities for protection. Vulnerable, irreplaceable communities should be actively managed to become more resilient (e.g. by reintroducing missing trophic groups, or improving spatial connectivity). Local initiatives, such as Cambodian farmers dedicating croplands to growing food for endangered red cranes (Pinto-Rodrigues, 2021), demonstrate the potential for food web conservation. Now we must scale up these actions in a systematic way to protect species biodiversity and nature's contributions to people. Only a network perspective on communities will achieve community resilience, protect keystone species, and the fluxes of energy and matter that sustain our natural world.

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Chapter 6

Spatial conservation of European vertebrate food webs

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Abstract

International conservation policies aim to protect 30% of area by 2030, including key areas for species and ecosystem services. These protected areas are often designated by considering individual species and typically ignore species interactions. Yet, species are interconnected and need to be protected within diverse, functional, resilient communities. Species interactions are crucial for species viability, ecosystem functioning and ecosystem services. There is evidence that, in order to conserve ecosystems effectively, it is essential to account for species interaction networks. Here, we propose and apply different methods to incorporate a metaweb in systematic conservation planning for European vertebrates. We first assessed the effectiveness of European protected areas for conserving terrestrial vertebrate species and their trophic interactions. Second, we investigated the extent to which spatial priorities are modified when accounting for interactions. We found that, on average, 31% of species ranges are protected, while 33% of species interaction ranges are protected. Interestingly, we found that there is no equivalence between the protection level of a species and the protection level of its interactions. We find that adding trophic information does not change top priorities in most instances, but that these small differences lead to a marginally higher representation of predators, their prey, and threatened species on average. While challenges remain to effectively integrate species and their trophic interactions in spatial conservation, our work highlights the need for a more holistic paradigm in conservation planning that considers biodiversity as an interconnected system.

6.1 Introduction

Some vertebrate species have experienced drastic declines [1]: over 300 terrestrial vertebrate species have been extirpated since 1500, and the abundance of remaining species has declined by 25% on average [2]. Because species are embedded in interaction networks, the loss (or decline) of one species can have indirect consequences on many other species [3, 4], and on the ecosystem functioning and services they provide. For example, agricultural production depends on pollinator visits and

pest regulation by predators that feed on rodents and other agricultural pests [5]. Ecosystem services also rely on sustainable trophic interactions: in particular, the prey of service-providing species are essential for maintaining services [6]. While there is evidence that protecting species together with their interactions would benefit conservation, conservation and management actions usually do not consider interactions explicitly. The scarcity of interaction data at large taxonomic and spatial scales on the one hand, and the lack of clear methods to use food webs in conservation, have made it particularly challenging to account for interactions in systematic conservation planning. Fortunately, large interaction networks are becoming increasingly available [7, 8] with untapped potential for conservation applications.

Systematic conservation planning (SCP) is a framework that allows for identifying priority areas for conservation, that optimise the cost-effective and balanced coverage of biodiversity features (species, ecosystem functions), across a region of interest [9]. Core principles of SCP state that protected areas should be representative (i.e. cover all the biodiversity features of an ecosystem); they should cover irreplaceable areas (i.e. areas that contain biodiversity features that are found nowhere else in the region of interest); and they should be complementary (to limit the redundancy of protected areas and thus optimise representativeness with limited means and in a limited area). These principles of SCP are usually applied for the protection of individual species, especially rare and/or threatened species. Interactions between species are not taken into account (or only to a limited extent) in conservation biology, even though rare or threatened species may depend on other species for their interactions. Consequently, there is no guarantee that species are protected simultaneously with their prey or predators or within functional and robust interaction networks. There is a risk that neglecting interactions in systematic conservation planning might lead to establishing suboptimal priorities for conservation.

Here, we ask two questions: 1) How well are species and their trophic interactions represented in protected areas? 2) To what extent does incorporating species interactions shift spatial priorities for conservation compared with the traditional species-based approach? We addressed these questions with a metaweb of trophic

interactions between all terrestrial vertebrate species in Europe [7]. We first investigated which species, trophic groups and trophic interactions are best and worst protected, relative to their range [10], following calls to evaluate the effectiveness of protected areas in terms of biodiversity outcomes [11]. We also investigated the relationship between protection level, trophic level and IUCN threat status of species. Second, we compared a prioritisation including species requirements in terms of both habitats and prey availability, with a traditional prioritisation approach that prioritises species by accounting for habitat suitability only.

6.2 Materials & Methods

6.2.1 Study area and resolution

The study area of 4,349,146km² includes the spatial extent of the European Union (EU) with the United Kingdom, Norway, Switzerland and the Western Balkans (Serbia, Kosovo, Northern Macedonia, Montenegro, Albania and Bosnia-Herzegovina) (EU28+). We excluded Iceland, Turkey and the outermost regions of Europe (Macaronesia, Cyprus). We worked at a resolution of 2 x 2 km² with the LAEA (Lambert Azimuthal Equal-Area) projection, which is frequently used at the European scale.

6.2.2 Species distributions

We extracted the geographic distributions of all terrestrial vertebrate species that occur naturally in the study area from Maiorano et al. (2013) [12]. We assumed a species to be present in a 2 x 2 km² grid cell if the grid cell was found within the extent of occurrence of the species (estimated by the IUCN) and contained at least 300 m² of suitable habitat for the species in the pixel. Otherwise, the species was assumed to be absent from the grid cell.

6.2.3 Metaweb of trophic interactions

We used the metaweb of the trophic interactions between all European terrestrial vertebrate species [7] (see Appendix ??). The metaweb is in the form of a binary adjacency matrix: element (i, j) is equal to 1 if species i is a predator of the adult life stage of species j . The database also details the non-vertebrate diet resources of each

species, among 22 categories: algae, aquatic plants, bark, berries, bulbs, coprophages, detritus, fish, flowers, grasses, fruits, waste, invertebrates, leaves, mosses and lichens, fungi, nectar, nuts, cultivated plants, other plants, seeds, woody plants. The species in the metaweb were aggregated within trophic groups where species have similar sets of prey and predators, following O'Connor et al. (2020) [13]. We then filtered the metaweb by removing interactions between species that never co-occur across the study area. The filtered metaweb contained 19,837 interactions between the 774 species, of which 200 have at least one prey species of terrestrial vertebrates. In total, there were 774 terrestrial vertebrate species for which these data were available (spatial distributions, interactions, red list status): 83 amphibians, 412 birds, 172 mammals and 107 reptiles. We represented the metaweb using the R package *metanetwork* [14].

6.2.4 Protected areas

For EU countries plus the UK, we considered Natura 2000 sites as protected areas (downloaded in 2020). For other countries in the study areas, we used the distribution of national parks from the World Database on Protected Areas (downloaded in 2022). We considered that a 2 x 2 km² grid cell was protected if it contained at least 50 hectares of protected areas. In total, 23.74% grid cells in the study area were considered to be protected.

6.2.5 Red list

We used the EEA database on the Red List of Species for Europe (November 2019 version) to define 'Threatened' species, including those that are listed as vulnerable (VU), endangered (EN) or critically endangered (CR).

6.2.6 Gap analysis

We investigated the effectiveness of European protected areas for species, interactions and trophic groups. The analyses were carried out in R (version 4.1.1).

We combined species distributions and the metaweb of trophic interactions to obtain local species interactions. We assumed a local interaction when two species interact in the metaweb and also co-occur in the grid cell. Similar to the species, we

defined the prevalence of an interaction as the number of pixels where the interaction is realised out of the total number of pixels in Europe. Some trophic interactions between pairs of species were only realised in one pixel (e.g. between the spotted eagle and the European souslik).

Then, we assigned conservation targets for species and trophic interactions. We combined the spatial distribution of protected areas with the distributions of species and their interactions to quantify the proportion of protected areas within the range of each species and each interaction. We then defined, for each species and each interaction, a protection objective, the minimum threshold of the distribution area that should be protected. We defined conservation targets for species and trophic interactions by building on the methodology of Thuiller et al. (2015) [10]: the 10% of the rarest species (or interactions) must be protected at 100%. The 10% most common species (or interactions) should be protected at 100%. Between these two thresholds, a logarithmic linear regression is performed. We were then able to quantify the protection level for each species and interaction, defined as the ratio between the protected percentage of the distribution area and the protection target. We explored how this level varied with the trophic level of species and the prevalence of the species or interaction (defined as the ratio between the number of grid cells in the range and the number of pixels in Europe).

6.2.7 Spatial prioritisation

We compared two spatial prioritisation scenarios. One scenario was the traditional approach (hereafter, “control scenario”): it optimises the representation of species, accounting for their suitable habitat but ignoring their trophic interactions. The second scenario optimises the representation of species accounting for both habitat and prey availability (hereafter, “trophic scenario”).

For the control scenario, the input layers were simply the individual distributions of the species considered. For the trophic scenario, we considered the overlap between predators and prey. For this, we combined the spatial distributions of species with the metaweb to produce spatial distributions that reflect the spatial overlap between predator species and its prey species, which we used as input layers

in Zonation. To obtain these, we multiplied the adjacency matrix of the metaweb with the distributions matrix of species to obtain a (species, pixel) matrix, where element (i, j) was equal to including the number of prey for species i in the grid cell j . We then divided the number of species in the pixel by the median number of prey richness across the study area, in order to not bias the prioritisation outcome to only a few areas with very high prey diversity. In ecological terms, this reflects the fact that having the maximum number of prey in a local community is not necessary neither for the predator's own survival, nor for the predator to have a beneficial effect (via top-down control) on the community. Note that our approach inherently includes the spatial distributions of species that are prey to several predators multiple times (both as their own distribution, and as resources for their predators). This is advantageous, because species that are prey for many species are essential for the robustness of food webs and related ecosystem services [6].

We combined the matrix thus obtained to the binary (species, pixel) matrix of presence/absence. In the resulting matrix, element (s, p) was equal to 0 if the habitat in pixel p is unsuitable for species s ; and non-zero elements ranged from 1 (if there is suitable habitat but no prey for species s) to 2 (suitable habitat and high prey diversity). Note that this means that the distribution maps are largely constrained by habitat suitability, but in grid cells that contain suitable habitat, we assign equal importance to habitat suitability and prey diversity. Moreover, for species that exclusively feed on terrestrial vertebrates, we set to 0 the grid cell where prey species are absent. We then transformed these matrices into individual rasters for each predator species.

We used version 5 of the conservation spatial planning software Zonation [15]. We included the distribution of protected areas as a binary hierarchical mask. We identified the top 7% priorities for the expansion of Natura 2000 areas (which corresponds to the European Green Deal's target of 30% protection). We then compared the results of the two scenarios, in terms of spatial overlap and representation of features (i.e., the spatial distribution of species, possibly weighted by its prey). To investigate whether the prioritisation outcome may be due to a dilution effect of

predator species (the majority of species in the metaweb do not feed on terrestrial vertebrates), we ran two variant prioritisation that only focused on the predator species (i.e. the 200 species with vertebrate prey in Europe).

6.3 Results

6.3.1 Protection level of species, trophic interactions and trophic groups

Species. We found that all species were protected in at least one location throughout their geographic range, but the percentage of their distribution within protected areas was highly variable: from 1.5 to 100%. On average, 30.72% of the species' ranges were protected. This is significantly better than if the protected areas were randomly located. The conservation target was met for only 245 species (31.6%), the vast majority of which are species with very large ranges (Figure 6.1). Unsurprisingly, for the most widespread species, the percentage of the range protected converges towards 23%, which is the coverage of protected areas in the study area. For example, the geographic range of *Parus major* covers 97% of Europe, and the percentage of its range protected is 22.9%. Concerning threatened species, out of the 94 species that are listed as threatened in Europe, only 8 are well protected, most of which are species with a widespread range (albeit in low abundance), such as *Myotis bechsteinii* (Figure 6.1). Note that our criterion does not account for abundance levels. That said, protected areas successfully cover a number of endemic species. For example, *Calotriton arnoldi*, a newt endemic to the Montseny massif in Spain, is protected in 100% of its range by the Montseny Natural Park). 84% of the range of the Iberian lynx (CR) is protected (for a target of 100%).

Trophic interactions. We found that 99.4% of the interactions (i.e. the areas of overlap between predators and their prey) were protected at least once in the study area. On average, 33% of the distributions of interactions were protected, which is significantly higher than random. Moreover, we found that 33.5% of the interactions reached their protection target. Interestingly, we found that the protection level of pairs of interacting species was not related to the protection level of their interactions

(Figure 6.1). In some cases, interactions reach their conservation target, while none of the interacting species reach their conservation target: in other words, the few areas where the species are protected are areas where they are both present. For example, the interaction between the Iberian lynx and one of its prey *Anas streptera* is well protected, even though the conservation target is not met for either protagonist species. In other cases, the conservation target can be met for two interacting species, but not their interaction: in other words, the locations where the species are protected are not in areas where they both occur. For example, *Aquila pomarina* and its prey *Crocidura russula* are both sufficiently protected (Figure 6.1), but their interaction is not (24% protection for a target of 77%).

Trophic groups. There was no relation between the trophic level of species and their protection level (Figures 6.2 and 6.5). Among basal species, *Calotriton arnoldi* was well protected, while *Somateria spectabilis* was very poorly protected. Among top predators, *Accipiter gentilis* is well protected, while *Ursus maritimus* is very poorly protected in the study area. We found that within trophic groups, the percentage of species that meet their conservation target varies widely from 7.7% (group 7, highly generalist top predators) to 72.7% (group 8, intermediate predators). Among groups of top predators, groups 11 (wolf, red fox, wild cats), 19 (birds of prey) and 25 (*Carnivora* and birds of prey) were, for example, rather well protected, while group 13, consisting of other *Carnivora* species (*Felidae* and *Mustelidae*), was poorly protected.

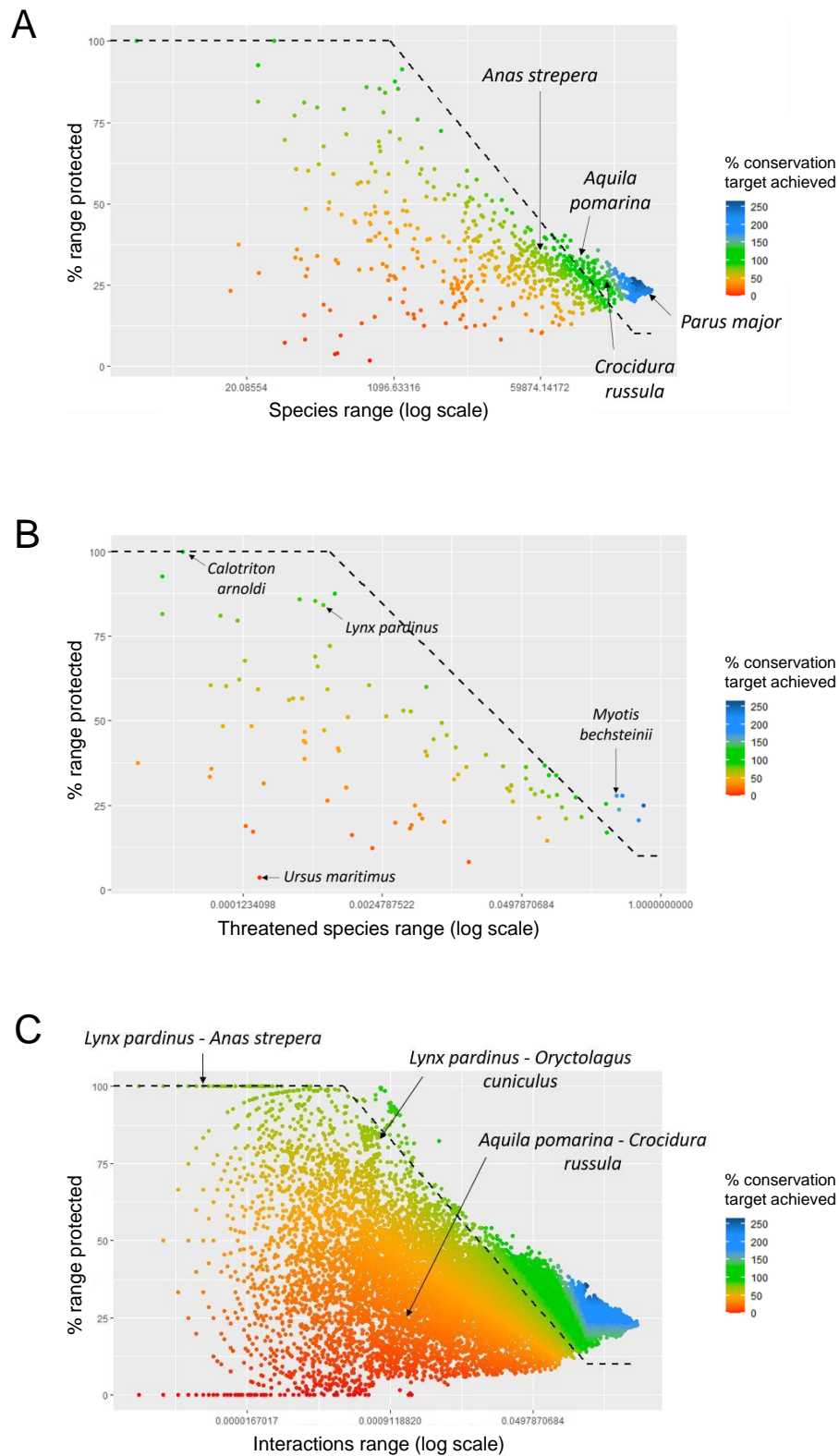


Figure 6.1: Protection of species relative to their targets for species (A), threatened species (B), and trophic interactions (C). Each dot represents one species (A and B) or an interaction (C). The dashed line represents the conservation target, deduced from the range of the species (or interaction), shown in the x-axis. Colours represent the protection level of the species (or interaction) (i.e. the distance from the conservation target) ranging from very poor (red) to sufficient (green) and very good (blue).

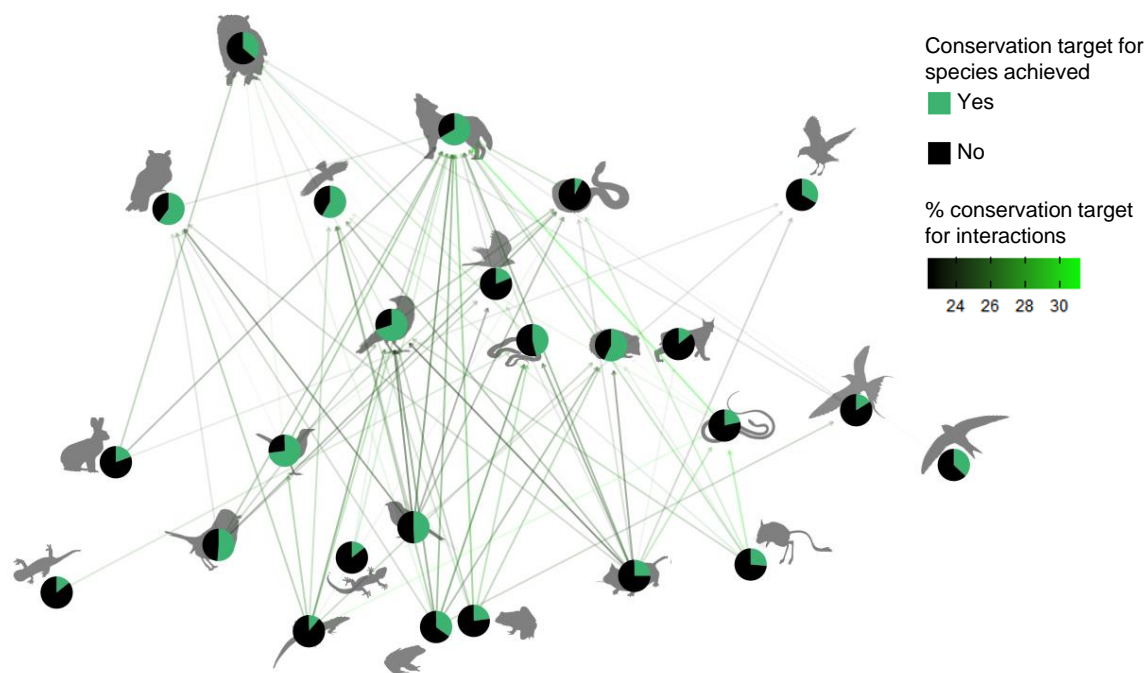


Figure 6.2: Protection level of trophic groups and interactions in the metaweb. In each trophic group, the pie-chart shows the proportion of species that achieve their conservation target (in green) or not (black). The colour of links shows the percentage of protected links between pairs of groups. Silhouettes (downloaded from <http://phylopic.org/>) illustrate the species typically found in each group.

6.3.2 Comparison of prioritisation outcomes with and without food web information

In both the species- and network-based prioritisations, top priority areas were mainly located in the Mediterranean region, known to be a biodiversity hotspot (Figure 6.3). There was 97.6% overlap between the top priorities in both scenarios. In other words, adding trophic information made a difference for only 2.4% of the top priority areas (i.e. 7 552 km²). These differences are mostly located in North-East Corsica, Sardinia, Sicily (top priorities only when ignoring interactions) and Greece (top priorities only when interactions were considered). When targeting the areas of overlap between predators and prey (the trophic scenario), top priority areas led to a marginally higher representation of species overall: predators' distributions (including prey richness) achieved 45.7% representation on average when considering interactions, vs. 44.9% when ignoring interactions; prey species achieved a representation of

51.9% when considering interactions vs. 50.3% when ignoring interactions; and threatened species achieved an average representation of 51.6% when considering interactions, vs. 48.7% when ignoring interactions. The prioritisation that considered interactions performed less well for the distributions of predators that included only habitat suitability, which were less well represented in the prioritisation that accounted for interactions (45.2% versus 49.0% when ignoring interactions).

In the variant prioritisation that focused on predator species only, the top priorities when accounting for interactions overlapped less with the top priorities when ignoring interactions: we found a 10.6% difference between the two types of priority areas (Figure 6.4). In addition to the Mediterranean islands and the Balkan peninsula with marked differences between the two types of priorities, new differences emerged. The eastern Alps, the Pyrenees, and Mallorca were top priorities for predator species habitats but not when accounting for prey diversity; Catalonia and some areas in Scandinavia emerged as top priorities for predators when accounting for prey diversity in addition to habitat.

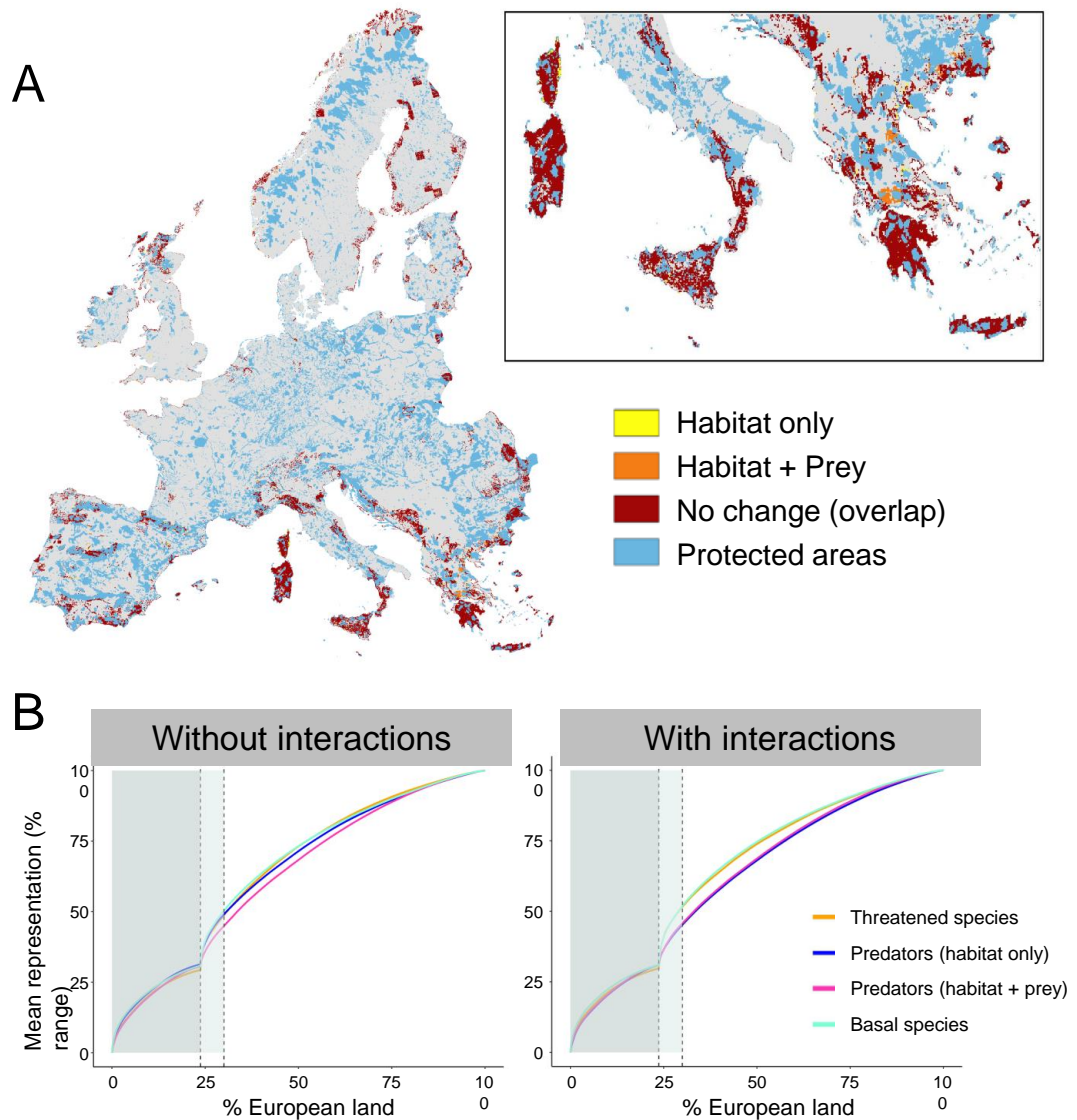


Figure 6.3: Comparison of prioritising species with and without considering interactions; in space (A) and in representation (B). The map shows top priorities for protected areas expansion in Europe for all species, when accounting for habitat only (yellow) or accounting for habitat and prey resource only (orange), or both (red). Protected areas are represented in blue. Below, the performance curves show the average representation gained as area is added in the prioritisation, in the run focusing on habitat only (left) and the run taking into account the prey resource (right). The dark grey area shows the fraction of Europe already protected; in light grey, the area needed to reach 30% protection of European land.

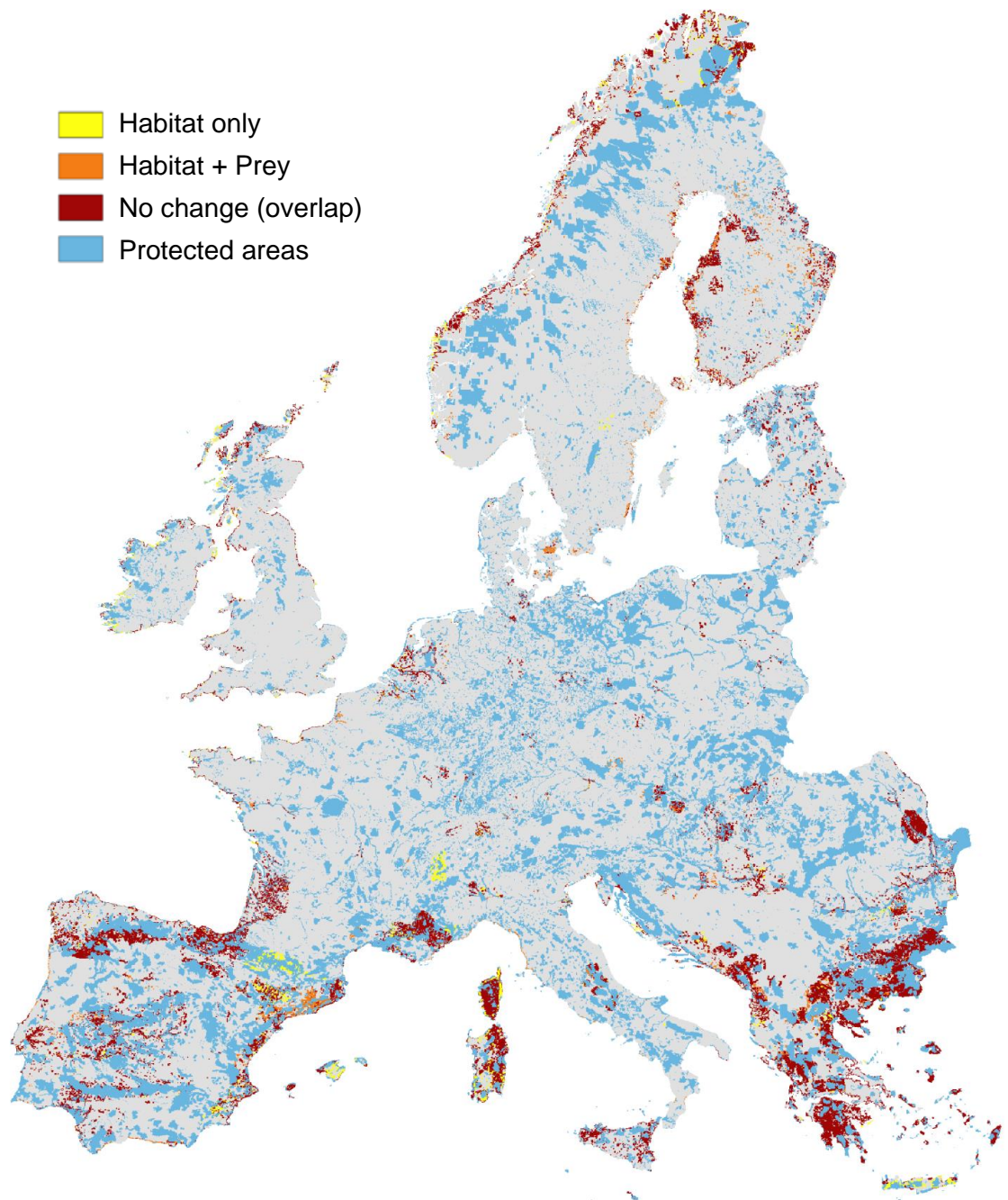


Figure 6.4: Top priorities for protected areas expansion in Europe for predator species, when accounting for habitat only (yellow) or accounting for habitat and prey resources only (orange), or both (red). Protected areas are shown in blue.

6.4 Discussion

Predators often cover vast spatial ranges with varying levels of prey (some areas have a high diversity of prey, while others are much poorer). Predators should be protected where a diversity of prey occurs for their populations to be viable in the long term, but we have found that this is not always the case. We found that the protection level of species and their interactions is suboptimal, but still better than random, which is in line with previous studies [9] that showed that the biodiversity representation in the Natura 2000 network is suboptimal for many species, but is still more effective than if the protected areas were randomly located.

We found that incorporating trophic interactions led to a highly similar prioritisation outcome compared with a prioritisation focused on species habitat suitability only - this is reassuring, because it suggests that top priority areas defined on the basis of species habitat suitability only (i.e., the traditional approach) also tend to be areas with sufficient prey diversity. However, it does shift priorities in a few specific areas: these rare spatial mismatches highlighted that priority areas identified on the basis of species habitat suitability only are not always favourable in terms of biotic interactions, i.e. may not sustain predators in the long term. These small differences thus highlight opportunities to improve the conservation of predator species together with their prey in the long term. In addition, despite the small differences, we showed that considering prey resources (when data is available) increased the representation of all species, including predators, prey, and threatened species - but only slightly. One explanation for the small differences observed between the two approaches is the fact that we used highly potential interactions, and focused on terrestrial vertebrates only. Indeed, priorities could differ more strongly if we excluded infrequent interactions (i.e., that do not make up the bulk of a predator's diet), and/or if we included interactions with other taxa, such as plants or invertebrates (which are a major source of food for a majority of terrestrial vertebrates). Thus, incorporating trophic interaction data for as many species as possible (when available) in systematic conservation planning could lead to significant gains for species conservation overall.

Incorporating interactions in systematic conservation planning requires examining trade-offs and synergies with other biodiversity facets. Our findings confirmed the status of the Mediterranean ecoregion as a biodiversity hotspot, including for species interactions. The Balkan Peninsula and the Iberian Peninsula emerged as top priorities when accounting for interactions in addition to habitat. This finding is in line with previous studies that have revealed densely connected networks and high trophic diversity in the Mediterranean region [16, 17, 13]. Yet, trade-offs do exist. For example, several Mediterranean islands contained top priorities when accounting for species habitats only, but they are not top priorities when accounting for interactions. This is consistent with a deficit observed in trophic interactions between terrestrial vertebrates (due in particular to a lower number of predators), even though they display high phylogenetic and functional diversity [16]. Yet, Mediterranean islands are extremely vital habitats for many endemic species and a large number of seabirds, some of which are endemic or endangered, and foster nutrient cycling between terrestrial and marine ecosystems - but the interactions of these island-dwelling species with plants, invertebrates or fish were neglected in our prioritisation. Similarly, the Western Alps harbour top priorities when accounting for predators' habitats only, but not when accounting for interactions. This can be explained by an interaction deficit in the Alps, due to the extermination of several top predator species by humans [16]. While considering trophic interactions can benefit many species, solely focusing on trophic interactions (especially with incomplete interaction data such as between terrestrial vertebrates only) might neglect other important biodiversity facets. This highlights the fact that we need to account for multiple biodiversity facets in systematic conservation planning.

Limitations and perspectives

Here, we considered potential interactions, which likely include many interactions that are actually infrequent or that are not essential for the predator's survival. For example, wolves can eat mice, but the bulk of their prey are large herbivores. The metaweb we used here does not distinguish between obligate and occasional interactions, but a new version has recently been developed (Maiorano et al., in

preparation). The next step for this work is to account for obligate interactions only in this analysis, because they are essential for the survival of predators.

We included the interactions indirectly by modifying input layers of predator species. Our approach is somewhat the opposite of the approach used in [18], who included the trophic level of species as a negative weight to identify refugia for prey. But many other approaches to integrate trophic information are possible (see Chapter 5). Food webs can be used to achieve a great number of desirable conservation outcomes: 1) Protecting areas where predators occur with high prey diversity; 2) Protecting keystone species (or trophic groups) in the food web can sustain many other species and ecosystem services; 3) high trophic diversity: this is linked to ecosystem functioning, and also makes the ecosystem less vulnerable to invasive species; 4) high trophic redundancy (many species with similar trophic roles) makes the associated ecosystem functions less sensitive to fluctuations in species abundance; 5) highly distinct food webs that are unique and irreplaceable at the regional level. One option would be to expand on previous work [19] to optimise the spatial connectivity between habitats of interacting species in the prioritisation, which is made possible via the interaction connectivity parameter in Zonation 5 (whether this is computationally feasible with a metaweb of several hundred species is to be confirmed). Using trophic-groups as input layers would prioritise ecosystems that contain i) high trophic diversity (more functional and less invadable networks), ii) high trophic redundancy (i.e. with many species in trophic groups (high resilience)), and iii) trophic groups that are represented by few and/or rare species (functionally irreplaceable). Another option would be to use the pagerank index to identify keystone species that are essential for the robustness of both species and the NCP they provide [6].

For this work to be relevant for European conservation policies, top priorities should focus on protecting species listed in the Birds and Habitats Directive, which countries are legally obliged to protect. This variant run would focus on 296 annex species, including 59 predator species. We could thus identify gap species that ought to be priority species because they are key to the robustness of entire food

webs and indirectly support NCP capacity. This approach would enable one to incorporate different values of nature (intrinsic, regulating, cultural) simultaneously in the prioritisation. Hopefully, new data and the development of methods should make it possible to take into account the interactions as well as the habitats of species, which is fundamental for effective long-term protection. While challenges remain for effectively integrating species, trophic interactions and NCP in spatial conservation, our work paves the way for more holistic conservation planning that considers biodiversity as an interconnected system [20].

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Supplementary figures

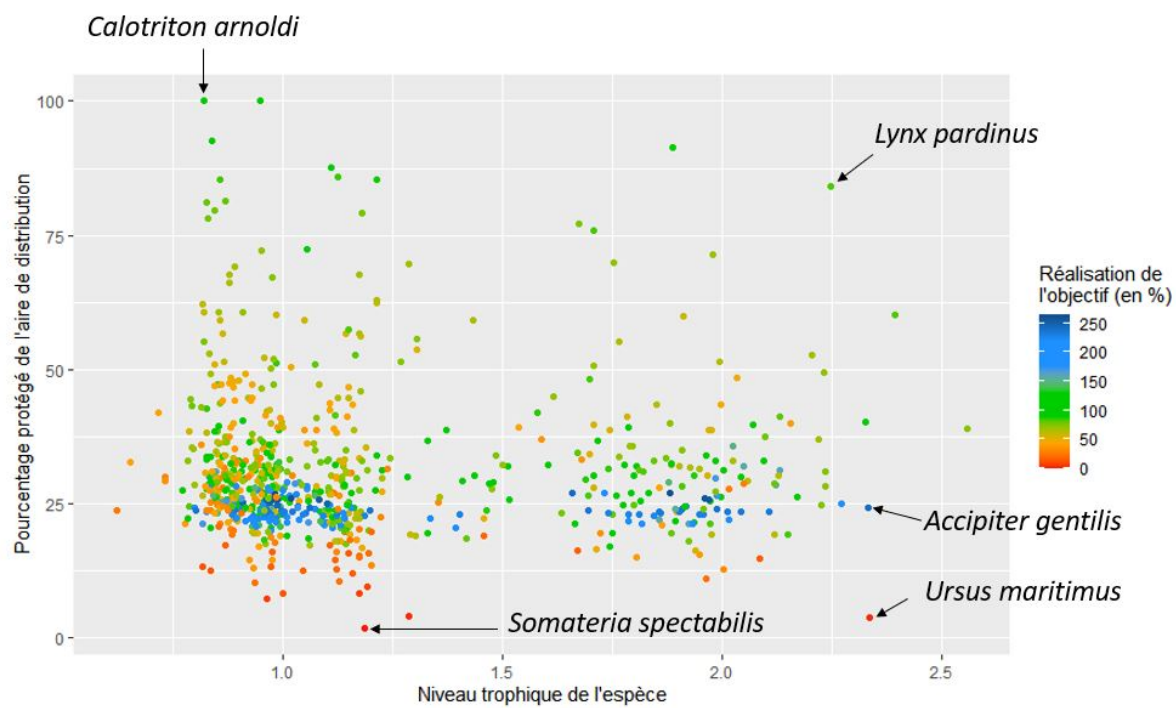


Figure 6.5: Protection status as a function of the trophic level of species.

Discussion

This thesis is a step forward in integrating information derived from food webs into biogeography and conservation. I first showed how using food webs can help characterise the functional role of species in an ecosystem, and investigate the spatial variation of biodiversity in a new light (Part I). Then, I showed that by accounting for trophic interactions, we can significantly improve our understanding of the potential impact of anthropogenic threats on biodiversity (Part II). Finally, I developed novel concepts and methods to improve the protection of species and nature's contributions to people (NCP), in particular by incorporating food web information into systematic conservation planning (Part III).

Here, I discuss the main findings of this thesis (see overview in Table 6.1). First, I review the ways in which food webs can be useful for biogeography and conservation: to i) understand the structure and functioning of biodiversity across space, to assess threats to biodiversity, ii) estimate the current and future potential impacts of anthropogenic pressures on species and NCP, including future climate and land use changes; iii) guide the conservation of functional and resilient ecosystems. Second, I highlight the limitations of my work and outline possible ways to address them. Finally, I suggest ways in which this thesis can be relevant for conservation in the context of the new European Biodiversity Strategy for 2030.

Discussion

Chapter	Objectives	Main findings
1. Functional biogeography of European food webs	Use the Eltonian niche concept to understand the spatial variation of food webs at a functional level.	Based on the metaweb, the stochastic block model aggregates species into functionally meaningful trophic groups. Trophic diversity (the number of trophic groups) varies along a latitudinal gradient which is driven by species richness and abiotic factors.
2. NCP provided by terrestrial vertebrates in Europe	Create a database on the NCP provided by terrestrial vertebrates and map the diversity of species associated with each NCP.	Terrestrial vertebrates are associated with 8 different regulating NCP through their trophic interactions: regulation of pests and pathogens, seed dispersal, pollination. They are also important for 4 cultural NCP (evolutionary heritage, cultural value, game, wildlife watching).
3. Direct and indirect threats to species via trophic interactions	Quantify and map the vulnerability of species, trophic groups, and interactions, to major anthropogenic threats in Europe.	Agricultural intensification and direct exploitation are the biggest threats to terrestrial vertebrate food webs. Wetland associated species and their interactions are vulnerable to multiple threats: hunting, pollution, IAS and diseases, and agricultural intensification.
4. Land use change impacts on species and NCP	Quantify the implications of the Nature Futures Framework on species and associated NCP through land use change scenarios.	All three NFF trajectories would benefit species-based NCP significantly more than SSP1.
5. Conservation priorities for nature and people in Europe	Analyse the differences between conservation priorities defined for species, <i>vs.</i> regulating NCP <i>vs.</i> cultural NCP.	Priorities for different values rarely overlap. Expanding protected areas in the 5% top priorities could double conservation gains for species and NCP.
6. Review: food webs and conservation	Propose ways forward to integrate food web information in SCP.	Using food web information can help achieve three conservation aims: prevent species extinctions, maintain ecosystem functioning, and foster robustness to perturbations.
7. Spatial conservation of European food webs	Analyse the difference between considering trophic information (in the form of prey diversity for predators) <i>vs.</i> only species habitats preferences (traditional approach) in a prioritisation.	We found few differences, but incorporating food web data leads to marginally higher representation of all species, including threatened species. Larger and more complete food web data are necessary to define conservation priorities.

Table 6.1: Overview of the thesis objectives and main findings.

Using food webs for biogeography and conservation

Food web biogeography sheds light on the structure and function of biodiversity across space. A few studies have investigated the spatial variation of the structure of food webs by using aggregate network metrics such as connectance [1, 2]. But these approaches have tended to overlook the functional structure of the food web. We sought to investigate the variation of food web structure from a functional perspective, *i.e.* at the level of the ecological role of species. In Chapter 1, I showed that the 1,152 species in the metaweb could be aggregated into a few dozen trophic groups (28 or 46, depending on the metaweb data used), on the basis of their trophic interactions alone. Species in the same trophic group were similar in terms of trophic level; number of prey and predators (degree); taxonomy; ecological traits (*e.g.* habitat type, foraging behaviour and activity time); and diet. In other words, using species interactions data only, the stochastic block model enabled us to reveal the Eltonian niche of species, and to summarise the functional structure of the metaweb.

Another dimension of a species' functional role in an ecosystem is the way in which they provide NCP, through their ecological traits and biotic interactions [3, 4]. In Chapter 2, I put together a database of the NCP provided by terrestrial vertebrate species. We reviewed the NCP that are underpinned by species and their interactions themselves (*e.g.* pest biocontrol, seed dispersal, and pollination). This information may be valuable to guide conservation priorities. Expanding on this work, we could harness these trophic groups and species-based NCP to quantify the functional irreplaceability, and the structural importance, of each species. For example, building on the framework developed by Keyes *et al.* [4], we could identify keystone species (or trophic groups) that are important for the robustness of both the food web and the supply of NCP across Europe, in particular in changing environmental conditions.

Across space, patterns of trophic diversity [5] and interaction diversity [6] showed that different European ecoregions harbour different assemblages of terrestrial vertebrates. In particular, the spatial variation of food web structure and diversity confirmed the status of the Mediterranean region as a biodiversity hotspot for all facets and values of biodiversity, and revealed that the Boreal and Arctic regions harbour trophically diverse and densely connected food webs (despite the relatively small number of species). Many EU-wide priorities for species, as well as win-win priority areas for multiple values of nature, are located in the Mediterranean. Yet, the Mediterranean and the Boreal and Arctic ecoregions already are, and will be, under considerable pressure due to climate change [7, 8]. What will happen to these ecosystems of exceptional biodiversity value in the future?

Food webs can help to better estimate the impacts of human activities on biodiversity. Human activities are almost never included in food webs - a study by Dunne *et al.* [9] was the first to include human hunter-gatherers alongside other species in the ecosystem, to describe prehistoric food webs. In a first attempt to analyse the vulnerability of species to multiple threats in the light of food web ecology, at a macroecological scale, I assessed the vulnerability of food webs are to major anthropogenic threats (Chapter 3). Findings suggested that species interactions can improve our understanding of the far-reaching impact of threats on biodiversity. I showed that quantifying threats to trophic interactions revealed much higher vulnerability than species-based assessments would suggest. Some predators have 100% of their prey vulnerable to major anthropogenic threats, which may imperil their long-term survival. In particular, agriculture expansion and intensification had the highest potential impact on the feeding resources of each predator species. This is consistent with recent findings that food webs complexity and diversity decreases in high intensity land uses (Botella *et al.*, in review; see Appendix B). It is also consistent with spatial patterns of species-based NCP (Chapter 2), where the diversity of NCP provided by terrestrial vertebrates and their trophic interactions declined with high intensity of land use (across all land systems):

most species that are culturally valued are absent from urban areas; and species that provide regulating NCP are mostly absent from high intensity agricultural landscapes. Top predators are also extremely vulnerable to direct exploitation (hunting, persecution); and pollution and invasive alien species are a major threat for wetland food webs. The next step will be to assess the risk of actual threat impact, using past, current or future estimates of land use change and climate change.

We need food webs to predict the impacts of future climate and land use change scenarios on species and nature's contributions to people. As both climate and land use change are projected to intensify, some species will lose suitable habitats, while others will be able to spread. In the Arctic, we are already seeing shifts in community composition due to climate warming: pollinators have declined by 80% within 20 years in Greenland, due to phenological mismatches with plant flowering periods [10]; in Canada, the majority of migratory caribou populations have declined in recent decades, due to food scarcity and the rise of insect pests [11]. Red foxes now compete with, and sometimes kill, arctic foxes; in Alaska, brown bears are killing musk ox juveniles. In other words, some interactions that are vital to species survival are lost; while other interactions arise, often posing a new threat to native species. The effects of climate change on biodiversity will be amplified by the heterogeneity in the ability of different (interacting) species to disperse to track climate changes, or to adapt locally. For example, birds can track climate changes across space through long-distance dispersal, while invertebrates may rather adjust their phenology [12]. These shifts in community composition can have knock-on effects on other species and NCP, via species interactions (*e.g.* secondary extinctions). Integrating food webs in global change impact assessments and in scenarios of biodiversity change can help disentangle the direct impacts of climate and land use changes on species, *versus* the indirect impacts via interactions (*e.g.* secondary extinctions, trophic cascades). Yet, modelling distributions in future scenarios has traditionally accounted for species-specific responses to climate change, and interactions are typically not accounted for, even though they are known

to have a large influence on species distributions. As a result, critical questions are left unanswered. Will competition become more extreme in the future, in fewer areas where food is available? What will be the consequences for other species and their biotic interactions, including for important prey resources such as insect populations? What consequences for ecosystem functions and NCP? Would locally extinct species be replaced by a functionally equivalent species (in terms of trophic role, NCP provision)? In addition, land use changes can either worsen (*e.g.* via habitat loss or land use intensification), or buffer (*e.g.* via habitat restoration or de-intensification of land use), the effects of climate change on biodiversity. So, what would food webs and associated NCP look like in future climate and land use change scenarios? These are questions that I hope to explore, together with colleagues from the FutureWeb project. Combining novel species distributions models (Poggiato *et al.*, in preparation), species dispersal capacity, high resolution climate change scenarios (Dirk Karger *et al.*, in preparation), future scenarios of the European land system (Dou *et al.*, in preparation) (see Appendix C) and the metaweb (Maiorano *et al.*, in preparation), we will be able to investigate how interacting communities will reorganise under different climate change and land use change scenarios (Figure 6.6). To measure changes in food webs structure in the future scenarios compared to current conditions, relevant metrics will include 1) changes in food web complexity [13, 6], or 2) the temporal turnover of food webs (temporal network β -diversity) [14], at the level of species and trophic groups [5] between future and current measures of food webs in each grid cell. We will also investigate the balance in gains and losses in species, trophic groups, and species-based NCP across Europe. The functional level of trophic groups and species-based NCP developed in this thesis will be used as a lens to quantify and map the direct and indirect effects of land use and climate changes on local assemblages of species and their interactions across Europe. Together, these results will highlight the hotspots and coldspots of communities and NCP that are most at risk, *versus* those that could be more resilient, under a range of future climate and land use change scenarios.

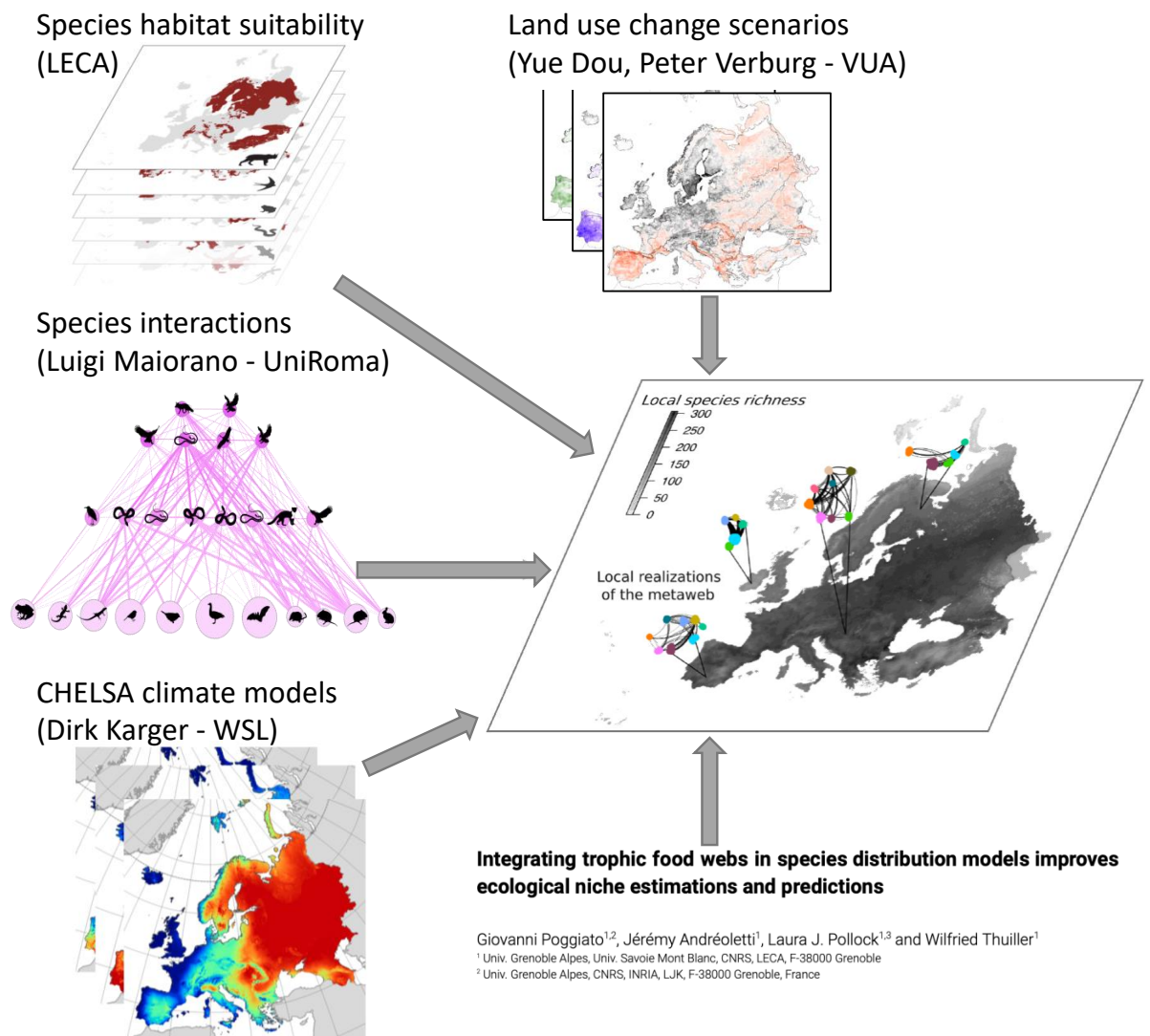


Figure 6.6: The FutureWeb project: predicting the impact of climate and land use change scenarios on terrestrial vertebrate food webs in Europe. By combining the European metaweb, trophic species distribution models, high-resolution regional climate models, land use change scenarios, species-based NCP, we can improve future projections of the distributions of species and associated NCP and give guidance on their protections.

Using food web information in conservation can help maintain and restore the functionality and resilience of ecosystems. Food webs underpin the persistence of species, as well as ecosystem functions and nature’s contributions to people [3]. Yet, so far, nature protection strategies do not systematically account for food webs. There are many options to consider food web information in conservation, which we reviewed in Chapter 5. At the level of species, interactions can be used to **protect**

predators together with their prey, or to **identify species that are structurally important** for the entire food web [4]. In particular, if a species is demonstrated to be structurally important for food webs, legally protecting this species (*e.g.* through legislation such as the Nature Directives in Europe) would incidentally benefit a large number of other species whose persistence depends on the keystone species [15].

At the community level, the diversity of species within and across trophic groups is essential for maintaining diversity, ecosystem functions, and whole network stability (Figure 6.7). Metrics of **food web diversity** (trophic diversity, interaction diversity, high network β -diversity) are highly relevant for protecting irreplaceable and functional food webs, that are resistant to biological invasions, and robust to extinctions [16]. The framework developed by Ohlmann *et al.* (2019) [14] can measure food web distinctiveness at different levels of network aggregation (species, trophic groups) and with different types of network data (binary or weighted). Further, the study led by Gaiüzère *et al.* (2022) [6] suggested that network diversity indices are not redundant with other diversity facets such as functional or phylogenetic diversity. Furthermore, **trophic redundancy** (*i.e.* diversity of species with overlapping trophic roles) is relevant for the robustness of food webs to species extinctions [17], and can ensure a high and stable supply of important ecosystem functions and NCP.

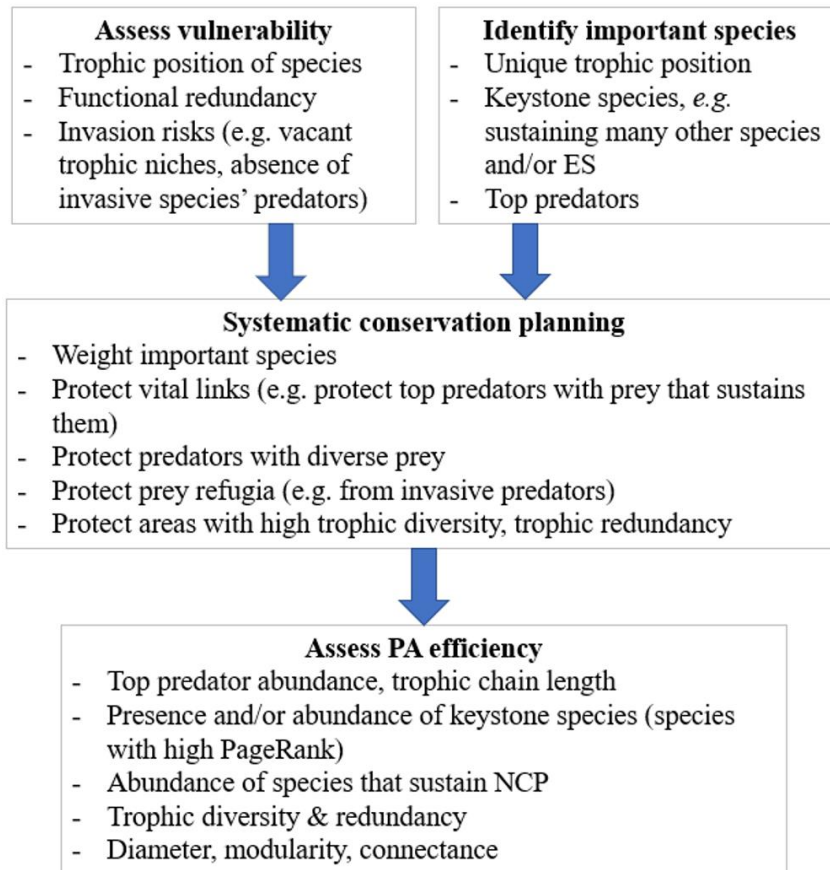


Figure 6.7: Overview of the steps in systematic conservation planning where information derives from food webs can be incorporated.

In Chapter 6, we tested the differences between a traditional prioritisation (based on species only) and a prioritisation that included food web information (*i.e.* diversity of prey within the habitat suitable range of predators). Preliminary results suggested that incorporating interactions in the prioritisation led to (slightly) higher conservation gains for all species (including threatened species) on average. The next step will be to perform the prioritisation again with new species distributions data (from Chapter 3.4) and obligate interactions only (Maiorano *et al.*, in prep.), and to test the performance of other approaches to incorporate food web data in the prioritisation, such as including trophic groups (Chapter 1) and species-based NCP (Chapter 2), and using the interaction connectivity framework in Zonation 5 [18]. Trade-offs with other biodiversity facets are likely, especially if we only include incomplete interactions data (*e.g.* only focusing on terrestrial vertebrates). For

example, many endangered or endemic seabirds are disconnected from terrestrial food webs, but they still require nesting habitat on land, even though they forage out at sea. This implies that, not only do we need larger and more complete data on species interactions and distributions, we also need to incorporate food web data alongside other biodiversity facets. It is possible that including trophic interactions in SCP may lead to even higher conservation gains when considering 1) obligate interactions only, 2) trophic interactions with other taxa (invertebrates, plants) and 3) future climate change scenarios. For example, the need for pest control in Europe will likely shift as a result of climate change. Agricultural pest species and disease transmitting organisms (*e.g.* ticks, mosquitoes) will expand their ranges northward as winters become milder in higher latitudes. It will be essential to protect and restore functional and diverse food webs, with natural predators that are able to control pest species in current and future conditions. We need a paradigm shift in conservation [19], as well as practical advances in addressing the Eltonian shortfall [20], to consider these essential aspects of the current and future state of biodiversity.

Limitations

Macroecology and conservation at a continental level requires high resolution maps of priorities for a large number of species. To identify conservation priorities that are robust, it is important to include as many species (or features) as possible for which we can obtain good quality data [21]. The main problem of working at a continental scale, and with over a thousand species, is the risk of overlooking complexity and uncertainty in the data. This thesis is based on the best available datasets for working at that scale, on the geographic distributions, and species interactions of terrestrial vertebrate species in Europe. European vertebrates are one of the best studied group of taxa around the world. Still, there are many assumptions and uncertainties at several steps in the workflow that we need to be aware of, and that would require further testing. Here, I outline the main limitations of my work, and how they might be addressed in the future.

The results presented in this thesis are based on a number of databases. How reliable are the biodiversity data that I have used throughout this thesis? The distributions and the trophic interactions (the core datasets used here) have in common that they are large scale data, they are based on expert knowledge and literature rather than observational records. I outline the methodological limitations associated with the use of these biodiversity data, and suggest ways forward to overcome these limitations.

Uncertainties in species distributions

To estimate the distributions of species, we built on previous work [8, 22], and assumed that a species is present in a grid cell if that grid cell is within the species extent of occurrence (estimated by the IUCN), and it contains suitable habitat for the species (based on existing databases and expert knowledge of species habitat preferences) and satisfies ecological requirements of the species (*e.g.* distance to water). This potential (binary) presence does not reflect an observation, but rather the assumption that, over a long time period, individuals or populations from this species will likely depend on its habitat for breeding, nesting or feeding. There are a few advantages associated with this method that should be mentioned here. Filtering species extent of occurrence with their preferred habitats enables us to overcome sampling biases that are present in observation records (*e.g.* GBIF or iNaturalist). They allow to obtain potential range maps of comparable quality across a large number of species (*i.e.* both well documented and less studied species), including different activity times (*e.g.* nocturnal species are less frequently observed by humans than diurnal species), taxonomy (*e.g.* amphibians are likely to be relatively less frequently observed than birds), habitat specialisation (species specialised in undisturbed habitat are likely to be less frequently observed than ubiquitous species).

However, several methodological limitations need to be acknowledged. First, this data is binary and static, and does not inform us about the abundance or the temporal dynamics of populations. Recently developed methods now enable to model population densities at large spatial scales for certain species – this is valuable information for biogeography and conservation applications [23]. For example, it is

well established that NCP delivery is (at least in part) driven by the abundance of NCP providers; thus, knowledge of population densities will help better quantify species-based NCP across space, and in turn, guide conservation priorities. Second, the species distributions data and framework we used here are strongly dependent on expert knowledge, and thus may not accurately estimate the actual presence or absence of a species. For example, it is possible that our conservative use of ‘suitable habitat’ (in Chapters 1, 3, 4 and 6) could create some false negatives, where we consider that the species is absent because the habitat is thought to be unsuitable for populations to persist, but where the species may actually be present in reality, for instance for hunting. Possible consequences of these uncertainties are that 1) the local food webs we reconstructed by sampling the metaweb with the local pool of species may be incomplete; 2) conservation priorities (Chapter 4) might miss areas that are important for species, but that were not reflected in the data we used. One way to quantify the biases in these data is to test the sensitivity of the results to different methodological choices. In Chapter 4, I showed that the results were robust to variations in the resolution of the distribution data (See Appendix D); but many other variables and methodological decisions remain to be tested, such as the distinction between primary and secondary habitats. Such sensitivity analyses would help identify what key results remain unchanged whatever the methodological choices. By contrast, in GBIF or iNaturalist, a species can be recorded in habitats where individuals are merely passing or vagrant (especially migrating species); but not necessarily in a location that the species requires for breeding, nesting or feeding. In fact, we investigated the overlap between habitat suitability models [8] and GBIF observation records for Chapter 4, and concluded that they are very different types of data and represent different things. How to resolve this conundrum? Integrated species distribution models may hold the answer. These models aim to combine observation records (*e.g.* GBIF) and presence-absence data (IUCN range maps) [24, 25, 26]. Recent studies compared the outputs of SDM using IUCN range maps and GBIF occurrence records, and concluded that the environmental niche estimated from these two different approaches are similar [27, 28]. Observation records

data requires pre-processing before using them for estimating species distributions. Fortunately, methods to correct for biases in opportunistic occurrence datasets (*e.g.* GBIF) have recently been developed [29] (see also Botella *et al.* in Appendix B).

In my thesis, I estimated the distributions of species in suitable habitats by accounting for land use intensity (in Chapters 2 and 3.4). For example, we assumed that if a land use class (*e.g.* high intensity cropland; high intensity forest) is associated with a threat to a certain species (*e.g.* agricultural intensification; logging), then the species is absent from this grid cell in the long term. In doing so, we assumed that the threat has a long term effect on the persistence of the local population of the species, because it affects its breeding, feeding, or nesting success. It is possible that the species may occasionally visit the ‘intensively managed’ habitat, but we assume that this habitat cannot sustain a viable population. Furthermore, we assumed that the extent of occurrence of a species is shaped by climate, therefore changes in land use alone would not change the extent of occurrence. This is a major assumption, because many other factors than climate are known to shape the range of species, including interactions, habitat suitability, human factors (*e.g.* human tolerance and persecution) [30, 31]. For example, the wolverine disappeared from the south of its European distribution (*e.g.* in Scandinavia and the Baltic states) in the 19th century because of deforestation and persecution [32]. We need to explore the relative contributions of these factors to improve predictions of species distributions in future conditions. The work of Giovanni Poggiato (in preparation) holds promise to improve our ability to estimate and predict species distributions by including known species interactions in species distribution models.

Uncertainties in reconstructing food webs

While the metaweb enables us to overcome interaction data paucity, this approach has its own limitations. We assumed that two species that co-occur, and that are known to interact in the metaweb, will interact locally. But the potential interactions between species may not be realised locally due to a variety of reasons, from uncertainty in species distribution estimates, phenological mismatches [33], low abundances of one or both interacting partners, or just by chance.

In this thesis, I did not consider the role of phenology. Yet the phenology of interactions is known to be a critical aspect for predators or mutually dependent species, especially in a changing climate: several studies have shown that phenological mismatches between interacting species can lead to the loss of the interaction [34].

Including dietary preference of predators would help to approach more realistic local food webs which contain frequent interactions only. Luigi Maiorano and colleagues been developing a new version of the metaweb which distinguishes the obligate (or frequent) interactions between a predator (*e.g.* the wolf is a specialised predator of ungulates), and the occasional (or infrequent) interactions (*e.g.* a wolf may occasionally eat a mouse) (I used these obligate interactions for Chapters 2 and 3).

It would be useful to compare food webs estimated with the metaweb approach, with sampled interactions in a given location, and analyse how different they are (and why). Note that, whatever the approach, it is extremely challenging to accurately map all the realised interactions in a given location: sampling or observing interactions is likely to underestimate the full interaction network (due to limited sampling effort); whereas sampling the metaweb with the local species pool is likely to overestimate the realised interactions (because it overlooks phenological mismatches, species abundances, *etc.*). The metaweb approach should perhaps be used in combination with other types of ecological data (*e.g.* abundance, population densities) in order to better estimate local food webs and estimate interaction weights (Antunes *et al.*, in preparation).

We need to consider more than terrestrial vertebrates

In this thesis, we focused on interactions between species of terrestrial vertebrates, and did not consider interactions with non-vertebrate species (*e.g.* invertebrates, plants, fish). Even though insects make up over 80% of all animal species, there are huge knowledge gaps for these taxa [35]. Consequently, they are frequently overlooked in conservation and biogeography. Yet, there is evidence that invertebrates are unevenly distributed in diversity and abundance, and 41% of invertebrates are

threatened with extinction, due to habitat loss caused by agricultural intensification, pesticides, and climate change [36]. This is worrying, because invertebrates are a major source of food for many terrestrial vertebrates (*e.g.* insectivorous bats and birds). We need to continue to address the Wallacean and Eltonian shortfalls [20] to include trophic interactions and spatial distributions of a broader set of taxa, specifically: invertebrates, plants, and fish.

Plants and terrestrial vertebrates also interact through seed dispersal, forming mutualistic bipartite networks. Seed dispersal is a vital function that enables plants to regenerate, thereby increasing carbon sequestration. The European Union's Green Deal proposes to plant 3 billion trees to increase carbon sequestration and mitigate climate change. But depending on the choice of which tree species to plant and where, reforestation can have positive or negative effects on biodiversity. Planning for reforestation should try to consider the spatial distributions of other species that may be influenced by new forest habitat. For example, we should ideally avoid planting new forests in wetlands or grasslands that endangered species depend on [37]. This would require careful evaluation of the benefits, costs, and trade-offs for different species or ecosystems of conservation interest in different planning scenarios. Such evaluation could inform reforestation scenarios, to try (as much as possible) to plant native tree species in places where their associated seed dispersers are potentially present. Integrating these considerations will be particularly challenging given that there are many competing interests in the already constrained landscapes of Europe.

Implications for the EU Biodiversity Strategy for 2030

“We are still losing our vital life support system. We urgently need to deliver on the commitments in the EU Biodiversity Strategy [for 2030] to reverse this decline for the benefit of nature, people, climate and the economy.”

Virginijus Sinkevičius, 2020

Protected area expansion

The EU Biodiversity Strategy for 2030 proposes to protect 30% of European surface by 2030. But depending on how biodiversity is valued - for itself, or for its benefits to people - the implementation of this target could lead to very different outcomes. In Chapter 4, I addressed the following questions: **What difference does it make to protect nature for the utilitarian *versus* the intrinsic value of nature? Are there any win-win areas? What is the best strategy to conserve species and nature’s contributions to people?** We showed that key ecosystems for species, regulating NCP and cultural NCP are rarely in the same areas, but a focus on species would lead to greater benefits for multiple values of nature (especially given that some species underpin several NCP). One explanation for this finding relates to the fact that individual NCP were more geographically widespread than species (even though we accounted for societal demand). Therefore, priorities defined for species could incidentally capture key ecosystems for NCP, while the reverse was not true. That said, in a future prioritisation, it may be more appropriate to consider geographically segregated ecosystems that deliver a given NCP as separate entities. In our analysis, all ecosystems that provided the same NCP were pooled in a single input layer - but a heritage forest in France and a heritage forest in Poland or in the Carpathians should perhaps be incorporated as separate features instead.

Another key finding from the study was the fact that focusing on all species performed well for threatened species, while focusing on threatened species only missed many important habitats for other species. This shows that keeping a narrow focus on listed species (*e.g.* the IUCN Red List, or Nature Directives) can lead to suboptimal conservation outcomes, especially given that i) species rely on one another via their interactions, ii) species lists necessarily overlook understudied species, many of which might be threatened [38] and iii) some species may become vulnerable in the future even though they are currently in favourable status. For the best outcomes, conservation prioritisation needs to be as comprehensive as possible, *i.e.* include as much good-quality biodiversity data as are available.

Protecting an additional 5% of EU land could double the current representation of species and NCP, but only if located in the top priority areas. The “30x30” target can lead to highly positive outcomes for biodiversity, but the new protected areas need to be carefully situated [39]. In particular, the rare win-win areas for different values represent opportunities to expand the European protected area network in areas that are crucial both for terrestrial vertebrate species and for ecosystems that we depend on for our livelihoods.

We also identified existing Natura 2000 sites with very high biodiversity value: these are areas where effective protection needs to be strengthened. Indeed, management is poor on many existing Natura 2000 sites. Because of loose regulation, these protected sites sometimes harbour hotels, ski resorts, golf courses, or renewable energy plants. Furthermore, many Natura 2000 sites are very small. Expanding and strengthening protection within and around the existing Natura 2000 sites with exceptional biodiversity value may be more easily achieved than creating a new protected area from scratch, and would ensure the long-term persistence of the species and NCP that they host.

Protecting biodiversity in current and future conditions will require spatially connected protected areas to ensure the resilience of species and their interactions in a context of environmental change. One of the main drawbacks of the study in Chapter 4 is that the priority areas identified may become unsuitable for species or may lose their capacity to provide NCP in future climatic conditions. A future prioritisation should aim to mitigate the possible impacts of climate change on species and NCP capacity, by identifying spatial priorities that would foster their resilience to climate change. One way of doing that is to improve the spatial connectivity between protected areas, and to preserve and restore habitat patches and ecological corridors that are important for the movements of species, *e.g.* for bird migration flyways, or for tracking climate changes. In previous work, I studied the importance of spatial connectivity for the recovery of metacommunities following environmental degradation [40] (see Appendix E). The need for spatial connectivity is recognized in conservation policies (*e.g.* ecological corridors). Protected areas need to be sufficiently large, and adequately connected across space, to maintain diverse and resilient populations. Yet, very few protected areas across the globe are structurally connected [41], and spatial connectivity is still poorly integrated in conservation planning due to myriad possible definitions and approaches [42, 43]. Only a few conservation planning studies integrate spatial connectivity as well as risks associated with climate and land use change [44, 45]. The next challenge will be to consider both spatial connectivity and species interactions in conservation planning [46], in order to restore the ecological flows within and between ecological communities [19].

Beyond protected areas: transforming European landscapes

We need more than protected areas to set nature on the path to recovery.

Protected areas are important and necessary, but they alone cannot bend the curve of biodiversity loss. Because the drivers of biodiversity loss are rooted in the way we produce, trade and consume goods, we need an integrated strategy for systemic change [47]. Outside of protected areas, we need to find ways to co-exist with non-human species.

Threat mitigation and de-intensification of land use can allow many species to recover, and species-based NCP supply to increase. In Chapter 3, we highlighted priorities for threat mitigation across Europe. Our findings support the need to regulate or ban direct exploitation of species (hunting, persecution, taking in the wild) and to de-intensify agricultural landscapes. We showed that, in some areas, a small number of vulnerable species are associated with a majority of interactions. Consequently, their loss may jeopardise local ecosystem structure and functioning. In other words, failing to reduce anthropogenic threats may lead to the collapse of interaction networks in these places. This is a problem because species interactions also underpin NCP. The work presented in Chapter 4 was a first attempt to investigate the potential benefits for species and associated NCP of implementing the EU Biodiversity Strategy targets through the lens of the Nature Futures Framework (NFF). We found that the NFF scenarios all lead to significantly higher gains on average for species-based NCP than the SSP1 scenario. Results suggested that land use changes that implement the EU biodiversity strategy in the light of the NFF would lead to a win-win situation for people and nature. Developments in the coming months on this study will include the addition of biophysical NCP estimates, societal demand for both biophysical and species-based NCP (in collaboration with Cecilia Zagaria and Peter Verburg (VUA)), and predictions of species distributions in future climate change scenarios.

The triple crises of climate change, biodiversity loss and food security need to be tackled together [48]. Climate change is leading to decreased agricultural yields and increased risk of pest plagues. In a 2°C warmer climate, the three most important grain crops around the world (rice, maize and wheat) are projected to experience a massive increase in pest-related crop losses [49]. Milder winters mean that agricultural pests are shifting northward, so temperate zones, including Europe, will be the hardest hit. Increasing the use of pesticides may be a short term solution, but would lead to the loss of many trophic niches, including natural predators of agricultural pests, subsequently benefitting agricultural pest species in the long term [50]. As Crowder *et al.* put it: “In farmlands, agricultural pest-management

practices often lead to altered food web structure and communities dominated by a few common species, which together contribute to pest outbreaks” [51]. The proposal in the EU Restoration Law to cut the use of chemical pesticides in half by 2030 is encouraging, but needs to be tightly coupled with the restoration of diverse and functional interaction networks within agricultural landscapes. High-diversity landscapes benefit agriculture: ambitious biodiversity targets are not a cost, but an investment in an agriculture that can provide food in the long term. However, the EU biodiversity strategy currently proposes to transform only 10% of agricultural areas into high diversity landscapes; and to manage a quarter of agricultural land organically by 2030. Given the massive impact of agricultural intensification on food webs and NCP, as well as the current and future challenges faced by biodiversity and agriculture, these targets are insufficient.

To quote Georgina Mace, “Required now are bold and well-defined goals and a credible set of actions to restore the abundance of nature to levels that enable both people and nature to thrive” [52]. But many targets in the EU biodiversity strategy are poorly defined - this leaves a lot of flexibility in the interpretation and subsequent implementation of targets, with varying outcomes for biodiversity depending on what is valued in nature (see Chapter 3.4, and Appendix C). Challenges posed by agricultural pests in future climate will likely be paralleled with those related to the spread of insect-borne diseases [53, 54]. Given the future risks posed by climate change to food security and public health, it is vital to protect and restore diverse and functional ecosystems that can provide regulating NCP (*e.g.* regulation of pests and pathogens, flood control, carbon sequestration).

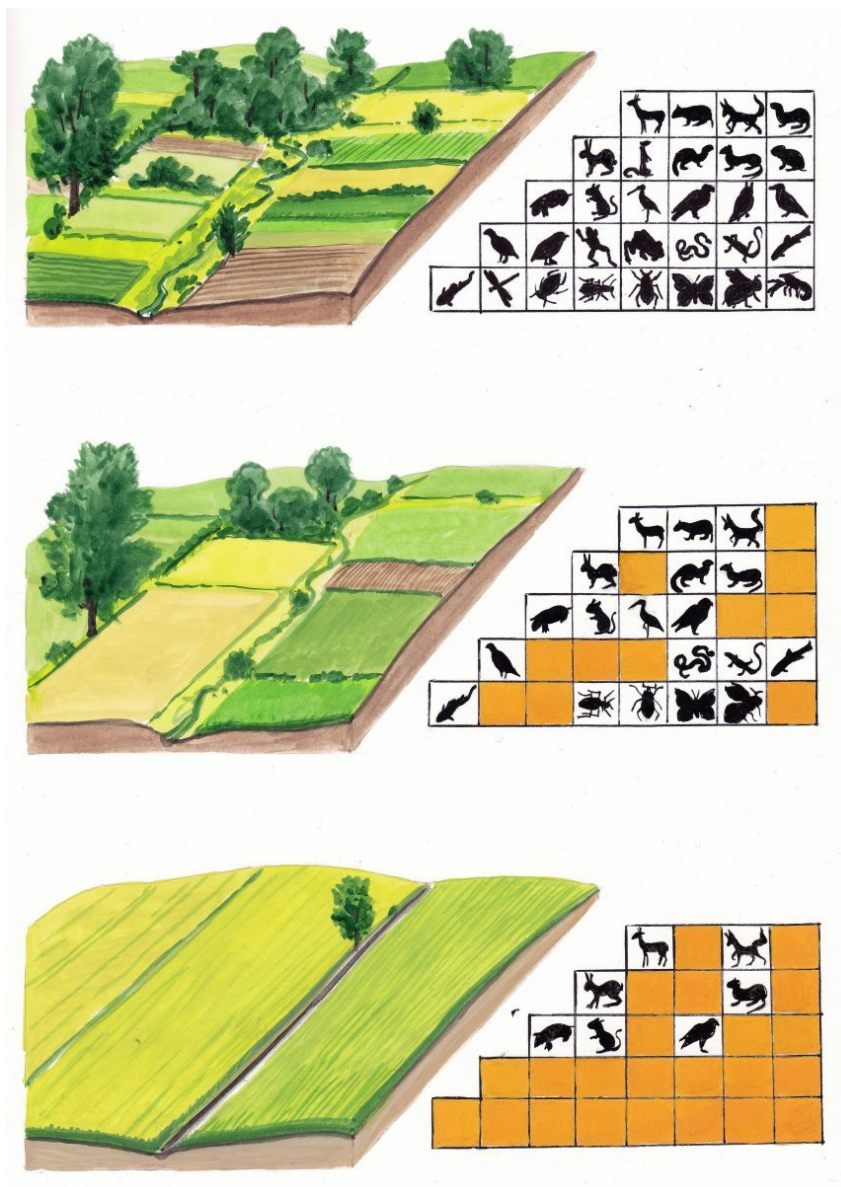


Figure 6.8: Habitat heterogeneity in agricultural landscapes benefits biodiversity, trophic interactions, and associated NCP. Adapted from Tscharntke *et al.* (2007).

Conservation measures and de-intensification of land use foster the recovery of wildlife. The recent comeback of several top predators and a number of other species in Europe has been explained by 1) land use change (*e.g.* agricultural abandonment for large carnivores) [55] and 2) conservation measures (particularly for birds). A recent report [56] reviewed the recovering trends (in population sizes, and geographic range) for 50 species (25 birds, 24 mammals, 1 reptile) that have bounced back from critical status in the past 50 years, thanks to the legal protection of

Discussion

species, the banning of harmful pesticides, and habitat protection. For example, legal protection from shooting and persecution and the ban of organochlorine pesticides have enabled the recovery of several bird species over the last few decades, such as the osprey (*Pandion haliaetus*) whose populations have increased by 45% between 1992 and 2019) and the white-tailed eagle (*Haliaeetus albicilla*), whose populations have increased by 445% between 1970 and 2018). All 25 bird species included in the report were able to recover thanks to the legal protection of these species, through the Birds and Habitats Directives, which forbids their killing and/or taking in the wild. The second most important driver of recovery was the protection of sites and habitats. Among mammals, grey wolves had hit a low point in the 1970 when only small and fragmented populations remained in the South and North-East of Europe, following decades of persecution. Since then, legislation and land abandonment in mountains has enabled the number of the grey wolves in Europe to rise by 1,800% (the current European population is estimated at 17,000), and the species has naturally recolonized former parts of its geographic range. The Eurasian beaver, historically hunted for its fur, meat and castoreum oil, has increased its range by 835% since 1955, thanks to legal protection and species reintroductions.

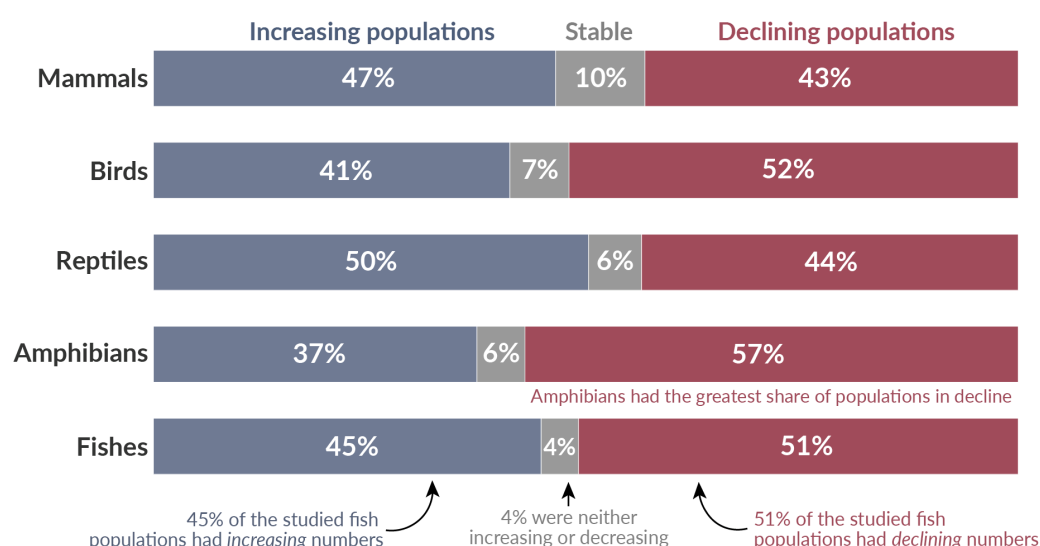


Figure 6.9: The percentage of surveyed populations in different taxonomic groups with increasing, stable, or declining trends in abundance. Source: 2022 Living Planet Index Report (WWF) (c) Hannah Ritchie, OurWorldInData.org

However, these recent recoveries follow centuries of decline, and we cannot simply assume that the recovering trends will just continue. For example, Dalmatian pelicans were recovering - but the construction of a new airport on a key wetland habitat in Albania may compromise their future. Furthermore, many species are still declining and threatened by sustained anthropogenic pressures (Chapter 3). The recent Living Planet Index reported a 69% average decline in wildlife population abundances since 1970 - even though almost half the surveyed populations are increasing (Figure 6.9). Understanding the drivers of the recovery of species, and why others are still declining, may help guide future conservation efforts to set more species on the path to recovery.

Take home messages

Species interactions underpin the persistence of all life on Earth (including human life). Yet, due to a lack of data at large spatial and taxonomic scales, species interactions had typically not been considered in biodiversity models and scenarios, in threat assessments, or in conservation applications. Fortunately, large-scale interaction datasets, such as the European metaweb of terrestrial vertebrates, are becoming increasingly available. As such, interaction networks open new perspectives for fundamental biogeography and applied conservation problems.

From a fundamental perspective, combined with species distributions, known interactions between species (*e.g.* through a metaweb) improve our understanding of the structure and functioning of communities in space but also in time. From an applied perspective, food web information can help quantify the vulnerability or resilience of ecosystems to various degrees of environmental changes. Certain food web components (*e.g.* trophic groups) are more threatened than others to major anthropogenic threats. This thesis shows that species interaction networks should be more widely considered to better understand and anticipate the structural and functional consequences of perturbations, at different levels of aggregation (species, interactions, trophic groups, whole network). For better outcomes, future work should include a more representative set of taxa (*e.g.* invertebrates, plants, soil organisms).

A holistic and comprehensive approach can lead to better outcomes for biodiversity and for multiple values of nature in general. To design an effective protected area network, it is essential to include as much (good-quality) biodiversity information as is available for the region of interest. There is evidence that accounting for interaction networks would benefit conservation, in particular to designate new protected areas. Several approaches are possible, but we need strong collaborations between disciplines (*i.e.* quantitative ecology, conservation science, social and political science) to evaluate their efficiency and their feasibility *in situ*. Applying this new paradigm in conservation actions on-the-ground is likely to be a difficult but rewarding challenge.

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“Aucune entité n’est vivante par elle-même si ce n’était pour les interactions entre ces entités.”

Jean-Claude Ameisen. *Sur les épaules de Darwin.*

“We are part of the world. We are part of one another. We are part of life which is all interconnected.”

David Attenborough (2020)

We have around us an infinite source of wonder: life, extraordinarily diverse, complex, abundant, resilient and yet fragile. Life on Earth appeared and evolved through historical contingencies. In fact, human life may have not existed at all! This urges us to realise how lucky we are to be alive, for a short moment, on this planet. Modern western civilisations have tended to take the gifts of nature for granted. Water, trees, food, a stable climate. Now, we are seeing that the greedy and limitless exploitation of finite resources in the last century has compromised the possibility of future generations of Earth’s inhabitants to thrive. The fragility of life is frightening - but it is also an invitation to not take anything for granted; and to contemplate, appreciate, preserve our environment, and nurture our bonds with one another. I would like to express my gratitude to all the people who sustained, nurtured, and helped me grow during this PhD journey.

Completing a PhD is a journey that is marked by a series of challenges. There are the scientific and technical challenges, which I have discussed extensively in this thesis. Then there are personal and global challenges that arise independently of the science, but that affect the scientist all the same. In the background of this thesis, multiple crises have reminded me of the fragility of life - a global pandemic, the brutality of war in Europe, droughts, heatwaves and megafires. In the last three years, I was also reminded of the fragility of life by the sudden loss of my dear grandfather; and, in other ways, by the choices made by my mother and father. I could not have faced any of these challenges alone. I am forever indebted to a rich support network of colleagues, family, and friends.

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I am incredibly fortunate to have had the support of a wonderful community of colleagues and friends throughout my PhD. I would like to thank my dear colleagues Camille, Irene, Giovanni, Pierre, Sarah, Billur, Xavier, Christophe, Emmanuel, Marie, Marc, Julien, and Maya. I am lucky that my work environment was made up of such brilliant, inspiring, caring, fun, and beautiful humans. I have deep gratitude for the bonds we created that now extend beyond work, and that I hope we will continue to nurture for a long time. I am also grateful to the flatmates with whom I shared a home during the past three years - Camille, Irene, Micha, Valentin, Nate, Cassandre, Matthieu, Tobias, Layla, Jeanne, Jacques - for their patience, understanding, and for all the great fun and great food we shared together. The team of injured climbers - Camicha, Amber & Nate, Los Jomos, Johan & Anca, Line, the climbing cats, and Jakes - thank you for showing me that conquering my fear of heights can be rewarding. To Rosalind, thank you for your presence and your poetry, which have comforted my soul when I needed it the most. To Alice, Chloé, Tatouille, Coco, Thomas, Riri, Titi, Anto, and Yasmine, thank you for always being there, despite the distance between us.

I am fortunate to have an incredibly supportive family: I thank my brother, sister, mother, grandparents, aunts, uncles and cousins for their unconditional love and kindness. They have been a constant source of inspiration and strength.

Finally, I would like to express my deepest gratitude to Jakes, my beloved partner, on my PhD journey. Thank you for your constant support, patience, and understanding throughout this journey. You have been a constant source of comfort, love, and encouragement, and I cannot imagine having gone through this without you. Thank you for being my rock, my sunshine, and for giving me the energy to blossom and develop with confidence. Your presence in my life is a true gift.

Appendix A

Supplementary Materials for Chapter

1

SUPPLEMENTARY MATERIAL

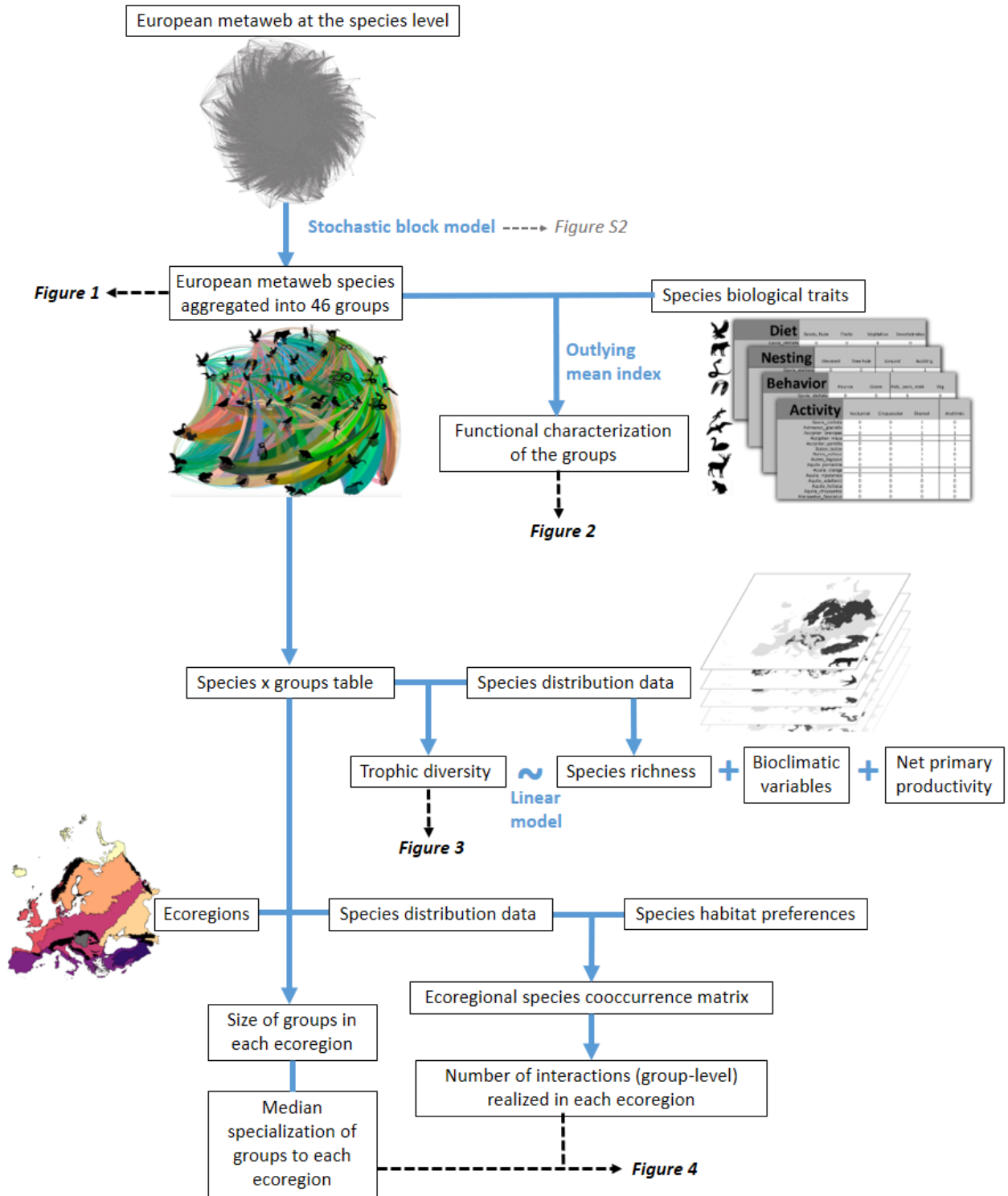
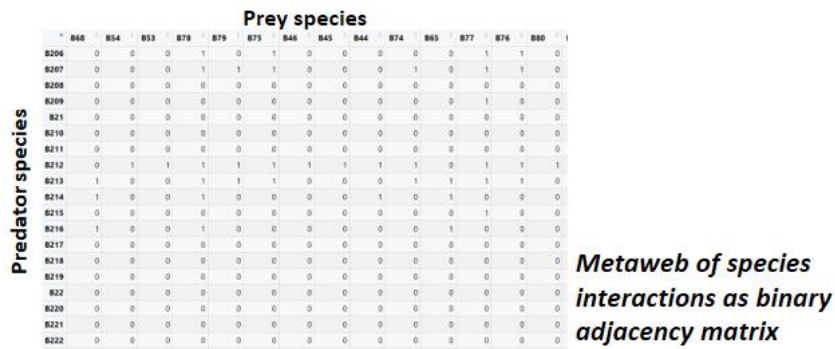


Figure S1 - Overview of the workflow, depicting how the different pieces of data (e.g. metaweb of trophic interactions, species biological traits, species distributions) come together to build and characterize the trophic groups, and then using them to analyse the structure and function of the metaweb across Europe.



1. For a given number of classes, the stochastic block model partitions the adjacency matrix into « blocks » of homogenous interaction probability



2. To select the optimal number of classes, the network is partitioned along a range of number of classes. The optimal number of classes is given by the highest ICL value.

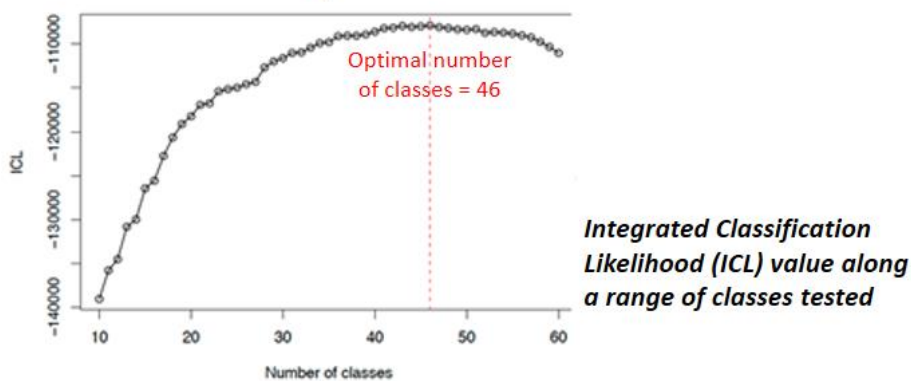


Figure S2 - Optimal partitioning of the metaweb by the stochastic block model. Given an adjacency matrix representing interactions between predator species (rows) and their prey (columns), the stochastic block model reorganized the adjacency matrix to group species into Q classes, such that each class has a given probability of interacting with all other classes. Upper panel: adjacency matrix of trophic interactions between species. Middle panel: reorganized adjacency matrix of the metaweb, where species (in rows and columns) are grouped within the 46 trophic groups (classes). Lower panel: Integrated classification likelihood information criterion as a function of the number of groups (or classes) that the stochastic block model built from the metaweb of potential trophic interactions between tetrapod species, exploring a range of partitionings of the metaweb along a range of 10 to 60 groups (or classes). The optimum partitioning of the metaweb maximises the Integrated Classification Likelihood and is highlighted with a vertical red line on the graph.

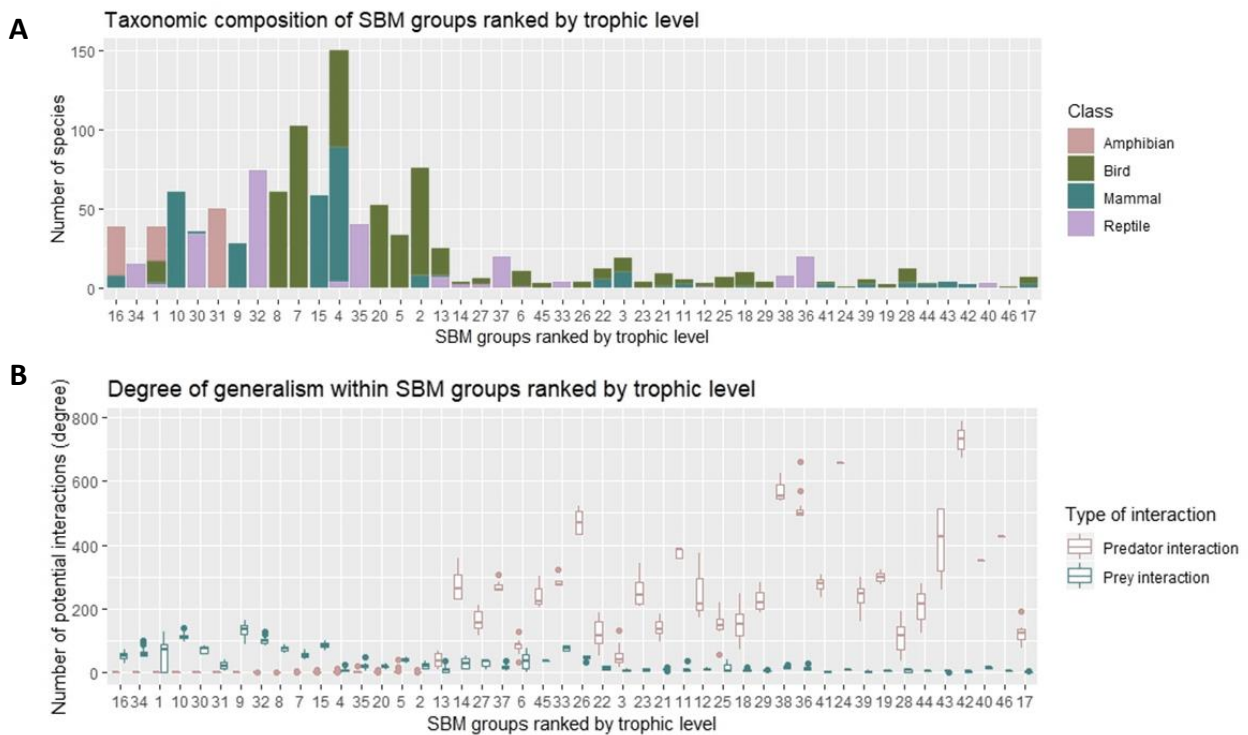


Figure S3 - Taxonomy and generalism of species within the trophic groups.

A. Trophic group composition in terms of species taxonomy. Colours represent the class of species. Trophic groups are on the x-axis, ranked from left (basal prey groups) to right (top predator groups) according to the average trophic level of species in the groups.

B. Boxplots representing the in-degree (i.e. number of predator interactions, in red) and out-degree (i.e. number of prey interactions, in blue) of species within the groups. Trophic groups are on the x axis, ranked from left (basal prey groups) to right (top predator groups) according to the average trophic level of species in the groups.

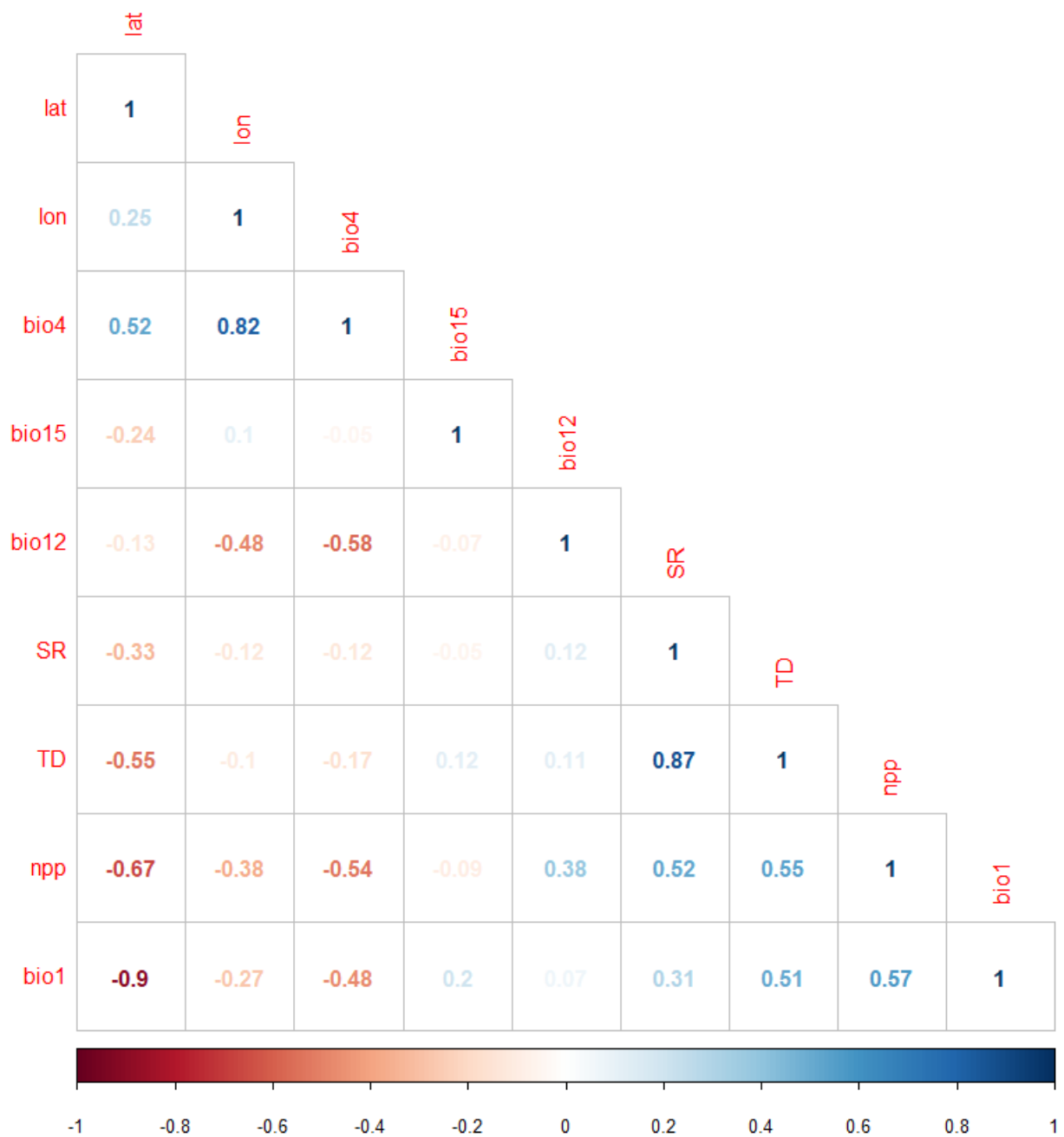
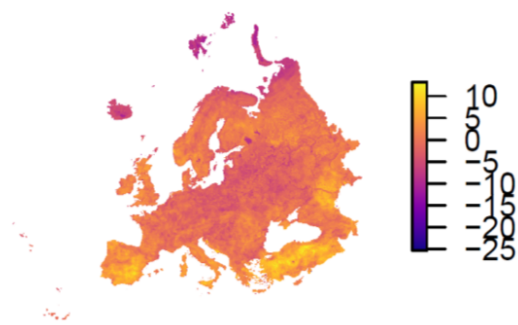


Figure S4 - Pairwise correlations between environmental variables. Lat: latitude, Lon: longitude, Bio1: annual mean temperature, Bio4: temperature seasonality (standard deviation *100), Bio12: annual precipitation, Bio15: Precipitation Seasonality (Coefficient of Variation), npp: net primary productivity, TD: trophic diversity, SR: species richness.

**Residuals of model
including species richness only**



$\text{lm}(\text{TD} \sim \text{SR01}, \text{data} = \text{scaled_EU_all})$

Residuals of full model



$\text{lm}(\text{TD} \sim \text{SR01} * \text{bio1} * \text{bio4} * \text{bio4_2} * \text{npp}, \text{data} = \text{scaled_EU_all})$

Figure S5 - Maps of the residuals of the linear models across the study area. Left panel: residuals of the model including species richness only as explanatory variable (AIC = 583,964.8). Right panel: residuals of the model including species richness and environmental variables (annual mean temperature (bio1), a quadratic relationship with temperature seasonality (bio4), net primary productivity (npp)) (AIC = 491,404).

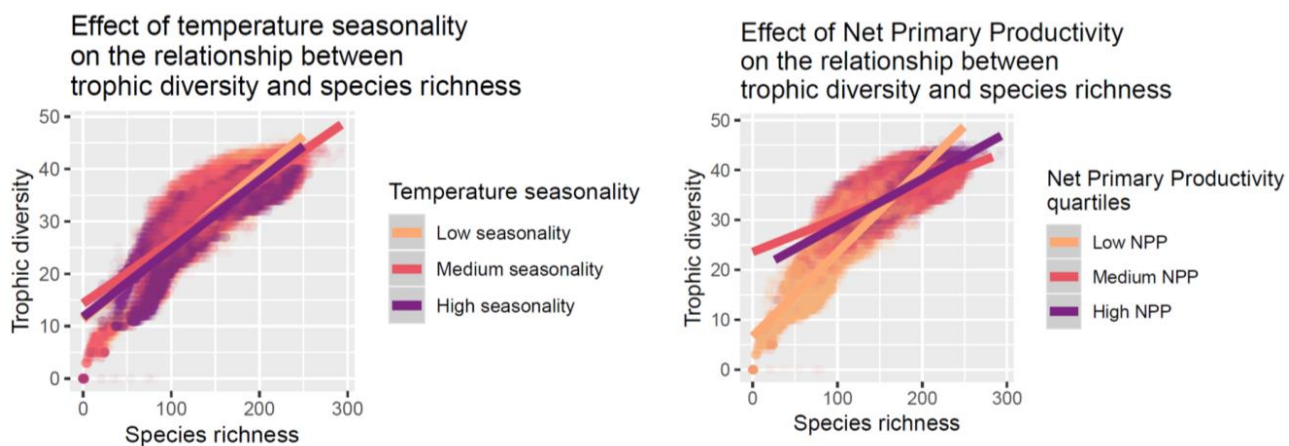


Figure S6 - Interaction plot between environmental variables (left: temperature seasonality; right: net primary productivity) and species richness in driving trophic diversity. These figures show a scatterplot of trophic diversity as a function of species richness, overlaid with the interaction plot between each environmental variable and species richness, using predictions from the linear model. The three categories represent the 1st, 2nd (median) and 3rd quartiles for each environmental variable. The lines representing the predictions and the data points in the scatterplot are coloured accordingly to these three categories.

	Estimate	Std. Error	t-value	Pr(> t)
Intercept	-26.463	1.142	-23.166	<2 e-16
SR01	196.814	4.917	40.024	<2 e-16
bio1	41.819	1.702	24.573	<2 e-16
bio4	151.157	9.2	16.429	<2 e-16
(bio4) ²	-302.267	21.1	14.325	<2 e-16
npp	32.261	8.471	3.808	0.0001
SR:bio1	-212.111	7.412	-28.616	<2 e-16
SR:bio4	-979.823	31.933	-30.684	<2 e-16
SR:npp	-314.654	18.999	-16.562	<2 e-16

Table S1. Output of the linear model testing the effects of (standardized) environmental variables (Bio1, Bio4, NPP), species richness (SR) and their interactions on trophic diversity (the number of trophic groups in any given pixel). Resolution used = 10 x 10 km pixels.

Appendix B

Studying the biogeography of interaction networks

Biodiversity is increasingly viewed as a multifaceted concept: it is the variety of life forms in terms of species (species diversity), evolutionary history (phylogenetic diversity), in terms of behaviour and life history (functional diversity). Trophic interactions are an emerging component of biodiversity which can bring additional insight in biogeography. While functional and phylogenetic diversity are now widely used biodiversity facets in biogeography and spatial conservation, we have a poor understanding of the way food web structure varies across space. In Chapter 1, I characterised the trophic role of species and investigated the variation of food web diversity across space.

In a study published in *Current Biology* led by Pierre Gaüzère, we investigated whether studying the spatial variation of interaction diversity provided additional insight to functional and phylogenetic diversity. Results showed that interaction diversity is not correlated to phylogenetic and functional diversity. Interestingly, the combination of the three diversity metrics led to biodiversity patterns that closely matched the European bioregions.

Work by Marc Ohlmann on developing diversity indices for interaction networks led to a publication in *Ecology Letters*, for which I prepared the figures and contributed to writing the manuscript. This framework for interaction network diversity indices holds promise for quantifying the spatial and temporal turnover of food web structure and functioning at different levels of aggregation (from species, to trophic groups, to the entire network), and is relevant for conservation applications (see Chapter 5).

In a study led by Christophe Botella, recently submitted to *Ecology Letters*, we investigated how land use intensity (in different land systems, and different bioregions) affect food web structure. Results suggested that high levels of land use intensity tended to have a negative impact on top predators and basal species, with more connected food webs in general in high intensity levels of land use.

These three papers are included in the following pages.

Report

The diversity of biotic interactions complements functional and phylogenetic facets of biodiversity

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SUMMARY

Taxonomic, functional, and phylogenetic diversities are important facets of biodiversity. Studying them together has improved our understanding of community dynamics, ecosystem functioning, and conservation values.^{1–3} In contrast to species, traits, and phylogenies, the diversity of biotic interactions has so far been largely ignored as a biodiversity facet in large-scale studies. This neglect represents a crucial shortfall because biotic interactions shape community dynamics, drive important aspects of ecosystem functioning,^{4–7} provide services to humans, and have intrinsic conservation value.^{8,9} Hence, the diversity of interactions can provide crucial and unique information with respect to other diversity facets. Here, we leveraged large datasets of trophic interactions, functional traits, phylogenies, and spatial distributions of >1,000 terrestrial vertebrate species across Europe at a 10-km resolution. We computed the diversity of interactions (interaction diversity [ID]) in addition to functional diversity (FD) and phylogenetic diversity (PD). After controlling for species richness, surplus and deficits of ID were neither correlated with FD nor with PD, thus representing unique and complementary information to the commonly studied facets of diversity. A three-dimensional mapping allowed for visualizing different combinations of ID-FD-PD simultaneously. Interestingly, the spatial distribution of these diversity combinations closely matched the boundaries between 10 European biogeographic regions and revealed new interaction-rich areas in the European Boreal region and interaction-poor areas in Central Europe. Our study demonstrates that the diversity of interactions adds new and ecologically relevant information to multifaceted, large-scale diversity studies with implications for understanding eco-evolutionary processes and informing conservation planning.

RESULTS AND DISCUSSION

Biodiversity—the diversity of life on Earth—was originally used to refer to species diversity, but it is now used to reflect a multifaceted concept.³ Given the evidence that species diversity alone cannot appropriately describe community assembly, ecosystem functioning, and variation in community composition,¹⁰ several complementary measures of biodiversity have emerged in the last three decades.^{1,2} The most important measure is the diversity of species' evolutionary histories (i.e., phylogenetic diversity [PD]) and their ecological functions (i.e., functional diversity [FD]), but while PD and FD are becoming central to many studies,^{11,12} the diversity of biotic interactions (i.e., interaction diversity [ID]) has been poorly considered as a biodiversity facet in large-scale studies (but see Thompson et al.⁸ and Dyer

et al.¹³). This is a major gap since biological interactions are tightly linked to species coexistence,¹⁴ ecosystem productivity, and functioning.^{4–7}

In its simplest form, ID is the total number of interactions shared by all species of a given assemblage.⁹ Interactions considered can be of different types and nature, for example, antagonistic (competition for resources), mutualistic (pollination^{15,16}), or trophic (predation¹⁷). Although the concept of ID is not novel^{8,13} and has its own methodological tools,^{18,19} the lack of information available on biotic interactions^{20,21} has limited its study across large taxonomical and spatial scales.^{22–26} Here, we leveraged unique and valuable data combining spatial distributions²⁷ (Figure 1A), trophic interactions (Figure 1B), functional traits,²⁸ and phylogenies²⁹ of most terrestrial vertebrate species in Europe³⁰ at a 10-km resolution.

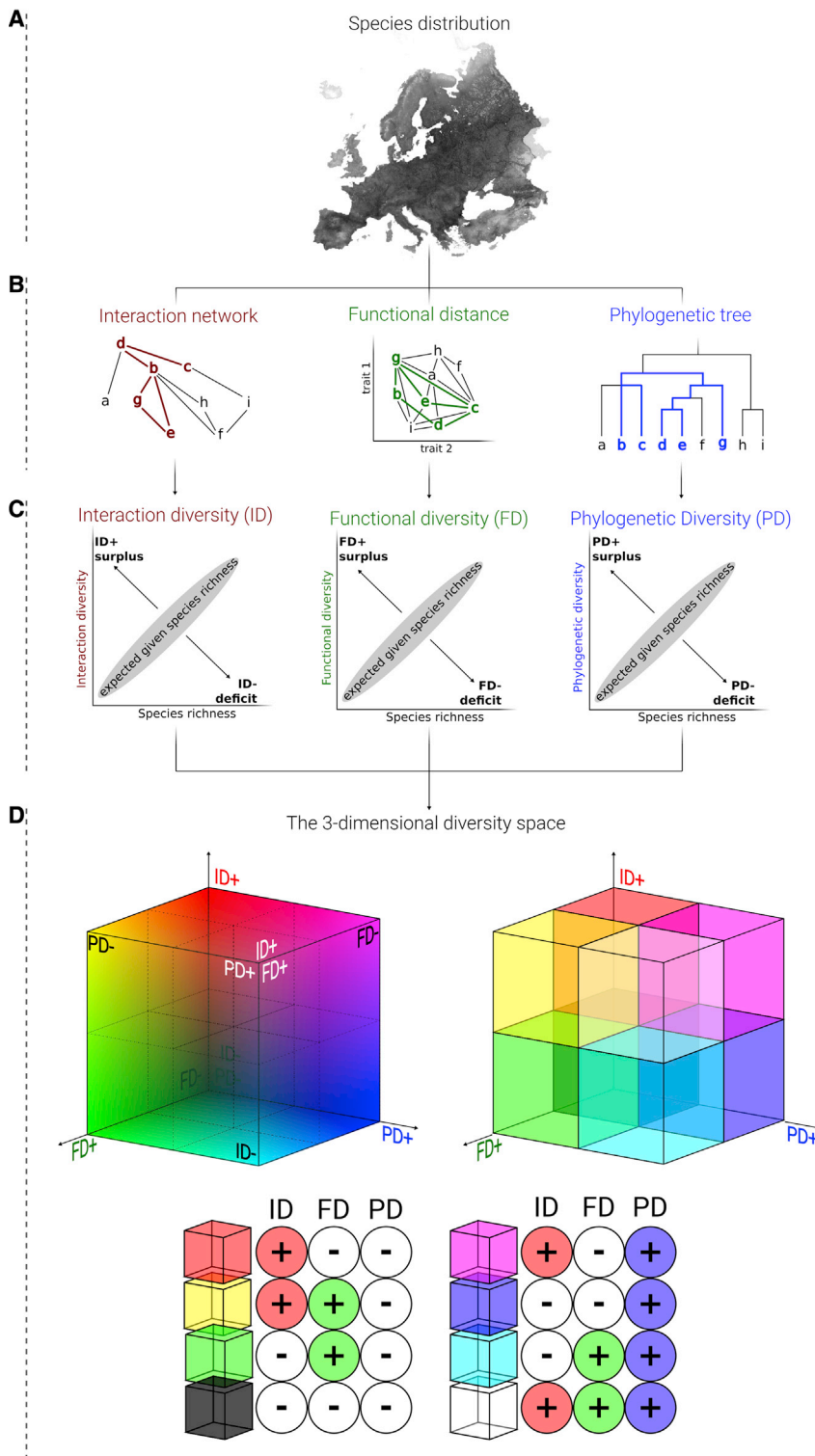


Figure 1. Conceptual workflow for a joint analysis of phylogenetic, functional, and interaction diversity (ID)

(A and B) Occurrences and probability of presence for 1,149 terrestrial vertebrate species on 117,000 10 × 10 km cells across Europe (A) are combined with the phylogenetic tree, a set of functional traits, and the trophic interactions of species (B).

(C) We combined species distribution with phylogenetic, functional, and trophic species attributes to compute local terrestrial vertebrate diversities using Hill numbers ($q = 0$, i.e., “richness”) and statistically corrected the diversity values by the local species richness. Note that the expected relationships (gray ellipses) are not necessarily linear.

(D) We projected the diversity values in a three-dimensional space with each axis representing a diversity facet and a color in the red-blue-green space ($x = PD/blue$, $y = FD/green$, and $z = ID/red$) and discretized particular types of combinations based on surplus and deficits of each diversity. Red identifies surpluses of ID and FD associated with deficits in FD and PD ($ID > 0$, $FD < 0$, and $PD < 0$); yellow identifies surpluses of ID and FD associated with deficits in PD ($ID > 0$, $FD > 0$, and $PD < 0$); green identifies deficits in ID and PD associated with FD surpluses ($ID < 0$, $FD > 0$, and $PD < 0$); black identifies deficits in ID, PD, and FD; pink identifies surpluses of ID and PD associated with FD deficits; dark blue identifies surpluses of PD associated with ID and FD deficits; light blue identifies surpluses of PD and FD associated with ID deficits; white identifies surpluses in ID, PD, and FD.

richness^{32,33} to measure and map deficits and surpluses of ID, FD, and PD (Figure 1C). We also investigated the correlation and complementarity between the three facets and created a three-dimensional diversity space that reveals different local combinations of ID-FD-PD (Figure 1D) and their distribution across biogeographical regions in Europe.

Surpluses and deficits of diversities

Trophic networks of terrestrial vertebrates found within 10-km cells in Europe contained up to 4,834 trophic interactions with an average of 1,958 interactions across cells (Figure 2A). Once corrected for species richness, ID ranged from a deficit of -942 interactions (1,667 observed interactions with 202 species involved) to a surplus of +968 interactions (3,730 interactions with 210 species involved). Because highly connected assemblages are often considered as the signature of functional and resilient ecosystems,^{34,35} areas with high ID are important from a conservation point of view.^{34,36} Furthermore, comparing spatial distributions of surplus and deficit IDs with those of FD or PD can complement our understanding of community dynamics and underlying processes. Because phylogenetic

Within each 10-km cell, we computed ID (as the number of trophic interactions), FD (as the sum of functional pairwise Gower distances between species in the cell), and PD (as the sum of the branch lengths of the phylogenetic tree containing all species present in the cell¹) using Hill numbers.^{18,31} We statistically corrected each diversity by the local species

richness^{32,33} to measure and map deficits and surpluses of ID, FD, and PD (Figure 1C). We also investigated the correlation and complementarity between the three facets and created a three-dimensional diversity space that reveals different local combinations of ID-FD-PD (Figure 1D) and their distribution across biogeographical regions in Europe.

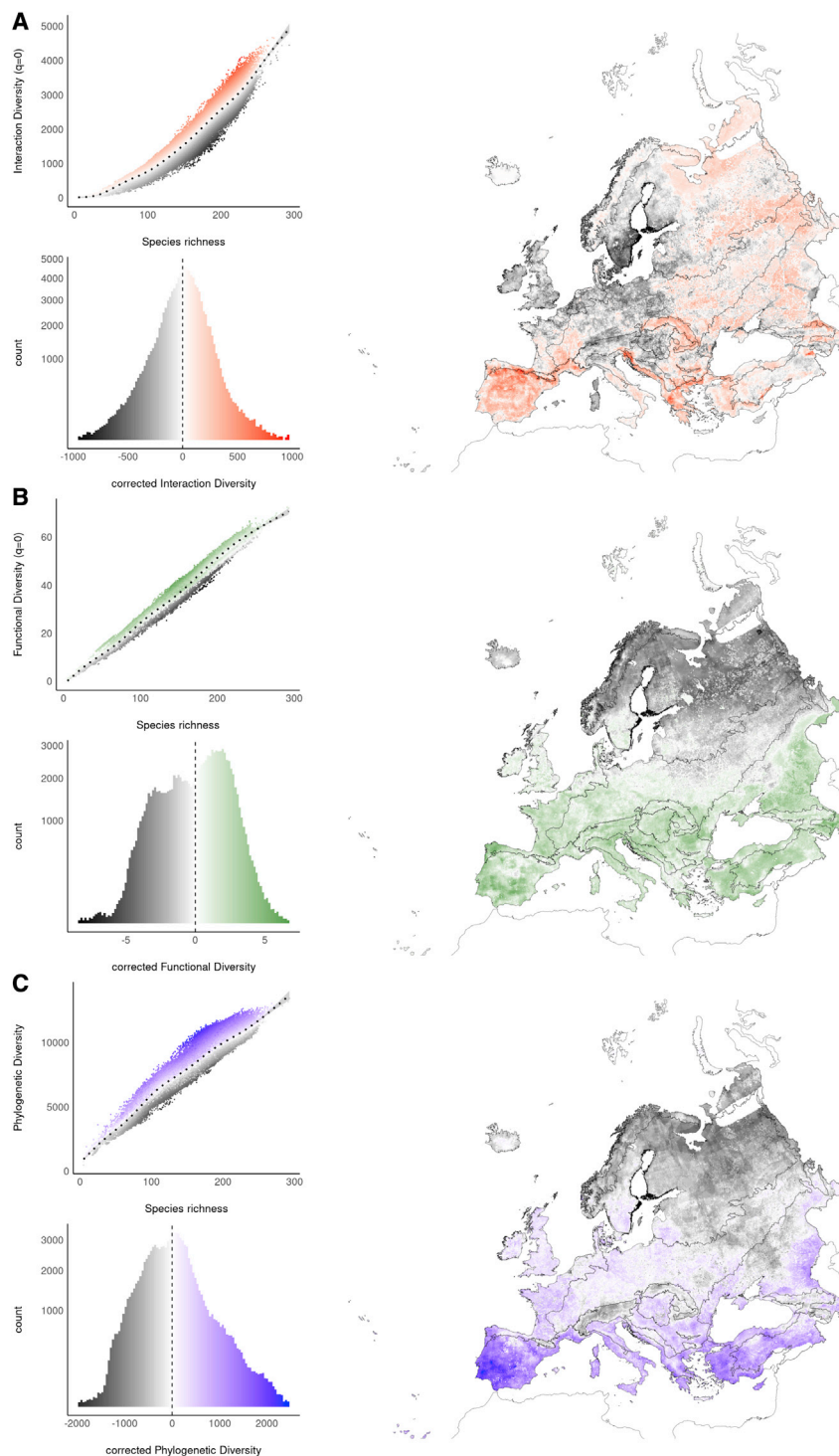


Figure 2. Patterns of diversity facets

(A) Interaction diversity (ID), in red.
(B) Functional diversity (FD), in green.
(C) Phylogenetic diversity (PD), in blue.

Top left: relationship between each diversity facet and the species richness. Dotted lines show relationships as fitted by generalized additive models. Bottom left: distribution of deficits and surpluses of diversities, where model residuals correspond to “corrected diversity” values with deficits (dark shades) and surpluses (red for ID, green for FD, and blue for PD). Right: spatial distribution of corrected values for each biodiversity facet color corresponds to distributions on the left. See also [Figures S1–S3](#).

locally viable traits or hierarchical competition where a given set of traits is the best adapted locally.⁴⁰ PD surplus ([Figures 1D](#) and [2C](#), dark blue color) could result from slow extinction rates of old and distant lineages (i.e., museums of biodiversity⁴¹) and PD deficit from rapid recent speciation (i.e., cradles of biodiversity). ID surplus and deficit bring additional information, as observed ID surplus ([Figures 1D](#) and [2A](#), red color) indicates particularly dense or long trophic networks, such as those emerging from high levels of omnivory and intraguild predation⁴² or from bottom-up control when large amounts of basal resources sustain longer trophic chains and the presence of top predators. ID deficits can result from weakened top-down control when top predators are absent from local assemblages, for example, following human-induced removal.^{43–45}

Overall, the different facets of diversity are shaped by eco-evolutionary drivers that are not mutually exclusive.⁴⁶ Any combination of ID-FD-PD could potentially exist locally and bring complementary information to the others, although one can expect the facets of diversity to be (partly) correlated when similar drivers influence multiple diversity facets. We showed that FD and PD were clearly and positively correlated ([Figure 3B](#)). This correlation is due to the fact that species tend to retain their ancestral traits through evolution^{38,47–49} and suggests an important effect of evolution and phylogenetic niche conservatism on biodiversity patterns.^{47,50,51} While one could expect ID to be related to FD (because of the link between trait similarity and competition for resources) or PD (because biotic interactions can drive the (co)evolutionary history of the species^{46,52}), this was not what we observed ([Figures 3C](#) and [3D](#)). Instead, ID represented unique and complementary information to the commonly studied facets of diversity.

and trait data contain information about evolutionary history and species niches, the spatial distribution of their diversity ([Figures 2B](#) and [2C](#)) is thought to hold the signature of the eco-evolutionary drivers that shape biodiversity patterns.^{37–39} For example, for a given species richness, an observed surplus of FD ([Figures 1D](#) and [2B](#), green color) could result from competitive exclusion between species with similar traits, while a deficit of FD might result from environmental filtering constraining the range of

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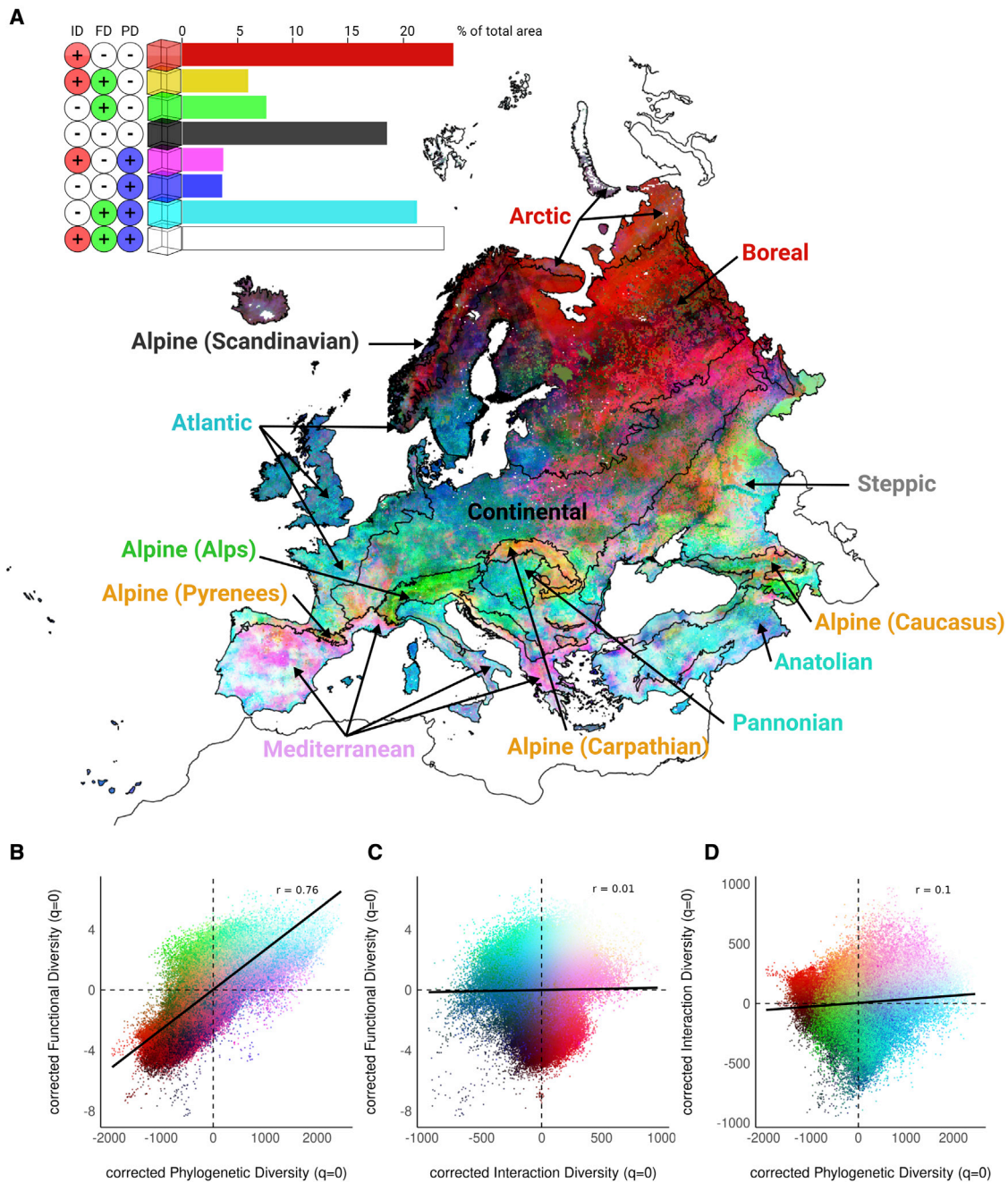


Figure 3. The combinations of diversities in the three-dimensional diversity space

(A) Geographic projection of the three-dimensional diversity space. In the top left barplot, we created eight discrete categories based on the combinations of deficits (–) and surpluses (+) of each diversity and reported the number of cells falling in each category. In the map, points are colored by their location in the red-green-blue three-dimensional color space, with each diversity facet corresponding to a distinct channel: red channel, ID; green channel, FD; blue channel, PD. Black shows lowest ID-FD-PD values, white shows highest ID-FD-PD, and so on for each combination. Black lines show the boundaries of the European biogeographical regions.

(B) Pair plot of corrected FD (y axis) versus corrected PD (x axis).

(C) Corrected FD (y axis) versus corrected ID (x axis).

(D) Corrected ID (y axis) versus corrected PD (x axis). In top right, r is the value of Pearson's product-moment correlation between y and x axes. Points' colors correspond to colors in the map.

Distribution of diversity combinations

To investigate the congruence among the interaction, functional, and phylogenetic facets of biodiversity, we created a three-dimensional space where each dimension represents one diversity facet. We further attributed a color channel for each diversity facet (red, ID; green, FD; blue, PD) to visualize all possible combinations of biodiversity facets (Figure 1D). Each combination of three color channels (red, blue, and green) resulted in a particular color in the RGB (red green blue) color space that corresponds to a given combination of three diversity facets and allowed us to identify a continuum of ID-FD-PD combinations (Figure 1D). We also interpreted particular types of combinations by discretizing colors based on the combinations of surplus and deficits of each diversity facet (Figure 1D).

This joint analysis of diversity facets highlighted various local combinations of ID-FD-PD, with all kinds of combinations being observed in different proportions (Figure 3A). The most commonly observed combinations were ID surpluses with FD and PD deficits (covering 21.8% of the total study area); surpluses in ID, FD, and PD (white, 21.6%); surpluses of FD and PD with deficits in ID (light blue 19.6%); and deficits in ID, FD, and PD (black, 17.3%), which is consistent with the positive correlation observed between FD and PD (Figure 3B). The spatial structure of diversity combinations aligned well with many boundaries of European biogeographical regions (Figure 3A), a striking spatial congruency considering that the identification and delimitation of bioregions are based on the geographic distribution of vegetation types.⁵³ Beyond species distribution, biodiversity facets such as PD already have been shown to match some ecological regions across the globe.⁵⁴ ID strongly varies between different regions (e.g., between the Mediterranean region and the Alps or between the Continental region and the Carpathian mountains) and thus further refines boundaries between them. These results suggest that species interactions (along with species co-occurrences and phylogeny) could have a strong structuring effect on (bio)regional species pools. Such a question, however, would require a deeper analysis based on the turnover of interactions within and between regions as regional diversity is connected to local diversity by the turnover in composition between locations. Interestingly, the mapping of diversity combinations also revealed the specificity of several sub-regions within their biogeographical region, for example, the Balkan peninsula subregion in the Mediterranean region or the Carpathian mountains in the Alpine region. These results further highlight that biotic ID adds new and independent information and that a dense network of trophic interactions can occur in areas of poor functional and PD.

Southern Europe showed strong diversity surpluses in all diversity facets (white/light color shades in Figure 3A), which confirms the Mediterranean bioregion as a multifaceted biodiversity hotspot.^{55,56} This result shows that, for a given number of species, local assemblages of Mediterranean terrestrial vertebrate species were particularly rich in terms of ecological strategies, contained long evolutionary history, and had particularly dense trophic networks. In the Mediterranean basin, the warm climate and the geographical proximity with Africa and Asia explain the high diversity of amphibians and reptiles, as well as the presence of unique evolutionary lineages, leading to high

functional and phylogenetic diversities compared with the rest of Europe. In addition to these high levels of functional and phylogenetic diversities, the Mediterranean region showed surpluses in ID, in particular in the subregion of the Balkan peninsula. The densely connected trophic networks observed in the Mediterranean region resulted from (1) numerous top predators in this region previously identified as birds, felids, and snakes preying upon small reptiles and rodents²² and (2) to a lesser extent from a high degree of omnivory in the Iberian peninsula.²³

Conversely, the northernmost areas tended to show low levels of diversities (black areas in North of Scandinavia and Iceland; Figure 3A). The Boreal and Arctic bioregions showed deficits in functional and phylogenetic diversities but tended to sustain surpluses in ID (red areas; Figure 3A). In these regions, FD deficits were likely to be driven by the cold climate constraining the range of functional traits that can be found in these regions and similarly for PD via trait conservatism. In particular, the fact that cold temperature limits the presence of ectotherms (amphibians and reptiles) in high latitudes reduces functional and phylogenetic diversities, in line with the expected effect of environmental filtering on these diversity facets.^{37,38} The consideration of ID brings additional and complementary information since FD-PD deficits are associated with ID surpluses in Northern Europe. The presence of ID surpluses in the Boreal and Arctic bioregions likely resulted from a high degree of omnivory,²³ which is known to increase trophic network connectance.^{26,57} Species that live under high latitudes tend to be trophic generalists²³ because the higher seasonality in high latitudes promotes the evolution of larger niche breadth, in accordance with the latitude-niche breadth hypothesis.^{57,58}

Within the Alpine bioregion, different mountain ranges displayed contrasting diversity combinations. The marked differentiation between the Alps and the Carpathian mountains subregions is a striking example supporting the consideration of ID in biodiversity studies and conservation biogeography. These two mountain ranges located in Central Europe are part of the same Alpine bioregion, which partly explains their similarity in terms of functional surpluses and phylogenetic deficits (Figures 2B and 2C). Based on functional and phylogenetic diversities alone, these two mountain ranges would be considered as similarly diverse, but they are markedly different in terms of ID. The Carpathians displayed a clear ID surplus (Figure 3, yellow), while the Alps displayed ID deficit (Figure 3, green). The proximate cause of such difference was the rarity of top predators in the Alps compared with the Carpathians (see maps of relevant network properties in supplemental information). Human influence likely explains this discrepancy because many apex predators (bears, wolves, and lynx) that are often trophic generalists are still present in the Carpathians, while they were exterminated in the Alps.⁵⁹

Potential drivers of diversity facets

While environmental filtering is likely to drive the decrease of FD and PD observed in high latitudes, ID might be more influenced by human activities than climate. As such, local deficits of trophic interactions appeared as a marker of high human impact across Europe. This is in line with the negative correlation between connectance and human influence previously reported for the

same study system²³ and suggests that the diversity of interactions is influenced by different drivers than functional and PD. It is, however, noteworthy that other studies reported higher connectance in more human-impacted systems.^{9,46} Indeed, the human-induced relative increase of generalist intermediate predators could counterbalance the decrease in ID due to the loss of a few top predators. The human influence on large-scale diversity has been considered and studied in terms of phylogeny and traits.⁶⁰ However, its consequences on large-scale patterns of ID have been largely overlooked although they are probably stronger. Indeed, human activities have been (and still are) particularly detrimental to large-bodied species.^{60–63} While this observation is generally viewed as a trait-induced consequence (humans are more detrimental to larger animals), it might also be a trophic-induced consequence (humans are more detrimental to apex and generalist predators).^{45,64}

The importance of ID

A clear understanding of the impact of human activities on ID has yet to emerge. More generally, ID is likely to be highly context and taxa dependent, and the understanding of its multi-scale drivers represents a research agenda for the years to come. Among others, the Eltonian shortfall is one big challenge that currently limits the description of ID in many parts of the world where information on biotic interactions is lacking.²¹ Here, we overcame this challenge for trophic interactions by inferring local interactions from species distributions and their known potential trophic interactions from the literature and expert knowledge (as commonly done; see, e.g., Poisot et al.¹⁹ and Gravel et al.²⁵). While this approach overestimates interactions at a given time, “realized” and “potential” number of interactions are very likely to converge in the long term. On the contrary, a field sampling approach would underestimate the realized ID. This underestimation can be quite severe and a massive sampling effort is required to detect most interactions.⁶⁵ Combining both approaches (inferring interactions from a metanetwork and species distribution versus observing interactions) and comparing their accuracy across a range of temporal and spatial scales will provide valuable insights in community ecology and biogeography.⁶⁶

Although ID patterns appear robust to spatial contexts (Figure S1) and data depletion (Figure S2), whether the patterns described in this study can be extrapolated to other biomes remain an open question. For example, our conclusions from European terrestrial vertebrates might not hold true for tropical rainforests, which shelter many trophic specialist species with narrow ecological niches (but comprehensive data on traits and interactions are lacking). Nonetheless, we argue that ID is a particularly valuable facet for biogeography and conservation planning. Although this view has been empirically challenged,³⁶ more densely connected trophic networks are generally considered as desirable from a conservation point of view.⁹ Areas with surpluses of interactions represent interaction networks that are expected to be more robust to cascading species extinctions³⁴ and consequently more resilient to perturbations. Coupled with its apparent sensitivity to human activities,²³ ID might be viewed as a marker of both ecosystem degradation and resistance to future degradation. We argue that a general consideration of ID as an important and meaningful diversity facet alongside the functional and

phylogenetic diversities should be a priority for macroecology and conservation biogeography.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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 - Materials availability
 - Data and code availability
- METHOD DETAILS
 - Study area and data
- QUANTIFICATION AND STATISTICAL ANALYSIS
 - Diversity measures and corrections
 - Building 3-dimensional diversity space

SUPPLEMENTAL INFORMATION

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AUTHOR CONTRIBUTIONS

P.G. and W.T. conceived the study, with early advice from L.O.C., C.B., G.P., and T.M. P.G. performed all analyses and wrote the first version of the manuscript with input from W.T., L.O.C., C.B., G.P., and T.M. All authors contributed substantially to the interpretation of the results and to the writing of the manuscripts and its revisions.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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METHOD

Diversity indices for ecological networks: a unifying framework using Hill numbers

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Abstract

Describing how ecological interactions change over space and time and how they are shaped by environmental conditions is crucial to understand and predict ecosystem trajectories. However, it requires having an appropriate framework to measure network diversity locally, regionally and between samples (α -, γ - and β -diversity). Here, we propose a unifying framework that builds on Hill numbers and accounts both for the probabilistic nature of biotic interactions and the abundances of species or groups. We emphasise the importance of analysing network diversity across different species aggregation levels (e.g. from species to trophic groups) to get a better understanding of network structure. We illustrate our framework with a simulation experiment and an empirical analysis using a global food-web database. We discuss further usages of the framework and show how it responds to recent calls on comparing ecological networks and analysing their variation across environmental gradients and time.

Keywords

Hill numbers, interaction network diversity, Metanetwork, species aggregation level.

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INTRODUCTION

Since the pioneering work of Humboldt (von Humboldt 1805), understanding the patterns of biodiversity across space and time has been a question central to both biogeography and community ecology (Gaston 2003). The recent upsurge of large-scale databases has made possible to produce comprehensive syntheses of biodiversity patterns (Belmaker *et al.* 2012; Mazel *et al.* 2017) by analysing local assemblages on the one hand (α -diversity, Hawkins *et al.* 2003). and composition turnover between such assemblages on the other (β -diversity, Mazel *et al.* 2017). A plethora of diversity indices and unifying frameworks have thus been proposed to partition biodiversity into α - and β -diversity components (Whittaker 1960; Routledge 1979; Ellison 2010; Chao *et al.* 2014b; Chao & Chiu 2016). However, not only does biodiversity reflect species coexistence but also the trophic and non-trophic interactions that link them to one another (Kéfi *et al.* 2016). The development of the trophic theory of island biogeography (Gravel *et al.* 2011; Massol *et al.* 2017) has recently paved the way for a new biogeography synthesis by accounting for trophic interactions in theoretical predictions of biodiversity patterns. Similarly, empiricists do not only investigate species distribution patterns but also analyse how ecological interactions (i.e. ecological networks) vary over space and time (Pellissier *et al.* 2017; Tylanakis & Morris 2017). To this aim, the *metanetwork* concept generalises the regional species-pool of classic community ecology by adding to this representation of biodiversity the potential trophic and non-trophic interactions

between species (Dunne 2006; Kéfi *et al.* 2016) at a regional scale. Thus, in the same way local assemblages are conceptualised as subsets of a regional species pool, local ecological networks are realisations of a subset of the regional metanetwork. This opens new perspectives in understanding the processes that shape the distribution of biodiversity in space and time. For instance, mapping, describing and comparing ecological networks along environmental or disturbance gradients are the first steps of a fascinating era to understand the organisation of life on Earth (Pellissier *et al.* 2017) and its effects on ecosystem functioning and associated services (Brose & Hillebrand 2016). The realisation, the frequency and the intensity of interactions within networks across space and time are driven by the compositional turnover of species or groups of species, changes in their abundances, their plasticity or behavioural variations, and finally by the environmental constraints on biotic interactions. Any of these variations may have direct or indirect consequences on ecosystem functioning (Barnes *et al.* 2014). Such knowledge would thus help not only to improve our understanding of multi-trophic assemblages and their influence on ecosystem functioning but also to help build a more robust predictive ecology at the interface between trophic ecology, community ecology and ecosystem ecology (Thompson *et al.* 2012).

There is thus a strong need to develop a framework to understand the structure and composition of ecological networks across spatial and temporal scales and along environmental gradients (Pellissier *et al.* 2017). To date, such a framework remains hampered by several issues.

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First, no appropriate diversity measure is available to describe the diversity of ecological networks, and partition it into α , β and γ components, that would account for both species abundances and the probabilistic nature of interactions, and that would relate to existing frameworks in biogeography or community ecology (Pellissier *et al.* 2017). Recent years have seen a prolific development of frameworks to measure diversity at both the taxonomic (Jost 2007; Ellison 2010; Chao & Chiu 2016) and phylogenetic or trait levels (Chao *et al.* 2014a; Tucker *et al.* 2016). These indices need to satisfy four mathematical properties (see Jost 2010): (1) α and β should be mathematically unrelated; (2) α , β and γ should be effective numbers (this enables to interpret a given measure of diversity in terms of the diversity of an evenly distributed community and therefore guarantees the comparability of diversity measures); (3) γ should be completely determined by α and β ; (4) α cannot be larger than γ . A fifth additional practical property of β -diversity, *invariance under shattering* (Reeve *et al.* 2014) assumes that each community represents a portion of the geographical space. This assumption implies that if a community is split into two and the abundances of the two resulting communities are equal, then the β -diversity of the overall metacommunity should not change. The framework recently proposed by Reeve *et al.* (2014) satisfies each of these fundamental properties (only when similarities between species are not considered) while Jost's framework satisfies the first four properties, and the fifth only for some particular cases. These indices are based on Hill numbers (Hill 1973), which are derived from Rényi's entropy (Rényi 1961) and have enabled a generalisation of the well-established diversity measures such as the Shannon entropy or the Simpson diversity index. An additional and interesting feature of Hill numbers is the introduction of a *viewpoint parameter* linked to the weight given to dominant vs. rare species onto assembly rules (Chalmandrier *et al.* 2015). While this framework could potentially be very useful for ecological networks, it is not yet applicable. So far, the few network-specific metrics are built on graph theory, with the aim to summarise the structure of a network through a single quantity (Poisot *et al.* 2012, 2016; Pellissier *et al.* 2017) – but none of them satisfy the five requirements listed above, nor are they able to manipulate species abundances or the probability of a given interaction occurring.

Second, diversity metrics depend on the way individuals are aggregated into larger groups (e.g. species, guilds, functional groups). In trophic networks, species can be aggregated based on their equivalent roles. Indeed, species richness or taxonomic turnover do not reveal much on how assemblages are truly structured in terms of resource exploitation, niche partitioning and co-existence mechanisms (Thompson *et al.* 2012), whereas functional or trophic groups enable to encapsulate more of the underlying ecological processes. In this respect, insights from graph theory (Luczkovich *et al.* 2003) and random models of networks (Group model, Allesina & Pascual 2009 or stochastic block model, Newman & Leicht 2007) have helped to mathematically formalise equivalence relationships between species using the topology of the ecological network alone. However, aggregating species in trophic or functional groups is often challenging (e.g. choosing an optimal number of groups) and there is no way of knowing whether a given grouping will provide a better

understanding of the diversity pattern than others. To address this issue, we believe it is necessary to describe and analyze patterns at different levels of species aggregation, as is now done in community phylogenetic analyses (Chalmandrier *et al.* 2015; Graham *et al.* 2018). In fact, analyses of ecological networks diversity (α , β , γ) should be carried out along a profile of species aggregation levels, ranging from characterising all species (their abundances, the abundance of their links and their probability of interactions, hereafter named the *microscopic scale*), to various species aggregation levels (hereafter coined the *mesoscopic scale*) until the *macroscopic scale*, represented by the single value of connectance (the probability of interaction between any two species). This multi-scale approach should provide novel insights to understand the processes that shape ecological networks. To overcome these limitations, we introduce a novel framework that allows measuring α , β , and γ diversities of ecological networks and combines Hill numbers (Hill 1973; Jost 2006; Chao & Chiu 2016) with different species aggregation levels. First, we build on the existing mathematical frameworks to derive new indices for ecological network diversity, which we partition into α , β , and γ components. We then demonstrate that existing network diversity indices (Bersier *et al.* 2002; Poisot *et al.* 2012, 2016) are particular cases of the proposed unified framework. We further extend our framework so it can be used across multiple levels of species aggregation. We then apply this framework to an intercontinental data set of stream water trophic networks (Thompson & Townsend 2003) and show that the drivers of the dissimilarity of ecological networks vary with the level of species aggregation. We finally provide an implementation of the framework in the R package *econetwork* available on CRAN (<https://cran.r-project.org>), guidelines for the interpretation of the results, and recommendations for the analyses of networks across space and time.

DIVERSITY FOR A SINGLE NETWORK

For the sake of simplicity, we first introduce the formalism behind our new indices with a single trophic network. We then generalise the framework to the case of a metanetwork, and provide the details and mathematical proofs in the Supporting Information.

A probabilistic model of interaction networks

We propose a generic model of ecological networks that considers both species abundances and the probabilities of interaction between species. It is an extension of the probabilistic network model (Poisot *et al.* 2016) with the additional property that it accounts for species abundances.

We consider a given region that contains individuals belonging to n different species with relative abundances $p = (p_1, \dots, p_n)$. p_q represents the probability of picking an individual of species q . We also assume that the probability of interaction between two individuals of species q and l follows a Bernoulli law of parameter π_{ql} . This allows to account for the potential variability on the realisation of an interaction event at the individual level (Albert *et al.* 2010; Gonzalez-Varo & Traveset 2016). We also assume that all interactions occur independently. We represent this regional model using a

weighted network G , with p_q the relative abundance of the node V_q , and π_{ql} the weight of the link (V_q, V_l) ($\mathbf{\Pi}$ is the adjacency matrix of G , see Table 1). The probability of picking a link that connects two individuals of species q and l is thus:

$$L_{ql} = \Pr(i \rightarrow j, i \in q, j \in l) \tag{1}$$

$$L_{ql} = \pi_{ql} p_q p_l \tag{2}$$

where

$$\pi_{ql} = \Pr(i \rightarrow j | i \in q, j \in l) \tag{3}$$

If this model represents the most complete case of a single network (abundances on nodes and weights on links), simpler cases can easily be derived by omitting the weights on links (i.e. for binary networks, π_{ql} is either 0 or 1) or the abundances of nodes (i.e. assuming evenly distributed species abundances).

Navigating across species aggregation levels

We initially described the probabilistic network model at a species level. However, species can have similar positions, roles (e.g. Eltonian niche, Elton 1927) or functions (Lindeman 1942; Lavorel & Garnier 2002; Luck *et al.* 2012), leading to inflated or deflated estimates with respect to functional diversity. It is thus crucial to represent and analyze the diversity of ecological networks at different aggregation levels, by grouping species into larger and more relevant entities. Here, we propose to use mathematical methods that group nodes using the topology of the ecological network without any prior knowledge (see Supporting Information for a brief review of these methods).

Assuming that we have established Q groups (C_1, \dots, C_Q) from the previous network ($Q \leq n$), we can represent the network at a coarser resolution (Fig. 1, mesoscopic scale), called the image network (Luczkovich *et al.* 2003; Allesina & Pascual 2009). The new set of nodes is $\tilde{V} = (\tilde{V}_1, \dots, \tilde{V}_Q)$ and each node is assigned a weight \tilde{p}_q that corresponds to the abundance of the group q .

$$\tilde{p}_q = \sum_{k \in C_q} p_k \tag{4}$$

Similarly, each link of the image network is assigned a weight $\tilde{\pi}_{ql}$ that corresponds to the probability of interaction between individuals from classes C_q and C_l .

$$\tilde{\pi}_{ql} = \frac{\sum_{k \in C_q, k' \in C_l} \pi_{kk'} p_k p_{k'}}{\sum_{k \in C_q} p_k \sum_{k' \in C_l} p_{k'}} \tag{5}$$

The link abundances between individuals of classes q and l , \tilde{L}_{ql} thus equates to:

$$\tilde{L}_{ql} = \sum_{k \in C_q, k' \in C_l} \pi_{kk'} p_k p_{k'} \tag{6}$$

We thus define the scale of the image network considered as:

$$s = \frac{Q}{n} \tag{7}$$

If $s = 1$, the network is considered at a microscopic scale (the image network corresponds to the original one). If $s = \frac{1}{n}$, the network is considered at a macroscopic scale. In this case, the image network is then made of a single node (with

Table 1 Notations, name of the different indices and ranges of values

Object	Name	Total margin
\mathbf{p}	Vector of relative group abundances	$\sum_{1 \leq q \leq Q} p_q = 1$
\mathbf{L}	Matrix of link abundances	$\sum_{1 \leq q, l \leq Q} L_{ql} = C$
$\mathbf{\Pi}$	Matrix of link probabilities (adjacency matrix of the weighted network)	$\sum_{1 \leq q, l \leq Q} \pi_{ql}$
\mathbf{P}	Matrix of group abundances of groups (metanetwork case)	$\sum_{q=1}^Q \sum_{k=1}^K P_{qk} = K$
\mathbf{L}	Tensor of links abundances (metanetwork case)	$\sum_{q,l=1}^Q \sum_{k=1}^K L_{qlk} = \sum_{k=1}^K C_k$
$\mathbf{\Pi}$	Tensor of link probabilities (metanetwork case)	$\sum_{q,l=1}^Q \sum_{k=1}^K \pi_{qlk}$

	Diversity index	Name & interpretation	Range
α -diversity	A_p^n	Overall α -diversity in group abundances	
		Average diversity in group abundances across local networks	$1 \leq A_p^n \leq Q$
	A_L^n	Overall α -diversity in link abundances	
		Average diversity in link abundances across local networks	$1 \leq A_L^n \leq N_L$
γ -diversity	A_{Π}^n	Overall α -diversity in link probabilities	
		Average diversity in link probabilities across local network	$1 \leq A_{\Pi}^n \leq N_L$
	G_p^n	γ -diversity in group abundances	
		Diversity in group abundances of the metanetwork	$1 \leq G_p^n \leq Q$
β -diversity	G_L^n	γ -diversity in link abundances	
		Diversity in link abundances of the metanetwork	$1 \leq G_L^n \leq N_L$
	G_{Π}^n	γ -diversity in link probabilities	
		Diversity in link probabilities of the metanetwork	$1 \leq G_{\Pi}^n \leq N_L$
β -diversity	B_p^n	β -diversity of group abundances	
		Effective numbers of distinct communities of groups	$1 \leq B_p^n \leq K$
	B_L^n	β -diversity of link abundances	
		Effective numbers of distinct networks	$1 \leq B_L^n \leq K$
β -diversity	B_{Π}^n	β -diversity of link probabilities	
		Effective numbers of distinct networks (with abundances rescaled at evenly distributed values)	$1 \leq B_{\Pi}^n \leq K$
	δ_p^n	Dissimilarity of group abundances	
		Effective average proportion of shared groups	$0 \leq \delta_p^n \leq 1$
dissimilarity	δ_L^n	Dissimilarity of link abundances	
		Effective average proportion of shared links	$0 \leq \delta_L^n \leq 1$
	δ_{Π}^n	Dissimilarity of link probabilities	
	Effective average proportion of shared links (with abundances rescaled at evenly distributed values)	$0 \leq \delta_{\Pi}^n \leq 1$	

Notes. C is the connectance of the considered network, Q is the number of groups of the considered metanetwork and N_L its number of different links and C_k is the connectance of the local network k .

abundance 1, the sum of species relative abundances) and a single link. The weight of this link represents the probability that any two nodes of the original networks are connected and is, consequently, the connectance of the original network.

$$C = \sum_{1 \leq q, l \leq n} \pi_{ql} p_q p_l \quad (8)$$

If $\frac{1}{n} < s < 1$, the network is considered at a mesoscopic scale.

Measuring diversity at different species aggregation levels

For a community vector $\mathbf{p} = (p_1, \dots, p_Q)$, the Hill number of order η is defined as:

$$D^\eta(\mathbf{p}) = \left(\sum_{i=1}^Q p_i^\eta \right)^{\frac{1}{1-\eta}}, \eta \geq 0, \eta \neq 1 \quad (9)$$

This number ranges between 1 and Q (Table 1), and translates into an effective number of groups (which can be species or group of species i.e., we define diversity indices on the image network while keeping the notations of the original one for the sake of simplicity). A Hill measure of Δ hence means that the system holds a diversity equivalent to a system made of Δ equally distributed groups. η is considered as a viewpoint parameter that modulates the weight given to group abundances. When $\eta = 0$, all groups equally contribute to the

index and D^0 is the richness of groups. For $\eta = 1$, eqn 8 is not defined but it converges towards the exponential of the Shannon entropy :

$$D^1(\mathbf{p}) = \lim_{\eta \rightarrow 1} D^\eta(\mathbf{p}) = \exp\left(\sum_{i=1}^Q -p_i \log p_i \right) \quad (10)$$

We propose to extend the use of Hill numbers to compute the diversity in link abundances and the diversity in link probabilities between groups. More precisely, we measure the entropy of the random variable associated to the experience: ‘A link is drawn uniformly in the network, what is the label of this link (the label is defined by the identity of the two groups that are connected by the link)’. Assuming that \mathbf{L} is the matrix of link abundances, the diversity in link abundances is:

$$D^\eta(\mathbf{L}) = \left(\sum_{1 \leq q, l \leq Q} \left(\frac{L_{ql}}{C} \right)^\eta \right)^{\frac{1}{1-\eta}} \quad (11)$$

where $C = \sum_{1 \leq q, l \leq Q} L_{ql}$. Similarly, assuming that $\mathbf{\Pi}$ is the adjacency matrix of the image graph, the diversity in link probabilities is defined as:

$$D^\eta(\mathbf{\Pi}) = \left(\sum_{1 \leq q, l \leq Q} \left(\frac{\pi_{ql}}{\pi_{++}} \right)^\eta \right)^{\frac{1}{1-\eta}} \quad (12)$$

where $\pi_{++} = \sum_{1 \leq q, l \leq Q} \pi_{ql}$.

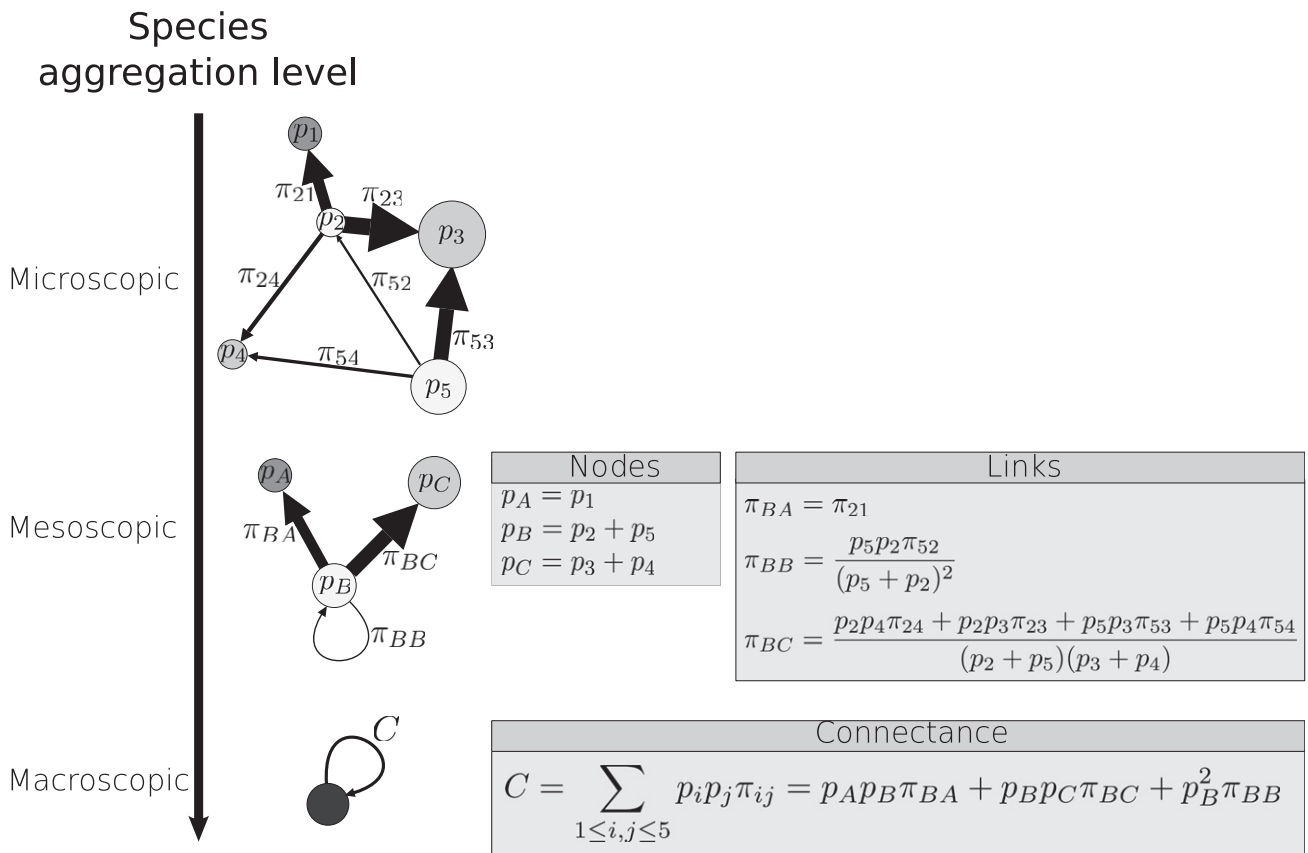


Figure 1 Navigating through species aggregation levels. From the original weighted network to image networks at mesoscopic and macroscopic scales, with the formulas giving the group abundances and link probabilities of the image networks.

$D^\eta(\mathbf{\Pi})$ is unrelated to $D^\eta(\mathbf{p})$ (*sensu* Chao & Chiu 2016), since the value of one of this measure does not constrain the value of the other. When $\eta = 0$, it measures the number of links of the image network. When $\eta \rightarrow 1$, it converges towards the exponential of the Shannon entropy of the probability of links (Bersier *et al.* 2002)

Both group abundances and the interaction probabilities determine the range of values of $D^\eta(\mathbf{L})$ which are therefore related. These last two indices translate into an effective numbers of links, either weighted ($D^\eta(\mathbf{L})$) or not ($D^\eta(\mathbf{\Pi})$) by the group abundances. Note that ($D^\eta(\mathbf{\Pi})$) could be used in studies where groups have different relative abundances, but these are not important in the analysis.

DIVERSITY FOR A METANETWORK

Measuring α -, β - and γ -diversity at different species aggregation levels

Mirroring the single network case, we propose to analyze the diversity of the metanetwork and its local realisations through different species aggregation levels. Importantly, we assume that any grouping is defined on the metanetwork. We thus define α -, β - and γ -diversity measures on the set of local networks and on the metanetwork at different species aggregation levels. We measure the diversity of group abundances, link abundances and link probabilities using Hill numbers. We extend the framework presented in Chao & Chiu 2016 since it satisfies the first four properties listed in the introduction and elegantly link the variance and decomposition perspective on β -diversity (see Chao & Chiu 2016 for details). For the sake of simplicity, we present the case $\eta \rightarrow 1$ (and therefore omit the exponent in the indices). The general case is presented in Supporting Information, together with our framework as an extension of Jost’s and Reeve’s framework and the mathematical links between the existing network diversity indices and the proposed unified framework. The proposed indices can be applied in several subcases (Fig. 2). We use the same probabilistic network model as presented before. The metanetwork is thus a weighted network, divided in K local networks (see Table 1 for notations and total margins).

α -diversity

For each local network, the α diversity is computed using Hill numbers (for $\eta \rightarrow 1$, it converges towards Shannon entropy). The overall α -diversity of groups across local networks is:

$$A_P = \exp\left(\sum_{q=1}^Q \sum_{k=1}^K -\frac{P_{qk}}{P_{++}} \log\left(\frac{P_{qk}}{P_{++}}\right) - \log(K)\right) \tag{13}$$

where $P_{++} = \sum_{1 \leq k \leq K} \sum_{1 \leq q \leq Q} P_{qk}$.

This is the mean equivalent number of groups across local networks. Similarly, the overall α -diversities in link abundances and link probabilities are equal to:

$$A_L = \exp\left(\sum_{q,l=1}^Q \sum_{k=1}^K -\frac{L_{qlk}}{L_{+++}} \log\left(\frac{L_{qlk}}{L_{+++}}\right) - \log(K)\right) \tag{14}$$

where $L_{+++} = \sum_{1 \leq k \leq K} \sum_{1 \leq q,l \leq Q} L_{qlk}$.

$$A_\Pi = \exp\left(\sum_{q,l=1}^Q \sum_{k=1}^K -\frac{\pi_{qlk}}{\pi_{+++}} \log\left(\frac{\pi_{qlk}}{\pi_{+++}}\right) - \log(K)\right) \tag{15}$$

where $\Pi_{+++} = \sum_{1 \leq k \leq K} \sum_{1 \leq q,l \leq Q} \pi_{qlk}$.

γ -diversity

The γ -diversity of group abundances is defined as:

$$G_P = \exp\left(\sum_{q=1}^Q -\frac{P_{q+}}{P_{++}} \log\left(\frac{P_{q+}}{P_{++}}\right)\right) \tag{16}$$

where $P_{q+} = \sum_{1 \leq k \leq K} P_{qk}$. This corresponds to the equivalent number of groups in the metanetwork. The γ -diversity of the link abundances is defined as:

$$G_L = \exp\left(\sum_{q,l=1}^Q -\frac{L_{ql+}}{L_{+++}} \log\left(\frac{L_{ql+}}{L_{+++}}\right)\right) \tag{17}$$

where $L_{ql+} = \sum_{1 \leq k \leq K} L_{qlk}$.

This corresponds to the equivalent number of links in the metanetwork. The γ -diversity in link probabilities is defined as:

$$G_\Pi = \exp\left(\sum_{q,l=1}^Q -\frac{\pi_{ql+}}{\pi_{+++}} \log\left(\frac{\pi_{ql+}}{\pi_{+++}}\right)\right) \tag{18}$$

where $\Pi_{ql+} = \sum_{1 \leq k \leq K} \pi_{qlk}$. This corresponds to the equivalent number of links in a network that contains the same probabilities of links as in the metanetwork, but where the relative abundances of groups are arbitrarily considered evenly distributed.

β -diversity and dissimilarity measures

The overall β -diversity can be calculated in group abundances, link abundances and link probabilities. The β -diversity in groups abundance is equal to:

$$B_P = \frac{G_P}{A_P} \tag{19}$$

This is the effective number of equally large and completely distinct communities of groups. It represents how many completely distinct communities of groups are present in the set of networks. The β -diversity in link abundances is equal to:

$$B_L = \frac{G_L}{A_L} \tag{20}$$

This is the effective number of equally large and completely distinct networks i.e., the number of networks made of distinct links across the considered region. The β -diversity in link probabilities is equal to:

$$B_\Pi = \frac{G_\Pi}{A_\Pi} \tag{21}$$

This translates to an effective number of equally large and completely distinct networks where group abundances would have arbitrarily been considered equal.

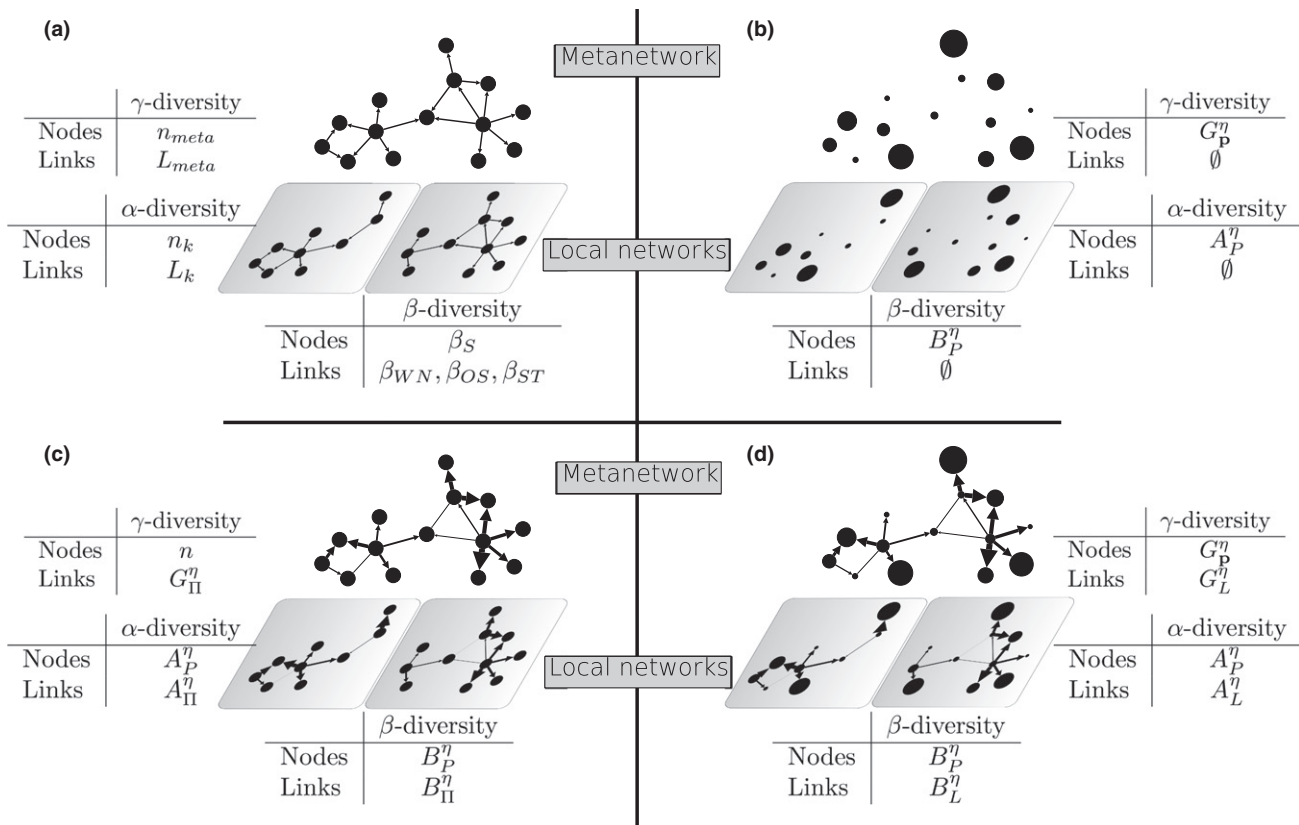


Figure 2 The metanetwork and the local realised networks in different cases: (a) binary network, unweighted links and without node abundances, (b) node abundances but absence of links, (c) weights on links but no node abundances and (d) weights and links and node abundances. The different indices to measure α -, β - and γ -diversity are associated to each particular case and presented more generally in Table 1.

Overlap measures can be built from β -diversity to obtain dissimilarity measures (Jost 2007, 2010; Chao & Chiu 2016). A class of parameterised Sorensen's based dissimilarity measures can be defined as non-linear transformation of β -diversity. When $\eta = 1$, it equals to the Horn dissimilarity index (the general case is presented in Supporting Information).

$$\delta_P = \frac{\log(G_P) - \log(A_P)}{\log K} \quad (22)$$

$$\delta_L = \frac{\log(G_L) - \log(A_L)}{\log K} \quad (23)$$

$$\delta_\Pi = \frac{\log(G_\Pi) - \log(A_\Pi)}{\log K} \quad (24)$$

These measures quantify the effective average proportion of shared groups/links/probability of links across networks and range between 0 and 1.

The framework is implemented in the R package *econetwork* available on CRAN (<https://www.cran.r-project.org>).

APPLICATION TO A CASE STUDY: WHEN THE AGGREGATION LEVEL REVERSES THE ASSESSMENT OF THE DRIVERS OF NETWORK DISSIMILARITY

Here, we re-analysed a data set used in Thompson & Townsend (2003). Using groups built *a priori* with three trophic levels, the authors concluded that stream water networks surrounded by pine or tussock grassland in New Zealand differ

in their structure at a mesoscopic level. They attributed this change of structure to differences of energy supply in the two systems. We proposed to extend this analysis to the entire dataset [ten stream water trophic networks sampled in the United States of America (USA hereafter) and New Zealand surrounded either by pines or not (Table 1)] using our novel framework together with trophic groups built using the topology of the metanetwork (Allesina & Pascual 2009; Gauzens *et al.* 2015). We hypothesised that at a species level, geographic location should have a major impact on network dissimilarity due to the different biogeographical histories of the two continents (e.g. dispersal limitation that leads to small species overlap, different life history traits due to different environmental constraints), whereas at a trophic group level, vegetation should have much more impact due to energy supply provided by the riparian vegetation (e.g. vegetation types select for certain groups of species and network structure, which is not discernible at a species level).

The data set consists of ten stream water trophic networks sampled in the USA and New Zealand (Thompson & Townsend 2003, https://www.nceas.ucsb.edu/interactionweb/resources.html#predator_preys, Fig. S1). The riparian vegetation of the American networks is a native species of pine, *Pinus strobus*. Two of the New Zealand networks are surrounded by planted pines, *Pinus radiata* (Table 2). All other networks in New Zealand are surrounded by bush and tussock. The networks contain species of algae, invertebrates and fishes. We

Table 2 The set of trophic networks and the covariates (adapted from Thompson & Townsend 2003)

Location	Site	Vegetation
Maine (USA)	Troy	<i>Pinus strobus</i>
Maine (USA)	Martins	<i>Pinus strobus</i>
North Carolina (USA)	Herlzler	<i>Pinus strobus</i>
North Carolina (USA)	Cooper	<i>Pinus strobus</i>
New Zealand	Venlaw	<i>Pinus radiata</i>
New Zealand	Berwick	<i>Pinus radiata</i>
New Zealand	North col	Native bush
New Zealand	Powder	Native bush
New Zealand	Trib C	Tussock
New Zealand	Sutton	Tussock

kept only the largest connected component of the metanetwork (Fig. S2). It contains 532 species and has a connectance value of 0.01.

To work at the mesoscale, we first determined the most relevant trophic groups using the stochastic block model implemented in the R package ‘mixer’ (Daudin *et al.* 2008). The optimal number of groups, 14, was identified using an information criterion (for simplicity we only used the optimal number of groups, but could have navigated through a wider range of aggregation levels). Therefore, the scale used to analyse the mesoscopic network dissimilarity is 14/532. We thereafter computed the dissimilarity matrices of link and group abundances at the microscopic and mesoscopic scales (using pairwise δ_L^η at two different aggregation levels) and the dissimilarity matrix of groups (using pairwise δ_p^η at two different aggregation levels) along a profile of weights attributed to

abundant groups or links by varying the values of η . We then assessed the influence of the riparian vegetation (presence/absence of pine trees) and the location (USA or New Zealand) on the four dissimilarity matrices per value of η using ANOSIM (Clarke 1993) for both covariates (location and riparian vegetation) along the range of η values. (Fig. 3).

These analyses revealed that at a microscopic scale, the pairwise dissimilarities of both group and link abundances (δ_p^η and δ_L^η) are best explained by the geographic location. At the mesoscopic scale, however, the riparian vegetation was the variable that best explains both the dissimilarity of group and link abundances for medium to high values of η ($\eta > 0.35$ for the groups dissimilarity and $\eta > 0.15$ for the links dissimilarity).

Since New Zealand and the USA have drastically different biogeographical histories, they have very few species in common (New Zealand and USA streams share, for example, almost no invertebrate species, Thompson & Townsend 2003). Consequently, the location is indeed expected to be a more powerful explanatory variable of the species dissimilarity (i.e. δ_p^η at a microscopic scale). Moreover, given that species turnover is partially responsible for the links turnover (i.e. δ_L^η at a microscopic scale), the latter is also expected to be predominantly explained by the location. Studying δ_p^η and δ_L^η at a mesoscopic scale allows to look beyond species turnover, and accounts for the role of the riparian vegetation in diversity, both for the group abundances and the link abundances. Importantly, riparian vegetation best explains group and link dissimilarities for medium to high values of η . So, the abundances of the largest trophic groups and the links between these groups are shaped by the riparian vegetation whereas

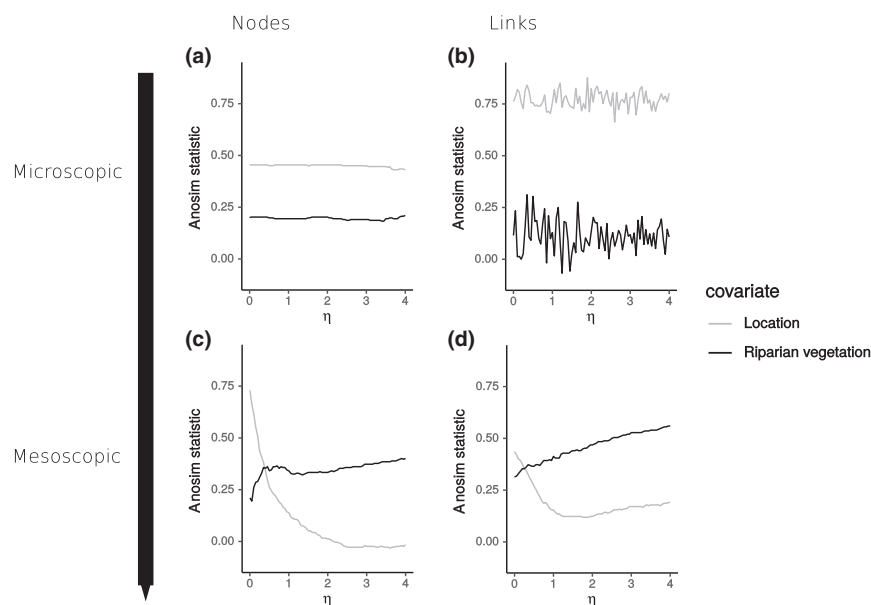


Figure 3 Assessing the drivers of dissimilarity in group abundances and link abundances at different species aggregation levels. Relative importance (ANOSIM statistic) of the location vs. the riparian vegetation regarding the (a) microscopic pairwise dissimilarity in groups abundances (δ_p^η at a microscopic scale) (b) microscopic pairwise β -diversity in link abundances (δ_L^η at a microscopic scale) (c) mesoscopic pairwise dissimilarity in group abundances (δ_p^η at a mesoscopic scale) (d) mesoscopic pairwise dissimilarity in link abundances (δ_L^η at a mesoscopic scale) across a range of η values (i.e. the viewpoint parameter controlling the weight given to entities (group abundances or link abundances) in the measure of the dissimilarity).




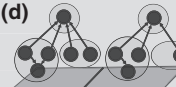
Local network		Networks in space and time										
Network aggregation	(a)  To what extent do ecological processes shape network structure?	(c)  To what extent do ecological processes shape networks across space and time at a species level?										
	Studies: Cohen <i>et al.</i> 2003 Dormann <i>et al.</i> 2017 (review)	Studies: Caradonna <i>et al.</i> 2017 Tylianakis & Morris 2017 (review)										
	Hypothesis: Traits and eco-evolutionary processes shape network structure	Hypothesis: Species composition and interactions change across space and time										
	Diversity index $C, D^n(\mathbf{p}), D^n(\mathbf{L}), D^n(\mathbf{II})$	<table border="1"> <thead> <tr> <th colspan="3">Mechanisms</th> </tr> <tr> <th>Change in species composition</th> <th>Change that alters probability of interactions</th> <th>Change in energy fluxes</th> </tr> </thead> <tbody> <tr> <td> Diversity index A_P^n, G_P^n B_P^n, δ_P^n </td> <td> A_{Π}^n, G_{Π}^n $B_{\Pi}^n, \delta_{\Pi}^n$ </td> <td> A_L^n, G_L^n B_L^n, δ_L^n </td> </tr> </tbody> </table>			Mechanisms			Change in species composition	Change that alters probability of interactions	Change in energy fluxes	Diversity index A_P^n, G_P^n B_P^n, δ_P^n	A_{Π}^n, G_{Π}^n $B_{\Pi}^n, \delta_{\Pi}^n$
Mechanisms												
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(b)  To what extent can species in a network be aggregated into groups while preserving the overall structure?	(d)  To what extent do ecological processes shape networks across space and time at a (trophic) group level?											
Studies: Allesina & Pascual 2009 Gauzens <i>et al.</i> 2015 Cirtwill <i>et al.</i> 2018 (review)	Studies: Thompson & Townsend 2003 (groups formed a priori) This study											
Hypothesis: Species that have similar traits are equivalent in terms of position in the network. Interpretation as trophic group (or trophospecies) in the case of trophic networks	Hypothesis: (Trophic) groups composition and interactions change across space and time											
Diversity index $D^n(\mathbf{p}), D^n(\mathbf{L}), D^n(\mathbf{II})$ (meso)	<table border="1"> <thead> <tr> <th colspan="3">Mechanisms</th> </tr> <tr> <th>Change in (trophic) groups composition</th> <th>Change that alters probability of interactions between groups</th> <th>Change in energy fluxes</th> </tr> </thead> <tbody> <tr> <td> Diversity index A_P^n, G_P^n (meso) B_P^n, δ_P^n (meso) </td> <td> A_{Π}^n, G_{Π}^n (meso) $B_{\Pi}^n, \delta_{\Pi}^n$ (meso) </td> <td> A_L^n, G_L^n (meso) B_L^n, δ_L^n (meso) </td> </tr> </tbody> </table>			Mechanisms			Change in (trophic) groups composition	Change that alters probability of interactions between groups	Change in energy fluxes	Diversity index A_P^n, G_P^n (meso) B_P^n, δ_P^n (meso)	A_{Π}^n, G_{Π}^n (meso) $B_{\Pi}^n, \delta_{\Pi}^n$ (meso)	A_L^n, G_L^n (meso) B_L^n, δ_L^n (meso)
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Figure 4 Reconciling two perspectives in ecological network analyses. Here, we represent the key questions, seminal studies and underlying hypotheses usually considered in studies of ecological networks, and our specific indices for investigating them. (a) Studying the structure of a local network. (b) Studying the structure of a network where species have been aggregated in meaningful groups (trophic groups in the case of trophic networks). (c) Studying how networks vary in space and time. (d) Studying how networks change in space and time at various aggregation levels (trophic groups in the case of trophic networks). (meso) means the diversity indices are computed at a mesoscopic scale.

their presence (i.e. while omitting their abundances) is explained by the location.

DISCUSSION

Diversity indices aim to describe and quantify the structure of ecological communities across space and time. There is currently a paradigm shift in the representation of a community, from a species assemblage to an interaction network (Thompson *et al.* 2012; Pellissier *et al.* 2017; Tylianakis & Morris 2017). While deciding which species belong to a community is made easier using a network representation of biodiversity (since a community is no more than a connected network), measuring and partitioning the diversity of these interaction networks is much more complex (Poisot *et al.* 2016; Pellissier *et al.* 2017). Diversity indices using Hill numbers provide a robust framework when ignoring interactions, as it gradually takes into account species abundances and satisfies theoretical properties. To be generic enough and to embrace the complexity of natural systems, these indices should take into account species abundances and the probabilistic nature of biotic interactions, while unifying the existing diversity frameworks. Moreover, they should be able to measure diversity at different species aggregation levels, so as to not inflate diversity indices or overestimate link turnover. In this paper, we defined a set of diversity indices that address each of these

requirements. The proposed framework is a generalisation of the Hill numbers to measure α -, β - and γ -diversity in link abundances and link probabilities. By doing so, we have extended the existing indices of network diversity (e.g. Poisot *et al.* 2012), while benefiting from key properties of Hill numbers. In other words, using this single framework on a single data set would enable one to not only investigate traditional relationships between species richness and energy as well as understand the compositional turnover across space, but also explore further by deciphering how variations in species abundance, probability of interactions and environmental gradients influence ecological networks.

The proposed framework is based on a probabilistic model of networks where parameters are species abundances and probabilities of interaction between species or groups of species. Consequently, it represents interactions as a random event rather than a deterministic event, thus assuming a plasticity of interactions at an individual level. While this constitutes an appealing representation from a theoretical standpoint, empirical datasets of interaction networks are often binary and lack abundance estimates. Binary networks constitute particular cases of our framework, that then connect with existing frameworks (Poisot *et al.* 2012). Our framework can also be applied to any weighted network (i.e. network containing interaction strength) even if the weights do not strictly represent a probability of interaction. The

viewpoint parameter η can then be used to modulate the weight given to interaction strength when assessing network diversity. The proposed diversity indices are based on Hill numbers that satisfy properties regarding group abundances but also link abundances. This is a fundamental condition to describe adequately network diversity over space and time and to build a robust spatial network ecology.

Additionally, our framework allows to compute diversity indices at different species aggregation levels (Fig. 4). In this paper, we have focused on methods that aggregate species based on the topology of the metanetwork (regular equivalence and stochastic block modelling). These methods aim to form trophic groups (Gauzens *et al.* 2015) and, in the general case, reduce the complexity of the network (i.e. the number of nodes) while preserving the overall structure. Grouping species using ecological and expert knowledge and computing diversity indices is possible using the developed framework. In this latter case, however, there is no guarantee that the structure of the image network will reflect the structure of the original network (Allecina & Pascual 2009; Gauzens *et al.* 2015; Leger *et al.* 2015).

Whatever the clustering method used, the image network can be viewed as a map at a coarser resolution than the original species network. A map which, depending on the method used, summarises faithfully the structure of the original network. Importantly, it changes the assessment of link turnover. Indeed, what appears as link turnover at a species level could disappear at a group level, provided that the species considered belong to the same group. In other words, network diversity patterns depend on the aggregation level we choose to study the network. This introduces a new notion of scale in the analysis of ecological networks and adds to the spatial and temporal scale used to describe network biogeographic patterns (Fig. 4). Studies aiming to describe network biogeography have so far mostly described macroscopic (i.e. connectance, Thompson & Townsend 2003) or microscopic (link turnover at a species level, Poisot *et al.* 2012, 2016; Carstensen *et al.* 2014; CaraDonna *et al.* 2017) scale patterns and occasionally mesoscopic scale using a priori groups based on the trophic level concept (Thompson & Townsend 2003). Statistical methods, such as the stochastic block model and regular equivalence, allow to select an optimal number of groups to cluster the nodes of a network, thus defining an appropriate scale to study network diversity when no ecological knowledge is available for the species described in the network. As shown by the case study, network diversity can be shaped by different ecological processes depending on the aggregation level considered, in the same way that species diversity is shaped by different processes depending on the spatial and aggregation level considered (Münkemüller *et al.* 2014). This encourages to study network diversity at micro-, macroscopic scale and along a profile of mesoscopic scales (i.e. by changing gradually the number of groups of the image network) to study the processes that govern network structure across space. Indeed, given that some empirical evidence suggests that network structure might be random at a species level (CaraDonna *et al.* 2017), one purpose of aggregating species into equivalent groups is to investigate beyond the stochastic plasticity of biotic interactions. For example, the simulation (Supporting Information) suggests a stochastic plasticity at a

species level but not at a group level since the image network is fixed at a given point of the ecological gradient. We hypothesise that, in the real world, there is an aggregation level below which stochastic processes drive the patterns of network diversity, and above which deterministic processes (i.e. ecological processes) are the main drivers. This hypothesis mirrors the use of the concept of emergent groups of organisms to assess the contribution of niche and neutral theory to community assembly (Héroult 2007).

Moreover, since ecological networks are now built using a wide spectrum of organisms, especially microorganisms with the advent of Next Generation Sequencing (Bohan *et al.* 2017) where the notion of species is hard to handle, using indices that allow to understand network diversity through different species aggregation levels will allow overcoming issues in the definition of the biological entity.

We thus believe that this unified framework should now pave the way for a better understanding of the spatial and temporal structure of biodiversity while considering biotic interactions. Indeed, it reconciles two perspectives on ecological networks analysis while building the associated indices. On the one hand, the study of how ecological processes shape an isolated network (Fig. 4a) and how meaningful groups can be derived from the topology of an ecological network (Fig. 4b), and on the other hand how networks vary across space and time (Fig. 4c). Importantly, it allows testing key ecological hypotheses on the processes shaping the spatial and temporal variation of ecological networks (case study, Fig. 3), by varying different aspects of the networks (Fig. 4d). Consequently, it should foster the emergence of spatial network ecology and allow the comparison, analysis and partitioning of multiple ecological networks, from the local community to the global metacommunity they are a part of, while considering various definitions of the organisms involved.

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AUTHORSHIP

MO developed a draft version of the framework that was further elaborated with WT. VM, SD, WT and MO conceptualised the final version of the framework. LO and LC gave additional perspectives to the paper. MO and WT wrote the first version of the paper and all authors contributed substantially to the revisions.

DATA ACCESSIBILITY STATEMENT

We used an open data set : https://www.nceas.ucsb.edu/interactionweb/resources.html#predator_prey. The code used to generate the simulated data is provided in section 5 of the Supporting Information. We implemented the method in the

R package *econetwork* available on CRAN (<https://cran.r-project.org>).

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Land-use intensity influences European tetrapod food-webs

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Statement of authorship: CB, PG, LO and WT conceptualised the study. CB, JR, YD, LM and PV collected and preprocessed the data. CB developed the code and analysis. CB, PG, MO and JR made the Figures. All authors validated the results. CB wrote the first draft. All authors read and reviewed the manuscript.

Data accessibility statement: The data used in this study is available at <https://zenodo.org/record/5831144>, and the R scripts to reproduce figures and results are provided at https://github.com/ChrisBotella/foodwebs_vs_land_use.

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41 **Abstract**

42 Land use intensification favours particular trophic groups which can induce architectural
43 changes in food-webs. These changes can deeply impact ecosystem functioning, stability and
44 robustness to extinctions. However, the imprint of land management intensity on food-web
45 architecture has rarely been characterised across large spatial extent and various land uses.
46 We investigated the influence of land management intensity on six facets of food-web
47 architecture for 67,051 European tetrapod communities, and its dependency on land use and
48 climate. We found that intensification promoted lower proportions of both apex and basal
49 species, with more connected and less compartmentalized food-webs, and unexpectedly,
50 favoured longer trophic chains in cities and decreased omnivory in mediterranean climates. By
51 favouring mesopredators and undermining basal tetrapods, intensification might lead to new
52 forestry and agricultural pest outbreaks. Our results support mesopredator regulation and apex
53 predator protection where possible, but urban and mediterranean contexts might need
54 alternative strategies.

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65 Introduction

66 Land use intensification and change have been identified as the most impactful factors of
67 biodiversity loss in terrestrial and freshwater ecosystems (Diaz et al., 2019), generating habitat
68 fragmentation or loss (Fahrig et al., 2003), introduction of invasive species (Doherty et al.,
69 2016), direct interactions between humans and wildlife (e.g. disturbances, exploitation, hunting)
70 and pollution. Increasingly, studies have documented how land use intensification leads to
71 changes in species composition across multiple trophic groups (Gossner et al., 2016). However,
72 species are not independent of each other: they interact in complex food-webs that reflect the
73 flow of energy and biomass in the system, the interdependency among species, and ecosystem
74 architecture and functioning (Link et al., 2005). In particular, food-webs sustain a number of
75 ecosystem functions and services, such as pest control (Montoya et al., 2003). Hence, changes
76 in food-web architecture, i.e. its topological properties (e.g. degree of omnivory, generalism,
77 compartmentalization, trophic chain lengths), following land use intensification might be
78 indicative of the potential for ecosystem collapse (Evans et al., 2013, Keyes et al., 2021, Saint-
79 Béat et al., 2015). We thus urgently need to understand how changes in land use will modify the
80 architecture of food-webs (Li et al., 2018, Rigal et al., 2021). Local studies focusing on specific
81 land uses or taxonomic groups can enable us to formulate hypotheses on how land
82 management intensity affects food-web architecture (Agostini et al., 2020, De Visser et al.,
83 2011, Gossner et al., 2016, Hallmann et al., 2014, Heger et al., 2018, Herbst et al., 2013);
84 however, we lack a macroecological assessment of these hypotheses and their context-
85 dependence.

86 Previous local-scale studies have shown that land use intensification favours a limited set of
87 synanthropic and generalist species, in terms of habitat (Clavel et al., 2011) and trophic
88 interactions (McKinney & Lockwood, 1999), at the expense of more specialist ones, leading to
89 biotic homogenization (Gossner et al., 2016, McKinney & Lockwood, 1999). For example,

90 intensive grassland management reduces plant diversity and induces local extinction cascades
91 in higher trophic levels (Herbst et al., 2013). Likewise, increased use of pesticides indirectly
92 affect species feeding on plants or invertebrates and is a well-known cause of the loss basal
93 tetrapod species, such as birds (Geiger et al., 2010, Hallmann et al., 2014) and amphibians
94 (Agostini et al., 2020, Sparling et al., 2001). Human presence tends to exclude top predators
95 like wolves or bears (De Visser et al., 2011, Estes et al., 2011), and human-induced habitat loss
96 affects these predators more quickly than lower trophic levels (Dobson et al., 2006). We may
97 then expect a loss of top-down control, potentially leading to competitive exclusion among prey
98 species, or offering opportunities for exotic meso-predator species to establish (Heger et al.,
99 2018), with a negative impact on basal species (Estes et al., 2011). Human activities are
100 expected to decrease the richness of top predators and basal species, inducing shorter trophic
101 chains and denser networks through replacement of specialists by generalists or omnivores.
102 These more frequent generalists and omnivores should also make networks less
103 compartmentalized (i.e. groups of species interacting more together than with others are
104 expected to be more rare). These ecological processes related to intensification should thus
105 translate into the following deviations on six different facets of food-web architecture (**Figure 1**)
106 that we test here: decreased proportions of (1) apex and (2) basal species, higher proportions of
107 (3) trophic generalists and (4) omnivores, (5) shorter trophic chains and (6) decreased
108 compartmentalization.

109 Here we build on a recent macro-scale study which suggested that human activities might affect
110 European tetrapods' food-web architectures (Braga et al., 2019). We used a recent high
111 resolution classification of land management intensity for different land uses (Dou et al., 2021),
112 along with massive presence-only observations collected across Europe (GBIF, iNaturalist) and
113 knowledge of European tetrapods potential trophic interactions (Maiorano et al., 2020). Through
114 a thorough spatial sampling analysis, we reconstructed 67,051 local food-webs at 1km²

115 resolution, representing a total of 756 tetrapod species and spanning five bioclimatic regions
116 and six land uses across Europe. We quantified the six above-mentioned architectural facets
117 (**Figure 1**) in each local food-web with network metrics, and evaluated how they were influenced
118 by land management intensity. To investigate the context-dependence of the response to
119 intensification, we tested this response per land use (forest, grasslands, arable and permanent
120 croplands, agricultural mosaics or human settlements) and bioclimatic region.

121 **Material and methods**

122 **Data**

123 **Species presence/absence/uncertainty rasters.** To quantify the effects of land management
124 intensity on European tetrapods trophic networks, we gridded species occurrences from GBIF
125 and iNaturalist. We chose to use occurrences because the extent of occurrence from IUCN or
126 BirdLife, commonly used previously (e.g. Braga et al., 2019, O'Connor et al., 2020), is not of
127 high enough resolution for our study. We considered 756 tetrapod species for which we found at
128 least one geolocated observation after data cleaning (see **Appendix S1** for data preprocessing)
129 in GBIF or iNaturalist across continental Europe (35 countries). For each species, we built a
130 raster indicating the presence, absence or uncertain status of that species in each 1km by 1km
131 cell of the land use raster described below (as shown in box 2 of **Figure S1.1**). As a
132 conservative strategy, we first considered a species as absent in a cell if it was out of the
133 species' distribution range provided by the IUCN Red List, including both native and invasive
134 ranges (IUCN, 2021). Within the IUCN range, cells having at least one occurrence of the focal
135 species either in GBIF or in iNaturalist were considered as presences. The remaining cells for
136 the same species (inside the IUCN range but without occurrence) were considered either as
137 absence, if the sampling effort in the cell exceeded a defined species-specific threshold, or
138 uncertain otherwise. The sampling effort in a cell for a given species was approximated by the

139 total number of occurrences across all species of the same taxonomic class (Aves, Mammalia,
140 Amphibia or Reptilia). The sampling effort threshold to consider this species as absent when
141 undetected was defined as the first decile of sampling effort values across all presence cells of
142 that species. We excluded from the study all cells where more than 30% of all 756 species (i.e.
143 227 species) had uncertain status or the observed richness was lower than 20 (box 3 of **Figure**
144 **S1.1**), because a lower richness is rare in tetrapod communities studied at comparable scale
145 (Braga et al., 2019, Gaüzere et al., 2022) and would likely be an artefact of a low sampling
146 effort.

147 After this filtering process, cells were grouped per combination of bioclimatic region and land
148 use (explained further below) only retaining combinations containing enough cells to compare
149 land management intensity levels (see box 4 of **Figure S1.1** for more detail). Given that climate
150 influences tetrapod food-web architecture (Braga et al., 2019), ignoring it could bias our results
151 on the influence of land management intensity. After cell filtering, we retained 67,051 cells
152 which are summarised by bioclimatic region, land use and management intensity in **Figure**
153 **S3.4**. The number of species with uncertain absence were generally a small proportion of the
154 richness per cell. For instance, the number of uncertain species was less than 20% of the
155 observed richness in 84% of cells, and less than 10% in 63% of cells. We acknowledge a
156 detection bias in favour of birds due to the large proportion of crowdsourcing data, and to a
157 lesser extent, mammals, while reptile and amphibian species tended to be less frequently
158 reported. Hence, our network metrics (described below) are likely more representative of
159 interaction among birds and mammals, and may hence underestimate the effect of other
160 important interactions such as birds preying diverse amphibians and reptiles.

161 **Local food-webs.** We used the metaweb of potential trophic interactions between European
162 tetrapod species (Maiorano et al., 2020), which we restricted to 756 selected species with
163 enough observations. The metaweb of these species is fully represented in **Figure S2.2** of the

164 Appendix, highlighting the decomposition of the 46 trophic groups introduced in O'Connor et al.
165 (2020); here we provide a simplified visualisation in **Figure 2** where species were aggregated
166 per trophic group. The metaweb was used to reconstruct the food-web associated with the set
167 of species present in each cell to create local food webs. Two species were assumed to interact
168 locally if they are both present in the cell and if they are known to interact in the metaweb.
169 Species having locally no prey and predator were kept, as they can feed on non-tetrapod
170 species (aquatic vertebrates, invertebrates, fungi, plants), without affecting most network
171 metrics (see architecture facets' section below).

172 **Land use and management intensity.** We used a new land system map that integrates
173 various land use and land cover data for Europe at 1km resolution (Dou et al., 2021), which
174 covers EU28+ (including the EU, the United Kingdom, Norway, Switzerland, and the Western
175 Balkans, but excluding Iceland, Turkey and Macaronesia). We considered six land uses: forest,
176 grassland (except grass wetlands), permanent cropland (vineyards, olive groves, fruit gardens),
177 arable cropland, agricultural mosaic (cropland and grassland) and human settlement (cities and
178 peri-urban landscapes). Each land use was decomposed into different levels of land
179 management intensity (low/high for permanent croplands, low/medium/high for others) based on
180 criteria that (i) depend on the land use (see **Table S3.2**) and (ii) have documented impacts on
181 biodiversity, which make these land use classifications suitable to our purpose.

182 **Bioclimatic regions.** We considered the biogeographical regions defined by the European
183 Environment Agency (European Environmental Agency, EEA 2021). These bioclimatic regions
184 represent large scale biodiversity units reflecting climatic contrasts and are based on an
185 interpretation of geobotanical data. Among the 11 original regions, 5 were used in our study, the
186 Alpine, Atlantic, Boreal, Continental and Mediterranean regions for which we had enough
187 sampled cells (**Figure S3.4**).

188 **Analysis methods**

189 Each hypothesis we tested concerns a specific facet of the food web architecture: proportions of
190 apex and basal species, proportions of trophic generalists and omnivores, length of trophic
191 chains, and compartmentalization (**Figure 1**). To evaluate the effect of land management
192 intensity on these facets, we selected one or several network metrics representing each facet.
193 We measured the mean deviation per metric related to an increase of land management
194 intensity (**Figure 4**) and tested, for each facet, the statistical significance of the multivariate
195 deviation between intensity levels per bioclimatic region and land use.

196 **Network architecture facets**

197 The network metrics composing each of the six architecture facets that we computed for each
198 local food-web are summarised in **Table 1**. Detailed explanations are presented in the Appendix
199 **S4**. For apex proportion, we computed the proportion of global apex predators (**pApexMeta**),
200 namely the number of apex predator species based on their trophic level (MacKay et al., 2020)
201 in the metaweb completed by species diets as additional nodes (as recommended in Maiorano
202 et al., 2020), divided by the total species richness of the local food-web. Diets were represented
203 along with tetrapod trophic groups in the full metaweb visualisation of **Figure 2**. For basal
204 proportions, we computed two metrics: **pBasalMeta** and **pBasal** are the proportion of observed
205 species having no tetrapod prey in the metaweb or local food web, respectively. Both versions
206 of the metric were considered because some of a species' potential prey (metaweb) might have
207 not been detected in local food-webs. For connectance, we computed the density of directed
208 trophic interactions among tetrapod species in a local food-web (**dirCon**). For omnivory levels,
209 we computed two metrics based on a continuous or categorical view of trophic levels: **omniLvl**
210 is the average over globally non-basal and non-apex species of the standard deviation of their
211 prey's trophic levels, while **omniProp** is the proportion of globally non-basal and non-apex

212 species predating several levels (basal / intermediary / apex, see Appendix **S4**). For chain
213 indices, we computed the longest (**maxPath**), mean (**meanPath**) and standard deviation
214 (**sdPath**) of the shortest-paths from locally basal species to top species. Finally, for
215 compartmentalization, we computed the local modularity (**modul**, Newman et al., 2006), and the
216 mean distance (**meanShortDist**) between species on the (undirected) local food-web. Several
217 metrics were chosen for one facet when one dimension alone could not capture the ecological
218 meaning well. As a logical consequence, metrics inside each facet were positively correlated but
219 weakly correlated between facets (see **Figure S5.5**). We later interpret land management
220 intensity as influencing a given facet only if all its metrics were influenced in the same way.

221 **Mean metric deviations related to land management intensity**

222 To assess the influence of land management intensity on architecture facets and its
223 context-dependence, we measured the mean deviation of each metric related to an increase in
224 land management intensity. We fitted a multivariate linear regression (Johnson & Wichern,
225 1992) over local food-webs where the metrics were set as dependent variables, and the
226 combination of bioclimatic region, land use and land management intensity as categorical
227 explanatory variable with nested contrasts, i.e. defined according to the following R formula:
228 $\text{metric} \sim \text{region} / \text{land_use} / \text{land_management_intensity}$.

229 As a result of this analysis, we obtained a mean deviation of each metric for each context,
230 namely combination of bioclimatic region, land use and couple of land use intensities (high
231 versus low, or mid versus low). We also obtained the mean deviation from one reference land
232 use to others per bioclimatic region (for low intensity cells) and the mean deviation from one
233 reference bioclimatic region to others (for low intensity cells and the reference land use). Some
234 combinations of land use, bioclimatic regions and intensity level pairs were not considered due
235 to a lack of well sampled cells (see **Figure S3.4**), and all cells from Black sea, Pannonian,

236 Steppic and Arctic bioclimatic regions were excluded. We ended up considering 38 contexts,
237 and the mean deviations are listed per context in Tables **S6.6 to S6.11**, where each table shows
238 one facet. **Figure 4-top** summarises the deviations per metric considering only the comparisons
239 between low and high management intensity.

240 **Tests of multivariate deviation significance**

241 We tested whether the deviation related to an increase of intensity was significant for each facet
242 and context. We tested the equality between the two multivariate distributions of food-web
243 metrics included in the facet, and detected significant deviations when the null hypothesis (i.e.
244 no effect of higher land management intensity) was rejected. This was done using a non-
245 parametric multivariate test based on Wilk's Lambda statistics which especially accounts for the
246 unbalanced number of cells between intensity levels (Liu et al., 2011) and is implemented in the
247 *npmv* R package (Burchett et al., 2017). For any combination of bioclimatic region and land use,
248 we set the first order risk α of detecting at least one false non-equality across our 6 facets to

249 5%, which translates into a risk of $1 - (1 - \alpha)^{\frac{1}{6}} \approx 0.009$ in each facet, a rather conservative
250 choice. Following the procedure of Burchett et al. (2017), when three intensity levels were
251 available for a combination, we first tested the equality between the three distributions with
252 risk α , and if equality was rejected, we tested the equality between each pair with risk $2\alpha/3$, to
253 maintain a strong control of the familywise error rate. The significance of the deviation in each
254 context is indicated by a blue background of cells in Tables **S6.6 to S6.11**. Deviation tests
255 across contexts are summarised per facet in **Figure 4-bottom**, representing the proportion of
256 deviations that are non-significant, that confirm or contradict our expectations, or that are
257 discordant when several metrics showed opposite deviations while the multivariate deviation
258 was significant.

259 **Results**

260 **Apex predator proportion generally decreased under higher land management intensity.**

261 In agreement with our hypothesis, apex predator proportion (pApexMeta) decreased with
262 increasing land management intensity and had the strongest average response of all food-web
263 metrics (deviation greater than 10% of the interquartile range, **Figure 4-top**). This general
264 decrease concerned 8 of the 9 highest trophic groups which included only apex predators
265 (**Figure 5**). Apex proportion decreased significantly in 77% of the 13 significant deviation
266 contexts (**Figure 4-bottom**, Table SXX), including Atlantic forests and croplands, and most
267 settlements (**Figure S6.6**). In contrast, it increased significantly in boreal settlements, which are
268 less aggregated than in other bioclimatic regions. Even though a minority of deviation contexts
269 were significant (13/36), 67% of deviations were negative overall while positive deviations
270 remained relatively small and rare.

271 **Basal species proportions tended to decrease under higher land management intensity.**

272 In agreement with our hypothesis, local and global proportions of basal species were both
273 lower, on average, in intensively managed landscapes (**Figure 4-top**). These decreases
274 included 12 of the 16 trophic groups containing basal species (**Figure 5**) and were significant in
275 34 contexts. Fifty percent of these significant contexts showed a decrease of both local and
276 global measures, including (**Figure 4-bottom**, Table 3) croplands from all bioclimatic regions,
277 except the Atlantic, and continental and boreal forests and Atlantic grasslands (**Figure S6.7**).
278 Contrary to our expectation, local and global basal proportions in local food-webs increased with
279 land management intensity in 26.5% of the 34 significant contexts, mainly in Atlantic croplands,
280 Mediterranean settlements and forests (**Figure S6.7**). The remaining 23.5% of the significant
281 contexts showed discordant deviations between global and local basal species proportions
282 (**Figure 4-bottom**).

283 **Connectance tended to increase under higher land management intensity.** In agreement
284 with our hypothesis, connectance generally increased with land management intensity (**Figure**
285 **4-top**), however with 11 significant contexts and a majority of non-significant contexts (25 of 36)
286 increasing in connectance. 64% of the 11 significant contexts showed increased connectance
287 with intensity (**Figure S6.8**), interpreted as higher trophic generalism and vulnerability in these
288 communities, including most forests, except the Mediterranean ones, and continental croplands.
289 The remaining 36% of significant contexts showed the opposite pattern and were mostly found
290 in the Mediterranean region (Figure S6.8).

291 **Omnivory showed contrasted responses to land management intensity.** OmniLev and
292 omniProp had weak and discrepant responses to land management intensity (**Figure 4-top**)
293 across bioclimates and land uses. While most contexts showed significant deviations (34/36),
294 only 23.5% of them showed an increase of both omnivory levels (**Figure 4-bottom**), challenging
295 our expectations. These contexts were mostly in forests, sometimes with important mean
296 deviations as for alpine forests (**Figure S6.9**). For a larger part (30%) of significant contexts, the
297 omnivory metrics had opposite mean deviations which were relatively small in amplitude, hence
298 showing no evident trend. Contrary to our expectations, omnivory levels both decreased in
299 47.1% of significant contexts, including all settlements, Atlantic grasslands and continental
300 croplands.

301 **Trophic chain lengths overall increased under high land management intensity.** Contrary
302 to our expectations, the three metrics describing trophic chain length globally increased on
303 average with land management intensity (**Figure 4-top**). Local food-webs under low land
304 management intensity had relatively more shortest-paths of length 1 (direct predation on a basal
305 species), while local food-webs under high land management intensity had more shortest-paths
306 of length 2 to 5 (see **Figure S7.12**). Responses across land uses and bioclimatic regions varied,
307 with 44% of the 34 significant deviation contexts showing an increase of all metrics, especially in

308 cities or peri-urban areas (Figure S6.10), and 30% showing a joint decrease in agreement with
309 our hypothesis (**Figure 4-bottom**).

310 **Compartmentalization overall decreased under high land management intensity.** Both
311 compartmentalization metrics decreased in average with increasing land management intensity
312 (**Figure 4-top**). Of the 34 significant contexts 56% showed a decrease and 27% an increase in
313 both metrics, with the remaining contexts showing discordant deviations between the metrics.
314 Most contexts where compartmentalization increased were located in Mediterranean and Alpine
315 regions, and in Atlantic croplands (see Figure S6.11). This result is confirmed by a higher
316 proportion of disconnected pairs of basal and top species in low intensity food-webs compared
317 to the high intensity ones (Figure S7.12), i.e. more frequent disconnected trophic chains or
318 species.

319 **The influence of higher land management intensity was context-dependent.** We observed
320 a significant deviation of basal proportions, omnivory levels, chain indices and
321 compartmentalization related to higher land management intensity for forest, croplands and
322 settlements in all our studied bioclimatic regions (Figures **S6.7, S6.9, S6.10, S6.11**). Deviations
323 of most facets were also significant for grasslands and agricultural mosaics in the Atlantic
324 region. The sign of the metric deviations in response to higher land management intensity
325 varied across land uses and bioclimatic regions (**Figures S6.6 to S6.11**). For instance, the
326 response of Mediterranean food-webs diverged from other regions and was quite consistent
327 across land uses: Connectance significantly decreased and compartmentalization significantly
328 increased when land management was more intense in forest, croplands and settlements
329 (**Figures S6.8 and S6.11**). Mediterranean forests and settlements also showed increased basal
330 proportions contrary to most other contexts (**Figure S6.7**). The singular response of
331 Mediterranean forests may be partly explained by a joint and significant increase of all
332 fragmentation metrics under high land management intensity, which is almost exclusive to this

333 context (**Figure S8.13**). Regarding land use, cities and peri-urban areas also showed a singular
334 response compared to other land uses independently of the bioclimatic region, with a decreased
335 omnivory and increased trophic chain lengths, which explain the unexpected general trends
336 stated above for these facets. Contrasted responses across land uses were observed for all
337 bioclimatic regions. In Atlantic areas, higher land management intensity was related to
338 decreased basal species proportions in grasslands and settlements while, surprisingly, it
339 increased it in croplands (**Figure S6.7**).

340 **Discussion**

341 Less intensively used landscapes hosted food-webs combining a higher proportion of basal
342 tetrapod species, greater compartmentalization and lower trophic generalism of predators. This
343 combination of properties strongly suggests that food-webs in these landscapes are
344 topologically more hierarchical (Clauset et al., 2008, see network on left of Figure 1 as an
345 illustration), namely networks that are similar to a tree. These findings support those of Mestre
346 et al. (2022), who showed that low human pressures favour scale-free architectures, i.e. where
347 the node degree distribution follows a power-law. A scale-free architecture combined with a high
348 compartmentalization characterises a hierarchical architecture (Barabási et al., 2003).
349 Hierarchical, and consequently scale-free, food-web architectures are more resilient to random
350 disturbances assumed to characterise natural ecosystems (Mestre et al., 2022). Such
351 architectures are thought to limit the effect of a variation in species' abundance on other trophic
352 chains, improving the global stability of the network (Tylianakis et al., 2010). Apex predators are
353 also relatively more diverse in areas of lower land management intensity, likely inducing a better
354 regulation of intermediary predators. This regulation should indirectly limit the predation
355 pressure on the basal layer, and distribute it more homogeneously across basal species given
356 the hierarchical architecture.

357 In contrast, food-webs under high land management intensity had a lower apex predator
358 species proportion, which decreases the pressure on mesopredators (Prugh et al., 2009), such
359 as many snakes and mustelids, and some large basal species, such as ungulates and wild
360 boars that can cause broad damage to ecosystems (Carpio et al., 2014, Ballouard et al., 2021).
361 A lower proportion of basal species are predated by a higher proportion of mesopredators that
362 exert a strong pressure on the basal layer (Prugh et al., 2009). The higher generalism may
363 result from the substitution of basal species by intermediary predators and even the selection of
364 generalist intermediary predators. This higher generalism was associated with less
365 compartmentalization and more frequent connections between pairs of basal and top species
366 (Figure S7.12), implying an increase of the vulnerability of basal tetrapods, i.e. basal species
367 tend to have more predators. This increased vulnerability of basal tetrapods species adds to
368 other threats such as the sensitivity of the less mobile tetrapod species (e.g. amphibians and
369 reptiles) to pollution (Lange et al., 2009) and overall question the sustainability of the food-web
370 architectures found under high land management intensity. Indeed, basal species extinctions
371 might eventually lead to more extinction via cascading effects, or increase the competition
372 between intermediary predators. Some studies have documented negative effects of land
373 management intensity on interaction network robustness (Evans et al., 2013) or community
374 persistence (Gilarranz et al., 2016), which are partly dependent on architectural change. Hence,
375 connecting large-scale empirical architecture changes to the theoretical knowledge of food-web
376 architecture-dynamic relationships can provide some insights on the impacts of intensification
377 on ecosystem stability. Further, a fruitful direction for future research would be to consider the
378 predictive power of these relationships in the context other impactful factors such as non-trophic
379 interactions (Kéfi et al., 2016), interaction strengths (Saint-Béat et al., 2015) and feeding
380 behaviour (Heckmann et al., 2012). In addition, land use intensification may act in tandem with
381 global warming by increasing the fragility of basal tetrapods resulting in more widespread losses
382 of ecosystem services fundamental to our economy, such as human health, as for instance the

383 control of mosquito borne diseases (Brugueras et al., 2020), and crop pest control (Civantos et
384 al., 2012). In addition, the partial collapse of basal tetrapods may favour bark beetle outbreaks
385 which can be catastrophic in forestry. Indeed, four woodpecker species predate them in Europe,
386 and favour the predation of bark beetles by a suite of other basal birds, while bark removal
387 enhances their regulation by parasitoids (Wermelinger et al., 2015).

388 Unexpectedly, food-webs under higher land use intensity tended to have longer shortest-path
389 lengths between basal and apex tetrapods. This apparent paradox is not easily resolved but
390 several factors might explain it. In food-webs under low land management intensity, the
391 presence of a few apex predators may exclude many mesopredators (Prugh et al., 2009). For
392 instance, wolves tend to exclude whip snakes, weasels or polecats. Besides, in our metaweb,
393 frequent apex predators have often more basal prey than frequent mesopredators, hence the
394 presence of the former generates many length one shortest-paths, while mesopredators might
395 often have to eat prey with a relatively higher trophic level in the absence of their basal prey.
396 Hence, we hypothesise that the replacement of apex predators by mesopredators under higher
397 land management intensity explain the lower proportions of shortest-paths of length one and the
398 longer average chain indices that we observed.

399 Beyond these global trends of food-web architecture response to land management intensity,
400 we observed a variety of more specific responses depending on the bioclimatic regions and land
401 uses. For instance, we documented a singular response in the Mediterranean region compared
402 to other bioclimates, characterised by a higher compartmentalization, a lower connectance and
403 smaller trophic chains under higher land management intensity, which illustrates how food-web
404 complexity may change the response to intensification. Regarding cities and peri-urban areas,
405 we observed a decrease of omnivory and an increase of trophic chain lengths in response to
406 higher land management intensity, which mostly explained the global trends for these facets.
407 Even though unexpected, these results support trophic dynamics phenomena previously

408 documented in urbanised habitats called prey specialisation and predator subsidy consumption
409 (Fischer et al., 2012): Dense urban habitats may select mesopredator species specialising on
410 prey adapted to such habitat (prey specialisation), such as certain small bird and rodent
411 species, or mesopredators consuming anthropogenic food (predator subsidy consumption) such
412 as garbage.

413 Our study used a space-for-time substitution approach (Walker et al., 2010, Blois et al., 2013) to
414 show the effects associated with varying land management intensity across space, which are
415 likely to result from temporal changes of past intensification over at least several decades.
416 However, spatial patterns might not necessarily mirror the effects of land use intensification or
417 other global changes (Gaüzère & Devictor, 2021). We compared areas with similar large scale
418 bioclimates and land use, but small scale environmental variations covarying with land
419 management intensity and impacting food-webs architecture could bias our results. This is likely
420 the case in the alpine region due to the strong relationship between elevation and land
421 management intensity.

422 Discrepant results could also be explained by other forms of human impacts that do not always
423 act in concert with intense land management. For instance, higher habitat fragmentation was
424 significantly associated with higher intensity only in Mediterranean and Alpine forests (Figure
425 S8.13). This result may partly explain the singular response of Mediterranean forests, with
426 decreased connectance and increased compartmentalization. Indeed, a higher agglomeration of
427 diverse land uses at a small spatial scale is thought to host more diverse independent trophic
428 chains even though empirical evidence is still rare (Gonzalez et al., 2011). In addition, the
429 increase of human footprint (a different indicator of human influence incorporating other aspects
430 of human influence such as night light intensity, traffic intensity and population density),
431 favoured food-webs with decreased connectance and higher compartmentalization metrics,
432 contrary to our results, in the same area based on earlier study (Braga et al., 2019).

433 Discrepancies between this study and Braga et al. (2019) could also be due to differences in
434 data analysis methods. For instance, these differences may be explained by the fact that we
435 chose food-web metrics normalised for species richness. Indeed, when not accounted for, food-
436 web size variability drives important variations in most metrics (Botella et al., 2021), which are
437 not interesting in our context because the effects of human pressures on species richness have
438 been well studied.

439 **Conclusion.** Land use intensification has already changed the architecture of food-webs, likely
440 inducing changes to ecosystem functions, services, stability and resilience. We found global
441 trends of the influence of land management intensity on European food-webs. According to our
442 expectations, food-webs in intensely used lands tended to have lower proportions of top
443 predator and basal species, higher connectance and lower compartmentalization. We identified
444 context-dependent influence of intensification, as in the Mediterranean region, where food-webs
445 were more compartmentalized and had lower connectance. Intensive urbanization unexpectedly
446 favoured longer trophic chains and lower omnivory. Overall, intensification has the potential to
447 decrease the regulation of intermediary predators and induce more predation pressure on the
448 basal layer, making the latter even more vulnerable to global changes, and questioning the
449 long-term stability of food-web architectures favoured by intensification. We stress the
450 importance of assessing these cascading consequences on ecosystem services such as pest
451 control in agriculture and forestry.

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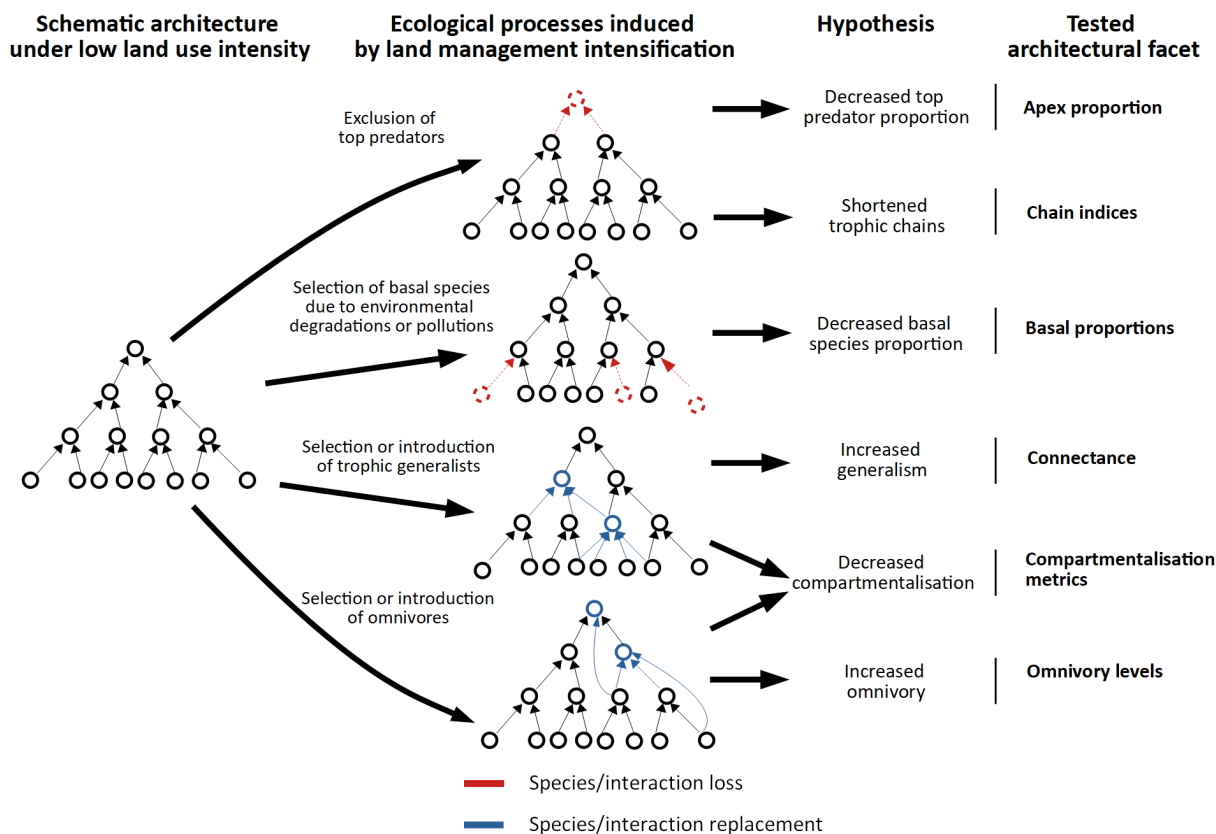
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624 **Figures**

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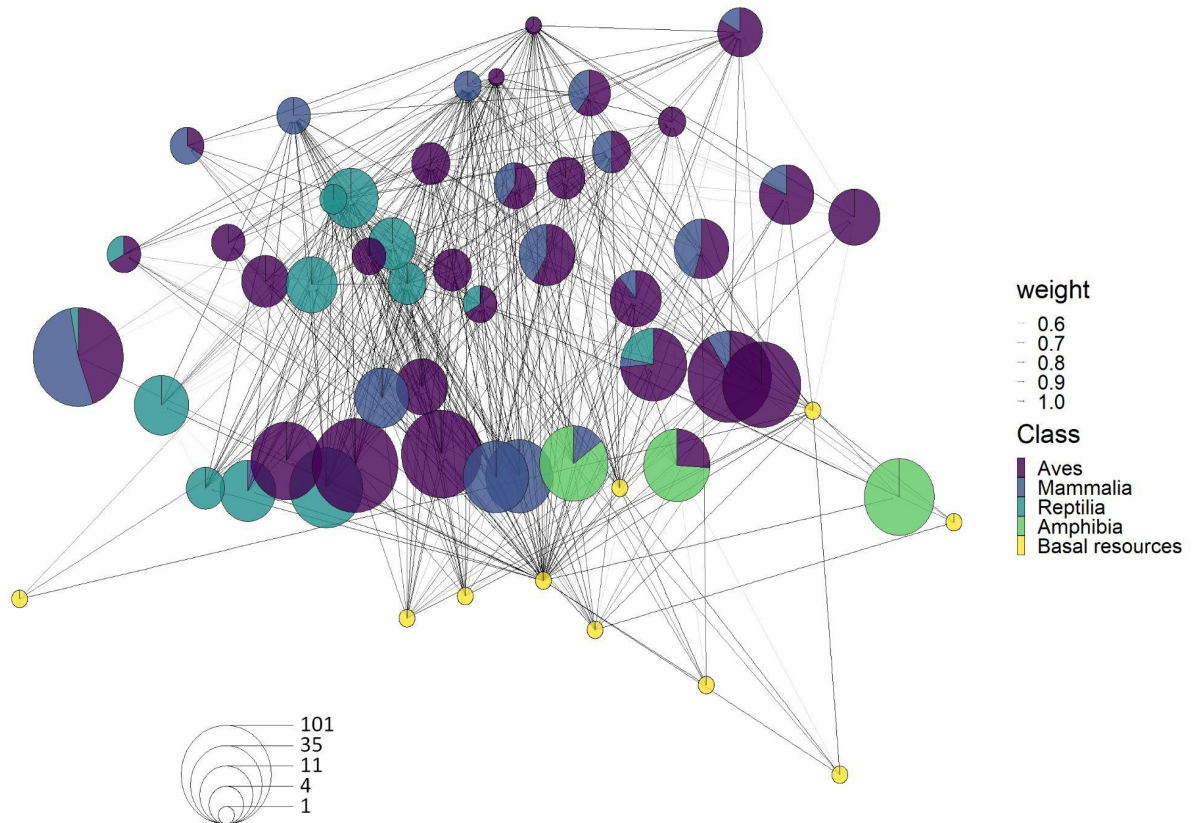


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627 **Figure 1.** Hypothetical food-web architectural changes related to land use intensification.

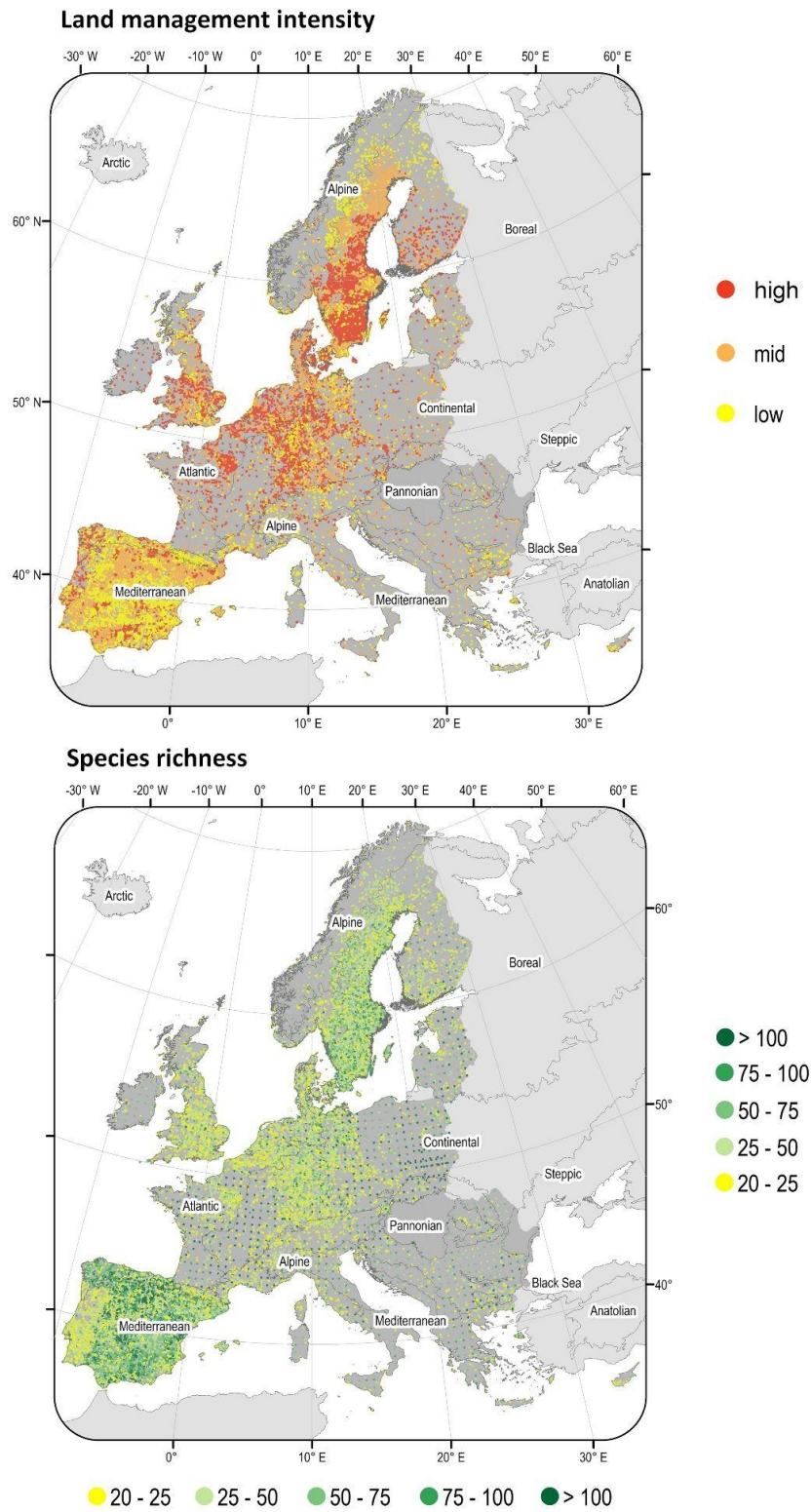
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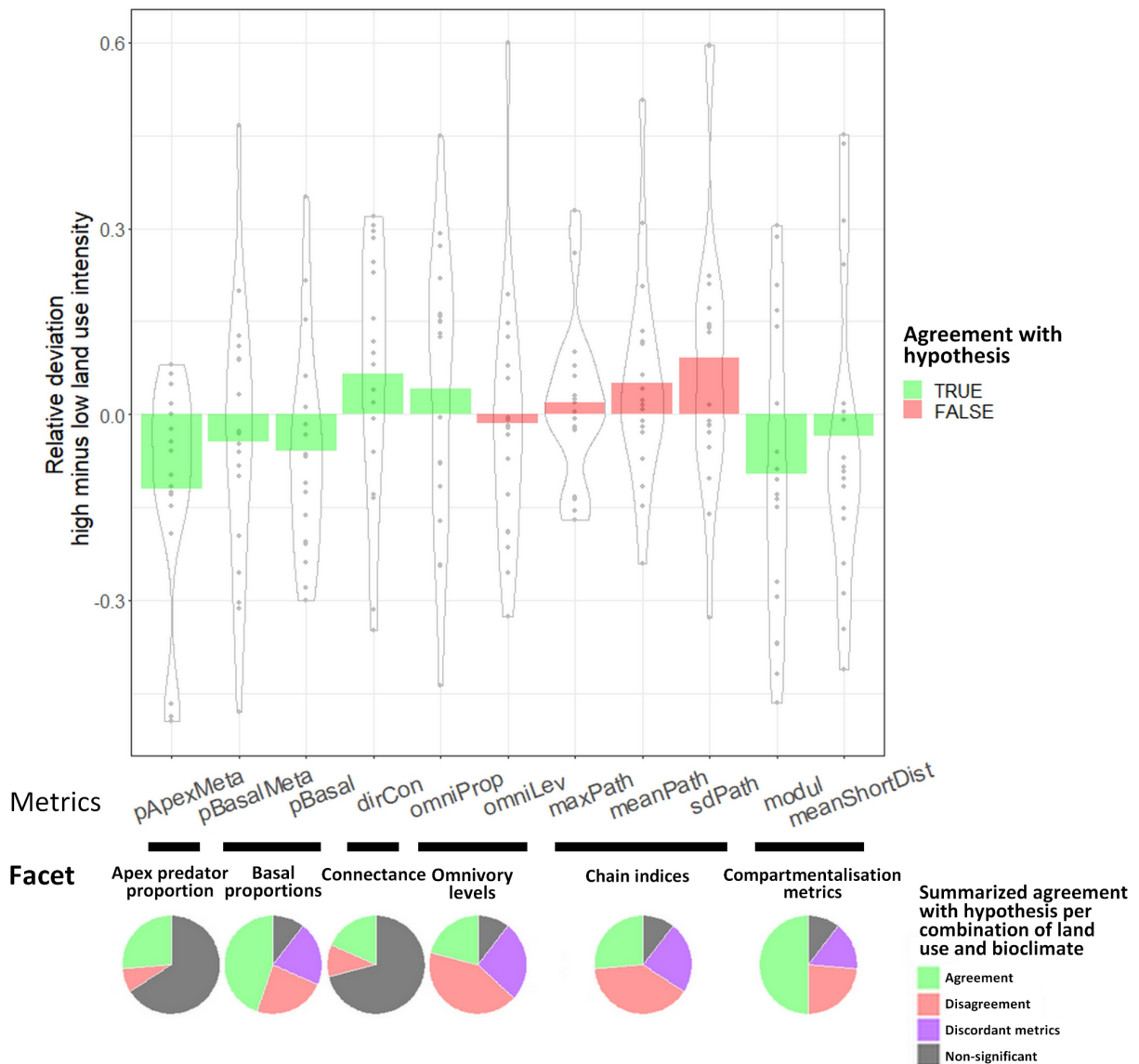
631 **Figure 2.** The metaweb of trophic interactions of our 756 European tetrapods aggregated per
632 trophic groups (O'Connor et al., 2020). Each node is one of the 46 trophic groups (detailed in
633 Table **S2.1**), its size represents the number of species while the colours represent the
634 proportion of classes. The trophic groups were automatically positioned vertically according to
635 their trophic level and horizontally so that connected groups are more aligned than non-
636 connected ones (TL-tsne layout method of the R package **metanetwork**:
637 <https://marcohlmann.github.io/metanetwork/>). Basal resources (i.e diets that are not wild
638 vertebrates) were included as yellow nodes.



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640 **Figure 3.** Map of the 67,512 studied local food-webs (1km² cells). **Top:** Cell locations colored
 641 by land management intensity. **Bottom:** Cell locations colored by observed species richness.

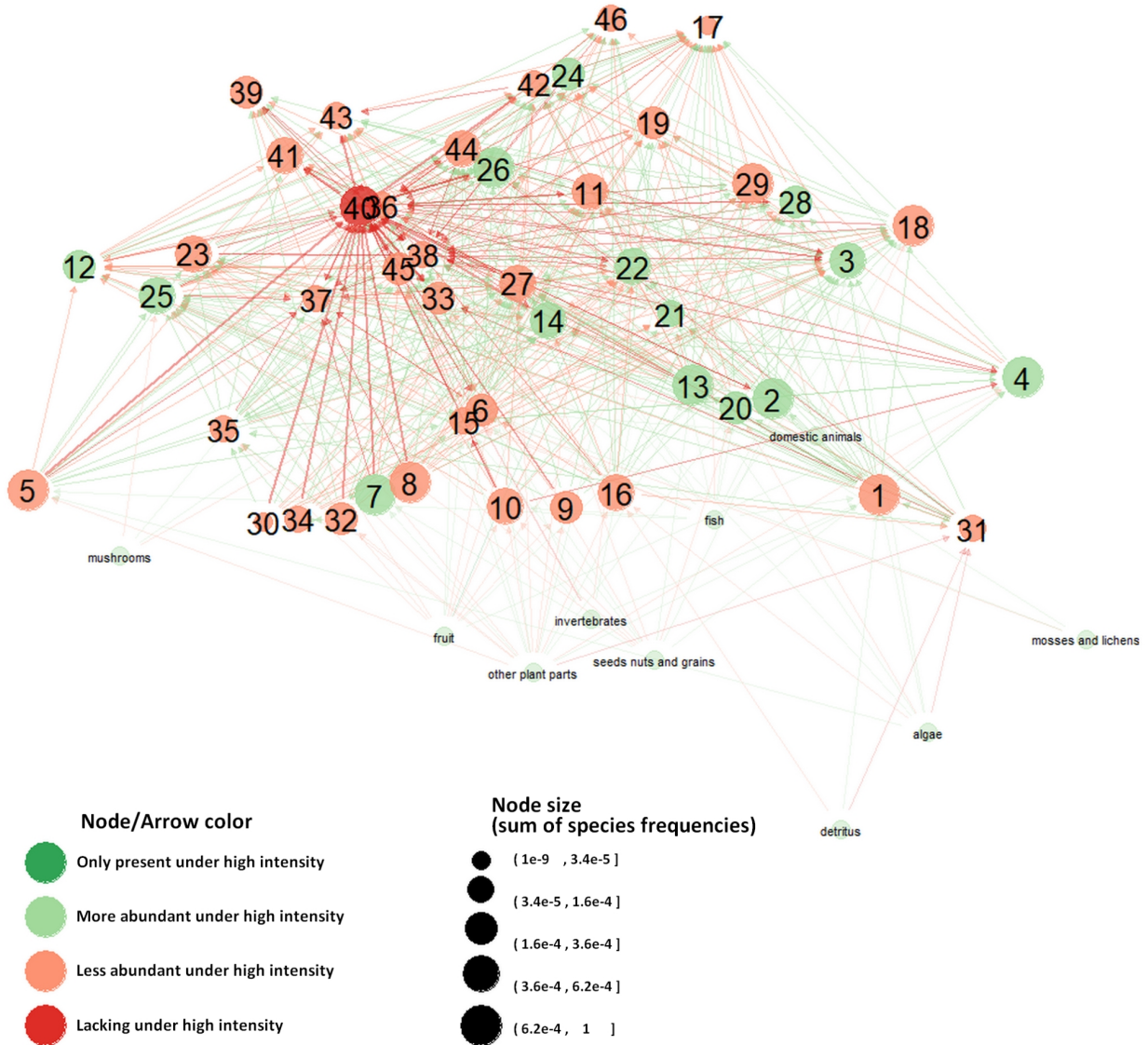
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644 **Figure 4.** Food-web metric deviations related to higher land management intensity per
 645 architecture facet and agreement with the initial hypothesis. **Top:** For each metric (abscisse),
 646 the relative deviation (ordinate) is the average metric in high intensity food-webs minus the
 647 average in low intensity food-webs divided by the interquartile range of the global metric
 648 distribution. The relative deviation is computed independently per combination of bioclimatic
 649 region and land use (grey dots) and averaged (barplot) to indicate the global response to land
 650 management intensity. The bar plot's colour indicates if the deviation is confirming (green) or
 651 contradicting (red) the initial hypothesis on the corresponding facet (see **Figure 1**). **Bottom:** For
 652 each facet, a pie plot summarises the tests of deviation significance across contexts into
 653 agreement (green) or disagreement (red) with the hypothesis, discordant metrics (purple) or
 654 non-significant, based on our multivariate test. The precise percentages are

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657 **Figure 5.** Changes of trophic group frequencies when increasing land management intensity.
 658 This difference plot between average networks in high and low land management intensity cells
 659 is produced by the `diff_plot` function in **metanetwork** R package. As in **Figure S2.2**, each node
 660 is one trophic group and its size represents the sum of species frequencies across the 67,051
 661 local food-webs. A red (resp. green) node color indicates a decrease (resp. increase) of the
 662 group frequency in high intensity cells compared to low intensity cells. More details on the
 663 trophic group compositions are provided in Table **S2.1**.

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669 **Tables**

670

Architecture facet	Metric acronym	Description	Range of values
Apex proportion	pApexMeta	Proportion of global apex predator species.	[0,0.3]
Basal proportions	pBasalMeta	Proportion of global basal species.	[0,1]
	pBasal	Proportion of species that are basal in the local network (have no preys).	[0.1,1]
Connectance	dirCon	Directed connectance: density of interactions in the local network.	[0,0.3]
Omnivory Levels	omniProp	Proportion of global omnivore species among non-basal and non-top species.	[0.3,1]
	omniLvl	Mean standard deviation of prey trophic levels of the non-basal and non-top species.	[0.1,0.7]
Chain indices	maxPath	Maximum length across shortest-paths from basal to apex species in the local network.	[0,12]
	meanPath	Mean length across shortest-paths from basal to apex species in the local network.	[0,3.8]
	sdPath	Standard deviation of lengths across shortest-paths from basal to apex species in the local network.	[0,2.4]
Compartment alization metrics	modul	Modularity (Newman et al., 2006): A measure of densely interconnected groups of species being less connected with other species.	[-1,0.4]
	meanShortDist	Mean path distance across species pairs in the undirected transform of the local network.	[1,4.3]

671 **Table 1.** Architectural facets and their constituent metrics computed for all local food-webs in
 672 this study.

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Appendices

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677 **Appendix S1 - Data preprocessing**

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679 **Figure S1.1** summarizes the 4 steps of our data preprocessing pipeline leading to the selection
 680 of the species, cells and combinations of bioclimatic region, land use and land management
 681 intensity in this study. In the text below, we also present in more detail the first step, namely
 682 data cleaning of the GBIF/iNaturalist occurrences. Finally, we explain how to reproduce the data
 683 preprocessing steps for transparency (optional) and the manuscript Figures using our online
 684 repositories.

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Data cleaning (step 1 of Figure S1.1). We extracted all tetrapod geolocated occurrences from the GBIF (except iNaturalist dataset) with date posterior to 1980, including only human observations, a geolocation uncertainty below 1km (resolution of our study cells). Besides, we extracted the tetrapod iNaturalist research grade occurrences using the rinat R package to add them to the GBIF ones. Then, we removed duplicates, and occurrences suffering from various coordinates errors using the **CoordinateCleaner** R library:

- Degree-minute to decimal degree conversion error (cd_ddmm function)
- Location too close to gbif headquarters or other biodiversity institutions, country capitals, country centroids.
- Occurrences outside of the IUCN range, if available, for the corresponding species. Indeed, we assumed that species presence outside of the IUCN range was either an identification error, a geolocation error, or a vagrant specimen not proving the existence of a local population. Species spatial ranges have been assessed in the context of the IUCN red list of threatened species (IUCN, 2021).

We globally removed datasets for which we detected a spatial rasterization of coordinates with a periodicity superior to 1km. Finally, for each species for which it was available, we removed occurrences lying outside of the IUCN spatial range, including the invasive range (spatial ranges are assessed in the context of the IUCN red list of threatened species, IUCN, 2021). Indeed, we assumed they were either identification errors, geolocation errors, or vagrant specimens not proving the existence of a local population. Species spatial ranges have been assessed in the context of the IUCN red list of threatened species (IUCN, 2021). Finally, the 756 species included in this study were those with at least one occurrence remaining and present in the tetrapod meta-web of trophic interactions (Maiorano et al., 2020).

Reproduction. To reproduce our result Figures, one can simply download **preprocessed_data** and **TrophicNetworksList** Rdata files from our Zenodo repository (<https://zenodo.org/record/5831144>) and run R script **analyse_preprocessed_data.R** provided in our Github repository (https://github.com/ChrisBotella/foodwebs_vs_land_use). It will generate the Figures of this manuscript locally. To reproduce steps 2 to 4 of the data preprocessing pipeline given in **Figure S1.1** from the cleaned GBIF/iNaturalist occurrences, it is possible to download the **raw_data** Rdata file from Zenodo (several Gb file) and run the **preprocess_data.R** script from our Github. It will re-generate **preprocessed_data** and **TrophicNetworksList** locally, which are the inputs for **analyse_preprocessed_data.R**.

Error control

Steps

**Access/
reproduction**

1) Data cleaning

N.B.: Step excluded from shared data & code
- Occurrence cleaning (exclude occurrence with rasterized, imprecise, corrupted location), taxonomic homogenization.
- Keep species with one occurrence and present in tetrapod metaweb (**756 species**).

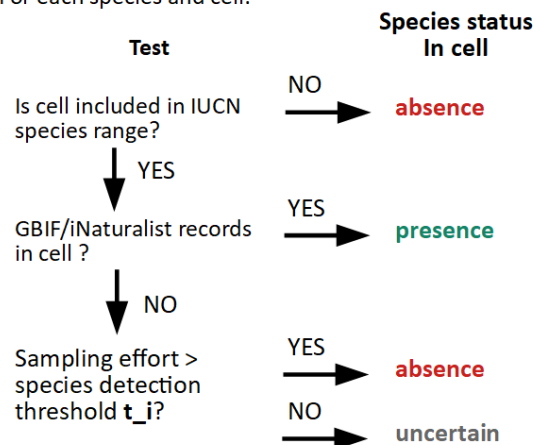
raw_data (Rdata file)



2) Assess species absence uncertainty

For each species and cell:

Risk of false presence (e.g. vagrant specimen) and false absence (non-detection).



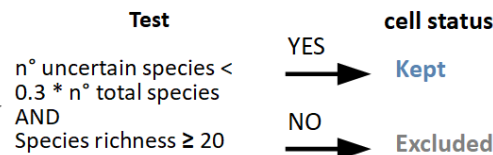
Github
R script



3) Filter uncertain cells

For each cell:

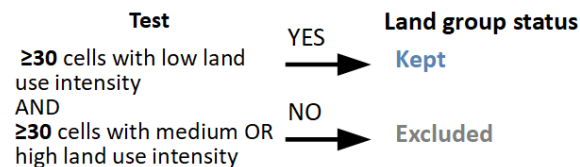
Risk of bias in undetected species affecting results



4) Filter incomplete/scarce land groups

For each land group = bioclimatic region and land system:

Risk of false rejection of equality between land use intensity levels because of small sample size.



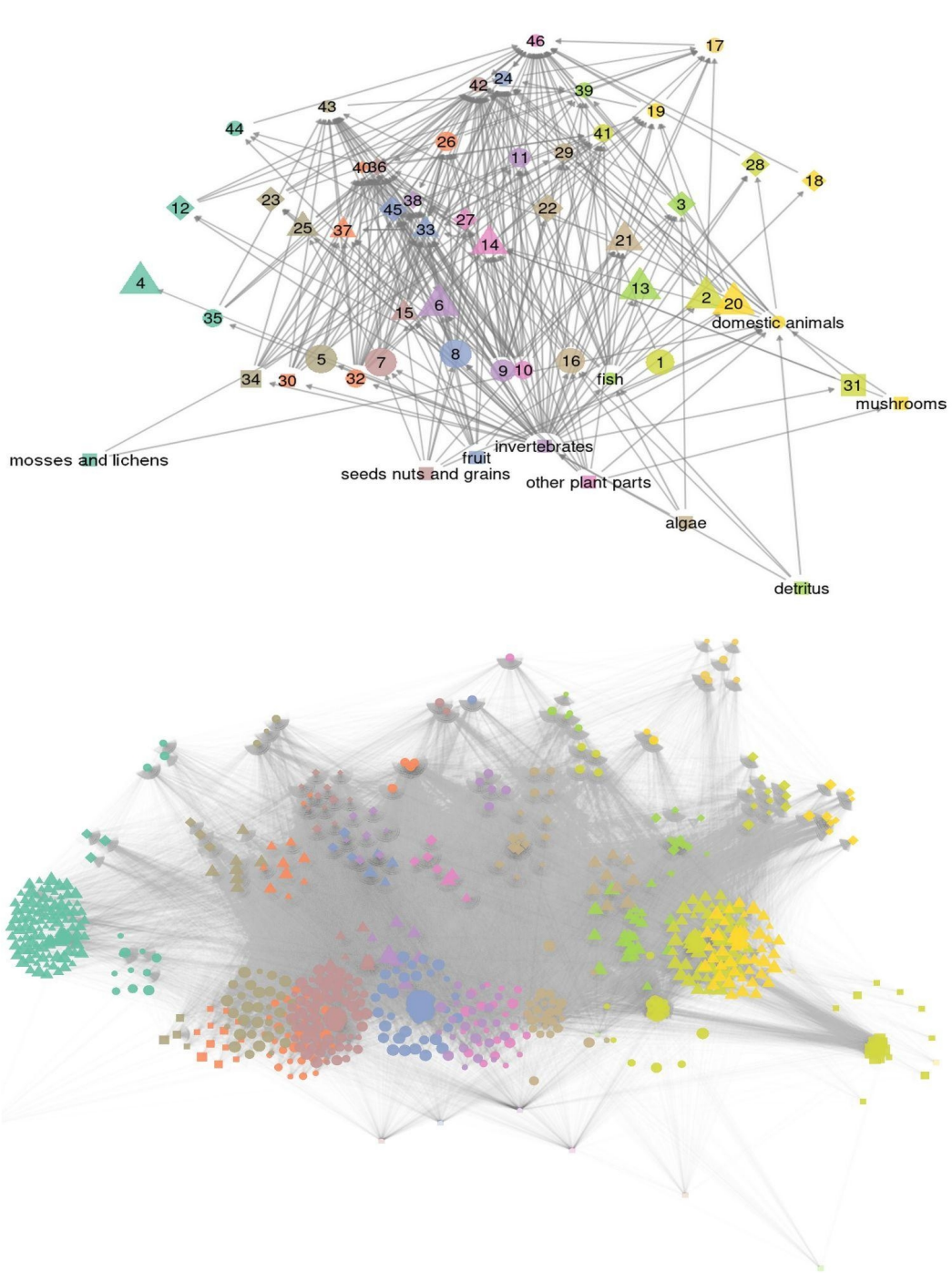
preprocessed_data (Rdata file)



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Figure S1.1. Data preprocessing pipeline (center), potential errors that each step is meant to control (left) and the websites where our material is provided for reproduction (right).

Appendix S2 - metaweb details



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 726 **Figure S2.2** The metaweb of trophic interactions of our 756 European tetrapod species and
 727 their 46 trophic groups. Top: The meso-scale metaweb where each node is one trophic group
 728 numbered as in Table S2.1, and identified by a combination of shape and colour. The vertical
 729 positioning is based on the trophic level, while the horizontal one is based on the proximity in
 730 the network (more connected groups are more aligned than non-connected ones). Diets are
 731 included as basal nodes. Each arrow indicates trophic interactions between species of two
 732 groups (going from prey to predator). Bottom: The micro scale metaweb where each node is
 733 one species and species belonging to a same trophic group are aggregated into clusters (group-

734 TL-tsne method of the R package metanetwork) with the same trophic group shape and colour
 735 code as in the above Figure.

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Group	nSpecies	Most frequent species	Most common class
46	1	Bubo bubo	Aves
17	6	Accipiter gentilis	Aves
24	1	Strix aluco	Aves
42	2	Vulpes vulpes	Mammalia
39	5	Aquila chrysaetos	Aves
43	3	Felis silvestris	Mammalia
19	2	Falco peregrinus	Aves
44	3	Circaetus gallicus	Mammalia
41	4	Ciconia ciconia	Aves,Mammalia
26	4	Corvus corone	Aves
29	4	Milvus milvus	Aves
11	5	Buteo buteo	Aves
28	11	Circus aeruginosus	Aves
36	11	Malpolon monspessulanus	Reptilia
40	2	Dolichophis caspius	Reptilia
18	9	Hieraaetus pennatus	Aves
23	3	Athene noctua	Aves
38	7	Vipera berus	Reptilia
3	11	Larus canus	Aves
12	3	Accipiter nisus	Aves
22	12	Chroicocephalus ridibundus	Aves
45	3	Lanius excubitor	Aves
27	4	Lanius collurio	Aves
25	7	Nucifraga caryocatactes	Aves
33	4	Timon lepidus	Reptilia
37	9	Coronella girondica	Reptilia
21	9	Ardea cinerea	Aves
14	3	Garrulus glandarius	Aves
4	101	Cuculus canorus	Mammalia
13	23	Vanellus vanellus	Aves
2	67	Columba palumbus	Aves
20	48	Gallinago gallinago	Aves
6	9	Turdus merula	Aves
15	11	Eliomys quercinus	Mammalia
35	11	Anguis fragilis	Reptilia
8	54	Fringilla coelebs	Aves
5	31	Hirundo rustica	Aves
16	27	Bufo bufo	Amphibia
1	23	Gyps fulvus	Amphibia
7	77	Parus major	Aves
10	24	Crocidura russula	Mammalia
9	22	Apodemus sylvaticus	Mammalia
32	35	Zootoca vivipara	Reptilia
34	4	Chalcides striatus	Reptilia
30	12	Chalcides bedriagai	Reptilia
31	29	Lissotriton vulgaris	Amphibia

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739 **Table S2.1.** The 46 trophic groups of the European tetrapod metaweb as defined in O'Connor et
 740 al. (2020) and represented in Figure S2.2-bottom above and Figure 4 of the main manuscript.

741 Groups are ordered by decreasing average trophic level. The table also shows their number of
 742 species (of the 756 studied here), the most frequently present species across the 67,051 local
 743 food-webs and the most common taxonomic class of the group.

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745 **Appendix S3- Land systems and study area coverage**

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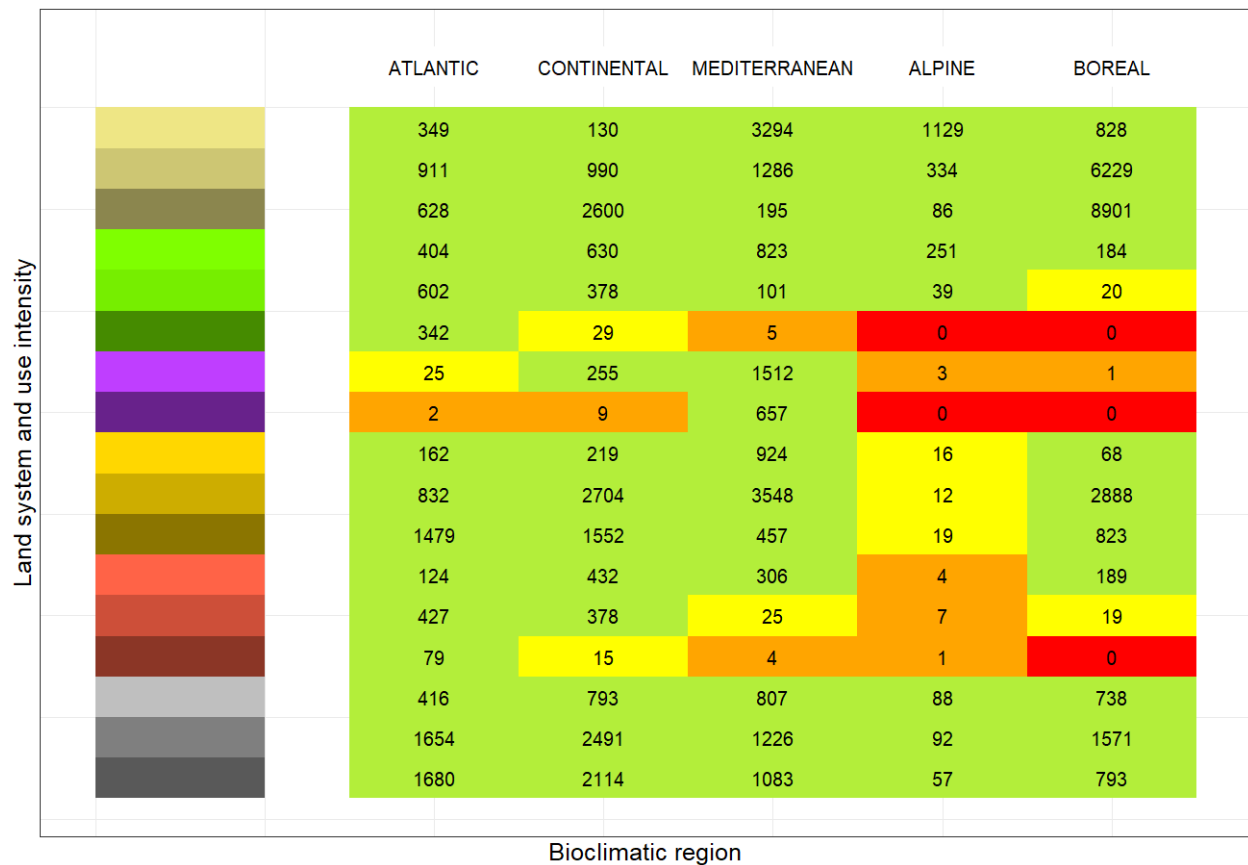
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land uses	Composition	Land management intensity classes	Indicators of intensity used
1. Forest	All forests except some clear cuts	Low, medium, high	Wood production, probability of primary forest
2. Grassland	All grasslands excluding grassed wetlands	Low, medium, high	Inorganic fertilizer input, mowing frequency, livestock density
3. Permanent cropland	vineyards, olive groves, fruit gardens	Extensive, Intensive	Understory vegetation
4. Arable land	Annual crops (wheat, etc)	Low, medium, high	Inorganic fertilizer input, field size
5. Agricultural mosaic	cropland and grassland	Low, medium, high	Inorganic fertilizer input, field size, livestock density
6. Settlement	Cities and surrounding urban areas	Low, medium, high	Population density, distance from urban core, imperviousness

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Table S3.2. Classification of land uses and land management intensity.

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Figure S3.4. Numbers of 1km² cells per land group (combination of bioclimatic region, land use and land management intensity included in the study) with >70% of all tetrapod species certainly present or absent and a richness >20. Land groups are colored based on their number of cells: No cell (red), 1 to 9 cells (orange), 10 to 29 (yellow) and more than 29 cells (green). We finally kept a total of 67,051 cells for our study, including only the green combinations above and discarding Black Sea and Pannonian regions because they lacked intensity levels for comparison.

Appendix S4- Detailed network metrics per architecture facet

Apex proportion: To define apex species, we first computed species trophic levels (MacKay et al., 2020) given the metaweb completed with species diets, as recommended by Maiorano et al.

770 (2020). There are 10 diets (1) “algae”, (2) “fish”, (3) “invertebrates”, (4) “domestic animals”, (5)
771 “mushrooms”, (6) “mosses and lichens”, (7) “detritus”, (8) “fruit”, (9) “seed, nuts and grains” and
772 (10) “other plant parts”. They were integrated as additional nodes in the metaweb along with
773 trophic relationships between them, that is: (1), (7) is eaten by (2) and (3). (3) is eaten by (2)
774 and (4). (5), (6), (7), (8), (9), (10) are eaten by (4). (10) is eaten by (5). This makes the trophic
775 levels more meaningful, especially for the many tetrapod species that otherwise have no prey
776 among tetrapods, because they can have variable height in the whole trophic chains including
777 non-tetrapod species. We set the trophic level lower threshold of 2.262 to define apex predators
778 in this study, so that the 59 selected species fitted best to those generally qualified as apex
779 predators, including wolf, brown bear, wolverine, foxes, badger, wild cat, eagles, falcons, owls,
780 and macro vipers. We then computed, in each local network, the proportion of apex predators,
781 hereafter called **pApexMeta**.

782 Basal proportions: We computed the proportion of basal species in the local network (species
783 with no prey), called **pBasal**, and the proportion of species that are basal in the metaweb, called
784 **pBasalMeta**. This gives a different perspective as a non-basal species in the metaweb can be
785 locally observed without its prey. By comparing proportions of basal and proportions of apex
786 species between two sets of networks, we can also deduce the variation of proportion of
787 intermediate species.

788 Connectance: We computed the directed connectance of the local network as the average
789 number of prey per species (i.e. the average in-degree, reflecting trophic generalism) divided by
790 species richness, called **dirCon**. This metric captures the density of trophic interactions in the
791 local network and enables to compare the level of generalism independently of richness. We
792 preferred it to the actual average in-degree which tends to scale linearly with species richness
793 and may thus bias our signal here as observed richness is partially biased by heterogeneous
794 sampling effort. Note that we only accounted here for predation on terrestrial vertebrates as we
795 lack data for assessing the full trophic generalism on non-tetrapod species (e.g. invertebrates,
796 marine vertebrates, plants, fungi).

797 Omnivory levels: We computed two metrics for each local network. **omniLvl** takes the average,
798 over globally (in the metaweb) non-basal and non-apex species from the local network, of the
799 standard deviation of prey trophic levels. This metric is based on a continuous view of omnivory.
800 **omniProp** computes the proportion of globally non-basal and non-apex species from the local
801 network that are classified as omnivores, namely feeding on several trophic level intervals. We

802 considered three trophic level intervals: basal (0 to the maximum trophic level of globally basal
803 tetrapods), intermediary (from the latter to the apex trophic level threshold, explained above),
804 and apex (above the apex trophic level threshold). This definition enables us to locally detect
805 surpluses of species that have a potentially broader trophic niche, even though many of their
806 prey are not locally present. As defined here, our omnivory metrics are insensitive to species
807 richness, basal and apex proportions in the local community.

808 Chain indices: For each local network, we computed the longest, the mean, and the standard
809 deviation of trophic chain lengths linking basal and top species, based on directed shortest-path
810 lengths. More precisely, we computed the matrix of shortest-path lengths between basal and top
811 species only. Each row of this matrix corresponds to a basal species (no prey in local network),
812 each column to a top species (no predator in local network) and the coefficient (i,j) indicates the
813 length of the shortest path in the network (trophic chain) starting from basal species i and going
814 to top species j. When no path exists from i to j, it is indicated by an infinite coefficient. Note that
815 species without any prey or predator are excluded. Then, we turned this matrix to a vector,
816 removing infinite coefficients, and summarized it with its maximum (**maxPath**), mean
817 (**meanPath**) and standard deviation (**sdPath**) values.

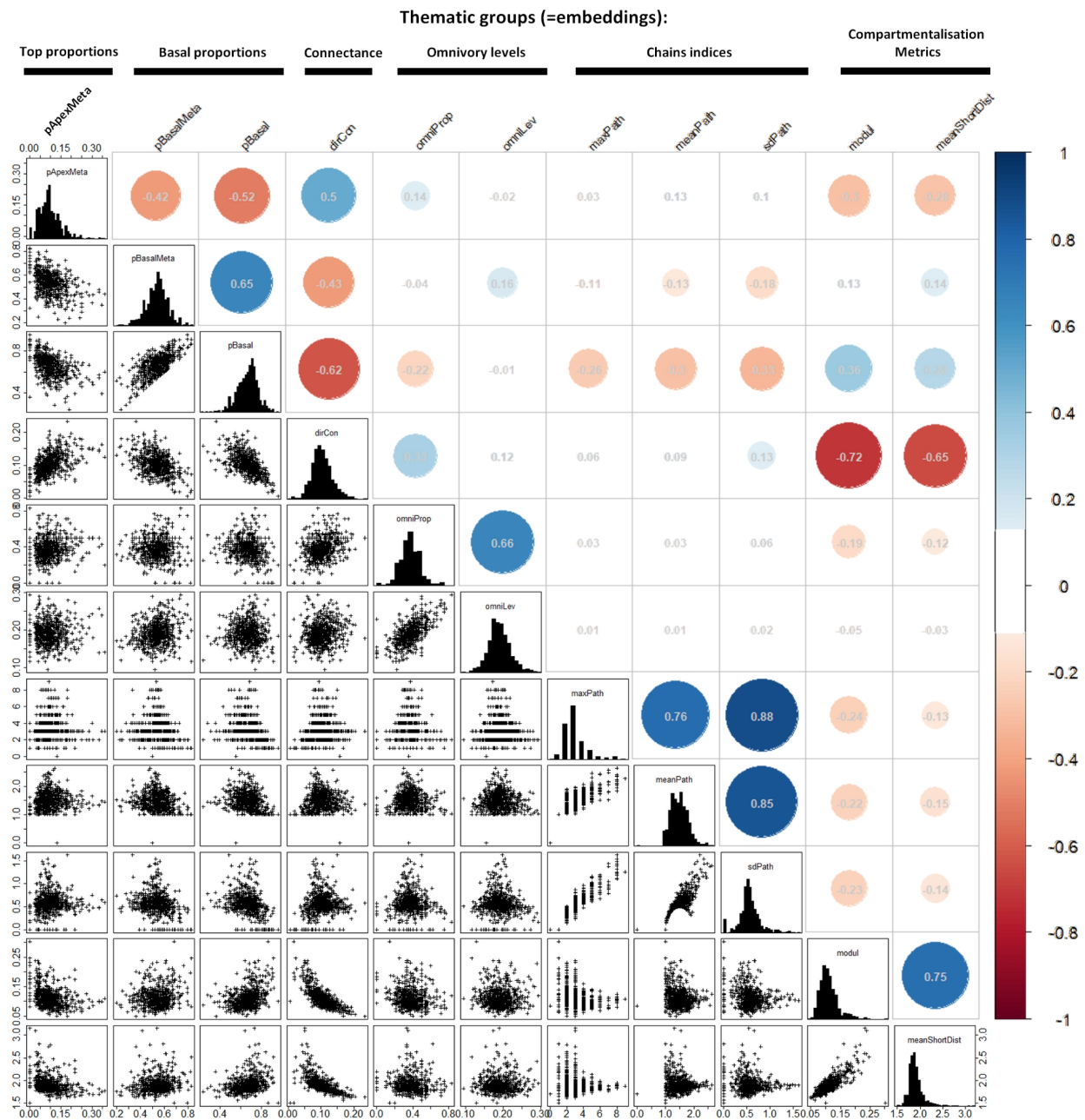
818 Compartmentalisation: We hypothesized that the replacement of trophic specialists with trophic
819 generalists and omnivores would tend to break up compartments within networks, i.e. sets of
820 species with denser interactions between them than with the rest of the network. More precisely,
821 it should translate into a decrease of network modularity (Newman et al., 2006), and a decrease
822 of mean distance between species in the undirected network (where the initial directed edges
823 are replaced by undirected ones). Thus, we computed those two metrics, respectively called
824 **modul**, **meanShortDist**, in this architectural facet.

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826 **Appendix S5- Relationships between network metrics**

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 830 **Figure S5.5.** Relationships between food-web metrics used in this study. Lower triangle: Scatter
 831 plots of metrics values over 650 randomly sampled cells. Upper triangle: Pearson correlations
 832 between metric pairs over all cells.

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837 **Appendix S6- Quantifying and testing effects of land management intensity**
 838 **on food-webs architecture per land use and bioclimatic region**
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	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	-0.372	-0.074	+0.009	-0.038	+0.043
high intensity forest	-0.467	-0.126	+0.081	-0.059	+0
medium intensity grassland	-0.101	-0.083	-0.059	-0.346	
high intensity grassland	-0.116	-0.098			
intensive perma. cropland			+0.017		
medium intensity cropland	-0.14	-0.032	+0.146		+0.065
high intensity cropland	-0.192	+0.049	+0.017		-0.129
medium intensity agri. mosaic	+0	+0.048			
high intensity agri. mosaic	-0.045				
medium intensity settlement	-0.014	-0.087	-0.588	-0.437	+0.055
high intensity settlement	-0.024	-0.148	-0.495	-0.487	+0.065

840
 841 **Figure S6.6.** food-web metrics deviations related to land management intensity, **Part 1: Apex**
 842 **proportion embedding (pApexMeta)**. For each bioclimatic region (columns), land use and
 843 land management intensity level (rows), we show the index of variation along each metric
 844 between the considered intensity level (medium/high) and the reference one (low). This index is
 845 the centroid coordinate of the highest intensity group minus the centroid coordinate of the lower
 846 intensity group, divided by the interquartile range of the metric across all studied cells (as in
 847 **Figure 2**). It indicates the direction of the deviation and its importance compared to the dataset
 848 variability. A blue cell indicates a significant multivariate deviation in the corresponding context,
 849 established with a non-parametric multivariate test, while a grey cell indicates a non-significant
 850 deviation and an empty cell indicates no data. A significant deviation is written in green when its
 851 direction confirms our initial expectation, in red when it contradicts it, and in black for discordant
 852 deviations.

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	+0.044,-0.073	-0.283,-0.09	+0.175,+0.171	+0.142,+0.014	-0.213,-0.265
high intensity forest	+0.11,-0.033	-0.256,-0.064	+0.465,+0.351	+0.127,-0.24	-0.195,-0.3
medium intensity grassland	-0.217,-0.049	+0.023,+0.093	+0.096,+0.003	+0.013,+0.292	
high intensity grassland	-0.1,-0.069	+0.088,-0.033			
intensive perma. cropland			-0.061,-0.205		
medium intensity cropland	+0.073,+0.076	-0.268,-0.217	-0.325,-0.171		-0.082,-0.228
high intensity cropland	+0.198,+0.153	-0.303,-0.279	-0.479,-0.162		-0.028,-0.111
medium intensity agri. mosaic	-0.205,-0.129	-0.112,-0.024			
high intensity agri. mosaic	+0.032,-0.015				
medium intensity settlement	-0.291,-0.214	-0.041,-0.035	+0.109,+0.195	+0.2,+0.273	+0.049,-0.12
high intensity settlement	-0.312,-0.208	-0.083,+0.012	+0.09,+0.216	-0.049,+0.063	-0.032,-0.126

853
854 **Figure S6.7.** food-webs modifications related to land management intensity, **Part 2: Basal**
855 **proportion facet** (pBasalMeta; pBasal).

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	+0.163	+0.14	-0.129	+0.083	+0.17
high intensity forest	+0.23	+0.284	-0.135	+0.245	+0.305
medium intensity grassland	+0.03	+0.094	+0.131	+0.018	
high intensity grassland	+0.039	+0.32			
intensive perma. cropland			+0.117		
medium intensity cropland	-0.152	+0.184	+0.114		+0.29
high intensity cropland	-0.13	+0.296	-0.062		+0.099
medium intensity agri. mosaic	+0.153	+0.043			
high intensity agri. mosaic	+0.155				
medium intensity settlement	+0.039	+0.022	-0.233	-0.329	+0.043
high intensity settlement	+0.081	+0.019	-0.348	-0.315	-0.006

856
857 **Figure S6.8.** food-webs modifications related to land management intensity, **Part 3:**
858 **Connectance embedding** (dirCon; preyPerPred;generalitySD;vulnerabilitySD).

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	-0.025;-0.045	+0.027;-0.036	+0.101;-0.025	+0.183;+0.186	+0.044;-0.053
high intensity forest	+0.131;+0.126	+0.163;+0.058	+0.292;-0.032	+0.45;+0.599	+0.159;-0.009
medium intensity grassland	-0.078;-0.175	-0.053;-0.001	-0.076;+0.126	-0.22;-0.172	
high intensity grassland	-0.077;-0.19	+0.272;+0.079			
intensive perma. cropland			-0.078;-0.004		
medium intensity cropland	+0.133;-0.112	-0.377;-0.298	+0.13;-0.11		+0.2;+0.196
high intensity cropland	+0.125;-0.13	-0.245;-0.214	+0.219;-0.017		+0.15;+0.193
medium intensity agri. mosaic	-0.131;-0.139	-0.085;-0.104			
high intensity agri. mosaic	+0.148;+0.147				
medium intensity settlement	+0.045;-0.029	-0.091;-0.109	-0.105;-0.17	-0.464;-0.218	-0.054;-0.026
high intensity settlement	-0.005;-0.022	-0.172;-0.189	-0.243;-0.326	-0.438;-0.255	-0.116;-0.073

859
860 **Figure S6.9.** food-webs modifications related to land management intensity, **Part 4: Omnivory**
861 **levels facet** (omniLev; omniProp).

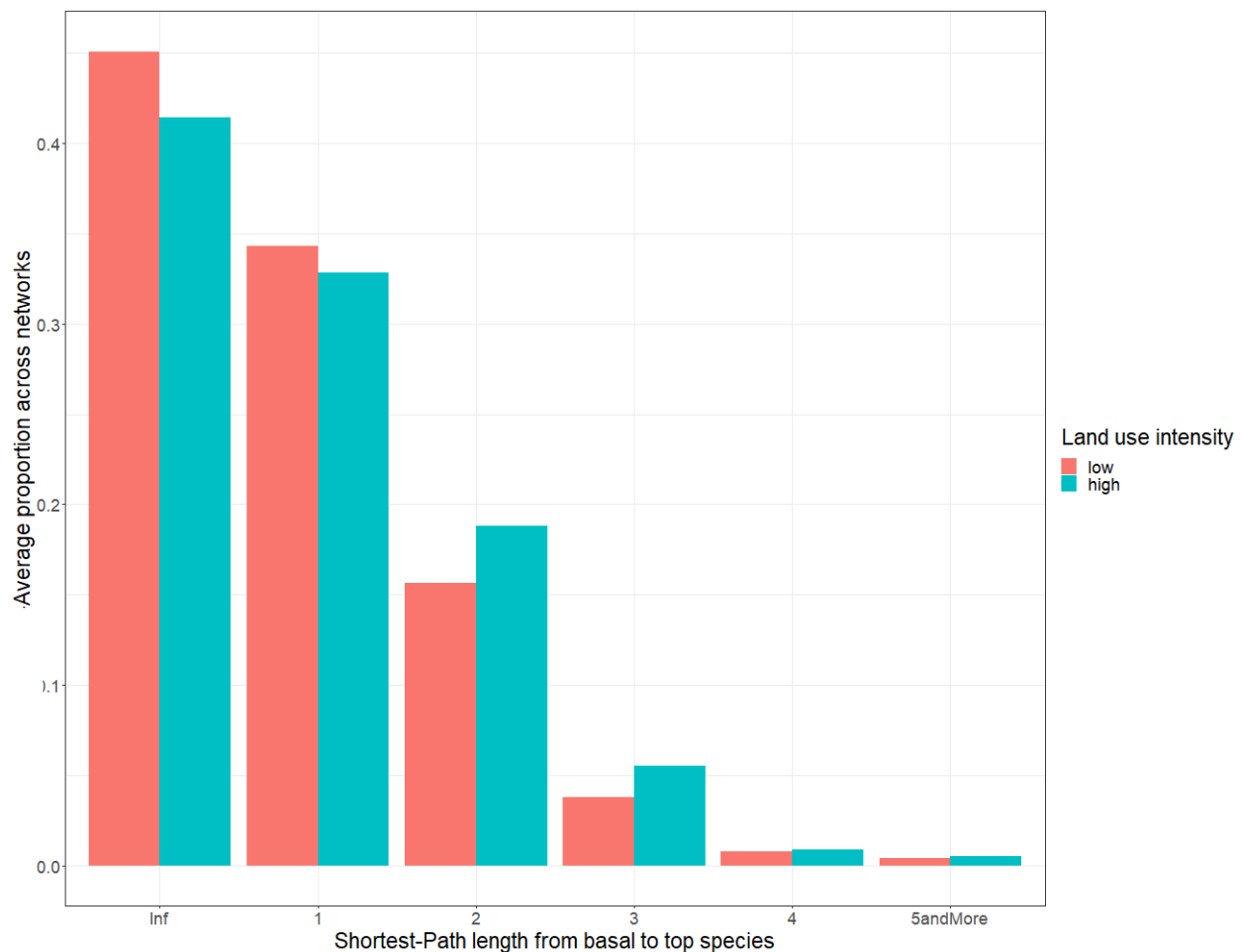
	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	-0.046;-0.052;+0.047	+0.148;+0.144;+0.283	-0.084;-0.098;-0.078	-0.05;+0.102;+0.036	+0.292;+0.332;+0.655
high intensity forest	-0.156;-0.149;-0.104	+0.1;+0.064;+0.211	-0.137;-0.117;-0.03	-0.025;+0.207;+0.224	+0.261;+0.308;+0.596
medium intensity grassland	+0.104;+0.075;+0.201	-0.091;-0.063;-0.106	+0.016;+0.042;+0.054	-0.027;-0.161;-0.127	
high intensity grassland	-0.019;-0.01;-0.019	-0.134;-0.072;-0.162			
intensive perma. cropland			+0.1;+0.134;+0.171		
medium intensity cropland	-0.137;-0.191;-0.282	+0.201;+0.27;+0.418	+0.029;-0.021;+0.053		+0.01;-0.003;-0.013
high intensity cropland	-0.17;-0.24;-0.328	+0.005;+0.042;+0.139	+0.063;+0.022;+0.133		+0.019;+0.007;-0.01
medium intensity agri. mosaic	-0.006;-0.06;-0.007	-0.098;-0.135;-0.211			
high intensity agri. mosaic	-0.006;+0.015;-0.016				
medium intensity settlement	+0.017;+0.096;+0.115	+0.054;+0.057;+0.079	+0.002;-0.065;-0.051	+0.029;+0.044;+0.179	+0.284;+0.396;+0.442
high intensity settlement	+0.03;+0.113;+0.142	+0.079;+0.118;+0.145	-0.021;-0.03;-0.053	+0.024;-0.02;+0.015	+0.329;+0.508;+0.595

862
863 **Figure S6.10.** food-webs modifications related to land management intensity, **Part 5: Chains**
864 **indices facet** (maxPath; meanPath;sdPath).

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	-0.214,-0.02	-0.25,-0.169	+0.129,+0.099	-0.219,-0.049	-0.243,+0.011
high intensity forest	-0.271,-0.085	-0.371,-0.412	+0.305,-0.093	-0.42,+0.018	-0.465,-0.168
medium intensity grassland	-0.007,+0.055	-0.161,-0.161	-0.051,-0.354	+0.016,-0.243	
high intensity grassland	-0.089,+0.004	-0.295,-0.241			
intensive perma. cropland			-0.138,-0.116		
medium intensity cropland	+0.238,+0.371	-0.115,-0.266	-0.056,-0.08		-0.491,-0.509
high intensity cropland	+0.168,+0.312	-0.13,-0.289	+0.208,+0.241		-0.368,-0.347
medium intensity agri. mosaic	-0.026,-0.066	+0.085,-0.013			
high intensity agri. mosaic	+0.017,-0.152				
medium intensity settlement	+0.003,+0.091	-0.116,-0.076	+0.181,+0.363	+0.08,+0.381	-0.21,-0.192
high intensity settlement	-0.061,-0.008	-0.15,-0.07	+0.286,+0.436	+0.141,+0.451	-0.105,-0.104

865
866 **Figure S6.11.** food-webs modifications related to land management intensity, **Part 6:**
867 **Compartmentalization metrics facet** (modul; meanShortDist; maxShortDist).
868

869 **Appendix S7- Shortest-Path lengths distribution in low vs high land**
870 **management intensity**



871

872 **Figure S7.12.** Average proportions of shortest-path lengths from basal to top species in
 873 European tetrapods food-webs under low (red) or high (blue) land management intensity. We
 874 used a weighted average to give an equal weight to each bioclimatic region and land use, i.e.
 875 we averaged proportions over networks in the same bioclimatic region, land use and land
 876 management intensity, before averaging over all networks in the same land management
 877 intensity.

878

879 **Appendix S8- Effect of land management intensity on landscape**
 880 **fragmentation per land use and bioclimatic region**

881

882 We computed for each study cell three complementary metrics of landscape fragmentation
 883 based on the 36km² square window of cells (9x9 cells) centered on the focal cell:
 884 **patchAntiArea**, **proxToBorder** and **divLandUse**. **patchAntiArea** is the opposite of the number
 885 of cells contained in the homogeneous patch of land system (land use and management
 886 intensity) containing the focal cell. **proxToBorder** is the opposite of the euclidean distance (in
 887 cells) to the closest cell border of this patch. We took the opposite of the last two quantities to
 888 ensure that an increase of value indicates higher fragmentation. **divLandUse** is the number of
 889 distinct land system (land use and management intensity) in the 8 adjacent cells to the focal
 890 one. The mean variation of each fragmentation metric related to higher land management

891 intensity and the significance of the multivariate deviation are reported per land group in **Figure**
 892 **S6.11**.

	ATLANTIC	CONTINENTAL	MEDITERRANEAN	ALPINE	BOREAL
medium intensity forest	+4.297;+0.008;+0.438	+8.927;+0.153;+0.244	+17.538;+0.202;+0.591	+16.725;+0.15;+0.757	+0.03;+0.017;+0.215
high intensity forest	-3.742;-0.038;-0.021	-4.378;+0.093;-0.087	+14.011;+0.196;+0.669	+19.688;+0.115;+1.092	-13.593;-0.083;+0.053
medium intensity grassland	-7.735;-0.039;-0.235	-4.638;-0.007;-0.084	+6.102;+0.04;+0.281	+4.603;+0.022;-0.231	
high intensity grassland	-20.038;-0.131;-0.704	-20.301;-0.227;-0.968			
intensive perma. cropland			-5.296;-0.061;-0.207		
medium intensity cropland	-13.167;-0.085;-0.361	-15.126;-0.154;-0.72	-17.607;-0.203;-0.725		-8.957;-0.03;-0.474
high intensity cropland	-20.349;-0.134;-0.551	-7.232;+0.004;-0.277	-4.596;-0.069;-0.358		-0.821;+0.004;-0.114
medium intensity agri. mosaic	-2.918;-0.012;-0.409	-0.704;+0.002;-0.224			
high intensity agri. mosaic	-4.142;+0;-0.318				
medium intensity settlement	-8.373;-0.014;-0.116	-6.621;-0.01;-0.205	-7.076;-0.01;-0.322	-5.337;-0.022;+0.042	-8.227;-0.028;-0.293
high intensity settlement	-24.051;-0.289;-1.069	-18.785;-0.229;-1.127	-14.258;-0.144;-0.891	-3.864;-0.035;+0.025	-7.714;-0.048;-0.68

893
 894 **Figure S8.13.** Landscape fragmentation metrics modifications related to land management
 895 intensity (patchAntiArea; proxToBorder; divLandUse). For each bioclimatic region (columns),
 896 land use and land management intensity level (rows), we show the mean variation along each
 897 fragmentation metric when taking the low intensity level as reference under constant land use
 898 and bioclimatic region. A blue cell indicates a significant multivariate deviation from the low
 899 low intensity level, established with a non-parametric multivariate test, while a grey cell indicates a
 900 non-significant deviation and a blank cell indicates no data. A significant deviation is written in
 901 green for a fragmentation increase (all metrics together), in red for a decrease, and in black for
 902 contrasted deviations.

Appendix C

Supplementary Materials for Chapter

4

Here, I include a study led by Yue Dou (in preparation for submission to *Global Environmental Change*) on modelling alternative land use change pathways that implement the EU Green Deal targets through the lens of the Nature Futures Framework. The work I presented in Chapter 3.4 is based on these land use change scenarios.

In this article, we used a spatial-explicit land system simulation model, CLUMondo to project European landscape changes up to 2050. We highlighted the importance of normative appreciations: Under the same societal demands and environmental targets, there are alternative land use pathways into the future, depending on how we prioritize the conservation purpose and how people appreciate nature's value. This is conducted using the Nature Future's Framework from IPBES, which reflects three dominant views of people's relations to nature: Nature for Nature, Nature as Culture, and Natural for Society where we used different spatial criteria to represent. The three nature futures scenarios, although sharing similar overall patterns, differ up to 40% land use spatially. The local land use trade-offs across three scenarios are mostly found in the South and East of Europe, where there are more biodiversity hotspots and remaining natural landscapes. To the best of our knowledge, this work is the very first to simulate plural land use futures, which is fundamentally different from the other scenario studies that compare projections from different socio-economic and climate settings.

For this study, I performed a European-wide prioritisation for terrestrial vertebrate species that was used as an input for the Nature for Nature scenario. I also contributed to reviewing and editing the manuscript.

1 Using Nature Futures as a lens for developing European land use scenarios

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12

13 Abstract

14 Ambitious international targets to protect and restore biodiversity have been set,
15 including the Convention on Biological Diversity's post-2020 targets and the
16 European Union's Green Deal. Yet, it is not clear how environmental targets can
17 be implemented across space, through land cover and land use change. Land
18 system scenario studies are needed address this gap.

19 We used CLUMondo, a spatial-explicit model to simulate land system pathways
20 for Europe until 2050. The model builds on current land system representations
21 of Europe and explores how and where environmental targets can be implemented
22 while delivering projected commodity demands by the SSP framework. We
23 created three alternative pathways to achieve the EU targets based on the Nature
24 Future's Framework, favoring landscapes providing carbon, species conservation,
25 or cultural heritage respectively.

26 Our results show that, irrespective of the NFF perspective, meeting
27 environmental targets will require European landscapes to change. In some areas,
28 commodity demands conflict with reaching the environmental targets. Although
29 similar land use changes (e.g., preserving natural grasslands and forests through
30 agricultural and forest intensification) are observed under different perspectives,
31 their magnitude and spatial distribution differ.

32 As different values and priorities may be claimed on land use, we perform
33 simulation studies with different ways to appreciate nature and reflect on how
34 these emerging land use pathways can enable a more comprehensive evaluation
35 of future biodiversity changes and collective well-being.

36 1. Introduction

37 Biodiversity loss is one of the major problems that society needs to tackle urgently.
38 Human activities including harvest and extraction have caused land cover change, habitat
39 fragmentation, land degradation, which are casting increasing pressure on biodiversity
40 (Newbold et al. 2015, Kehoe et al. 2017, Winkler et al. 2021). Scientists, policymakers, and
41 practitioners have set ambitious targets at both regional and international scales, to overcome
42 the threats to biodiversity due to environmental degradation and climate change (Pattberg et al.
43 2019, Maron et al. 2021). For example, the Convention on Biological Diversity (CBD) and the
44 European Union's Green Deal both have several transformative targets, relating to no-net-loss
45 of natural areas, the extension of protected areas to cover 30% of all land, the expansion of
46 forested area, and reduction of nitrogen use. All these targets imply a need for drastic
47 reconfiguration of the way our land is currently used and managed.

48 There is growing recognition of landscape changes in biodiversity assessment. Various
49 facets of land system change, as the outcome of different human activities altering the land
50 cover and use, can affect species and biodiversity. Direct human encroachment on habitat leads
51 to suitable habitat loss and fragmentation (Powers and Jetz 2019, Gonçalves-Souza et al. 2020).
52 While the current trend already shows land-use intensification may have surpassed the
53 magnitude of land cover change (Zabel et al. 2019, Hu et al. 2020), unsustainable management
54 and intensive use of land will degrade ecosystems thus affecting species interactions (Newbold
55 et al. 2015, Kehoe et al. 2017, Beckmann et al. 2019, Horák et al. 2019). Landscapes also
56 provide several essential services and functions to human society. Projected future societal
57 changes of population, economy, behaviors call for a growing demand on land use to produce
58 sufficient shelter, crop, livestock, and forest products. For example, the shared socio-economic
59 pathways projections (SSPs) estimate a 20% increase in wood products from forests in the EU
60 by 2050, mostly resulting from intensively-managed forest plantations (Lauri et al. 2019).
61 Existing land use projections also indicate that the intensification of croplands will likely
62 replace the multi-functional agro-silvo-pastoral mosaics that are traditional Mediterranean
63 landscapes (Malek et al. 2018). All these changes that capture different types of land use should
64 be taken into account when designing future environment protection and assessing the impacts
65 to biodiversity, yet limited studies have done so.

66 The desired landscape future has to balance the competing claims of land resources and
67 achieve synergies from different land use. Besides the direct material and shelter demands, the
68 implementation of the above-mentioned environmental targets also asks for sparing land to
69 protect and restore a healthy living environment for species and human beings. How, and
70 especially where, to implement landscape changes remains, however, unspecified, and is
71 dependent on which landscape services we choose to value as a society (Meyfroidt et al. 2022).
72 Scientists have tried to map key areas for protection and restoration based on different values.
73 For instance, (Strassburg et al. 2020) identified the global priority areas using multiple criteria
74 including sole targets of biodiversity, mitigation of climate change, and minimizing costs
75 respectively, as well as combined targets of biodiversity and mitigation of climate, and all
76 criteria. Single criteria optimization results in wide variation in spatial patterns, and may not
77 perform well for other targets and priorities. At the European scale, (Louise M. J. O'Connor
78 et al. 2021) identified areas that can lead to the most conservation outcomes when considering
79 three different targets of species preservation, the cultural value of landscapes, and the
80 regulating service of ecosystem services. Even using the same targets, the multiple ways of
81 target counting can also lead to substantially different land use patterns, which is proved by a

82 simulation study that used land degradation as a goal (Schulze et al. 2021). Therefore, a
83 comprehensive framework that allows space and guidance to navigate among different
84 appreciations of nature is adopted in this study for future landscape projections.

85 The Nature Futures Framework (NFF) is being developed by a group of experts in the
86 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)
87 to illustrate the different ways in which society can value nature (Kim et al. n.d.). Using a
88 simplified triangle space (Figure 1), NFF places the human-nature relationships at its core and
89 integrates several concepts and definitions such as nature’s contribution to people, good quality
90 of life, and ecosystem services. According to the framework, three primary perspectives
91 capture people’s relations to nature; these have been termed “Nature for Nature”, “Nature as
92 Culture” and “Nature for Society”. This framework has been used to engage stakeholders to
93 explore and co-design plausible futures for protected areas (Kuiper et al. 2021) and can be used
94 as a tool to elaborate different desirable pathways of the future under plural perspectives across
95 stakeholders (Kim et al. n.d., Pereira et al. 2020).

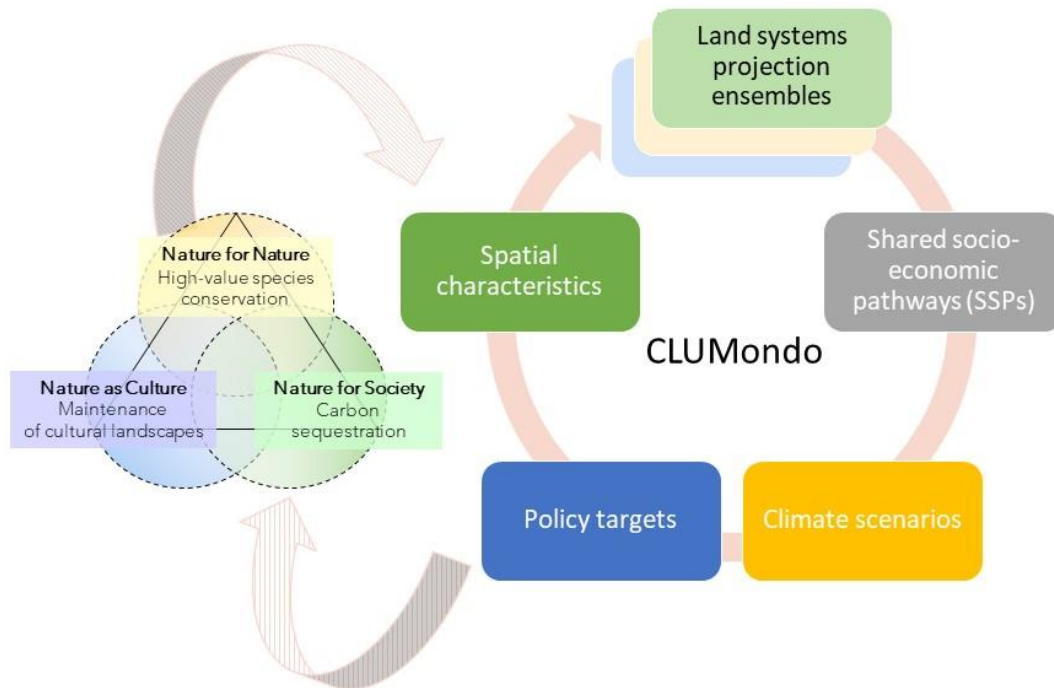
96 Given the plurality of perspectives on environmental priorities, in this paper, we
97 adopted the NFF to guide the future land use change modeling. Under each scenario, we
98 compare how different value perspectives on nature can be used to determine where and how
99 to implement the same environmental targets. While the landscape changes have to produce
100 enough materials and provide shelter to human society, environmental restoration and
101 biodiversity safeguard are also essential. To explore how future land use changes can meet
102 these different targets, we inclusively demonstrated different values of nature appreciation
103 when implementing regional and global environmental targets. We also adopted land systems
104 approach and incorporated the multiple facets of human activities affecting land use. Several
105 plausible land use pathways for Europe are simulated and compared to show the tradeoffs when
106 prioritizing different values, which provides concrete information for stakeholders and policy-
107 makers to navigate among different options.

108 **2. Methods**

109 **2.1 Vision future land system changes through a normative lens**

110 Land system scenarios call for stronger engagement with normative implications
111 (Nielsen et al. 2019, Meyfroidt et al. 2022). Achieving sustainability and biodiversity goals
112 require joint efforts from people and stakeholders who may have fundamentally different
113 relationships with nature. Therefore, future land systems change should take into
114 consideration various visions on the relationships between nature and people.

115 To guide such normative implementation, we applied the Nature Futures Framework
116 (NFF) as a holistic tool. To model how various values will influence the land systems to
117 change, we integrated NFF in the use of CLUMondo, a land systems simulation approach
118 (Figure 1). CLUMondo is a spatial-explicit model that optimizes the spatial allocation of land
119 systems accounting for the local suitability and transition rules, through which it delivers the
120 required service from land use (Malek et al. 2018, Wolff et al. 2018, Schulze et al. 2021).
121 Land systems characterize the human-environmental interactions and represent the causes
122 and consequences in landscape units. Each land system can produce a list of goods and
123 services contributing to the requirement from future projections.



124

125 *Figure 1 Integrating Nature Futures Framework with land system change simulation*

126 To set up the reference scenario, we looked at a specific climate and societal
 127 projection: SSP1 – taken the green road storyline and the corresponding climate scenario
 128 (Representative Concentration Pathway (RCPs) - RCP2.6). A recently developed land
 129 systems classification (Dou et al. 2021) was used as the initial land system distribution.
 130 Therefore, the future land systems have to change to produce enough services for the
 131 sustainability scenario. These changes are also subject to spatial suitability that is quantified
 132 by a list of biophysical and socio-economic factors (Table S1).

133 The outcome from the SSP1 scenario is compared to scenarios in which
 134 environmental targets are additionally implemented. The generic targets and statements in the
 135 broad policy frameworks can be interpreted and implemented differently using different
 136 visions and perspectives framed by NFF (Pereira et al. 2020), therefore leading to various
 137 pathways of land system changes and creating different environmental and social outcomes.
 138 Based on the three core value perspectives in NFF, namely *Nature for Nature*, *Nature as*
 139 *Culture*, and *Nature for Society*, we contrasted the measures and rules of land systems change
 140 to meet the generic policy targets. The societal and policy targets remain the same across
 141 different scenarios, but underlying spatial characteristics and conversion rules change
 142 accordingly to the specific nature of futures value. For example, the target of planting 3
 143 billion new trees, in a “Nature for Nature” future, is implemented through reforestation in
 144 areas with higher species conservation values; while from the “Nature for Society”
 145 perspective, tree plantations are implemented within areas with higher carbon sequestration
 146 potential. Lastly, in the “Nature as Culture” scenario, reforested aim to preserve existing
 147 cultural landscapes, thereby favoring the persistence of traditional, mosaic agricultural land
 148 across Europe.

149

150 2.2 Scenarios defined by societal and environmental targets

151 2.2.2 SSP 1 reference scenario overview

152 To identify policy impacts on environmental sustainability and biodiversity, we
153 developed one reference scenario that is based on the Shared Socioeconomic Pathways
154 (SSP1) (Table 1). This reference scenario was implemented in CLUMondo simulation for a
155 period of thirty-five years, from 2015 to 2050. The storylines in the reference scenario were
156 translated to the following aspects in the model: society demands for land use related goods
157 and services, the productivity from different land systems, and preferred land use transition
158 rules. As the production of goods and services depends on global trade and global demand-
159 supply relations, we based the SSP1 scenario on the results of global integrated assessment
160 models (Table 1) (i.e., IIASA's SUSFANS project (Frank et al. 2018) that specifically
161 elaborated scenarios for Europe and the FAO food and agricultural projections (Food and
162 Agriculture Organization of the United Nations 2018)). These production quantities were
163 supplemented with our interpretations of the storylines in terms of land use conversion and
164 other spatial model settings (Table S4). Each European region (e.g., north, south, west, east),
165 although following the general storylines of the scenarios, has some distinct assumptions to
166 account for the specificities of land use in these regions. Specifically, we separated annual
167 crops (e.g., wheat, rice, maize, barley) and permanent crops (e.g., olives, grapes, fruits) as
168 two demands, because they differ in terms of diets and importance to biodiversity. In
169 addition, the corresponding climate projection, namely RCP 2.6, was used to account for the
170 changing climatic conditions in the reference scenario. Details are documented in **Table S1-**
171 **S6.**

172

173

Table 1 Storyline for SSP 1 reference scenario

GLOBAL MODEL STORYLINE	A slight increase is assumed for both EU's population (7.6%) and economic development. Although international trade is more liberalized with a reduced tariff, the stagnating EU household income and high agricultural production from the rest of the world only increase EU's agricultural demand modestly (3.2%). The shifting social norm to consume less meat contributes to a reduction of livestock products and the higher demand for permanent crops that complements EU's dietary needs. There is also a high demand for wood production caused by the demand for biofuel.
REGIONAL DIFFERENCES	Regional difference is particularly noticeable in the demand of population and agricultural production. A marginal increase in population is anticipated for the whole EU. However, because free movement of people is guaranteed, the east region is having a negative 8% population growth while the other three regions are having positive growth, particularly the north with a 32% increase. While all three regions have a stable increase of annual crop production (6% growth in the west to 12% in the north), the south experiences a 25% decreased demand in 2050 compared to the year 2015. However, south and west have reduced demand for livestock products (i.e., -18.7% and -9.3%) while north and east have

***URBANIZATION
PROCESS***

positive growth. All four regions have increasing demands for forest products.

Environmental awareness and values have become dominant and led to strict environmental legislation toward the protection of natural landscapes, pro-environmental farming strategies, and sustainable food consumption. Environmental protection is implemented in our simulation through strict rules for the urbanization process. To represent the preferred lifestyle in villages and peri-urban, this is implemented in CLUMondo by allowing village and peri-urban land systems to host marginal agricultural activities.

***AGRICULTURAL
CHANGES***

In the simulation, we assumed agricultural production is diverse, innovative, and thriving, focusing on sustainable forms of production. We implemented this narrative in CLUMondo by promoting crop and livestock production in a variety of land systems, particularly the mosaic systems containing forest/shrubs with cropland, and agricultural mosaics of cropland and grassland, instead of focusing on highly specialized cropland and grassland. Although agricultural production will become less profitable in the future, short-term marginalization from currently high-intensity cropland and grassland to low-intensity is not allowed. Over the simulation period, however, re-wilding from high-intensity agricultural land areas to natural areas (e.g., low-intensity grassland and shrubs) is possible. The reduced profit in the agricultural business is compensated through the transition from current industrial farming and grazing systems to more diversified and multi-functional mosaic landscapes, to balance the product quality, quantity, and environmental costs.

***PRODUCTION
EFFICIENCY***

Agricultural productivity changes due to various underline causes: climate change, technology development, decline/improvement of ecosystem service. The regional variation of productivity change, shown in GloBiom, is more visible than the differences between scenarios. Europe's farms benefit from increased productivity in general, yet, in the south crop yield decreased by 14%. We used the productivity change implemented in GloBiom to our land system projections, and assumed that productivity change only occurs on medium to high-intensity agricultural land uses. Productivity of low-intensity agricultural land uses, however, remains the same as no technology development or improvement will be applied on land that is extensive and marginal used.

***CLIMATE
CHANGE
IMPACTS***





The Representative Concentration Pathway (RCPs) - RCP2.6 for Sustainable scenario (SSP1) was selected based on the probability of how RCPs correspond to SSPs and the combinations of other existing land use models (Engström et al. 2016, Brown et al. 2019). Five bioclimatic variables (i.e., bio1, 2, 4, 12, 15), along with 12 other social-environmental variables, were used in our model to predict the suitability of different land systems. Climate projections of these bioclimatic variables were obtained from CHELSA dataset, which is statistically downscaled from Coupled Model Intercomparison Projects (CMIP6) to 30 arcsec, ~1km resolution

(Karger et al. 2017). We extracted the region of Europe from the global projections, and calculated the averaged projections from five climate models for each scenario. Climate change effects were implemented through the spatial preference for different land systems. While other driving factors (e.g., soil characters, elevation, road density) for spatial preference remain constant over time, climate variables are updated annually to calculate the spatial preference map hence affecting the spatial probability of each land system.

2.2.2 Synthesis of environment targets

The post-2020 Global Biodiversity Framework of the Convention on Biological Diversity (CBD) and European Union's Green Deal have set out ambitious plans to overcome the twin challenges of climate change and environmental degradation. Some of their most transformative targets (relating to no-net-loss of natural areas, the extension of protected areas to cover 30% of all land, the expansion of forested area, and reduction of nitrogen use) all imply a drastic reconfiguration of the way our land is currently used and managed. We reviewed and compiled a series of policy targets from the CBD and the Green Deal, and translated them to different targets and rules for land system change. Most of these targets are designed with a timeline to 2030, we then extended the targets to the year 2050 (Table 2).

Table 2 Environmental targets influence future landscape change across Europe (comparing to current condition)

Environmental targets for 2030		For 2050
	(1) Reduce fertilizer use by >20%	1) Reduce fertilizer use by >30%
	(2) Plant 3 billion new trees	(2) Plant 5 billion new trees
	(3) No-net-loss of natural areas	(3) Restoration of natural ecosystems by 20%
	(4) Protect 30% of land	(4) Protect 45% of land

We summarized compatible policies from Green Deal and CBD into three main sectors: **protection and restoration**, **agriculture**, and **forestry** (Table 2). If a specific goal has not been mentioned in (one of) the two policy statements, we used targets from the other policy or assumed a reasonable goal. The action points regarding **protection and restoration** include expanding the current protection area (Natura2000 covering 18%) to cover a total of 30% European land by 2030, and no net loss of natural ecosystems by 2030. After 2030, we assumed about 1% increase of natural areas will be restored annually outside of the protected areas until 2050. For **agriculture**, we selected the policy that aims at reducing the excessive use of nitrogen. The total use of nitrogen in agricultural production should be reduced by 20% by 2030, compared to 2015. Furthermore, we assumed the reduction to be 30% by 2050. Europe also plans to plant 3 billion new trees by 2030 in the **forest** sector according to the Green Deal, which we implemented in the policy scenarios and assumed that 2 billion more

199 trees will be planted between 2030-2050. In addition to the targets in the three sectors, we
200 implemented specific rules addressing the process of **urbanization**. Details of targets
201 implemented in the model as demands can be found in **Table S3**.

202

203 2.3 Model implementation with normative scenarios

204 The comparison between the nature futures scenarios and the SSP1 reference scenario
205 is that, while keeping the same material demands and storylines from SSP1, land system
206 change has to account for additional specific goals and restrictions following the policy
207 statements.

208 From the *Nature for Nature* perspective, priority is given to preserving the intrinsic
209 value of nature and species conservation. To identify the additional protected areas, we
210 identified the top priority areas for expanding the European network of protected areas,
211 considering all vertebrate species known to occur in the study area (Maiorano et al. 2013,
212 O'Connor et al. 2021). Top priorities for expansion complement existing protected areas
213 (Natura 2000 for EU28 countries, and national parks for non-EU countries in the study area).
214 We performed the prioritization using Zonation software (Lehtomäki & Moilanen 2013).
215 Areas with higher gains for the protection of terrestrial vertebrates are given priority to be
216 allocated as protected areas. Restoration of natural habitats also focuses on areas that have
217 high conservation value but are currently occupied by land systems with lower natural
218 components. More trees are planted in forests that are used as natural habitats for species,
219 which are low and medium-intensity forests and not intensively managed forests. Under this
220 perspective, population density in settlement systems is increased over time to permit land
221 sparing for natural landscapes.

222 The *Nature as Culture* perspective focuses on the cultural contexts and highlights
223 Nature's nonmaterial contributions to People. Therefore, when identifying the expansion of
224 protected areas and restoration, areas that have a high capacity of cultural ecosystem services
225 (i.e., food foraging, heritage forests, heritage agriculture, natural tourism) are given priority
226 (Tieskens et al. 2017). However, the additional trees are planted outside of the high cultural
227 value landscapes, since priorities are given to the cultural value appreciation of typical
228 agricultural mosaics. Among the different human settlement landscapes, village landscapes
229 are preferred over peri-urban landscapes, for their higher cultural value.

230 The *Nature for Society* perspective highlights the benefits that nature provides to
231 people and society. The restoration of ecosystems focuses on areas with high carbon
232 potentials but currently occupied by land systems with low carbon storage (Cook-Patton et al.
233 2020). Trees are planted in all forest classes and mosaic systems in areas with high carbon
234 potentials first, under the perspective of prioritizing Nature's regulating contribution to
235 people. Rules of slowly decreasing population density and increasing urban green space were
236 introduced compared to the reference scenarios under this value perspective.

237 Following different spatial priorities, these specific targets were implemented in
238 CLUMondo by two approaches: (1) target measured by numeric indicators, and (2) changes
239 of land system management. For example, the targets of 3 billion new trees and 20%
240 restoration were added in addition to the SSP1 demands. The average value of these
241 indicators in every land system was estimated based on reference datasets (JRC; Crowther et

242 al., 2015; Copernicus). We estimated the tree density in low-intensity forests in Southern
243 Europe is more than 42 thousand, and in forest and grassland mosaic is 18 thousand. The total
244 number of trees from different land systems in 2030 has to be exceeding the 3 billion targets.
245 For the restoration, we counted the areas of low-intensity forest and grasslands and increased
246 the areas by 20% as the demand for natural ecosystem restoration. In other words, the total
247 area of low-intensity forest and grassland has to be 20% more at the end of the simulation
248 than in the initial year.

249 We also represented the land management changes in the model. We assumed that
250 half of the nitrogen application reduction goal is fulfilled by the overall reduction of nitrogen
251 application, while the other half is fulfilled by lowering the unit nitrogen input in the high-
252 intensity cropland system. This is also the case for settlement systems, where we assumed
253 different development patterns. For example, in *Nature for Society* scenario population
254 density for urban and peri-urban decreased by 0.5% every year, which suggests that residents
255 prefer less-dense residential areas and more green space. The sum of these indicators from
256 accountable land systems, however, should meet the change target in each scenario.

257 Land system changes were simulated for each model region and each value
258 perspective accounting for rules from protection and restoration, agriculture, forestry, and
259 urbanization, therefore resulting in three policy scenarios: *a-Nature for Nature* scenario, *b-*
260 *Nature as Culture* scenario, and *c-Nature for Society* scenario (Table 3, Table S7, Figure S3-
261 5). Spatial data of the three categories priority areas for EU28 were from (Tieskens et al.
262 2017, Cook-Patton et al. 2020, O'Connor 2021). Global maps were used for other regions
263 (Balkans, Norway, and Switzerland).

Table 3 General policy statements and implementation in CLUMondo simulation according to the Nature Futures Framework

SECTOR	EU GREEN DEAL	CBD-POST 2020 GLOBAL BIODIVERSITY FRAMEWORK	A - NATURE FOR NATURE	B - NATURE AS CULTURE	C - NATURE FOR SOCIETY
1 STRICT PROTECTION-AREA TARGET	Protect 30% of land in Europe by 2030;	Action Target 2: By 2030, protect and conserve ... at least 30 per cent of the planet with the focus on areas particularly important for biodiversity	The expansion of protected area focusses on priority areas for terrestrial vertebrates	The expansion of protected area focusses on priority areas for cultural NCPs	The expansion of protected area focusses on priority areas for regulating NCPs (carbon storage)
2 RESTORATION-AREA TARGET BY 2050	Restoring degraded ecosystems	Increased extent of natural ecosystems by at least 15%	No net loss of natural areas by 2030, and around an annual 1% increase after 2030. We consider low-intensity forest and grassland areas as natural landscapes. The restoration focuses on areas having specific conservation values that currently are occupied by land systems with low natural values	The restoration focuses on areas with high cultural value but that are currently occupied by land systems with lower natural values	The restoration focuses on areas with high carbon potential and that are currently land systems with low carbon storage capacity
3 AGRICULTURE	...resulting in the reduction of the use of fertilisers by at least 20% by 2030	By 2030, reduce pollution from all sources, including reducing excess nutrients by 40%	Total nitrogen application from all agricultural systems reduce by 10%, and the application from high-intensity cropland reduce by 10% by 2030. By 2050, an additional 10% decrease in nitrogen application		
4 FORESTRY	Plant 3 billion new trees by 2030; we assumed 2 billion more trees will be	Increase in secondary natural forest cover	Accounting for trees in all land systems. Forest expansion (e.g., low and medium	Forest restoration happens outside of high cultural value landscapes	Accounting for trees in all land systems. Forest expansion (e.g., low-

	planted by 2050		forest) focus on areas with high species conservation values.		high intensity and forest mosaics) focus on areas with high carbon potentials
5 URBANIZATION		By 2030, increase benefits from biodiversity and green/blue spaces for human health and wellbeing, including the proportion of people with access to such spaces by at least [100%], especially for urban dwellers.	Increase the population density in all urban classes; allow villages to be bewildering after a certain long period.	Preferences for villages over peri-urban.	Slow decrease of urban population density and increase of urban green space.

3. Results

3.1 Alternative land use patterns are required to meet the environmental targets

3.1.1 More natural forest and grassland need to be preserved

Under the SSP1 scenario (Figure 3), there will be more forest areas but fewer natural (low-intensity) forests (4% loss) in 2050 in comparison to 2015 (Figure 2). In contrast, the three nature futures scenarios all result in increasing low-intensity forest. The expansion of low-intensity forests ranges from 1% in the Nature as Culture scenario to 10% in the Nature for Nature scenario. This increase mainly occurs through the de-intensification of medium and high-intensity forest classes.

The difference between SSP1 and nature future scenarios is even more pronounced for grassland areas. In the SSP1 scenario, besides the loss of natural grassland (13%), medium and high-intensity grassland will lose three-quarters of its area, whereas nature futures scenarios expand, rather than decline, low and medium intensity grasslands. The Nature as Culture scenario is associated to the largest natural grassland areas in 2050 (i.e., 84.8% higher compared to the baseline and 113% times bigger than the SSP1 scenario). The large preservation of low-intensity forest and grassland areas in the NFF scenarios is the result of the explicit environmental target of no-net-loss and restoration, as these land systems are considered to be natural ecosystems in the model.

The change of use intensities contributes to the restoration of forests, however, the restoration of natural grassland is most frequently the result of conversion from forest/grassland mosaics instead of changing the intensity of use (except for the Netherlands, where de-intensification affects 25-47% of grassland areas). For example, around 34% of the low-

intensity grassland was forest/mosaic land use in 2015 under the Nature for Nature scenario (Figure 4).

3.1.2 Croplands to undergo simultaneous intensification and multi-functional mosaic landscape expansion

All cropland areas decreased in the SSP1 scenario, mostly within the low and medium intensity classes (together by 74.2%). Agricultural mosaics that constitute cropland and grassland have expanded towards high-intensity (three times bigger than current) and decreased (63%) in low and medium-intensity classes.

The three nature futures scenarios show a different pattern compared to the SSP1 scenario. Both low and medium-intensity cropland decrease, but high-intensity cropland increases up to 37.6%. This occurs as large areas of forest/cropland mosaics and medium intensity cropland are converted to high-intensity cropland (Figure 4). Simultaneously, large quantities of medium-intensity cropland are also converted into forest/cropland mosaics in all three nature futures scenarios, leading to greater extents than under the SSP1 scenario. The spatial coverage of this multi-functional land system almost doubles (97%) in the Nature as Culture scenario and is 1.4 times larger in the Nature for Nature scenario (Figure 3). Agriculture is becoming either highly intensively managed or converted to a multi-functional landscape.

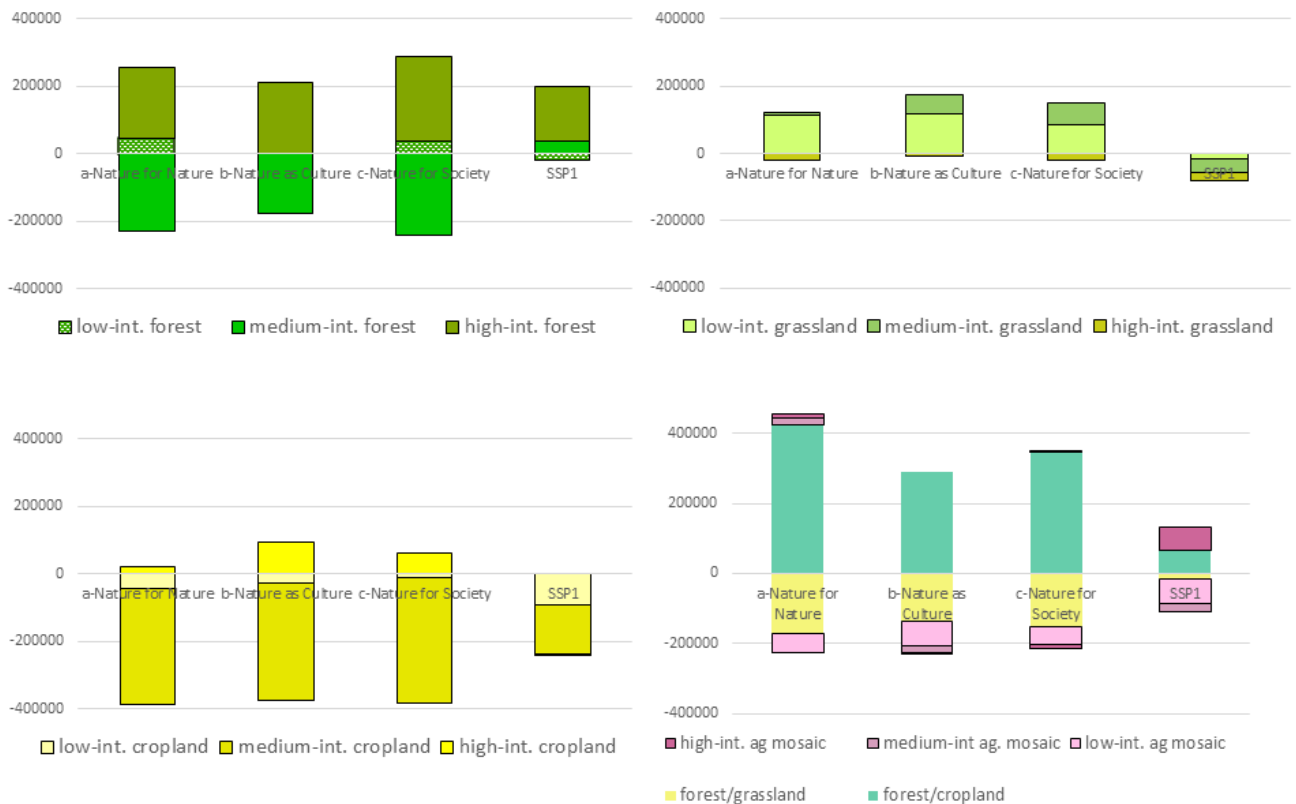


Figure 2 Amount of land systems changes in SSP1 and three nature futures scenarios

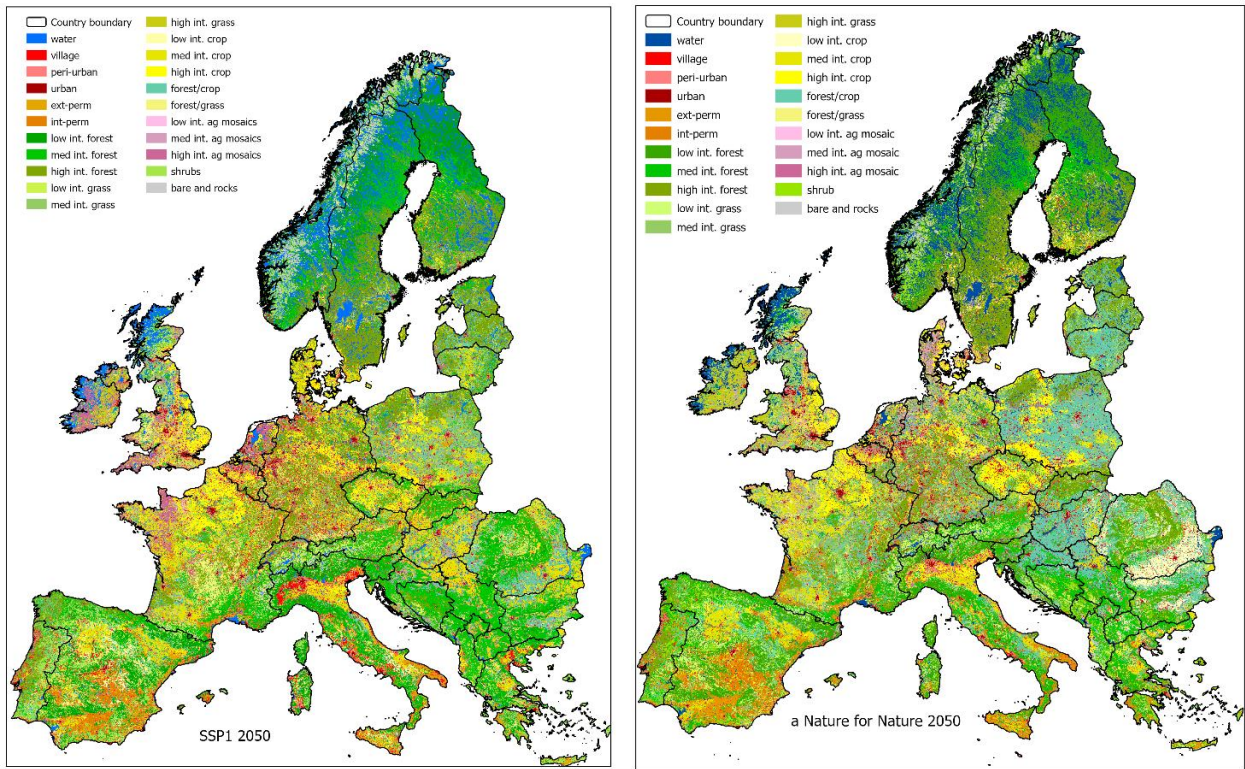


Figure 3 land system simulation of SSP1 and Nature for Nature scenario

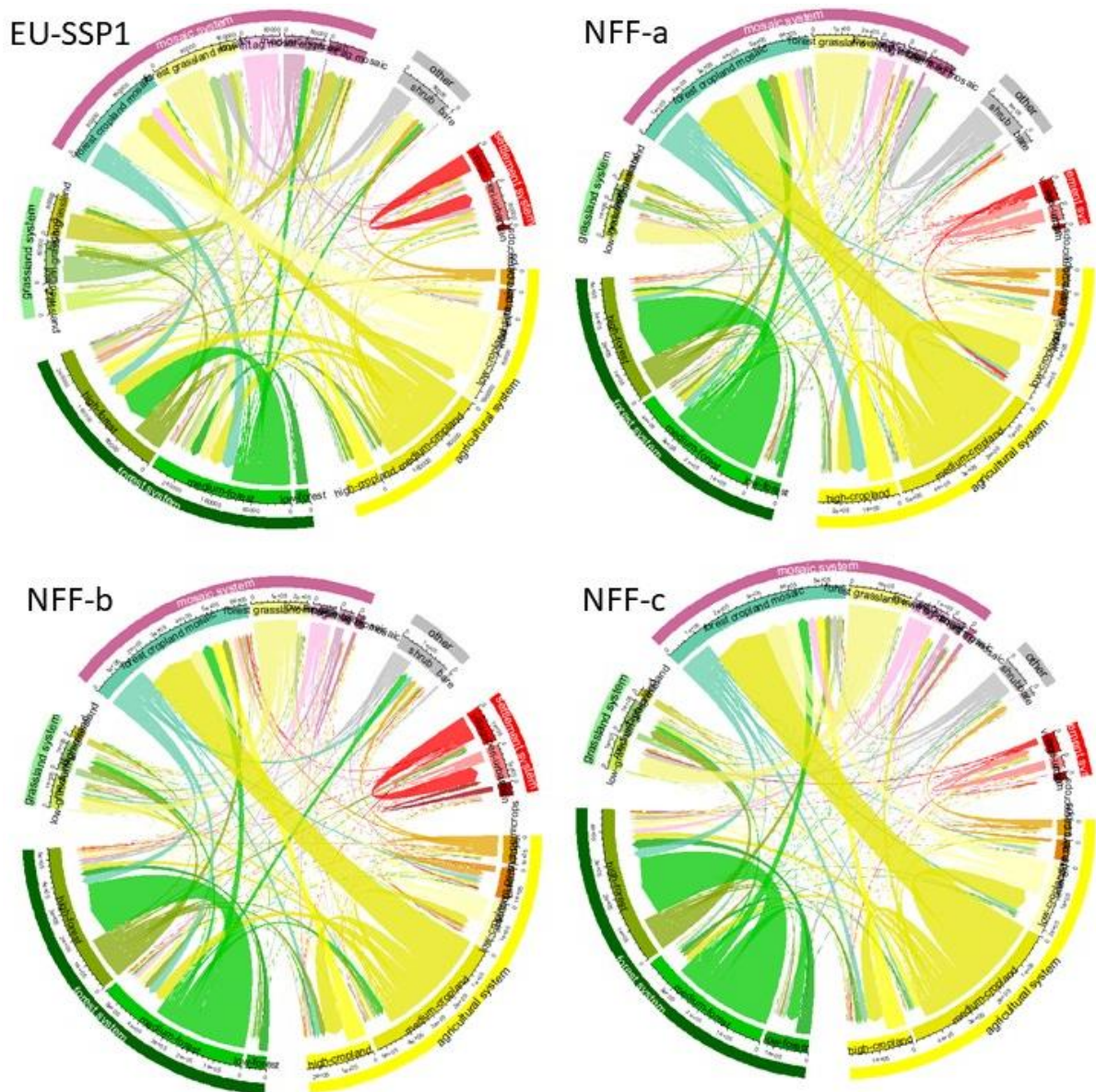


Figure 4 Land systems change trajectories in SSP1 and three nature futures scenarios. Land system changes include both land class conversion and intensity changes within the same class.

3.2 Tradeoffs and synergies across Nature futures scenarios

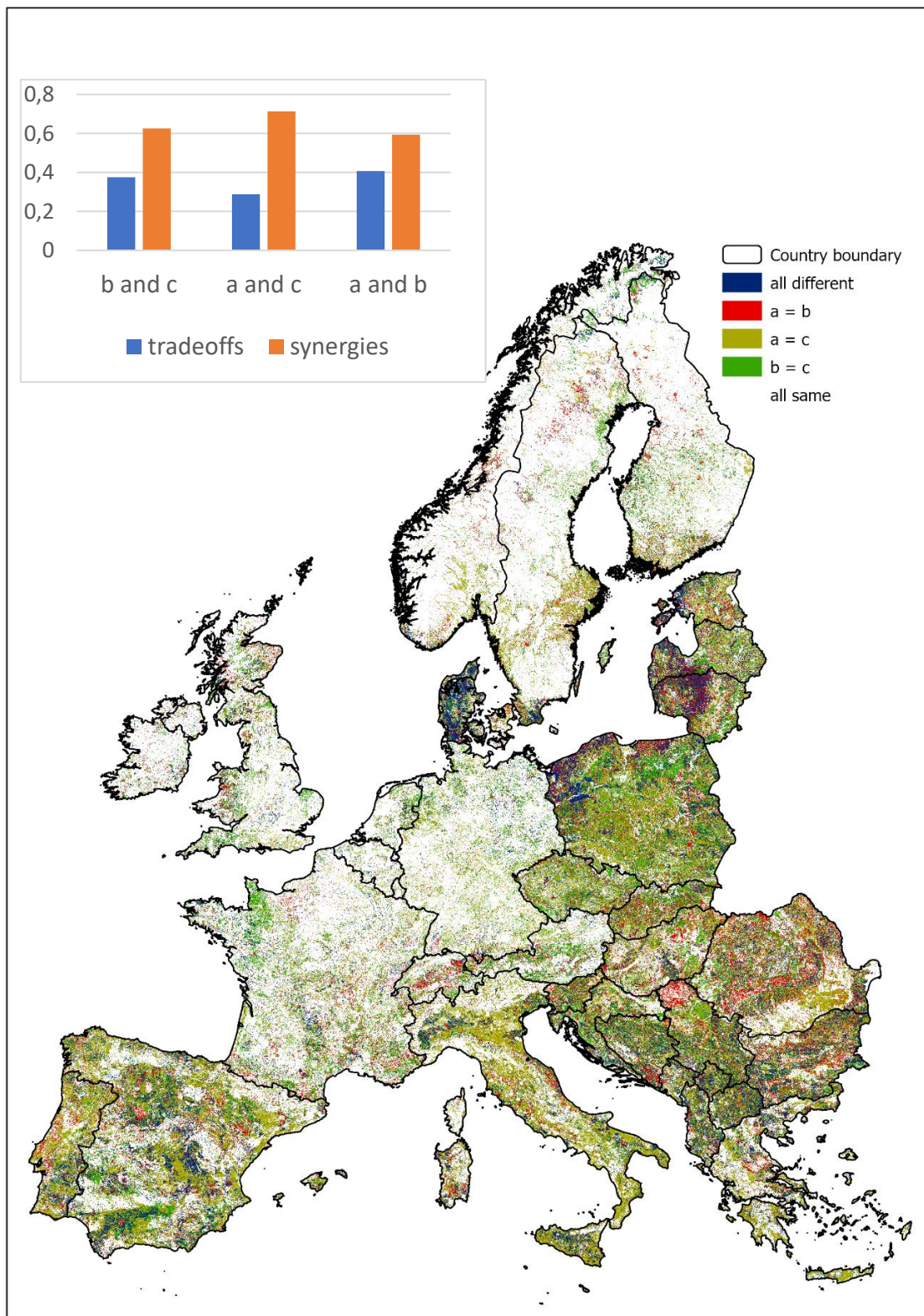


Figure 5 Consistent land system classes across three Nature Futures scenarios (a Nature for Nature, b Nature as Culture, c Nature for Society). Imbedded figure shows the portion for same and different land systems between two compared scenarios.

3.2.1 Spatial synergies

Overall, more than half of the landscapes across Europe share the same land use across the three nature futures scenarios (Figure 5). Most areas in the west and north of Europe are more likely to remain unchanged or convert to the same land system classes regardless of the preferred value. However, large diverging patterns of land system trajectories are found in the south and even more so in the east. Several land system classes stand out in the consistent landscapes: low and high-intensity forest, low-intensity grassland, medium and high-intensity croplands, and forest and cropland mosaics. Low-intensity forest and grassland achieve spatially consistent maybe because of the existing Natura 2000 network, along with the strict environmental targets. The conversion from low and medium-intensity forest to high-intensity forest consistently occurs primarily in Sweden, Finland, Norway Romania, and France, while patterns of forest de-intensification largely occur in Romania under all NFF scenarios (10-14% of all de-intensification). Also consistent across all three NFF scenarios are areas of significant concurrent cropland expansion and intensification, occurring in Spain, Poland, and the Czech Republic.

Within the three nature futures scenarios, the Nature as Culture scenario is the one that differs most from the other two scenarios (Figure 5). More than 70% of the landscapes reach the same land uses between Nature for Nature and Nature for Society scenarios, while their agreement with Nature as Culture is 10% less.

3.2.2 Areas with different trajectories

There are large local variations of land systems shown across the three scenarios. Most of these differences are shown in the south and east of Europe (Figure 6 and Figure 7). For example, many of the medium-intensity forests and medium-intensity cropland in Spain in the Nature for Nature scenarios are modeled into forest and crop mosaics in Nature as Culture and Nature for Society scenarios (Figure 6). In contrast, a Nature for Nature scenario favors the expansion of mosaics in Poland (Figure 7) rather than in southern European countries.

Low-intensity grassland in Portugal simulated in Nature for Nature scenario are changed into forest and grassland mosaics in Nature for Society scenarios. Different intensities of cropland are found in the valley in Italy across the three scenarios, so are the extensive and intensive permanent crops in south Italy. A Nature for Nature scenario foresees the greatest extent of new grassland emerging primarily in southern and eastern European countries, while the other two nature futures scenarios see greater grassland expansion in northern and western Europe respectively, rather than in the south. This may be explained by the higher species values in the south that is used in Nature for Nature scenario. While the Nature as Culture scenario sees forest de-intensification occurring within central-eastern European countries (Romania, Poland, Slovakia, and Hungary), the other two scenarios foresee forest de-intensification occurring primarily also in Finland, Sweden, and Bosnia. Another profound difference in the Nature as Culture scenario is that all large urban areas are de-intensified into peri-urban areas in the east. This may not happen in reality, but it also reflects the tension to fulfill all targets required from land systems change.

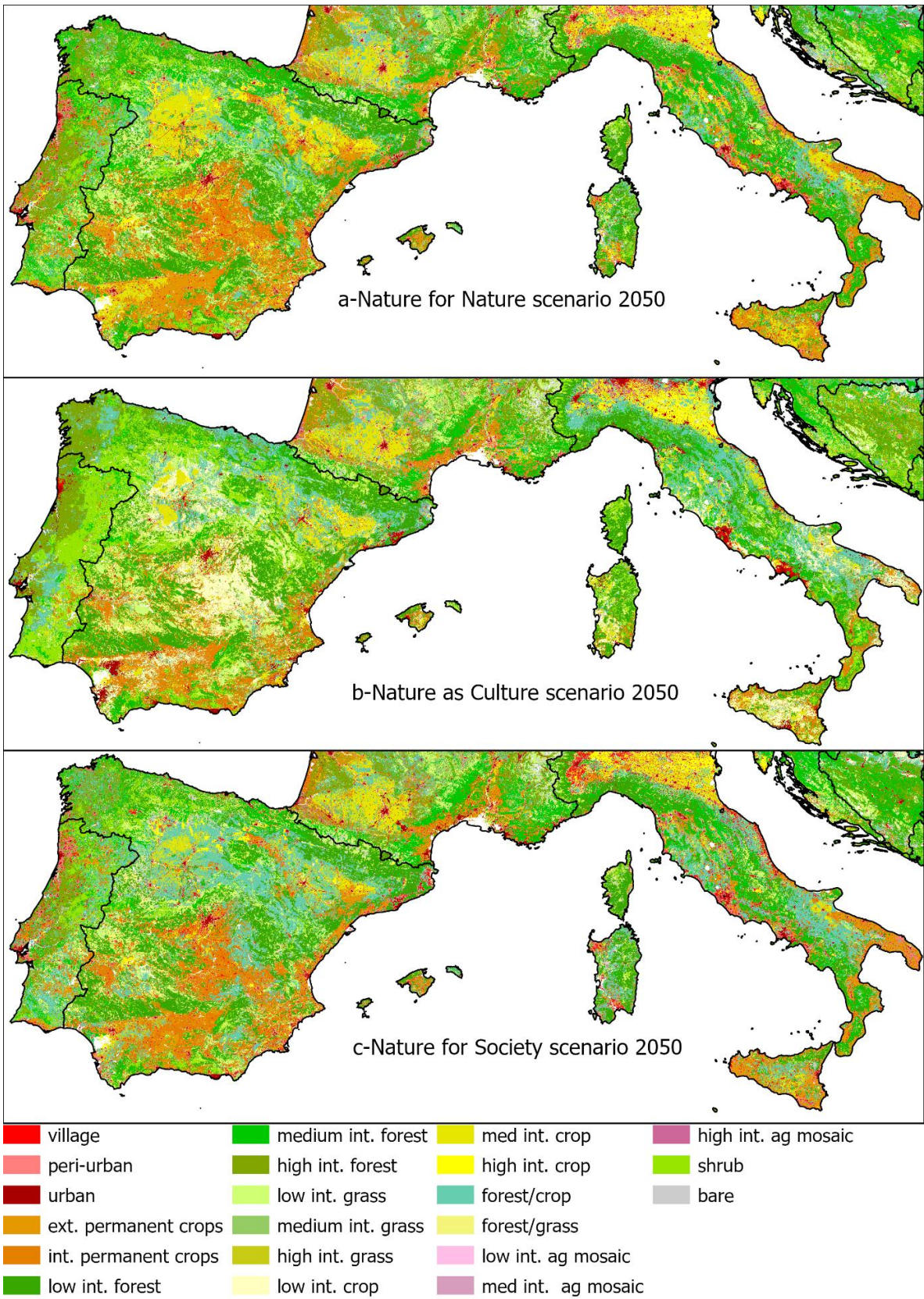


Figure 6. Modeled different land systems (2050) in southern Europe (Portugal, Spain, Italy) across three Nature Futures scenarios. (a) Land systems in Nature For Nature scenario; (b)

Land systems modeled for Nature as Culture scenario; (c) Land systems modeled for Nature for Society scenario.

4. Discussion

4.1 Importance of additional environmental targets

Environmental targets established under the Convention on Biological Diversity and the European Union's Green Deal imply a structural reconfiguration of Europe's current landscapes. In this study, we investigated if and where future landscape changes can take place to deliver all targets. We compared land system changes in Shared Socio-economic Pathways 1 (SSP1)– Taking the green road-- and the changes in nature futures scenarios when additional environmental targets are implemented. Our simulations, when comparing the SSP1 and the nature futures scenarios, show the importance of having these additional targets. The most striking effects appear on grassland systems. Without the implementation of “no-net-loss” and “restoration” targets, Europe would lose a quarter of its grassland landscape due to the declining demand for livestock and growing demand for wood and crop production in SSP1. Similar patterns also appear as the implementation of environmental targets changed forest intensification from low and medium-intensity forest to forest plantations that the main purpose is wood production and serves little to no role in maintaining biodiversity (Chaudhary et al. 2016, Horák et al. 2019).

Besides the forests and grassland systems, the implementation of additional targets also transformed European cropland landscapes substantially. This is caused directly by the target on the reduction of nitrogen use, which shifted medium-intensity cropland to both high-intensity cropland and multi-functional forest and cropland mosaics. However, it may also be the indirect effect of the preservation of natural forests and grasslands, resulting in fewer monoculture agricultural lands with less land use efficiency (e.g., low to medium intensity cropland) and achieving synergies in multi-functional landscapes. Our results show that to achieve sustainability-focused growth in the future, strict environmental regulations are still needed besides the already less demanding requests from the landscapes in SSP1 in comparison to other SSPs. This also indicates the necessity of taking a holistic view of land systems, which provides material and habitat service for human society but also has many other functions for nature conservation.

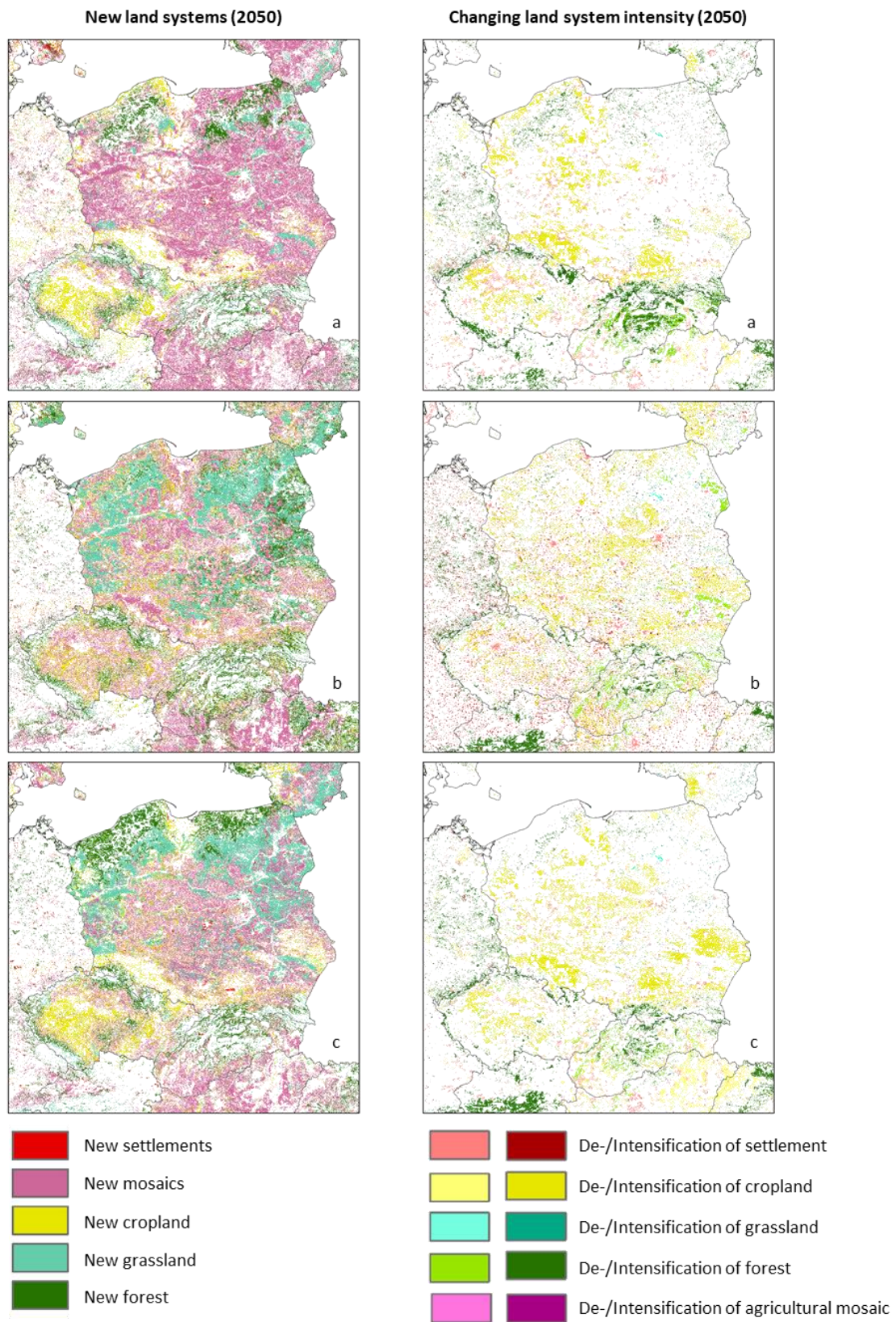


Figure 7. Land system conversions in eastern Europe between 2015 and 2050 under each NFF scenario. The left column illustrates conversions between different land system types (e.g., from forest to cropland), while the right column illustrates cases of intensification or

de-intensification within the same land system type (e.g., low intensity to high intensity grassland)

4.2 Alternative futures when prioritizing different values

Scenario studies have been useful tools to demonstrate how different societal development, emissions, and policy choices can lead to alternative futures. However, most scenario studies describe and compare plural singular future outlooks, each under different, unique settings. In this study, we adopted the Nature Futures Framework that explores plural desirable futures. The targets and objectives for land use changes remain consistent across scenarios, so are the underlying socio-economic and climate change patterns. Yet only people's valuations of nature differ in each scenario. This plurality of the underlying spatial prioritization is, to the best of our knowledge, the first among scenario studies, which differentiates from existing scenario studies that may have potentially missed the normative implications of their underlying assumptions at a continental scale. The different visions of nature are implemented in our scenarios through the prioritization of either carbon sequestration, species conservation, or the preservation of cultural landscapes, hence resulting in different landscape configurations and compositions.

The different pathways simulated by our study underline the importance to articulate normative positions in modeling practice and scenario designs (Nielsen et al. 2019, Meyfroidt et al. 2022). Previous scenario studies focused on analyzing and comparing the differences caused by tangible socio-ecological settings, or the uncertainties embedded in modeling and parameter ranges (Sun et al. 2012, Prestele et al. 2016, Doelman et al. 2018, Wolff et al. 2018, Malek and Verburg 2021). However, how different values and norms under the same socio-economic conditions affect the futures have been less investigated. While our results show some similarity across different scenarios, they also demonstrate significant tradeoffs among different land use and spatial locations that would be overlooked when ignoring value assumptions. Taking a normative lens through the Nature Futures Framework, we explicitly reflect on the underlying assumptions regarding the priorities in spatial planning, and showcase the alternative land use futures in a more transparent mode.

Our results call for more explicit policy-making on what to prioritize and how to implement environmental targets. This is amplified by even under the same targets and same value appreciation, different methods can be used to implement and regulate the changes which may also lead to various outcomes as shown by (Schulze et al. 2021). However, our results highlight potential strategies policy-makers can employ. For example, the expansion of protected areas can aim at the natural landscapes coincided in all three nature futures scenarios, to avoid risks and maximize the valuation across different stakeholder groups. Alternatively, policymakers can take the risk-seeking strategy to protect key natural areas that are consistently converted to other land use in different scenarios.

4.3 Feasibility of targets across regions and scales

Our simulation study shows that landscape changes can deliver environmental targets while also meeting societal demands for shelter, food, timber, and livestock projected by SSP1. The addition of the environmental targets would transform landscape changes to both land sparing and land sharing (Fischer et al. 2014). For example, about 10% more medium-intensity cropland in the three nature futures scenarios converted to high-intensity cropland for the high yield productivity, and 30% more to forest and cropland mosaics for the balance of nature and

agriculture, compared to the SSP1 scenario. This trend is aligned with the co-existence but a slight preference for land sharing identified by other studies (Karner et al. 2019). However, south and east regions face higher land use pressure than other regions hence certain targets were relaxed. The target of reducing the nitrogen applications by 40% in 2050 was relaxed to 30 % in 2050 in the south region, resulting in 1.2 million kilograms higher nitrogen input than the original target. Yet the total nitrogen application rate in the south is less than a fifth of the nitrogen use in the west in 2050.

For the south and east regions, there are more challenges in certain nature future scenarios than in other scenarios. Although Nature as Culture results in the most distinctive landscapes in the two regions, Nature for Nature scenario is the one that required the most attempts and iterations until CLUMondo can finally find a solution. The restoration target for the south was lowered to remain at 30% and stopped expansion after the 2030 goal for Nature for Nature scenario. The reasons for the high land use pressure in the south are multiple: the famously complex southern mosaic land systems, scattered natural land systems over a large extent, rich species conservation and cultural value, and future climate change stress. By contrast, there are few land use changes in the west, with or without the additional environmental targets (e.g., UK and Germany experience few land use changes in the simulation). The landscapes in the west can be easily optimized via a consistent pathway up to 2050 across all three value scenarios. Possible reasons are that i) most areas in the west are already in the medium to high-intensity use (e.g., currently 5% of the total cropland is low-intensity, while this number is 27% in the south) and ii) relatively low additional environment targets are implemented to its future changes.

How these environmental targets will be implemented in practice needs to address fairness and account for regional heterogeneity. In this scenario study, we divided these environmental targets based on the size of these targeted variables in the baseline, to account for the regional characteristics. For instance, the north currently has 38.8% of all trees in Europe, implying the north as the wood production and forest center of Europe. We also considered the size of each region, with the north accounting for 22.2% of the terrestrial areas. Therefore, the target of newly planted trees in the north is the average of the two variables. However, we also acknowledge that this approach is relatively simple and crude, while real targets will need to bread down to finer scales as national and even sub-national levels. Furthermore, the spatial priorities are simply implemented in the model. Across the whole Europe, we used the distribution of a single variable to address the same normative value, where multiple criteria can be used for the same priority.

4.4 Potential methodological improvement

The translation of ambitious environmental targets into CLUMondo model setting has some limitations. For example, the target related to excessive nitrogen use was implemented in two modules in the model: the reduced nitrogen application rate per agricultural land system, and the decline of the total nitrogen application in the region. However, how different land systems will respond to per unit nitrogen reduction and affect crop yield is unclear. Yet we assumed the management and technology will compensate and hence maintain the same yield increase from the SSP outlook. The implementation of restoration targets on low-intensity forest and grassland introduced another type of uncertainty. In this simulation, we counted the size of the areas designated for low-intensity grassland and forest systems as natural habitats, although they may not always reconcile as natural ecosystems. Furthermore, different ways of counting restoration targets also matter. For instance, binary counting on the dynamic loss and

gains of natural systems, or numeric counting based on the natural elements in different systems, will lead to different outcomes (Schulze et al. 2021). Based on the three natural futures scenarios, these counting systems and criteria used can be different as well. In addition, the restoration of natural ecosystems will take years and decades. Reflected in our model settings, we began the restoration target a few years ahead of 2030 to account for the lag-off effect. Yet this can only reserve the land use as the low-intensity grassland and forest, and does not guarantee the successful restoration of such systems.

5. Conclusion

Using a land system simulation approach, we showed the potential for sustainable land use futures in Europe. In particular, our study highlights the importance of having specific environmental targets even under the SSP1 sustainable pathways. Without the various environmental targets established under the Convention on Biological Diversity and the European Union's Green Deal, Europe would further lose its already-at-risk low-intensity forest and grassland ecosystems up to 13% compared to now. These additional environmental targets further transformed European landscapes to higher intensification within the same systems (e.g., more high-intensity cropland and forests) as well as converting to more multi-functional mosaic systems (e.g., converting medium-intensity croplands to forest/shrub and cropland mosaics). However, how and where to implement these targets in real-world needs further exploration, to account for the heterogeneity of regional capacity and characteristics.

The multiple value appreciation of nature, implemented through the Nature Futures Framework, guided the prioritization of different targets at different locations. Our results show a large variety of the land use change pathways and the local tradeoffs and synergies across three nature future scenarios. When the prioritization differs, the pixel-based tradeoffs in land systems in future projection can be as large as 41% of the whole terrestrial area of Europe. This suggests that scenario studies can and should incorporate a variety of values. Our simulation, being the first to reveal the underlying values for different assumptions, can help identify the alternative pathways to achieve the corresponding prioritized goals. The comparison of different land system projections in the future is an exploration of plural futures of the same targets, to provide information to reach the optimal potential synergies for better decision-making.

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Appendix D

Supplementary Materials for Chapter

5



Supplementary Materials for

5

Balancing conservation priorities for nature and for people in Europe

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Materials and Methods

1. Study area, species distribution and Nature's Contribution to People (NCP) data.

The study area included all countries from the European Union plus the United Kingdom (formerly part of the EU), covering all European terrestrial ecosystems. We excluded Croatia, Cyprus and Macaronesia from the study area due to lack of data on NCP for these areas. All spatial data consisted of raster layers at a resolution of 1.44 km² (grid cells of length 1.2 km) (projection LAEA / GRS90); for the sake of simplicity, in the text we refer to this as simply 1 km². The total surface of the study area was 4,349,146 km² (i.e. 3,020,240 grid cells of length 1.2 km). We used the European Commission countries shapefile (version of 03/06/2019) at the scale of 1:3 million to harmonize the study area for all spatial data used:
<https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/countries>.

We classified spatial data into three categories of nature's values (Fig. S1): 1) the *intrinsic* value of biodiversity, represented by all vertebrate species known to occur in the European Union (785 species, including 124 that are threatened), 2) the *cultural* value of landscapes (wild food foraging, heritage forests, heritage agriculture, nature tourism), and 3) the *regulating* value of ecosystems that sustain life on Earth as we know it through flood regulation, carbon sequestration, pollination and air quality regulation. We sought to compare spatial priorities when the focus was either species, cultural NCP or regulating NCP. Therefore, we performed separate prioritizations for species, cultural NCP, and regulating NCP. Then, we compared them in a post hoc analysis.

a. Species distributions

We extracted the distribution for all 785 terrestrial vertebrates naturally occurring in the study area from Maiorano *et al.* (2013) (37). These 785 species are: 84 amphibian, 416 bird, 171 mammal and 114 reptile species (Fig. S3). Original species distributions data from Maiorano *et al.* (2013) followed a regular grid of 300 m resolution. The authors performed an independent validation of these distribution data against field observation data for 38 species of amphibians, 283 species of birds, 93 mammals and 36 squamates. The coverage of the points considered for model evaluation was from 22 different countries of Europe, including most of the EU27. 100% of refined EOOs evaluated for mammals performed significantly better than random, while the percentage was lower for squamates (97.1% of the refined EOOs performing better than random) and breeding birds (96.3% of the refined EOOs performing better than random). Full details of the model evaluation procedure are provided in the supplementary material in Maiorano *et al.* (2013) (37).

The species distribution data assume that a species is present in a grid cell if that cell meets the three following criteria: i) is within the species EOO (IUCN 2013), ii) contains primary habitat for the species (based on land cover data), and iii) meets species requirements in terms of elevation and distance from water. Spatial ecological data (e.g. land cover, species distributions) is tied to some inevitable uncertainties. First, since the data were published in 2013, we evaluated whether these EOO are still in agreement with the latest estimates from the IUCN Red List website (Table S2). For a random selection of 10% of our species database, there was a 92.3% of agreement between the datasets (Table S2). This demonstrates that the data used still offer a fairly good estimate of the ranges of most vertebrate species. Second, a comparison between the

GlobCover dataset (version of 2006, which was used to refine species distribution data) and CORINE land cover dataset (version of 2018) (Table S3) suggested that at the resolution of 1km², habitat types have remained similar in general, except for some local variations. Because of these different potential sources of uncertainty in the spatial data, the highlighted priority areas (Fig. 1 and 2) should be considered as potentially valuable for species conservation.

The habitat suitability of each land cover class for each species was determined in Maiorano *et al.* (2013). The authors used data available in the literature to assign to each of the 46 GlobCover land-use / land-cover classes a habitat suitability score with 3 possible values: 0, for habitat where the species cannot be found except for vagrant individuals; 1, for marginal habitat (habitat where the species can be present, but does not maintain viable populations in the absence of primary habitat); 2, for optimal habitat where the species can persist. The reclassification of habitats was intersected with elevation bands (outside of the known elevation bands all pixels get automatically a value of zero), with distance to water (for species depending on the presence of permanent water the species gets a value only within the water buffer), and with the extent of occurrence for the species (such that all pixels outside of the known EOO automatically go to zero). All species range maps were up-scaled to a 1 km² equal-size area grid. We aggregated the 300 x 300m cells using a factor of 4, such that the up-scaled raster contained the coverage of optimal habitat within each aggregated cell (1.2 km x 1.2 km, hereafter referred to as 1 km² resolution to simplify). Considering only the optimal habitat in species distributions enables us to prioritize the landscape based on habitat that is essential to species persistence. This is a conservative method which has also been suggested to provide a better prediction of the species' actual distributions (38, 39), and ultimately helps to focus conservation efforts on habitats that can host viable populations of species. These species distributions (% optimal habitat per grid cell) were used as individual input layers for the spatial prioritization.

b. Threatened species

We investigated priorities for threatened species in addition to all species, using data from the IUCN red list of species for the EU region, downloaded from www.eea.europa.eu/data-and-maps/data/european-red-lists-7 (version of November 2019). The European red list data for mammals (261 species assessed) and herptiles (237 species assessed) was delivered in 2009; the data for birds (533 species assessed) was delivered in 2015. We defined as threatened the vertebrate species that were listed either as vulnerable (VU), endangered (EN), or critically endangered (CR).

Mismatches between species names from the IUCN red list and from our dataset (derived from Maiorano *et al.* 2013) were recorded for 19 species. Taxonomical synonyms for nine species were identified and corrected: *Hierophis cypriensis* (changed to *Dolichophis cypriensis*), *Clanga clanga* (*Aquila clanga*), *Mareca penelope* (*Anas penelope*), *Spatula querquedula* (*Anas querquedula*), *Vanellus spinosus* (*Hoplopterus spinosus*), *Calidris pugnax* (*Philomachus pugnax*), *Turnix sylvaticus* (*Turnix sylvatica*), *Hydrobates leucorhous* (*Oceanodroma leucorhoa*), *Bubo scandiacus* (*Nyctea scandiaca*).

In total, 124 (18 amphibians, 71 birds, 20 mammals, 15 reptiles) of the 785 vertebrate species in the EU were listed as threatened in the EU regional list of threatened species. By contrast, 73 vertebrate species (18 amphibians, 23 birds, 18 mammals, 14 reptiles) of the same set of species were defined as threatened according to the global red list. Appendix 2 includes a

comparison of the prioritizations for these two different sets of threatened species (EU regional red list and global red list) (Fig. S17-S19).

Species richness maps for all vertebrate species, threatened species only and within each class (amphibians, birds, mammals and reptiles) are shown in Fig. S3, but species richness maps were not used as such in the prioritization analysis, which required all the species distributions as individual spatial layers.

c. Nature's contributions to people (NCP) spatial data

We selected four regulating and four cultural (also known as nonmaterial) NCP (Table S1). Nature's contributions to people build on the ecosystem service concept (40) and we define them as the match between the capacity of an ecosystem to provide the NCP and the human demand for this NCP, in keeping with previous work including human demand to identify ecosystem services priorities (18). To identify priorities in ecosystems where a high supply for the NCP coincides spatially with a high demand for the NCP, areas with both high NCP capacity and high demand for this NCP were assigned the highest value. If either the capacity to provide the NCP or the demand for the NCP were low in the cell, then the cell had lower NCP value; the NCP value was lowest when both capacity and demand were low. In practice, the preparation of the NCP layers required four consecutive steps (although not all were needed for each individual NCP) 1) mapping the spatial distribution of NCP capacity (*sensu* Verhagen *et al.* (2017), i.e. the capacity of the ecosystem to supply the NCP irrespective of demand), 2) identifying the type of NCP flow (local, regional, global) 3) mapping the spatial distribution of demand for those NCP with non-global flows, 4) allocating ecosystem demand to areas of NCP capacity based on spatial rules and finally 5) multiplying the demand for the NCP with the ecosystem capacity to supply the NCP.

Table S1 provides an overview of the description of the data for capacity and demand of the different NCP.

i. Carbon sequestration

We mapped the spatial distribution of carbon sequestration capacity using the dataset built by Schulp *et al.* (2008) (41), and retrieved the data from: <https://www.environmentalgeography.nl/site/data-models/data/ecosystem-service-public-goodbiodiversity-data/>. Carbon sequestration is a combination of both belowground carbon sequestration for all land-cover types and aboveground carbon sequestration in forests. Soil carbon sequestration values are determined using information on soil type, soil organic carbon content and land-use specific emission factors. Above-ground carbon sequestration in forests is determined based on forest carbon content, deforestation and forest age. We set negative carbon sequestration values (i.e. carbon emission) to zero to focus the prioritization on carbon sequestration benefits. The global carbon cycle means that benefits from carbon sequestration are irrespective of location. As such, carbon sequestration is a global flow NCP and there is no spatial variation in the demand for carbon sequestration. Therefore, the demanded capacity was equal to the capacity for carbon sequestration.

ii. Pollination

We mapped both the spatial distribution of pollination capacity and pollination demand based on a dataset from Schulp *et al.* (2014) (42), publicly available at: <https://www.environmentalgeography.nl/site/data-models/data/pollination-data/>. Pollination

capacity for the entire EU consisted of pollinator habitat with high probability of pollinator visitation. Pollination capacity was obtained from a multiplication between the proportion of pollinator habitat per grid cell (using land cover suitability, forest edge habitats and green linear elements within a grid cell) and the visitation probability by pollinators (proxied by *Apis* and *Bombus* species) of these habitats (42). Pollination demand consisted of the coverage of pollinator dependent cropland per grid cell, weighted by pollinator dependency of the crop type (Fig. S6). Pollination is a local flow NCP, in which the visitation probability of a pollination demand (crop) cell depends on the distance to pollinator habitat, constrained by the flight distance of pollinators (here: wild bees) (43).

To assign pollination demand to areas of pollination capacity at 1km² resolution, we assigned the pollination demand value of each grid cell containing pollinator dependent cropland, to the 8 neighbouring cells (Moore neighbourhood) using the function raster::adjacent in R, in line with previous efforts to combine capacity and demand for pollination (18). Thus, we were able to match pollination NCP capacity with demand, by placing a high NCP value on pollinator-abundant locations with natural vegetation and/or hedgerows surrounding pollinator-dependent croplands (i.e. within a ~ 2-3 km vicinity of the cropland). High pollination capacity areas further than 3 km from pollinator dependent cropland, were not assigned a pollination demand. We then winsorized the demand values based on the 95th percentile; that is, we assigned the 95th percentile value to all locations with values higher than the 95th percentile, to avoid disproportionately skewing the NCP demand layer towards 5% outlier cells (Fig. S6, Table S4). Last, we normalized both demand and capacity layers, and multiplied the demand and capacity layers, thereby assigning high NCP value to pollination habitat within the proximity of pollination-dependent crops.

The approach presented here follows previous mapping exercises (44, 45) at the scale of landscapes to continents, and has also been applied in prioritization studies before (18). An important simplification is the use of an aggregated wild bee to proxy pollinator habitat and flight distances. Previous work has shown the relation between bees functional traits, sensitivity to land use and land use intensity and differences in flight distance (46). Accounting for these differences between wild bee species would alter both the pollination capacity, pollination demand and the determination of spatial overlay of both demand and supply. However, these insights on functional traits and pollination have not been used in large-scale mapping exercises at the extent of countries let alone the EU, and requires a level of detail around habitat mapping and spatial resolution for which currently data are not available at the scale of the EU. Therefore, we consider the use of an average wild bee species to be a reasonable assumption and in line with best-practices for mapping pollination across large extents (44, 45).

iii. Flood control

The flood regulation capacity and demand dataset was obtained from a previous study by Stürck *et al.* (2014) (47), which we retrieved from <https://www.environmentalgeography.nl/site/data-models/data/flood-regulation-supply-data/>. Flood capacity and demand were determined at the subcatchment level, delineating Europe in Strahler 5-order catchments (18, 47). Flood regulation capacity was determined using meta-models accounting for a combination of land cover, catchment type and zone, water holding capacity and a combination of land use and management intensity. Flood regulation demand was proxied using an estimated flood damage (euro/ha), using land cover damages for a 50-year flood inundation level (48). Damages were aggregated at the subcatchment level. This resulted in

a value of flood regulation capacity and flood regulation demand for each subcatchment. However, across a wider river catchment area, upstream subcatchment often have high flood regulation capacity whereas downstream subcatchment often have high damage (demand). For each subcatchment with flood regulation capacity, the demand for flood regulation was
 5 calculated using the aggregated downstream damage weighted by the aggregated upstream area capable of providing flood regulation capacity (18, 47). This approach assigns high demand values to flood regulation capacity subcatchment with high downstream demand. Flood demand data was winsorized for values above 95th percentile: all values above 95th percentile were set to this value to correct extremely skewed data (in Northern Italy). Prior to winsorization of the
 10 demand data, the 95th percentile value was equal to 0.0901, while the maximum value was equal to 1 (Fig. S7, Table S4). Both demand and capacity values were normalized, prior to multiplication.

iv. Air quality regulation

Maps of the spatial distribution of air quality regulation capacity and demand are based on
 15 European scale maps from Lavallo *et al.*, (2015) (49) and further explained in Verhagen *et al.* (2017) (18). The authors quantified air quality capacity using deposition velocity (m/s) mainly determined by the leaf area of plants. Air quality demand was proxied using NO2 emissions. It assumes that demand for air quality regulation is highest in the locations with the highest pollution levels. All data are accessible at: <http://data.europa.eu/89h/jrc-luisa-1f511-no2-removal-by-urban-vegetation-ref-2014>. The interaction between (urban) vegetation and air quality is
 20 highly local and vegetation can significantly reduce concentrations from air traffic (50, 51). Although the exact contribution of urban vegetation to air quality regulation is contested (50), even small reductions in air pollution can result in significant benefits in highly populated areas (50, 51). Given the local flow of this NCP, we directly multiplied the cell-to-cell values of air
 25 quality demand and capacity.

v. Wild foods

For wild foods foraging, both the NCP capacity (edible vascular plants and mushrooms species richness) and demand (foraging) were obtained from a study by Schulp *et al.*, 2014 (52), and was retrieved from: <https://www.environmentalgeography.nl/site/data-models/data/wild-food-data/>. Wild food capacity was mapped for mushrooms and vascular plants, using a species
 30 distribution map filtered for edible wild food species (52). The demand for wild food foraging is based on a combination of factors on demography (age), GDP per capita, land use, regulations around accessibility and cultural importance of wild food in the cuisine. Furthermore, the demand for wild food was spatially restricted based on population density. The demand for wild
 35 food already includes accessibility and population density, and therefore limits the spatial match between demand and supply. We combined capacity and demand such that the resulting wild foods NCP was equal to:

$$(\text{demand}_{\text{mushrooms}} * \text{capacity}_{\text{mushrooms}}) + (\text{demand}_{\text{plants}} * \text{capacity}_{\text{plants}})$$

vi. Heritage forests and heritage agriculture

40 The location of heritage ecosystems, both forest and agriculture, were obtained from Tieskens *et al.*, 2017 (53). We retrieved the dataset from <https://www.environmentalgeography.nl/site/data-models/data/ecosystem-service-public-good-biodiversity-data/>. Heritage agriculture and heritage forest were mapped based on a

combination of management intensity variables (farm size, n-input, energy output crops, and forest harvest intensity), landscape structure (land use/cover, green linear elements, forest age) and two indicators capturing value & meaning (photo density and products of designated origin). Mapping the demand and the spatial flow for cultural NCP is challenging. There are both
5 localized flow components (such as sense of place) as well as regional to global flows associated with heritage agriculture and forest (tourism and products of designated origin). In contrast to the regulating NCP, the indicators of cultural heritage already include spatial indicators of capacity, use and benefit (value and meaning). As such the spatial distribution already captures a
10 combination of capacity and demanded capacity. We therefore did not separately map demand and capacity for heritage agriculture and heritage forest besides the above mentioned indicators.

vii. Nature tourism

The capacity for nature tourism NCP is based on a publication by Van Berkel & Verburg 2011 (54), where capacity for nature tourism is defined as the ability of the region to provide tourist activities that take place outside urban areas, and involve overnight stays. We retrieved
15 the dataset from <https://www.environmentalgeography.nl/site/data-models/data/ecosystem-servicepublic-goodbiodiversity-data/>. It is modelled with a combination of assets of sun, sea and sand tourism; winter tourism assets; assets for nature tourism; and symbolic capital. Symbolic capital is a collective sense of place and/or place identity. Again, the approach used to map nature tourism already includes aspects of capacity (presence of beaches, winter precipitation)
20 combined with aspects of use (distance to urban centers, presence of camping sites). As such, the indicator used already combines the capacity of an area to supply an ecosystem NCP, with the benefits and use. We therefore used this indicator to directly map demanded capacity for nature tourism. Given the fact that the indicator measures the opportunities for nature tourism with overnight stay, we assume the flow to be of global nature (i.e. people travelling long-distance for
25 beach and winter tourism) and the demanded capacity to be limited only by accessibility.

d. Natura 2000

We downloaded the Natura 2000 database from the European Environmental Agency website: <https://www.eea.europa.eu/data-and-maps/data/natura-11/natura-2000-spatial-data>
30 (version of end 2019). Marine and sea inlets were removed from the layer, using the European Commission countries shapefile at the scale of 1:3 million, to avoid inflating the protection of coastal grid cells. Then the layer was rasterized at a 100m resolution. Finally, the number of 100 m protected cells were counted in each cell of the 1200 m and 12000 m reference grids, to match the biodiversity and NCP data. The total area covered by Natura 2000 sites in the study area was 750,515 km² (this represented 17.26 % of the study area). The smallest percentage covered by a
35 Natura 2000 site in a 1.44km² grid cell was 0.69%; 25% of the protected cells contained 27% of Natura 2000 or less (first quartile); the median protection per grid cell was 77%; the mean protection per grid cell was 62%; the 3rd quartile and the maximum protection per grid cell were both 100% (Fig. S2). The mask used in the prioritization was an ordinal raster, where grid cells that contained at least 100 hectares of Natura 2000 sites were assigned a value of 2, and were
40 ranked first in the prioritization; cells that contained a non-zero proportion of Natura 2000 sites but less than 100 ha of Natura 2000 (either because these Natura 2000 sites are small or because the grid cell is on the edge of a larger Natura 2000 site) were assigned a value of 1, and were ranked next; cells that did not contain any proportion of Natura 2000 were assigned a value of 0, and were ranked last in the prioritization (Fig. 3 and S10B). We tested the influence of the

definition of protected cells on the prioritization outcome in a sensitivity analysis (Appendix 4, Fig. S20).

Other area-based conservation schemes in Europe exist and complement Natura 2000 (14) but were omitted from this analysis for the sake of consistency.

5

2. Spatial conservation prioritization

We ran prioritizations using the spatial conservation planning software Zonation (55, 56), to prioritize locations that maximized the representation of each species and each NCP, that were complementary to each other, where endemic species occurred or where NCP had a particularly high value.

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The software Zonation is a prioritization tool that maximizes both the representation of all features considered as well as the complementarity between priority sites. Using the input raster layers, Zonation computes the value of all the cells across the landscape and removes the cells which have the lowest value, and it repeats this iteratively until all cells in the landscape are removed. The prioritization process uses the fraction of the distribution of each feature (individual species or NCP) in a cell (Zonation automatically applies a normalization to all individual spatial layers prior to commencing the ranking process). Therefore, the biodiversity feature layers do not need to have the same units and they do not need to be rescaled to the same scale, as the prioritization is relative to the individual features' spatial coverage (57). We ran a total of 53 prioritization scenarios, including 6 for the results presented in the main text and an additional 47 for the sensitivity analyses (Appendices 2-4). The main prioritizations are run separately for: 1) all vertebrate species, 2) regulating NCP, 3) cultural NCP. We present results from the other prioritizations in the Appendices 2-4. We chose the prioritization algorithm "Core Area Zonation" to determine the priority value (i.e. order of removal) of cells across the landscape during the prioritization process. This algorithm maximizes the representation of individual features rather than local richness. This means that for each run, the algorithm prioritized locations that maximized the representation of each feature (i.e. species or NCP), that were complementary to each other, where endemic species occurred (for the species runs) or where NCP had a particularly high value (for the NCP runs). We ran the prioritizations for two spatial allocation approaches: 1) ignoring existing protected areas (referred to as "optimal") and 2) including Natura 2000 by using Natura 2000 as a mask, such that cells within and outside Natura 2000 were prioritized sequentially, to first perform a gap analysis and then prioritize areas for the expansion of Natura 2000 that would complement the current protected areas.

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For each prioritization, Zonation produces a map where each cell is assigned a value based on its order of removal during the prioritization: this is the priority rank of the cell, between 0 (lowest priority) and 1 (highest priority). We set the number of cells removed at each iteration (warp factor) to 1,000.

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Outputs of the six main Zonation runs (i.e., those presented in the main figures) are accessible online at <https://doi.org/10.34894/TCNKPJ>.

3. Comparing priorities in space and in representation

Two quantities can be used to compare the efficiency of a prioritization for a given set of features:

- 1) The optimal representation that can be gained within a fixed amount of land.
- 2) The amount of land needed to achieve a fixed representation.

The first, quantifying the average representation of features of interest in a limited amount of space, is directly relevant to conservation applications. It enables us to identify key areas to protect, given fixed resources.

In the main text, in order to compare the locations and representativeness of different types of priorities, we used a threshold to define top priority cells: these cells correspond to the top 10% area in the optimal prioritization, and to the top 5% area in the Natura 2000 analyses.

a. Comparing priorities across space

Fig. S17 shows the spatial correlations between different prioritizations.

In each scenario, we quantified the spatial overlap between top priorities. For the optimal scenario, the top priorities consisted of the top 10% ranked area (Fig. 2, S11 and S18). For the scenario including Natura 2000 as a mask, top priorities within or outside Natura 2000 consisted of the top 5% ranked area within (small and large Natura 2000 sites) or outside Natura 2000, respectively (Fig. 3).

We then overlapped the priority maps and quantified the area that was associated with top priorities for one value, for two values (2-way spatial overlap), and for all three values (3-way spatial overlap).

b. Quantifying the representation of each value in each prioritization

Fig. S19 shows the differences in representation between different prioritizations for different groups of features (species or NCP).

Representation (or conservation gains) is the average proportion of the distributions of features (species or NCP) covered in a given amount of land, and is used to assess the performance of a prioritization. Performance curves show the conservation gains in a prioritization as the cumulative sum of representation as area is added in a prioritization (Fig. 3D-F and S10). In practice, the representation in a given cell is equal to the sum across the features considered (species or NCP) of the fractions q_{ij} of the distribution of the feature j occurring in the cell i :

$$we_i = \sum_j q_{ij}$$

The representation in a given area is normalized by the total number of species or NCP considered in the prioritization to make the metric comparable across all values, with the final 'representation metric ranging from 0 (0% of all distributions covered) to 1 (when 100% of the distributions of all features is covered). To quantify the confidence interval of the mean representation, we computed the standard error (s.e.) which is equal to:

$$s.e. = \frac{\sigma}{\sqrt{n}}$$

Where σ is the standard deviation in the fractions q_i of the distributions of the features i represented in the area considered, for a given group of features (e.g. all species; all cultural NCP) (Fig. 2C).

Appendix 1. Ecosystem diversity and composition in top conservation priorities and in Natura 2000 sites

We used the habitat types of widespread interest for ecosystem-based conservation in Europe (*e.g.*, those listed in the habitat assessment under article 17, accessible at <https://nature-art17.eionet.europa.eu/article17/habitat/summary/>). These are equivalent to the EUNIS L1 ecosystem types B to H: Coastal; Freshwater; Mires & bogs; Grasslands; Heathland, scrubland, tundra; Forests; Sparsely vegetated, Rocky. The two other EUNIS L1 ecosystem types are arable lands (ecosystem type I) and artificial, constructed areas (ecosystem type J) (Fig. S8).

We used the European terrestrial ecosystem types version 3.1, downloaded in August 2020 from <https://www.eea.europa.eu/themes/biodiversity/mapping-europes-ecosystems>. The initial data is at a resolution of 100 x 100 m grid cells. We up-scaled this map to fit the 1km² resolution and projection of the data used in the analysis, using the nearest neighbour method (used for categorical data).

We then quantified the proportion of ecosystem types within each type of top priority (top 10% of optimal prioritizations and top 5% priorities for Natura 2000 expansion), as well as within fully protected cells (containing 1km² Natura 2000) and partially protected cells (containing less than 1km² Natura 2000). Results are shown in Fig. S9.

Appendix 2: Sensitivity of the main results to the spatial resolution of input data

5 The main analysis was performed using data at 1km² resolution. We tested whether our results were consistent at a coarser spatial resolution by re-running the entire analysis with input data at a 100-fold coarser resolution than the main analysis.

We up-scaled species distributions from 300x300m to 12x12km² resolution by aggregating cells with a factor of 40 and computing the continuous coverage of optimal habitat within the larger cell. At this resolution, 782 species were found to occur in the study area.

10 We up-scaled the NCP data layers (demanded capacity) from 1km² to 12x12km² resolution by first aggregating the NCP layers by a factor of 10, conserving the mean value of the aggregated pixels. We then resampled the cells using bilinear interpolation to match the aggregated species distributions layers described in the previous paragraph. This methodology enabled us to minimize the encroachment of NA and optimize the similarity with the initial raster when resampling. We then repeated the pre-processing methodology for each NCP layer, in the
15 same way as for the main analysis.

In this Appendix, we also present how different the main results would be if the chosen threshold for top priorities was different (i.e. for a smaller or greater amount of land than presented in the main text). We quantify the spatial overlap between different types of priorities
20 and the average representation of features of interest, from 1 to 20% top priority area. Results are shown in Fig. S13.

Appendix 3: Sensitivity of the prioritization to input data

One traditional way of testing the sensitivity of a prioritization output is to use partial data, as the selected input data tends to have the largest effect on the priority ranking (57). To test the influence of different groups of input data, we ran a total of twelve individual prioritizations for the following groups of input data (on a 1 km² resolution, ignoring Natura 2000):

- species: 1) threatened vertebrates only, according to the EU regional red list; 2) threatened vertebrates, according to the Global red list; 3) all vertebrate species; 4) mammals only, 5) amphibians, 6) reptiles, 7) birds; 8) all vertebrates weighted by their evolutionary distinctiveness (Fig. S15).
- regulating NCP and cultural NCP: 1) capacity only, 2) both capacity and demand (which makes a difference especially for regulating NCP).

Concerning the distinction between the capacity and demanded capacity data for the NCP: the indicators of the cultural NCP (heritage ecosystems, nature tourism) already combine indicators on capacity with indicators on use, value and accessibility. The cultural benefits of heritage landscapes and areas for nature tourism (but not wild foods) are not only physical, they can also be psychological (or remote). We have therefore characterized the flow as global in scope. This is different for the regulating NCP, for which locations of capacity (bee habitat, upstream basins) are spatially disjoint from locations of demand (crop areas, downstream value).

Evolutionary distinctiveness

We used the 100 maximum likelihood trees from the phylogenetic dataset for European terrestrial vertebrates from (58). We identified and corrected 48 taxonomical synonyms to match species names in our dataset. In total, 747 out of the 785 EU vertebrate species were in the phylogenetic dataset. We pruned all trees to this subset of species occurring in our study area, and computed the median evolutionary distinctiveness for each of these species across the 100 maximum likelihood trees. We used the *evol.distinct()* function from the *picante* R package (version 1.8). The individual distributions of these 747 species were used as input layers for the prioritization and they were each weighted by their evolutionary distinctiveness value (Fig. S15).

We compared the outcome of all twelve different prioritizations (Fig. S16) by computing:

- 1) the pairwise Pearson rank correlation of the cell rankings (Fig. S17)
- 2) the proportion of spatial overlap between the top 10% priorities (Fig. S18)
- 3) the difference between the accumulation curves *s-o*, with *s* the area under the curve of the surrogate scenario, *o* the area under the curve of the optimal scenario. (Fig. S19). This metric quantifies the similarity between two prioritizations in terms of representation. The closer to 0, the more similar the performance curves are (i.e. the better the incidental representation); the more negative, the worse the surrogate run performs compared to the optimal run.

Appendix 4: Sensitivity of the prioritization to the definition of protected cells with Natura 2000 site size

Here, we tested how the thresholds to define the (binary) status of protection of a 1km² grid cell influences the prioritization with Natura 2000. We consider the following thresholds: 1) non-zero protection: a 1.44 km² grid cell is considered protected if it contains a proportion (between 0 and 1) of Natura 2000 site; 2) a grid cell is considered protected if it contains Natura 2000 surface of at least 27ha (the first quartile); 3) a grid cell is considered protected if it contains at least 89ha of Natura 2000 (the average coverage); 4) a grid cell is considered protected if it contains at least 100 ha (1km²) of a Natura 2000 site; 5) 4) a grid cell is considered protected if it contains at least 111 ha of a Natura 2000 site (the median coverage) (see Fig S2 and S20).

The results (depicted in Fig. S20) show that the estimates of the protected proportion of species and NCP spatial distributions varies with the size threshold of Natura 2000 used to define the protection status of a grid cell: the average proportion of distributions of species or NCP covered by cells that are minimally protected is two to three times higher than the representation in grid cells that contain at least 100ha of Natura 2000.

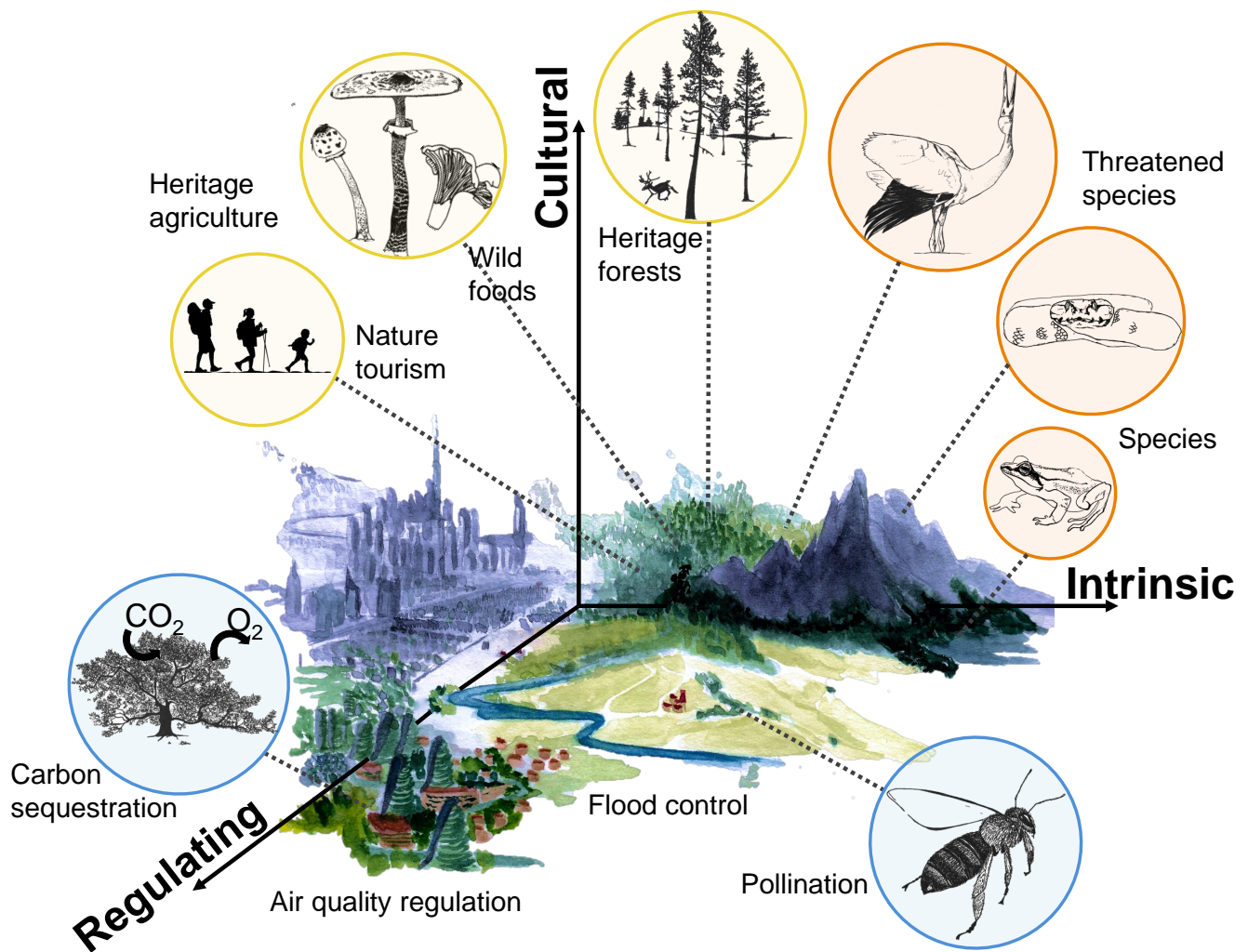


Fig. S1. The multiplicity of nature's values relevant for conservation. Different values of nature (regulating, intrinsic and cultural) are represented in orthogonal dimensions. The intrinsic value places high perceived value on biodiversity (e.g. species) and ecosystem functioning, independently of human presence. The cultural value places high value on culturally valuable landscapes (e.g. wild foods diversity for foraging, heritage agriculture and forests, popular nature tourism destinations). The regulating value places high value on ecosystems that provide regulating benefits upon which societies depend, such as flood control, air quality regulation, pollination, climate regulation.

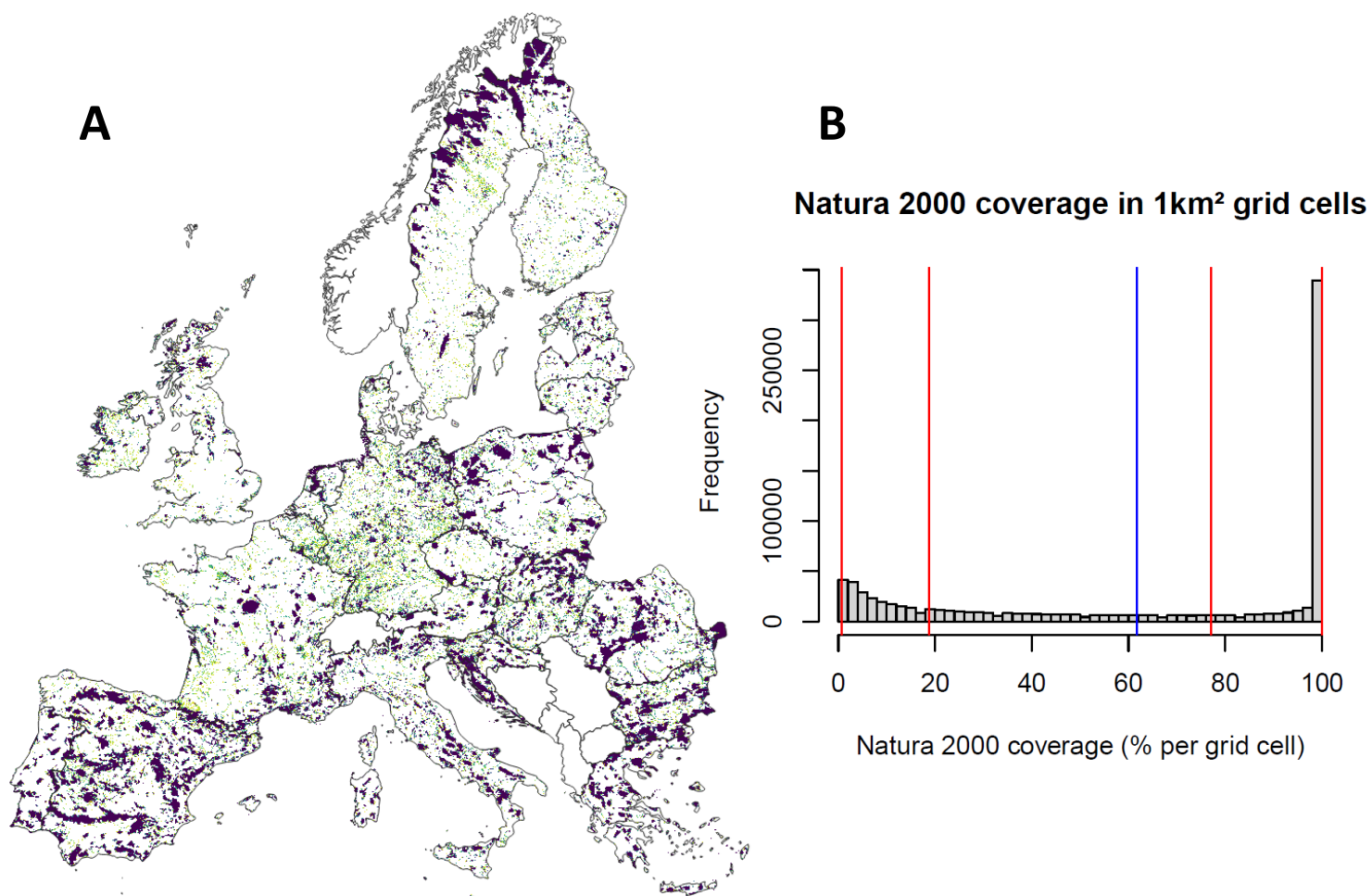


Fig. S2. (A) Map and (B) bar plot of (non-zero) proportion of grid cells covered by Natura 2000 site. In (B), vertical red lines indicate the quartiles (minimum; 1st quartile; median; and 3rd quartile = maximum coverage) and vertical blue line indicates the average Natura 2000 coverage within 'protected' 1.44 km² grid cells.

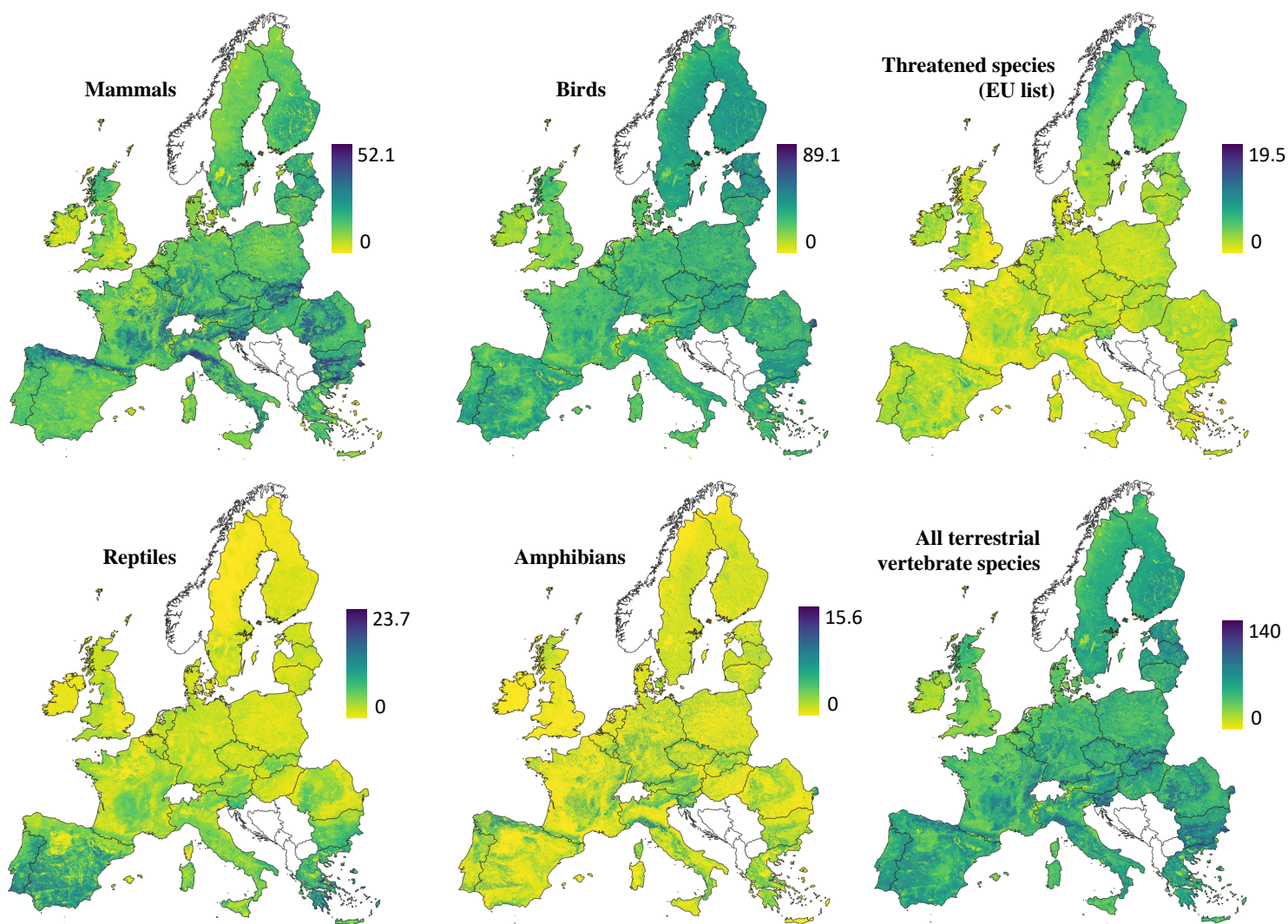
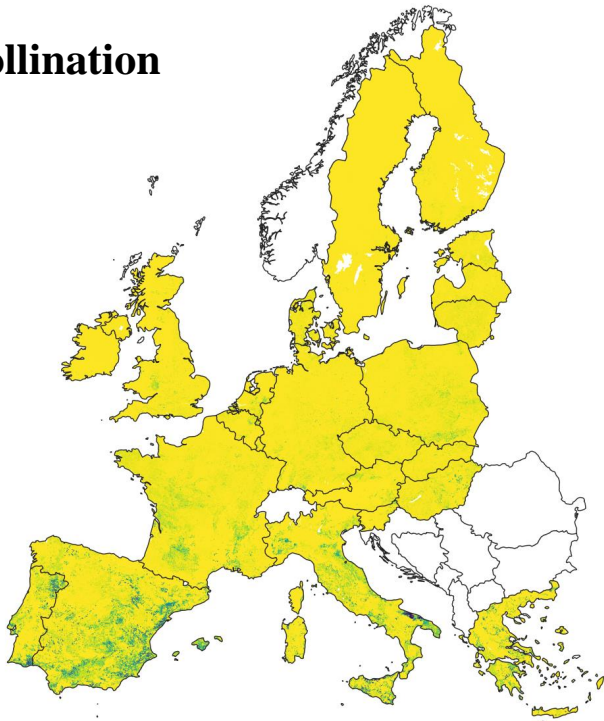
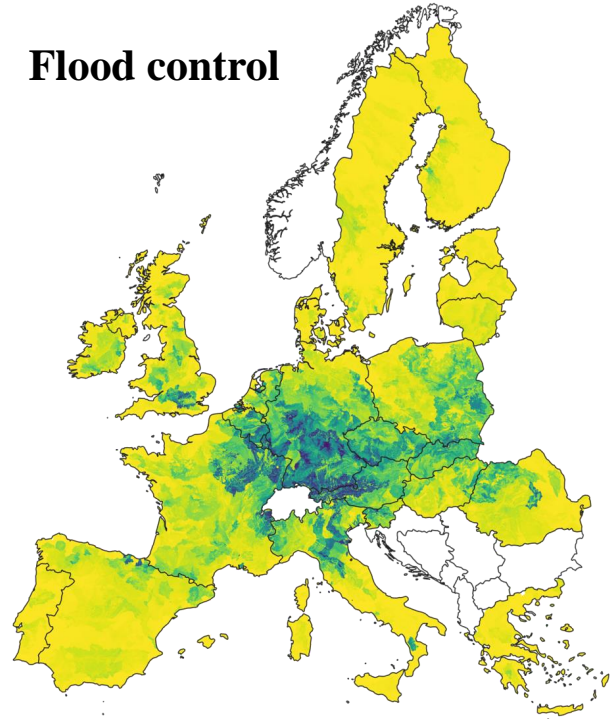


Fig. S3. Species richness maps. These maps show the sum of all species distributions per taxonomic class. Darker shades indicate higher local species diversity per grid cell.

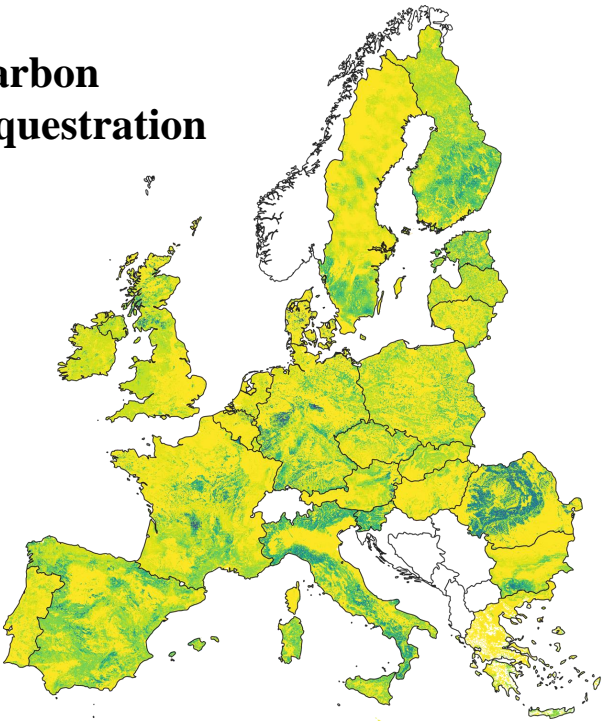
Pollination



Flood control



Carbon sequestration



Air quality regulation

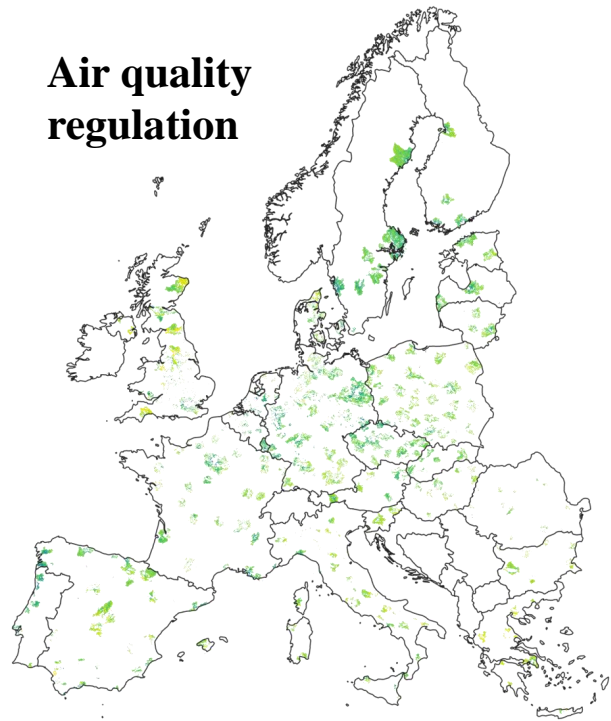
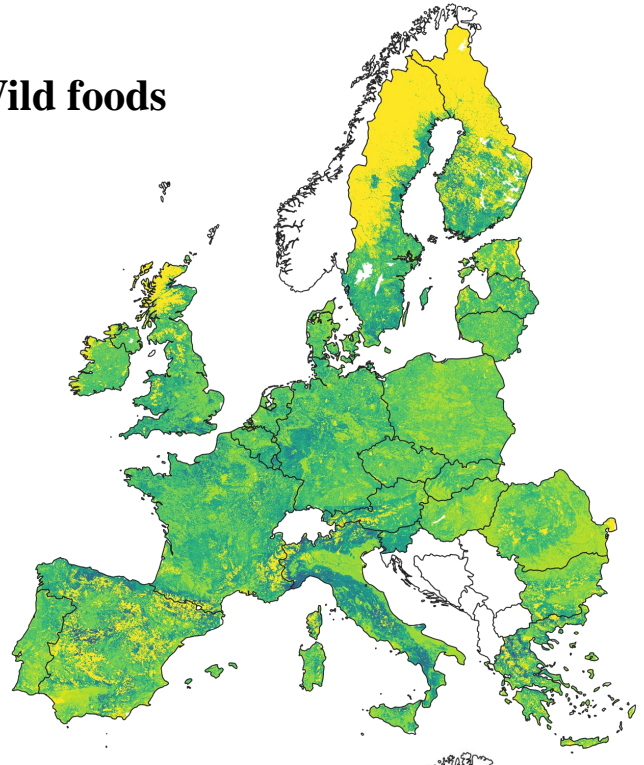


Fig. S4. Regulating NCP. These maps show the spatial distributions of each of the four regulating NCP considered in this study. Darker shades indicate higher local NCP value (demanded capacity) per grid cell.

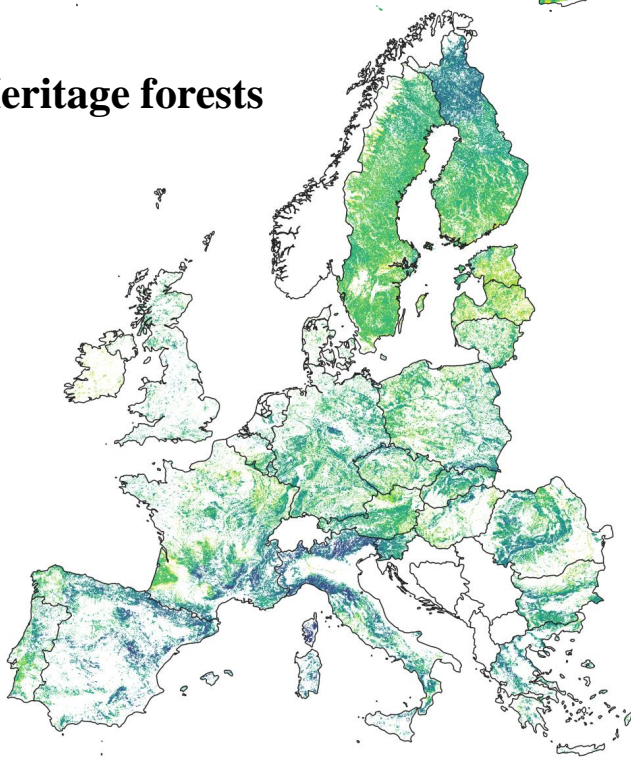
Nature tourism



Wild foods



Heritage forests



Heritage agriculture

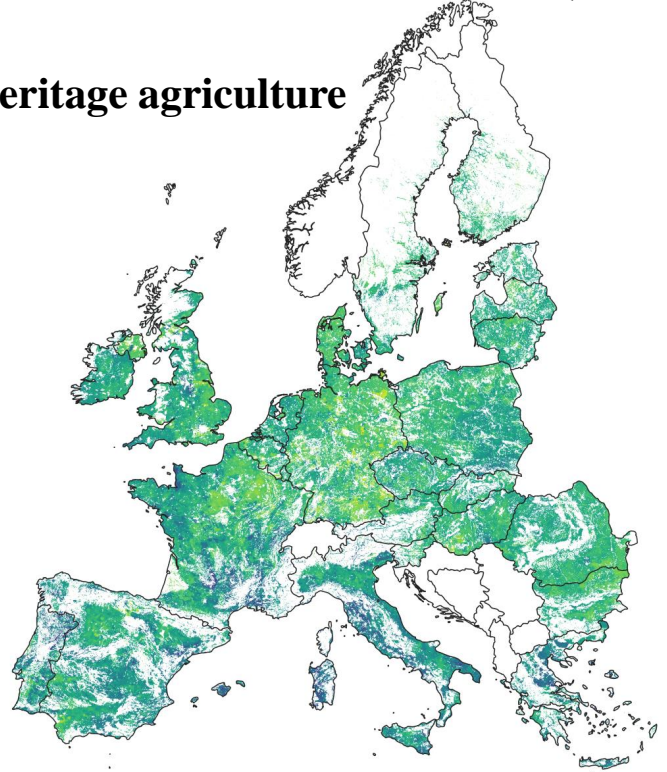


Fig. S5. Cultural NCP. These maps show the spatial distributions of each of the four cultural NCP considered in this study. Darker shades indicate higher local NCP value (demanded capacity) per grid cell.

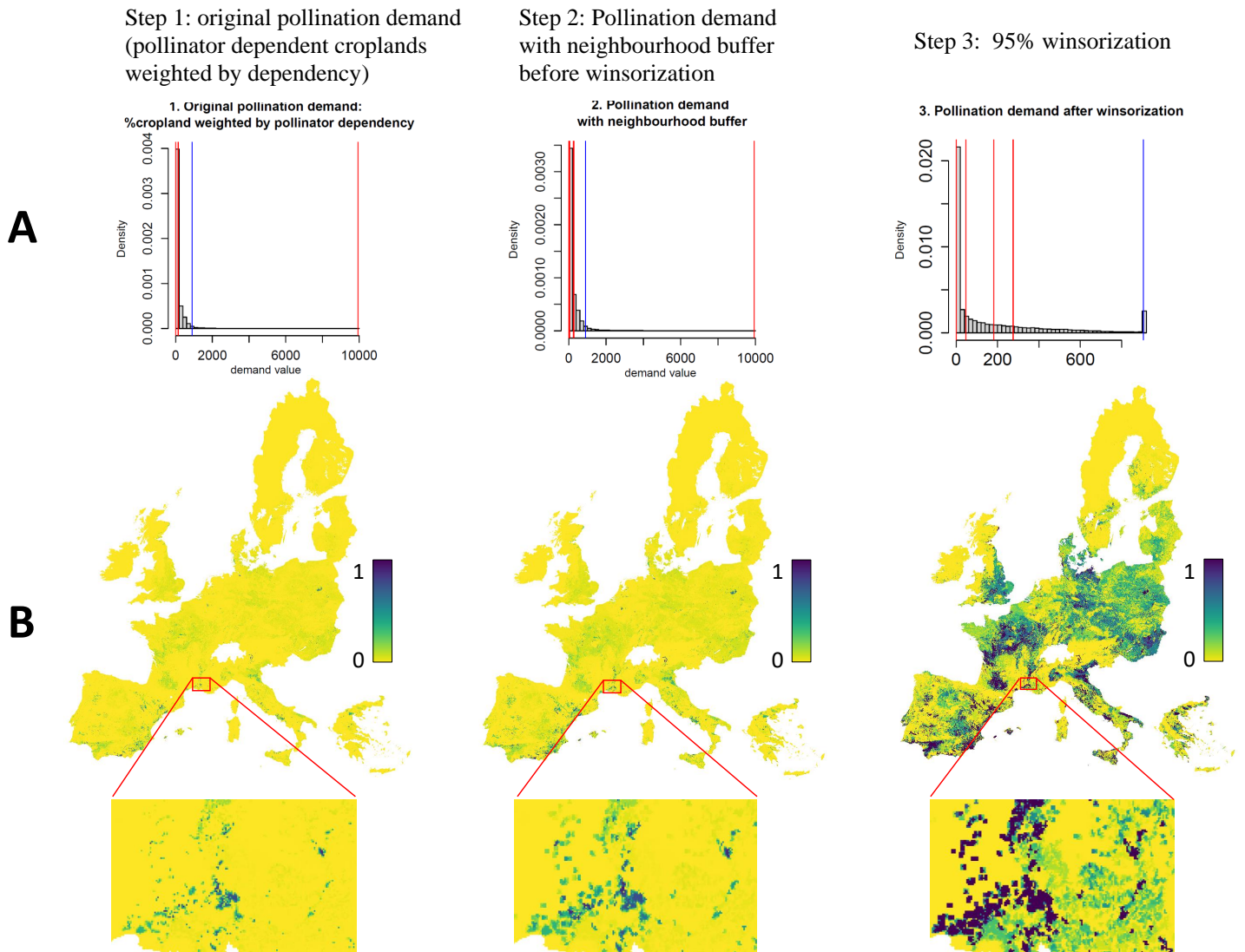


Fig. S6. Pre-processing steps for the pollination demand map. (A) Histograms show the distribution of demand values in each step (top of Fig.). Vertical red lines indicate the quartiles (minimum, lower quartile, median, upper quartile and maximum); the vertical blue line indicates the value of the 95th percentile prior to winsorization in step 3. (B) Demand map in each step, including an inset of pollinator dependent croplands (e.g. orchards) in Southern France.

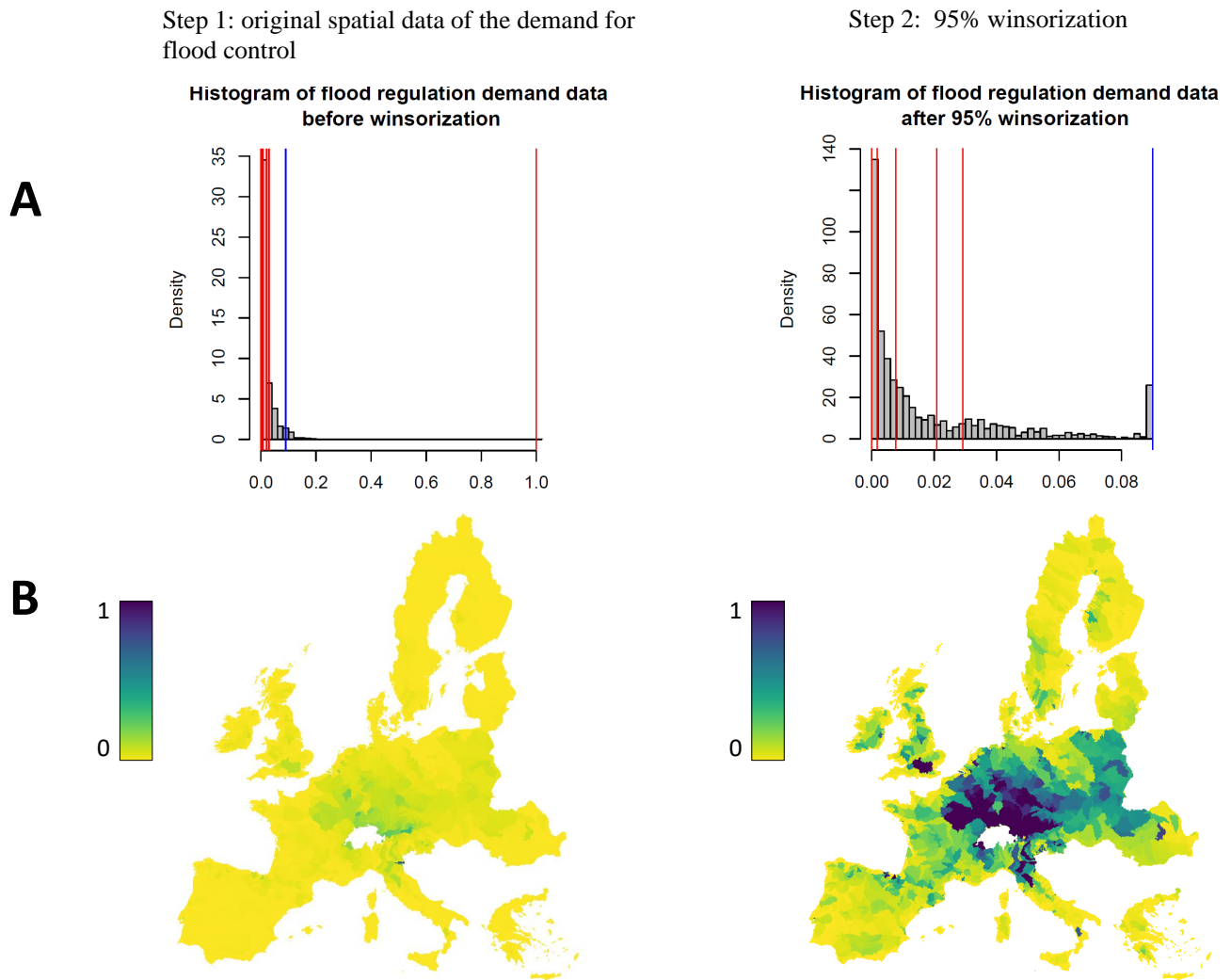
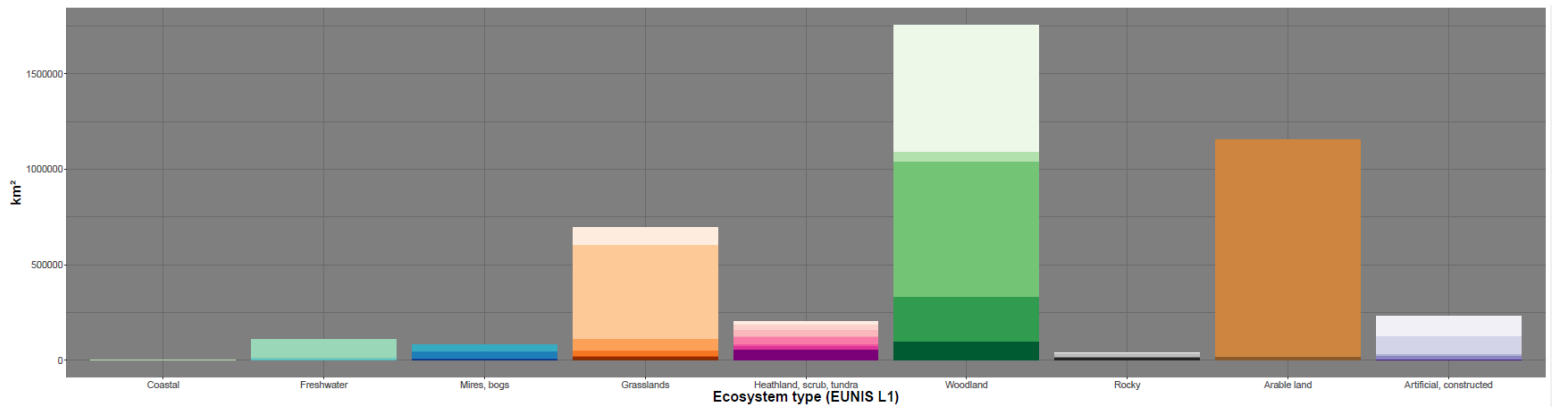


Fig. S7. Pre-processing steps for the flood control demand map. (A) Histograms show the distribution of flood control demand values in each step (top of Fig.). Vertical red lines indicate the quartiles (minimum, lower quartile, median, upper quartile and maximum); the vertical blue line indicates the value of the 95th percentile prior to winsorization in step 3. (B) Demand map in the two pre-processing steps.



Ecosystem subtype (EUNIS L2)

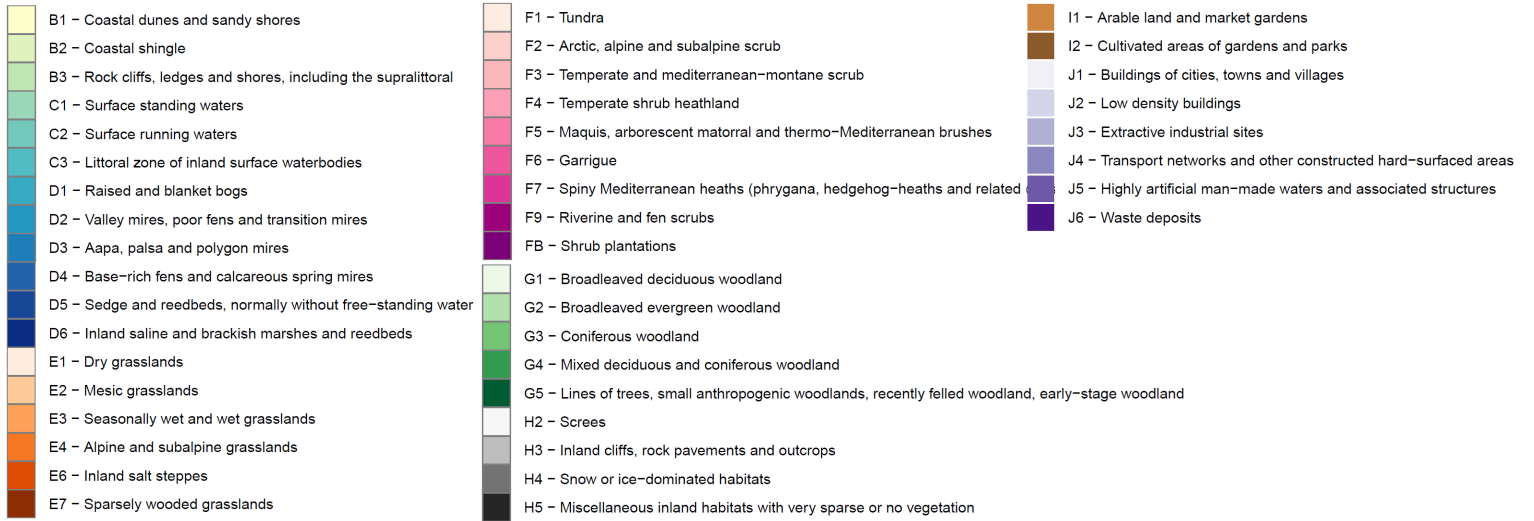


Fig. S8. Diversity and spatial coverage of ecosystem types in Europe. The bar plot shows the area covered by each ecosystem type according to the EUNIS L2 classification (see legend); the x-axis corresponds to the broader EUNIS L1 classification of the European terrestrial ecosystem types. Woodlands and arable lands are the two most frequent ecosystem types in the EU.

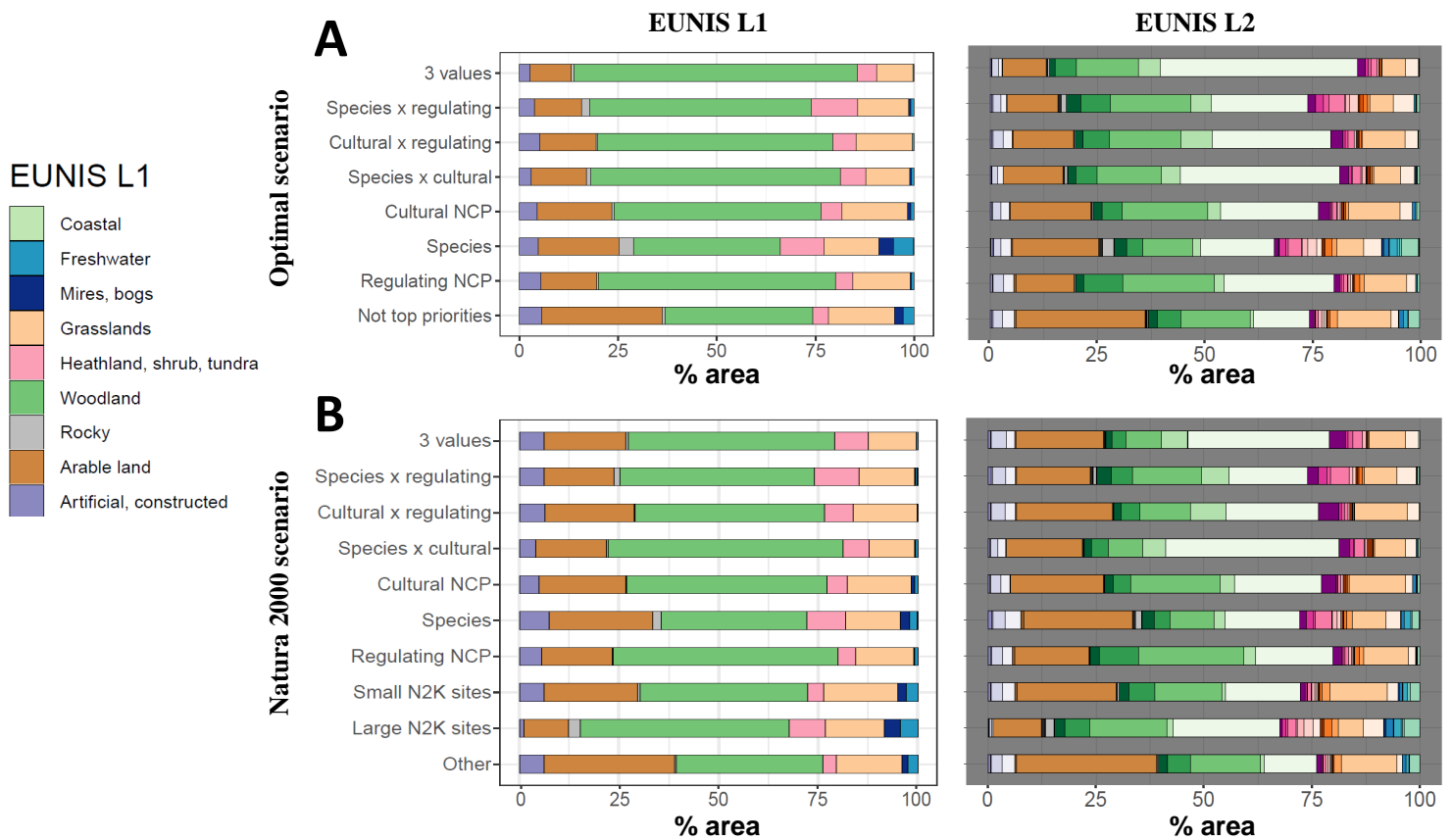


Fig. S9. Diversity and spatial coverage of ecosystem types in optimal priorities (A) and in the Natura 2000 scenario (B). Colours represent the ecosystem type in EUNIS L1 (left, with colour legend on the left) and EUNIS L2 (right, with colour legend in Fig. S8). The y-axis represents the type of top priorities: for example, top priorities for species contain the highest diversity of ecosystem types (considering evenness) across all other types of priorities. In particular, heathlands and scrublands, aquatic ecosystems and sparsely vegetated (rocky) ecosystems represent a high proportion of the top priorities for species, while they are of low value for NCP, and they are not particularly abundant types of ecosystems in the EU (Fig. S8). Areas of spatial overlap between all three values (species, cultural and regulating NCP) are mostly found in (broadleaved deciduous) woodlands. Arable lands are widely represented in Europe (Fig. S8), but they represent a relatively small proportion of top conservation priorities for either species or NCP.

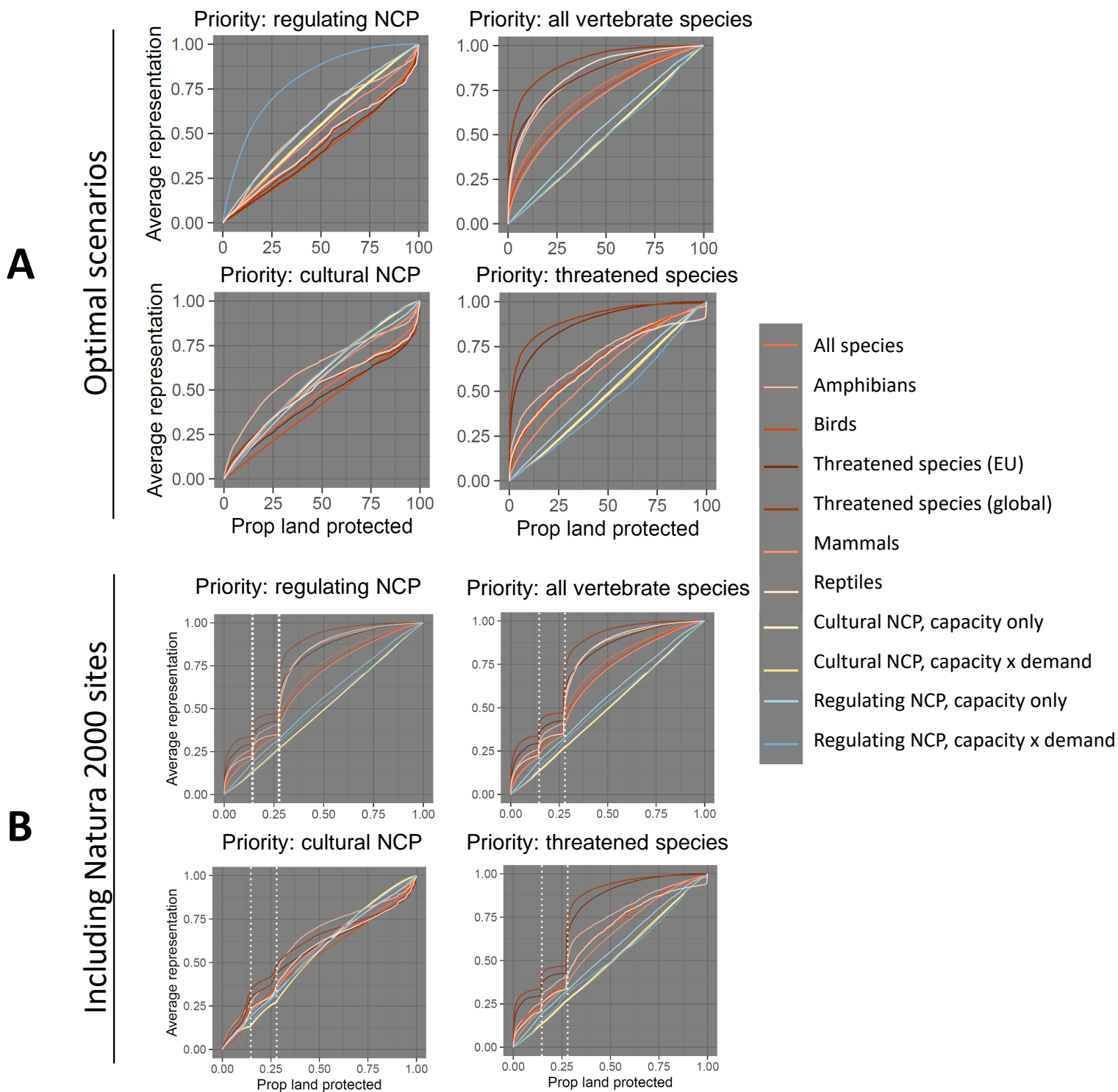


Fig. S10. Performance curves for (A) an optimal allocation of land and (B) accounting for Natura 2000 protected areas. Each graph represents the performance curve for each prioritization run. The x-axis represents the percentage land protected, where the order of the cells in the landscape is determined by the prioritization scenario (corresponding to each of the different graphs). In each graph, the coloured curves quantify the representation (i.e. the average proportion of distributions) of the features optimized as well as all the incidental representation of other features (each colour corresponds to a group of features, e.g. amphibian species; cultural NCP capacity).

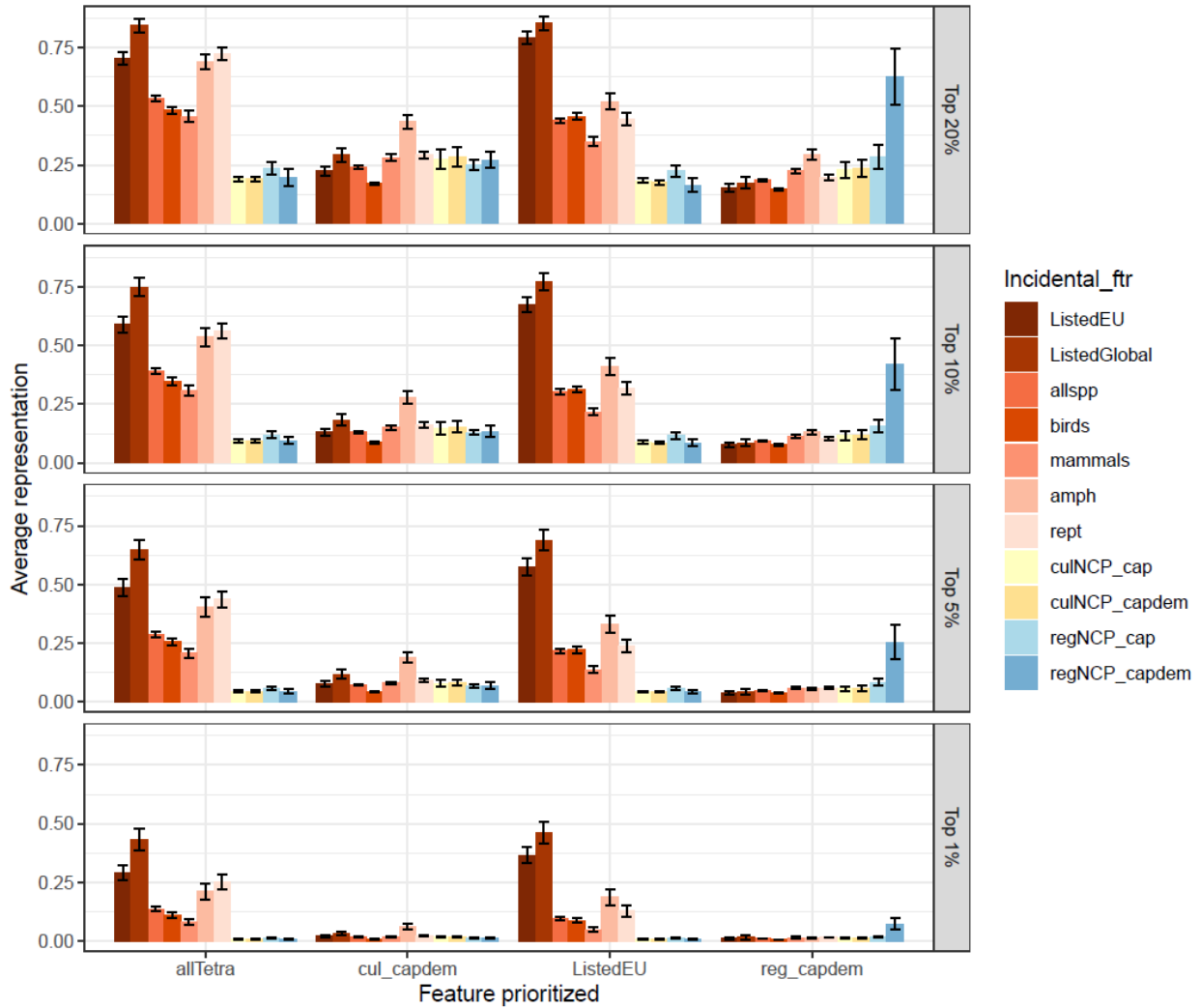


Fig. S11. Representation of different groups of features (species or NCP) in different prioritizations, for different top priority cut-off thresholds. This graph shows that, for example, top 10% priorities for species cover on average 39% (standard error (s.e.) = 1.2%) of all species distributions, including 59% of threatened species distributions, 53% of amphibians, 56% of reptiles, 34% of birds, and 31% of mammal species distributions. Fig. 2 shows only the top 10% priority areas; this figure shows that a large proportion of species distributions is contained just 1% of the study area (but not for NCP). In particular, almost half of globally threatened species distributions on average are contained in just 1% of the study region (EU27).

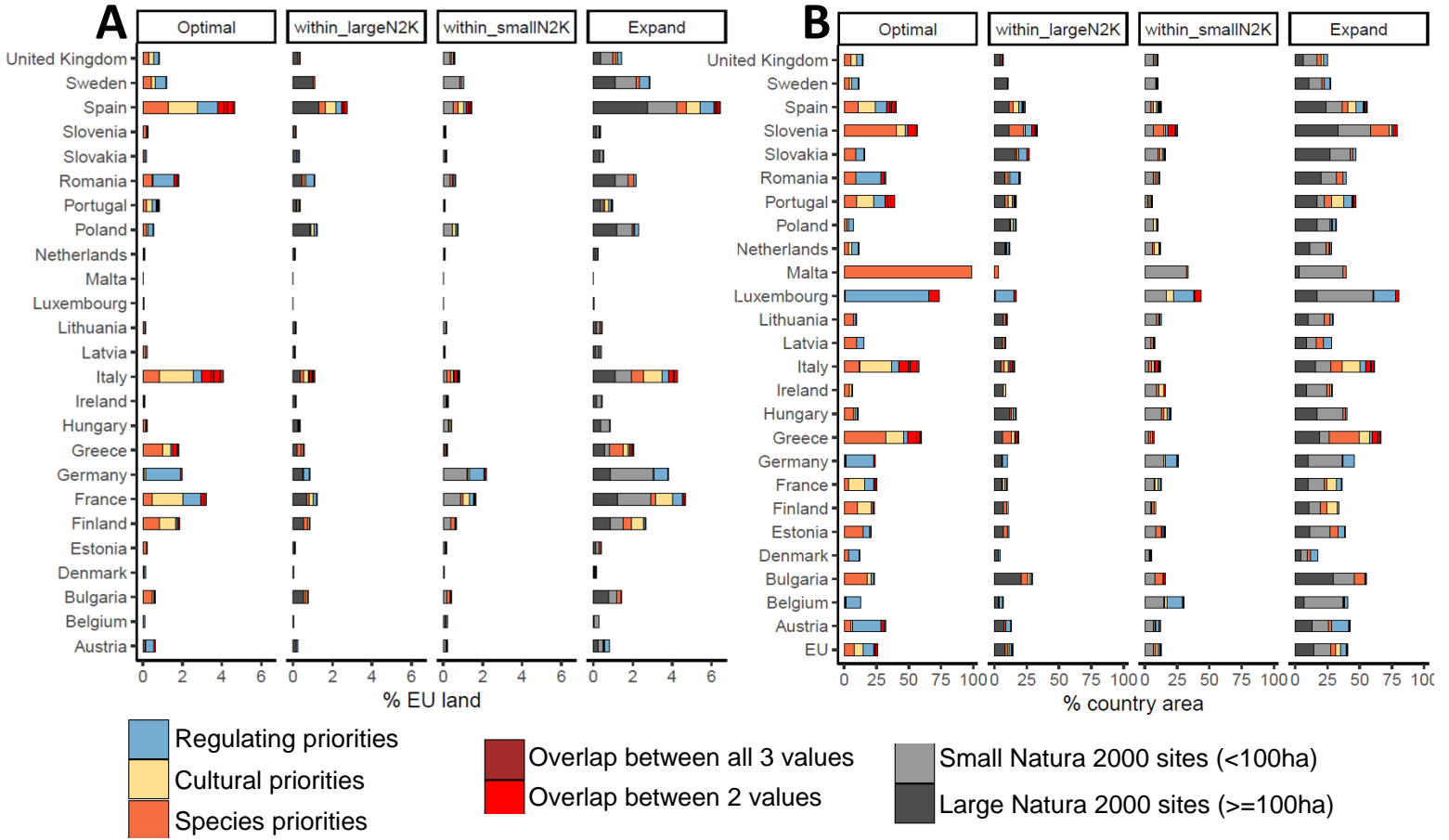


Fig. S12. NCP and biodiversity priorities are unequally distributed between countries. Bar charts represent the surface covered by each type of priority (orange: species, yellow: cultural, blue: regulating, red: total surface of spatial overlap between at least two values) for each country in the study region. In (A) the surface is expressed in terms of % EU surface, and in (B) the surface is expressed as the proportion of each country's surface. Each panel represents the different top priorities for each scenario, from left to right: top 10% optimal, top 2.5% within large Natura 2000 sites, top 2.5% within small Natura 2000 sites, top 5% to expand the Natura 2000 network. The surface covered by Natura 2000 areas (large in dark grey, small in lighter grey) is represented in grey.

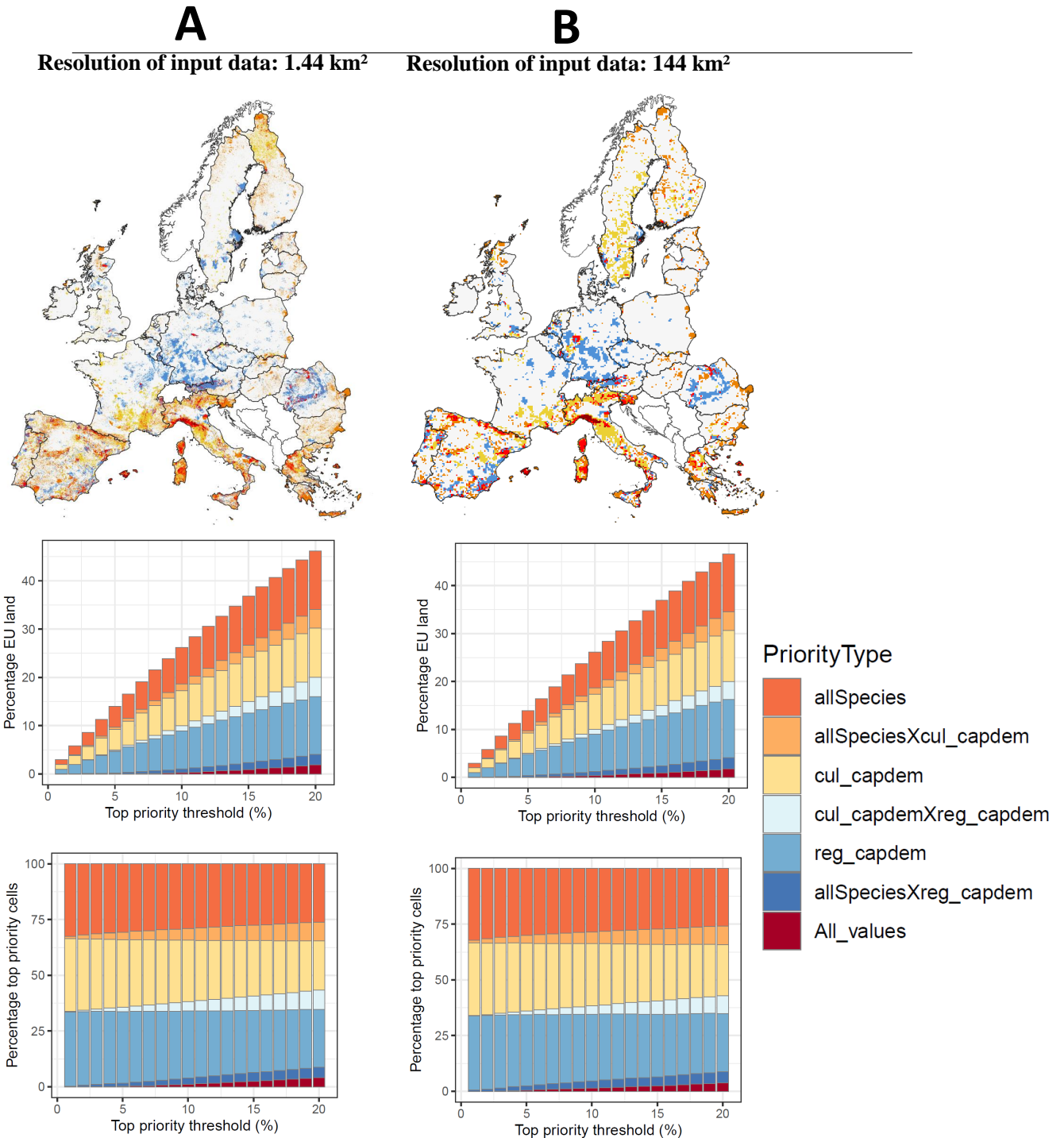


Fig. S13. Spatial overlap (y-axis) between different top priorities cut-off threshold (x-axis) of the 3 main prioritizations, for (A) 1.44km² input data and (B) 144km² input data.

Colours represent the type of top priority: top priorities for all terrestrial vertebrate species only in orange; top priorities for cultural NCP in yellow; top priorities for regulating NCP in blue.

Dark red represents the surface covered by spatial overlap between all 3 values. In the maps, areas of spatial overlap between priorities for 2 different values are bright red. In the bar plots, different pairwise spatial overlaps are represented in different colours: light orange represents the surface covered by spatial overlaps between top priorities for species and for cultural NCP; light blue represents spatial overlap between top priorities for regulating NCP and for cultural NCP; dark blue represents spatial overlap between top priorities for species and for regulating NCP. The comparison between (A) and (B) shows that the spatial outcome of the prioritization are the same when using a 100-fold coarser spatial resolution.

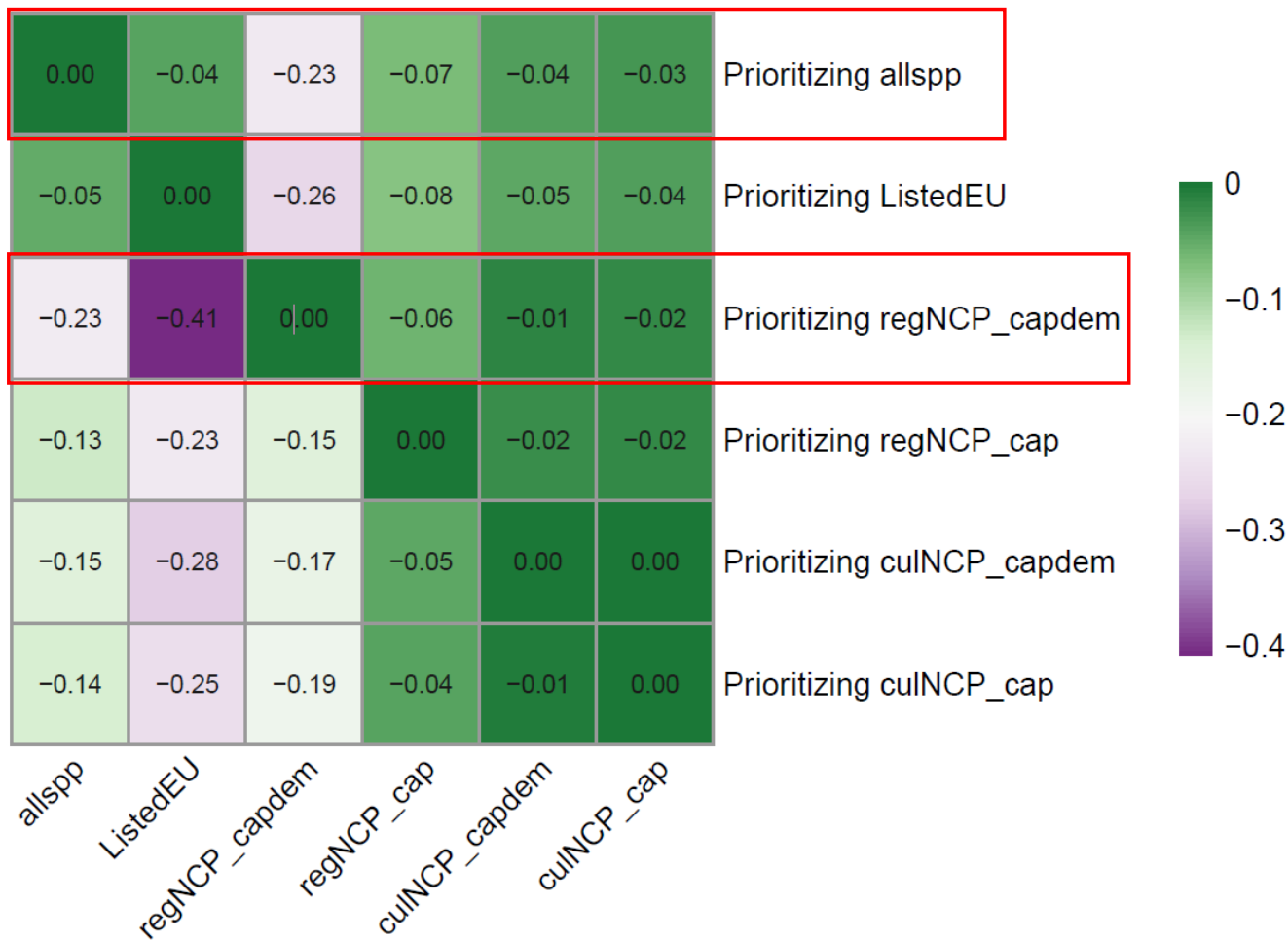


Fig. S14. Heat map representing the (dis)similarity between performance curves, for input data at 144 km² resolution. Numbers show the difference between the incidental representation and the optimal representation, quantified by: $AUC(\text{incidental}) - AUC(\text{optimal})$ (AUC stands for area under the curve). Each element of the heat map shows the difference between the incidental representation in the prioritization on the right (from top to bottom), and the optimal AUC of the features on the X axis (from left to right). The closer to 0, the more similar the performance curves are (i.e. the better the incidental representation); the more negative, the worse the surrogate run performs compared to the optimal run. Comparison of this figure with Fig. S19 shows that these results are largely unchanged when up-scaling the resolution of input data by a factor of 100.

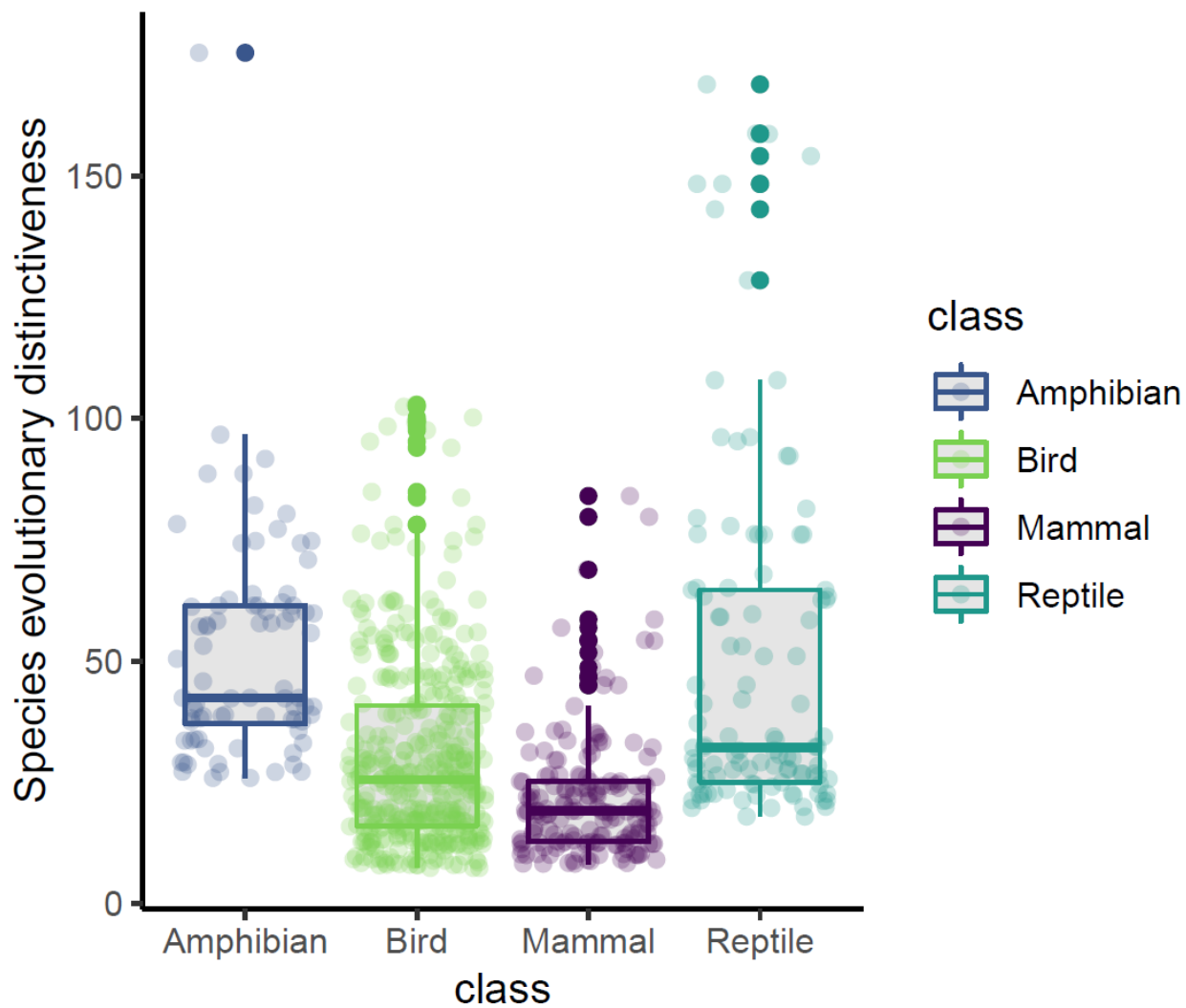


Fig. S15. Evolutionary distinctiveness (ED) (y-axis) of terrestrial vertebrate species, per taxonomic class (x-axis). Each dot in the boxplot is a species' evolutionary distinctiveness value, used as a weight (multiplying factor of individual species distributions) in the ED prioritization.

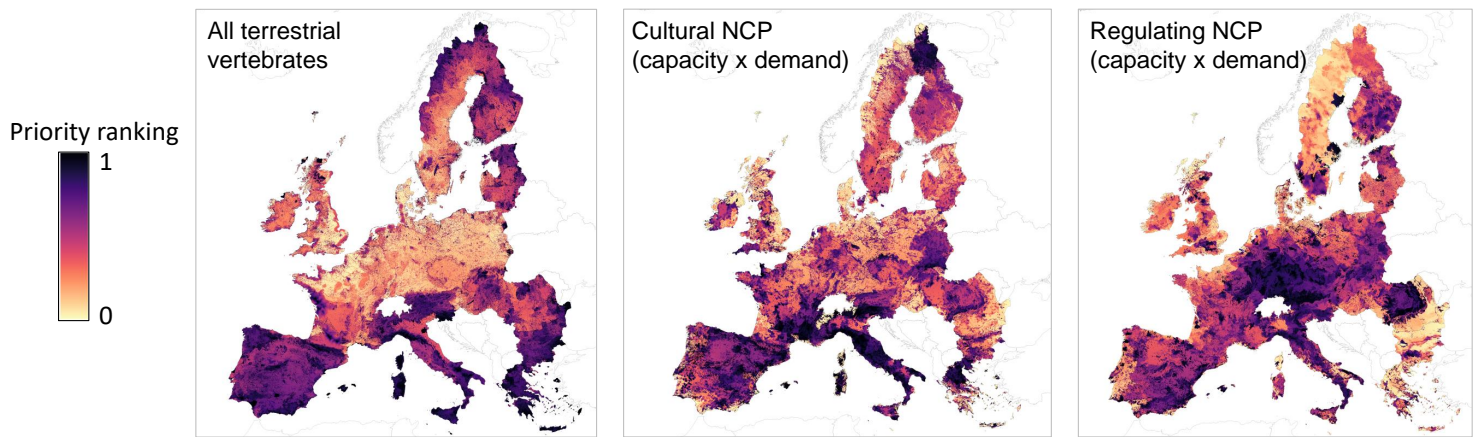


Fig. S16. Priority rankings for vertebrate species, cultural NCP and regulating NCP in an optimal allocation of land for conservation (ignoring existing Natura 2000 areas). Each map represents the conservation value across the study region, quantified by the priority ranking of grid cells, in each prioritization. Values range from 0 (lowest conservation value) to 1 (highest conservation value). In the main text, we present only the top 10% priorities in these three prioritizations, i.e. the cells that have a priority ranking between 0.9 and 1.

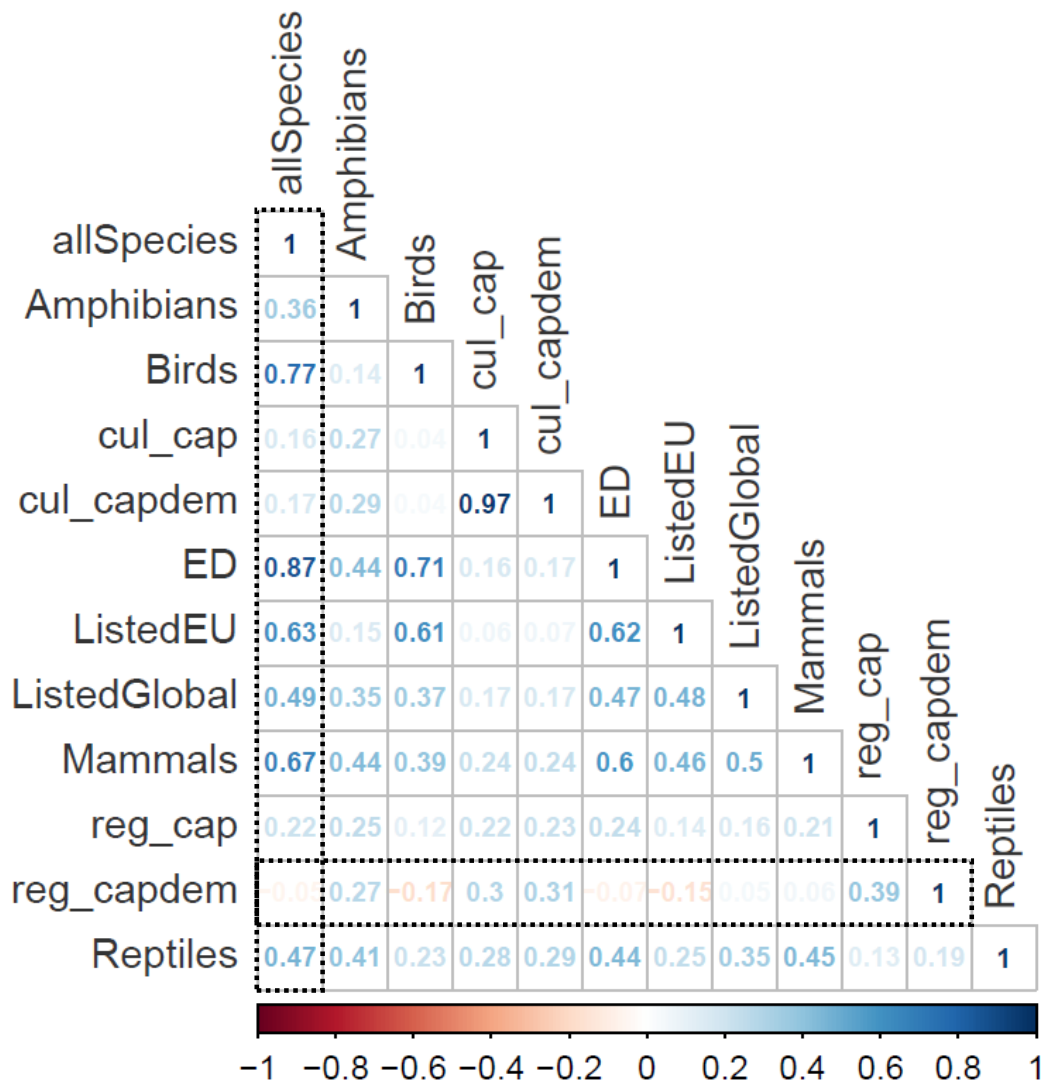


Fig. S17. Spatial similarity between prioritizations performed on different groups of focal features. Numbers correspond to the pairwise spatial R^2 (Spearman rank correlation) of grid cell rankings (ignoring Natura 2000 sites, using input data at a resolution of 1.44 km²).

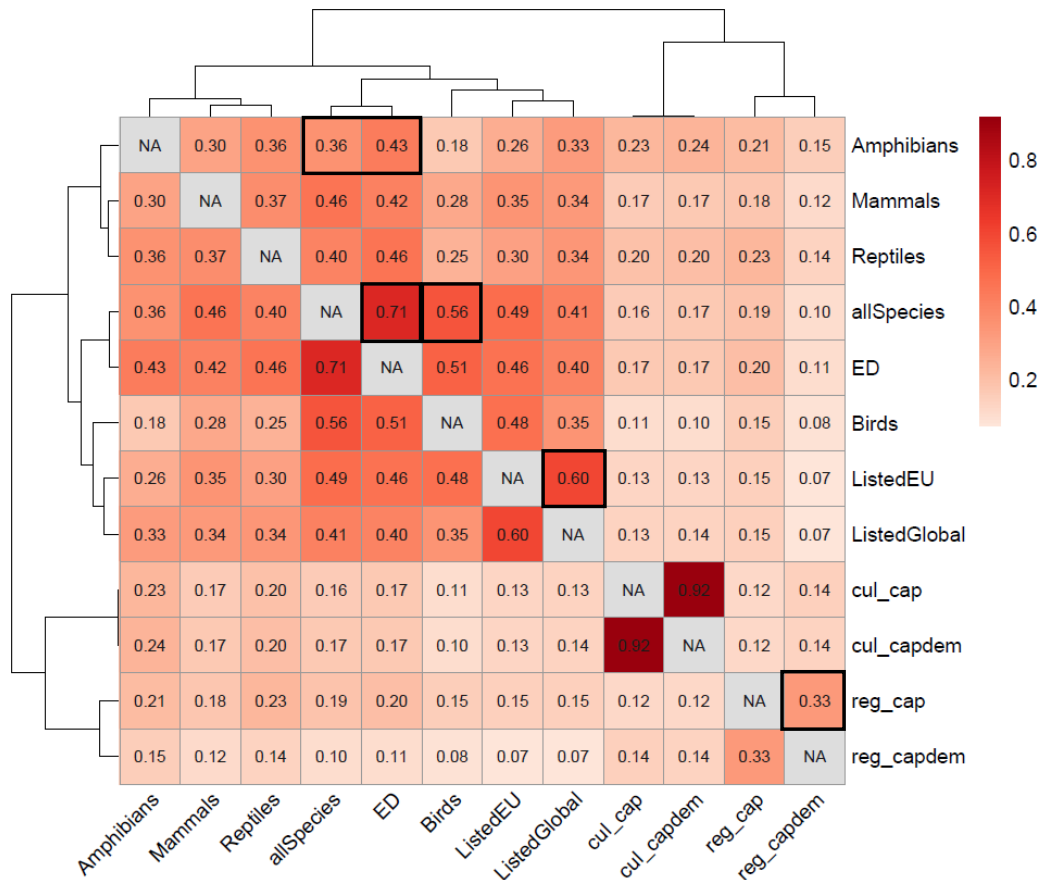


Fig. S18. Heat map representing the pairwise spatial overlap between top 10% priorities obtained from prioritizations for different sets of features. For example, the row ‘Amphibians’ presents the spatial overlap between top 10% priorities defined for amphibians only, with top priorities defined for other groups of features. Interestingly, top priorities for amphibians coincide more often with top priorities defined with the evolutionary distinctiveness of species, than with priorities defined for all species regardless of their evolutionary distinctiveness. This is because amphibians are more evolutionarily distinct on average than the three other taxonomic classes (Fig. S15). Top priorities defined with the evolutionary distinctiveness of species are largely similar (71% overlap) to priorities defined for all species regardless of evolutionary distinctiveness. Top priorities defined for birds coincide more with priorities defined for all species than any other taxonomic group of species, because birds represent half of all species considered in this study. The overlap is relatively high between top priorities for threatened species defined at the EU level, and top priorities for globally threatened species (60% overlap) – the 40% mismatch is due to a few species that do not belong to both sets and that strongly influence the prioritization due to their small geographic ranges. The mismatch is high between priorities for regulating NCP including demand and priorities for regulating NCP capacity only (only 33% overlap), because the demand for regulating NCP is strongly structured spatially.

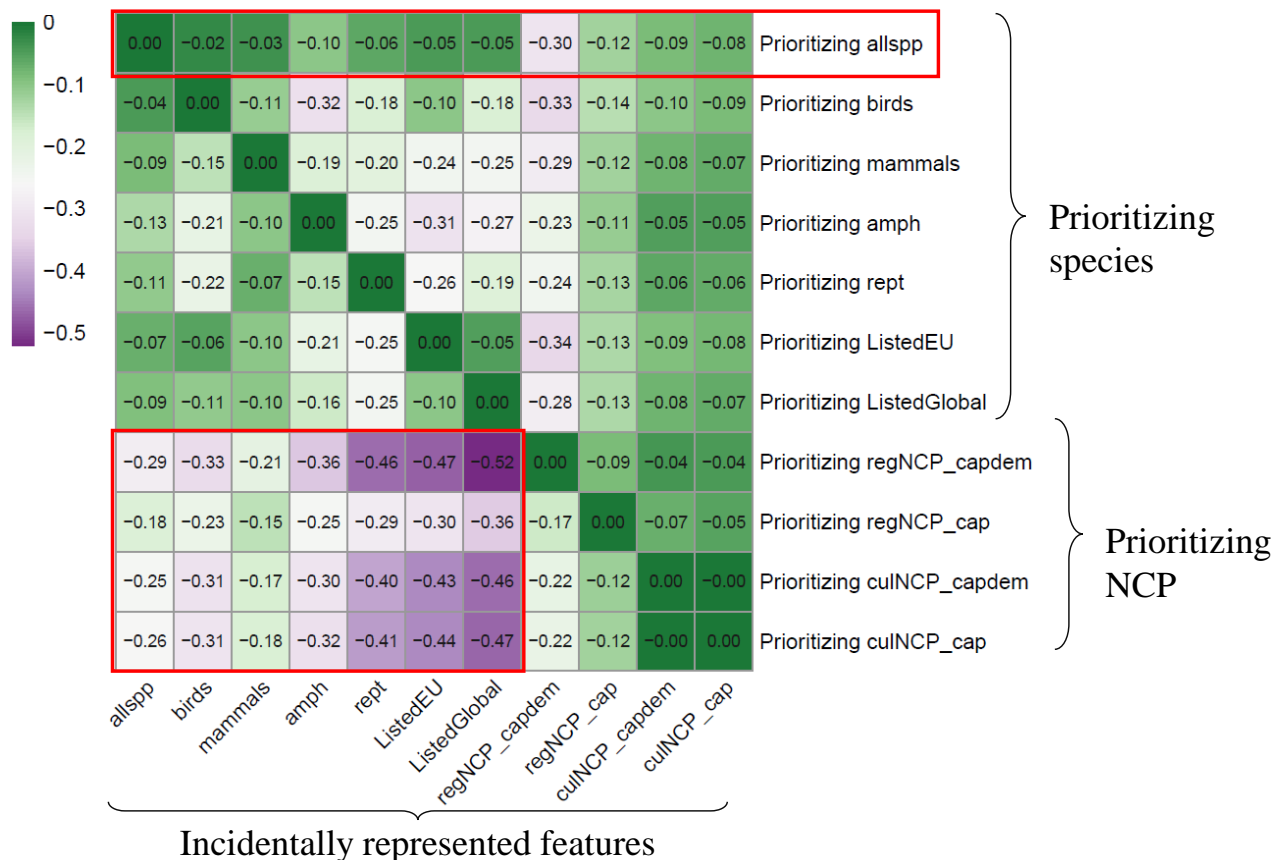


Fig. S19. Heat map representing (dis)similarity between performance curves, for input data at a resolution of 1.44 km². Numbers represent the difference between the incidental representation of a group of features and their optimal representation – this difference is best quantified by the difference between the corresponding areas under the curve: $AUC(\text{incidental}) - AUC(\text{optimal})$. These prioritizations ignore Natura 2000 sites, and input data is at a resolution of 1.44km². Each element of the heat map shows the difference between the incidental representation in the prioritization on the right (from top to bottom), and the optimal AUC of the features on the x-axis (from left to right). The closer to 0 (deeper green), the more similar the performance curves are (i.e. the better the incidental representation). Conversely, the more negative (deeper purple), the worse the surrogate run performs compared to the optimal run. This Fig. shows that prioritizing for species (first row) leads to the highest incidental representation across all features (left to right), i.e. the highest conservation gains across all nature's values. By contrast, prioritizing for nature contributions (both regulating and cultural) lead to high losses for all groups of vertebrate species considered compared with their optimal representation – particularly regulating priorities, that lead to the highest losses in representation of all groups of features considered.

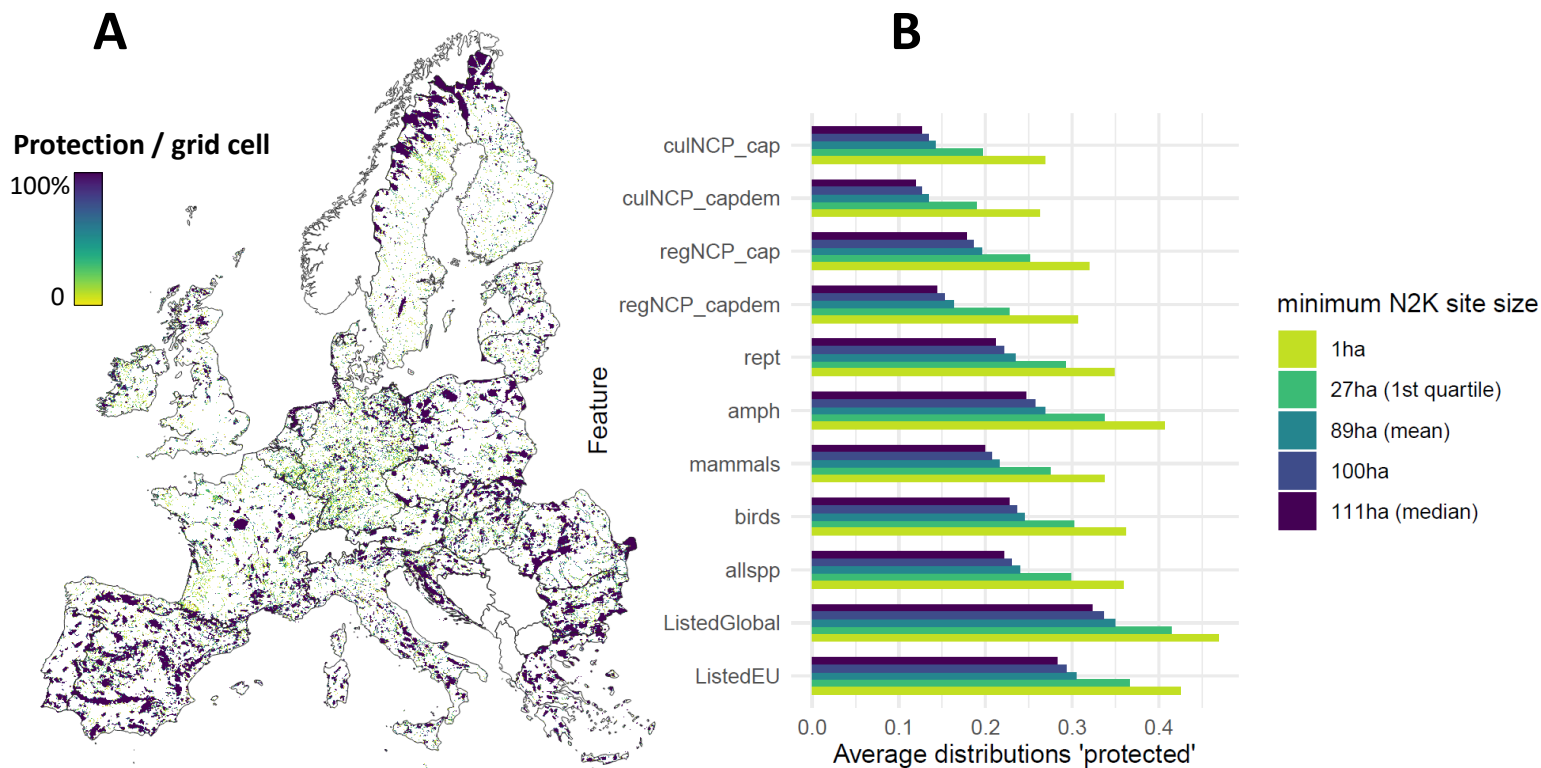


Fig. S20. The proportion of different nature's values protected vary with the size of Natura 2000 used to define the protection status of a grid cell. (A) Map of the percentage of Natura 2000 coverage in 1.44km² grid cells. (B) Bar plot quantifying the proportion of distributions 'protected' for different groups of features (y-axis) along a gradient of Natura 2000 size thresholds. Colours represent the minimum size of a Natura 2000 site for a grid cell to be considered 'protected'. Lighter shades indicate that cells with a smaller proportion of Natura 2000 are considered to be protected, while darker shades indicate cells that are considered 'protected' if they contain higher proportions of Natura 2000. The proportions of distributions within these 'protected' cells are then quantified (x-axis).

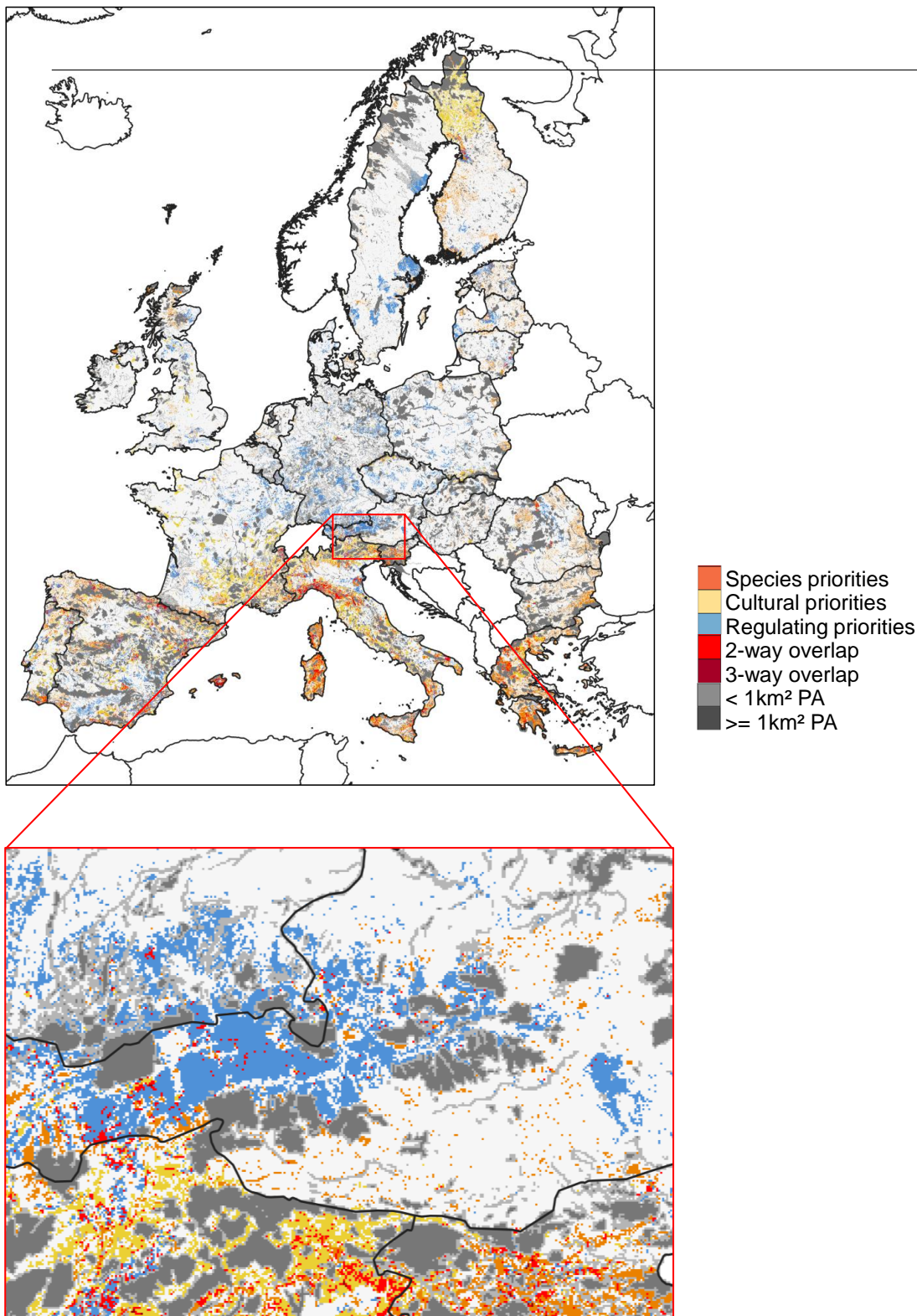


Fig. S21. Map of top 5% priority areas for the expansion of the Natura 2000 protected area network. The map above represents the entire study region (EU27) coloured in light grey, and the map below shows an inset on the national borders between Italy, Austria, Germany and Slovenia. Grid cells containing less than 1km² of Natura 2000 sites are shown in grey; those containing larger Natura 2000 sites are shown in darker grey. In blue are top priority areas for regulating NCP; in yellow for cultural NCP; in orange for all vertebrate species. Areas of spatial overlap between top priorities for two values are bright red; areas of spatial overlap between 3 values are in brown.

Nature's contribution to people	NCP capacity (without demand)	Demand for NCP
Carbon sequestration	Sequestration rates for different land cover types (cropland, pasture, and wetlands, together with country-specific emission factors for forests). Emissions (i.e. negative sequestration rates) were set to 0 (18, 41).	Global.
Pollination	Percentage of potential wild bee habitat per cell, based on land cover and hedgerow (green linear elements) density. (42)	Pollination dependency of a crop type multiplied by the percentage of that crop type within cells that overlapped or were adjacent to cells containing bee habitat.
Flood control	Water retention capacity (large patches of natural vegetation or extensive agriculture). (47)	Potential monetary flood damage in a downstream basin for a specific water inundation. Downstream flood damages are distributed towards upstream basins providing flood regulation.
Air quality	Air quality capacity was adapted from Lavalle <i>et al.</i> 2015 (49), who quantified using deposition velocity (m/s), mainly determined by the leaf area of plants. (18)	Modelled NO ₂ concentrations (micrograms per cubic meter) as a proxy for air-quality-regulation demand, assuming demand is high in locations with relatively higher air pollution.
Heritage agriculture	Landscape characterization based on cultural landscape and land use intensity (economic farm size, N-input, Energy content output, harvest intensity, field size, photo density). (53)	Indicator for NCP capacity includes value & meaning through photo density.
Heritage forests	Landscape characterization based on cultural landscape and land use intensity (forest age; photo density). (53)	Indicator for NCP capacity includes value & Meaning through photo density.
Nature tourism	Supply of assets for tourism supported by ecosystems. (54)	Indicator for NCP capacity includes distance to cities and presence of camping sites
Wild foods foraging	Species richness of wild edible plants and mushrooms. (52)	Culturally important areas for wild foods foraging

Table S1. Overview of NCP data

Species	Year Assessed	Concordance (%) between Maiorano et al. And IUCN
<i>Fulica atra</i>	2019	97.17%
<i>Gelochelidon nilotica</i>	2019	36.95%
<i>Remiz pendulinus</i>	2019	86.33%
<i>Gavia stellata</i>	2018	97.17%
<i>Falco vespertinus</i>	2018	66.66%
<i>Calidris maritima</i>	2018	82.33%
<i>Stercorarius longicaudus</i>	2018	99.99%
<i>Pterocles alchata</i>	2018	76.95%
<i>Calandrella brachydactyla</i>	2018	82.77%
<i>Anthus campestris</i>	2018	89.88%
<i>Regulus regulus</i>	2018	98.09%
<i>Prunella modularis</i>	2018	98.48%
<i>Turdus philomelos</i>	2018	98.12%
<i>Acrocephalus melanopogon</i>	2018	49.96%
<i>Ficedula hypoleuca</i>	2018	95.47%
<i>Miliaria calandra</i>	2018	91.19%
<i>Carduelis cannabina</i>	2018	99.38%
<i>Circus macrourus</i>	2018	85.48%
<i>Aquila clanga</i>	2016	89.28%
<i>Lagopus mutus</i>	2016	92.85%
<i>Vanellus vanellus</i>	2016	96.60%
<i>Charadrius alexandrinus</i>	2016	86.03%
<i>Chlidonias hybridus</i>	2016	82.86%
<i>Clamator glandarius</i>	2016	88.57%
<i>Dendrocopos syriacus</i>	2016	95.13%
<i>Nycticorax nycticorax</i>	2016	58.47%
<i>Tarsiger cyanurus</i>	2016	11.55%
<i>Aegithalos caudatus</i>	2016	96.22%
<i>Garrulus glandarius</i>	2016	98.62%
<i>Cygnus cygnus</i>	2016	96.71%
<i>Emberiza hortulana</i>	2016	93.90%

<i>Loxia scotica</i>	2016	69.84%
<i>Corvus corone</i>	2016	99.11%
<i>Anas crecca</i>	2016	95.59%
<i>Milvus migrans</i>	2016	81.04%
<i>Grus grus</i>	2015	98.19%
<i>Strix uralensis</i>	2015	68.71%
<i>Riparia riparia</i>	2015	94.94%
<i>Oenanthe oenanthe</i>	2015	97.77%
<i>Rupicapra pyrenaica</i>	2020	100%
<i>Miniopterus schreibersi</i>	2019	100%
<i>Plecotus auritus</i>	2019	99.99%
<i>Microtus felteni</i>	2018	100.00%
<i>Crocidura zimmermanni</i>	2018	100%
<i>Microtus agrestis</i>	2016	100%
<i>Microtus multiplex</i>	2016	100%
<i>Myopus schisticolor</i>	2016	100%
<i>Neomys fodiens</i>	2016	99.74%
<i>Sorex minutissimus</i>	2016	100%
<i>Crocidura armenica</i>	2016	100%
<i>Eliomys melanurus</i>	2016	100%
<i>Erinaceus europaeus</i>	2016	100%
<i>Glis glis</i>	2016	100%
<i>Lemmus lemmus</i>	2016	100.00%
<i>Mustela lutreola</i>	2015	92.57%
<i>Capreolus pygargus</i>	2015	100%
<i>Alopex lagopus</i>	2014	100%
<i>Myotis emarginatus</i>	2016	98.86%
<i>Bison bonasus</i>	2008	100%
<i>Alytes cisternasii</i>	2008	99.96%
<i>Discoglossus galganoi</i>	2008	100.00%
<i>Hyla intermedia</i>	2008	98.69%
<i>Pelodytes ibericus</i>	2008	100.00%
<i>Bombina bombina</i>	2008	100.00%

<i>Pelophylax lessonae</i>	2008	100.00%
<i>Salamandra corsica</i>	2008	100.00%
<i>Atylodes genei</i>	2008	100.00%
<i>Triturus cristatus</i>	2008	100.00%
<i>Iberolacerta aurelioi</i>	2008	100.00%
<i>Lacerta bilineata</i>	2008	99.15%
<i>Podarcis hispanica</i>	2008	100.00%
<i>Podarcis taurica</i>	2008	99.84%
<i>Chalcides bedriagai</i>	2008	100.00%
<i>Vipera aspis</i>	2008	100.00%
<i>Podarcis cretensis</i>	2008	100.00%
<i>Algyroides fitzingeri</i>	2008	100.00%

Table S2: Concordance between the latest estimates of species extent of occurrence from the IUCN red list, and the original extent of occurrence data used in Maiorano *et al.*, 2013 for a random sample of 10% of the species considered in this study across all taxonomic classes (38 birds, 20 mammals, 9 amphibians, 8 reptiles). The values are the results of a spatially explicit comparison of the ranges from Maiorano *et al.* (2013) with those downloaded from the IUCN website on December 7th, 2020. On average, using the IUCN ranges as reference, the concordance among the two databases at the species level was 92.3% (percentage of a species range from IUCN which fall within the range from Maiorano *et al.*). For 37 species (8 reptiles, 8 amphibians, 18 mammals, 3 birds; 48.7% of the species) the concordance was perfect (>99%), and it was >95% for 54 species (71% of the species). In short, all amphibians, reptiles, and mammals obtained from Maiorano *et al.*, 2013 correspond almost perfectly to what is currently available online today from IUCN (average concordance of 99.9% for both amphibians and reptiles and of 100% for mammals). For some birds, the range can change significantly even in short periods. Note that these figures are relative to individual extents of occurrences, therefore large percentages can correspond to a fairly small area (*e.g.* *Tarsiger cyanurus*, a species only occurring partially in Finland).

Land cover class	Pearson correlation R ²
agriculture	0.82
forests	0.87
urban	1
other natural vegetation	0.55
bare areas / sparse vegetation	0.72

Table S3: Correlation (cell-by-cell Pearson) between the GlobCover dataset (version of 2006, used to refine the species EOO) and the CCI 2018 (Copernicus), at the same spatial resolution (300 m). To make the two comparable and in line with the spatial resolution we have in our study, we performed a focal analysis with a circular moving window with a 1km radius over the entire EU27 and calculated the correlation between the two land cover maps. To account for the different classifications between the two datasets, we used coarse classes: agriculture, forests, other natural areas, urban, bare areas.

	Pollination demand	Flood control demand
Maximum	9933.73	1.0
99th percentile	3272.38	0.14
98th percentile	1915.29	0.1
95th percentile	905	0.090
75th percentile	275	0.029
Mean	251	0.021
50th percentile (median)	47	0.0077
25th percentile	0	0.0017
Minimum	0	0

Table S4: Summary statistics of the demand for pollination (Fig. S6) and flood control (Fig. S7) prior to winsorization. See section 1. c. ii) and iii) of the materials and methods for more information.

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Appendix E

Understanding the importance of spatial habitat connectivity

Parallel to my PhD, I finalized publications from previous research projects I had been involved with.

In 2017, I worked in the Gonzalez lab in McGill University, to study the diversification and adaptation of microbial metacommunities to environmental stress (antibiotic). This work, in collaboration with Vincent Fugère and Andy Gonzalez, was published in 2020 in *Frontiers in Ecology and Evolution*.

In 2018, I spent four months in Melbourne University, supervised by Heini Kujala in the Quantitative Ecology (QAEco) lab. I worked on metapopulation viability analysis for a set of species of conservation interest in the Hunter region in NSW (Australia): the Powerful Owl, the Northern Brown Bandicoot, and the Squirrel Glider. A main drawback of metapopulation viability models is that they require large amounts of data on the demographics and ecology of the species (e.g. dispersal distance, initial population size, population growth rate). Yet, there is often some uncertainty associated with these values, which may have an impact on key outputs of the population viability models (e.g. expected minimum abundance). For this project, I performed sensitivity analyses to test the sensitivity of key parameters that expected to influence the output of the models. This work fed into a study led by Erica Marshall, which is now published in *Conservation Biology*. A key message from this study is that species need to be explicitly accounted for in spatial planning (specifically for offsets), and that using habitat as a proxy does not guarantee conservation gains for species.

These projects have in common that they incorporate spatial connectivity between

patches of habitat, to study population dynamics following a perturbation (i.e. harsh concentrations of antibiotics in the first; mining developments in the second). The study systems could not be more different. In the first, I experimentally studied metacommunities of the rapidly evolving bacterium *Pseudomonas fluorescens*. In the other, we modelled the viability of three terrestrial vertebrate species across a region of 90,500 ha.

In my thesis, I did not consider spatial connectivity; but it would be essential to include in future work to adequately connect protected areas for long term population persistence, especially in the context of climate and land use changes.

Both of these publications are included in the following pages.



Evolutionary Rescue Is Mediated by the History of Selection and Dispersal in Diversifying Metacommunities

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Rapid evolution can sometimes prevent population extirpation in stressful environments, but the conditions leading to “evolutionary rescue” in metacommunities are unclear. Here we studied the eco-evolutionary response of microbial metacommunities adapting to selection by the antibiotic streptomycin. Our experiment tested how the history of antibiotic selection and contrasting modes of dispersal influenced diversification and subsequent evolutionary rescue in microbial metacommunities undergoing adaptive radiation. We first tracked the change in diversity and density of *Pseudomonas fluorescens* morphotypes selected on a gradient of antibiotic stress. We then examined the recovery of these metacommunities following abrupt application of a high concentration of streptomycin lethal to the ancestral organisms. We show that dispersal increases diversity within the stressed metacommunities, that exposure to stress alters diversification dynamics, and that community composition, dispersal, and past exposure to stress mediate the speed at which evolutionary rescue occurs, but not the final outcome of recovery in abundance and diversity. These findings extend recent experiments on evolutionary rescue to the case of metacommunities undergoing adaptive diversification, and should motivate new theory on this question. Our findings are also relevant to evolutionary conservation biology and research on antimicrobial resistance.

Keywords: evolutionary rescue, metacommunity, spatially explicit dispersal, biodiversity, eco-evolutionary dynamics, stress gradient, antibiotic resistance, *Pseudomonas fluorescens*

INTRODUCTION

Biodiversity is organized across multiple scales, from populations of individual species to communities of multiple species, that evolve and move across a range of spatial scales, from local ecosystems to entire continents. Situated within this hierarchy are metacommunities, defined as a set of local communities that are connected by dispersal (Leibold et al., 2004). Metacommunities face increasing pressure from human-induced environmental degradation, often leading to population decline, local extinctions, and biodiversity loss (Pereira et al., 2010; Haddad et al., 2015). Species occupying metacommunities can respond to these pressures by moving to other communities, by adapting *in situ*, or they can undergo extinction. Under some circumstances, populations can rapidly evolve resistance to stressors and persist in severely degraded environments (Bürger and Lynch, 1995; Hufbauer et al., 2015; Reid et al., 2016). This phenomenon is described by

the theory of evolutionary rescue (Gomulkiewicz and Holt, 1995; Bell and Gonzalez, 2009; Gonzalez et al., 2013; Bell, 2017), which explains how populations can recover from extreme environmental stress through rapid adaptation.

Evolutionary rescue occurs when stress-resistant individuals are selected within a perturbed population, allowing abundance to recover and a viable population to be maintained in conditions that would otherwise cause population extirpation in the absence of evolution. Resistant types responsible for evolutionary rescue may already be present in a population before rescue is needed (due to past *in situ* evolution or to the immigration of resistant types from connected habitats), or evolve *de novo* after the onset of extreme stress. Theory and laboratory experiments have described key drivers of evolutionary rescue for single-species populations. First, evolutionary rescue is more likely if populations were previously exposed to lower levels of the same stressor (leading to an increase in the abundance of stress-resistant genotypes through selection). Second, large population sizes favor evolutionary rescue by reducing the risk of stochastic extinction (Gomulkiewicz and Holt, 1995; Bell and Gonzalez, 2009; Gienapp et al., 2013). Third, if populations are spatially connected to others, the dispersal of stress-resistant genotypes among local populations can enable rescue even in environments that were not previously contaminated by the stressor (Bell and Gonzalez, 2011; Carlson et al., 2014). Understanding the conditions that favor evolutionary rescue has clear implications for both biodiversity conservation and for the management of pests and pathogens evolving resistance to biocides (Alexander et al., 2014).

A few recent studies have expanded the scope of evolutionary rescue from populations to diverse assemblages of species and examined evolutionary rescue in entire communities confronted with severe stress (Fussmann and Gonzalez, 2013; Low-Décarie et al., 2015; Bell et al., 2019; Fugère et al., 2020). Community rescue occurs when the populations of multiple species recover rapidly following exposure to levels of stress that were lethal to the community in its ancestral form, allowing a community to recover both abundance and diversity in severely degraded environments (Low-Décarie et al., 2015). Some key factors promoting evolutionary rescue of populations were also found to favor community rescue (Low-Décarie et al., 2015; Bell et al., 2019; Fugère et al., 2020). First, a history of stress exposure increases the relative frequency of stress-resistant individuals in communities, which provides a correlated advantage at a higher dose of stress and thus facilitates rescue. Second, just as intraspecific genetic diversity can promote the evolutionary rescue of individual populations (Carlson et al., 2014), a greater diversity of species can also favor rescue, as communities holding a more diverse set of species are more likely to contain resistant types (Low-Décarie et al., 2015). Finally, when local communities are spatially connected, thus forming a metacommunity, dispersal was found to favor evolutionary rescue in local communities by moving resistant genotypes within a heterogeneous metacommunity (Low-Décarie et al., 2015). Nonetheless, only a few recent studies have tested the conditions that promote evolutionary rescue in communities of multiple species, and much remains to be uncovered.

Here, we expand on previous work testing evolutionary rescue in communities, and ask whether a history of stress, greater biodiversity, and the presence of dispersal favor evolutionary rescue in metacommunities across a heterogeneous landscape. In contrast to previous community rescue experiments that have used microbial assemblages with existing intra and interspecific variation, we examined evolutionary rescue in an experimental system in which all diversity and stress resistance is generated *de novo* through rapid evolution. We also manipulated not only the presence of dispersal prior to exposure to extreme levels of stress, but also its spatial structure, contrasting global vs. local dispersal in metacommunities. These two modes of dispersal were shown to have distinct effects on the likelihood of evolutionary rescue in metapopulations of the yeast, *Saccharomyces cerevisiae* (Bell and Gonzalez, 2011), but how the spatial structure of dispersal affects evolutionary rescue in metacommunities remains unknown. Global dispersal connects all communities to each other, mixing individuals from the whole metacommunity. This mode of dispersal brings in diversity upon which natural selection will act and potentially enable evolutionary rescue. At the same time, the resulting migrants could be maladapted to their new habitat, thus hampering adaptation and subsequent evolutionary rescue by migration load (Bell and Gonzalez, 2011; Schiffers et al., 2013; Carlson et al., 2014; Hao et al., 2015). On the other hand, local dispersal [also known as “stepping-stone” dispersal (Bell et al., 2019)] is a mode of dispersal where communities are only connected by directional migration up a gradient of environmental stress. Local dispersal is expected to favor evolutionary rescue, because it will more likely bring better-adapted individuals as they move up the stress gradient (Bell and Gonzalez, 2011). Over longer time-scales in communities undergoing adaptive diversification and speciation, dispersal may also favor the generation of diversity and productivity (Venail et al., 2008), which would also promote the likelihood of rescue following environmental degradation.

To address how stress and dispersal interact to modulate the adaptation and diversification of metacommunities across a heterogeneous landscape, and subsequent evolutionary rescue, we used the plant symbiont *Pseudomonas fluorescens* SBW25 as a model system exposed to the antibiotic streptomycin. We build on previous studies with this organism (Rainey and Travisano, 1998; Kassen et al., 2000; Massin and Gonzalez, 2006; Perron et al., 2006; Venail et al., 2008, 2010; Ramsayer et al., 2013). This bacterium shows rapid and repeatable *in vitro* diversification when grown in a heterogeneous environment. As they grow, individuals of this aerobic bacterium compete for oxygen, thus creating a vertical gradient of oxygen in the liquid medium. The resulting environment favors mutants able to colonize the air-liquid interface (Rainey and Travisano, 1998) via the formation of a biofilm composed of cellulose-based polymer (McDonald et al., 2009; Lind et al., 2018). Diversification can be recorded at the phenotypic level by growing these bacteria on solid media where they display striking differences in colony morphology that relates to their niche preference. These morphotypes are easy to detect and are heritable (Rainey and Travisano, 1998). In our experiment, the ancestral cells were derived from a single isomorphic

colony (“smooth” opaque morph) which then grew asexually. This means that mutations are only transferred to the next generation by single cell division. Consequently, adaptive mutations that arise in one morphotype are independent from the evolutionary pathway of other morphotypes. Quantifying the emerging morphological diversity allows us to track this evolution occurring *in vitro*. The species concept does not readily apply to bacteria (Rosselló-Mora and Amann, 2001; Riley and Lizotte-Waniewski, 2009), but the subsequent rapid diversification, niche specialization, and growth by asexual reproduction in *P. fluorescens* allows us to consider different morphotypes analogous to different species, and to consider our diversified bacterial assemblages as a model for communities of multiple species. Previous studies have documented the capacity of *P. fluorescens* to rapidly evolve resistance to the antibiotic streptomycin (Ramsayer et al., 2013), a versatile and widely used antibiotic (World Health Organization, 2015). This work, combined with the tendency for *P. fluorescens* to adaptively radiate (MacLean and Bell, 2002; Barrett and Bell, 2006), makes it an excellent system to study the factors promoting adaptation to stressors and evolutionary rescue in the context of rapidly diversifying communities.

Following previous experiments (Bell and Gonzalez, 2011; Low-Décarie et al., 2015; Bell et al., 2019; Fugère et al., 2020), we conducted an experiment which proceeded in two phases. In the first phase, communities evolved and diversified across a gradient of streptomycin. We created replicated four-patch metacommunities with one of three modes of dispersal: local dispersal, global dispersal, and a control with no dispersal. We recorded the dynamics of adaptation by quantifying the growth and morphological diversification of each community across the gradient of stress. In the second phase, we transferred each community regardless of its history of stress to a severe dose of streptomycin which was established to be lethal to the majority of ancestral organisms, following the method employed by previous community rescue experiments (Low-Décarie et al., 2015). In this second phase, dispersal was ceased such that any recovery of abundance and diversity could be attributed to local eco-evolutionary processes – and not demographic rescue due to dispersal. We quantified the trajectory and outcome of evolutionary rescue in Phase 2 of the experiment and linked these responses to three potential drivers of rescue manipulated in Phase 1: the history of exposure to sublethal doses of streptomycin, the mode of dispersal within the metacommunity, and the morphotype diversity of the community (i.e., the outcome of diversification occurring during Phase 1). Based on previous experiments (Bell and Gonzalez, 2011; Low-Décarie et al., 2015; Fugère et al., 2020) we expected that: (1) a history of streptomycin exposure in Phase 1 would facilitate evolutionary rescue in Phase 2; (2) the presence of dispersal in heterogeneous metacommunities would increase local morphotype diversity and would spread resistant genotypes during Phase 1, both of which would facilitate adaptation to, and rescue from, severe antibiotic stress—especially in communities naive to the stressor; and (3) that local dispersal would have a greater influence on the likelihood of evolutionary rescue than global dispersal.

MATERIALS AND METHODS

Bacterial Cultures

We used the ancestral strain of *Pseudomonas fluorescens* SBW25 (Rainey and Bailey, 1996) cultured in basic growth medium was King's B (KB) medium (20.00 g/L Proteose Peptone (Difco no.3), 15 mL/L glycerol, 1.50 g/L K₂HPO₄, 1.50 g/L MgSO₄, distilled water). Populations in stressful treatments were supplemented with streptomycin (MilliporeSigma; Montreal, Canada). We initiated bacterial cultures from a single isolate clone of *P. fluorescens* SBW25 in a 125-mL glass vial supplied with 50 mL of King's B medium, grown for 24 h at 28°C and shaken at 150 rpm. One percentage of this culture was transferred to 96-well plates supplied with 200 μL KB and grown for a further 24 h at 28°C, to initiate separate experimental populations. These were not shaken to allow diversification into morphologically diverse communities of *P. fluorescens* morphotypes over the course of the experiment (Rainey and Travisano, 1998). We thus refer to the “ancestral cells” at the onset of the experiment, and then to “communities” once microwells contained a diverse assemblage of morphotypes.

Abundance was measured spectrophotometrically as the optical density at 590 nm (OD₅₉₀), using a microplate reader (BioTek; Winooski, USA). Correspondence between absorbance readings and cell density was verified by growing bacterial cultures with known OD₅₉₀ values on at least 3 replicate KB-Agar plates and by counting the number of colony-forming units. The relationship between cell density and OD₅₉₀ ($R^2 = 0.6$) was: y (cells/mL) = $-3 \times 10^8 + 5 \times 10^9 \times \text{OD}_{590}$ (**Supplementary Figure 1**). Population size of the ancestral population was recorded after 24 h of growth in benign media, where it reached an abundance of $\sim 12 \times 10^9$ cells/mL (cell density recorded on agar, after 10⁶-fold dilution). This population served to initiate the experimental metapopulations with a standardized initial abundance of 10⁵ cells/mL in 96-well plates supplied with 200 μL of KB medium (see below). Then, throughout the experiment, we tracked community abundance by measuring the OD₅₉₀ of all plates every 24 h.

To determine the susceptibility of the ancestral bacteria to streptomycin, we inoculated the ancestral bacteria of *P. fluorescens* SBW25 in densities of 10⁵ cells/mL in wells with 200 μL of KB medium supplemented with 10 different concentrations of streptomycin, ranging from 0 to 500 μg/mL. Eight replicate populations were treated with one of 10 streptomycin concentrations for 24 h (incubated at 28°C), during which OD₅₉₀ was read every 30 min (**Supplementary Figure 2**). This served to identify the dose of streptomycin that was lethal to the majority of ancestral cells, the precondition required for evolutionary rescue. Note that, just as in previous experiments that tested population and community rescue, this dose is not required to be lethal to all individuals (Bell and Gonzalez, 2009; Low-Décarie et al., 2015).

Experimental Design

We randomly assigned metacommunities to streptomycin or control treatments crossed with three modes of dispersal (global, local, and none). Each metacommunity consisted of

four communities. Streptomycin-treated metacommunities were composed of four communities exposed to concentrations of 0, 100, 200, and 400 $\mu\text{g}/\text{mL}$, replicated 4 times (Figure 1A). These concentrations partially inhibited growth and represented a selection pressure on *P. fluorescens* during the first part of the experiment, which is expected to generate a correlated genetic response conferring some degree of tolerance to severe stress before it was actually experienced in Phase 2 of the experiment. Control metacommunities had the same dispersal treatments but were unexposed to streptomycin. This factorial design resulted in 96 local communities arrayed into 24 metacommunities distributed evenly on 4 separate 96-well plates.

During Phase 1 of the experiment, 1% of each culture was transferred to a new plate with fresh medium every 24 h to maintain growth. Dispersal treatments within metacommunities occurred simultaneously with the transfers. In the two dispersal treatments, 2 μL of grown culture was moved from each well to a dispersal pool, to match the rate of 1% dispersal used in previous studies with this bacterial strain (Venail et al., 2008). In the local dispersal treatments, this pool contained a contribution from the well with the next lower streptomycin concentration on the old plate: 2 μL of this dispersal pool was transferred to the next higher level of streptomycin, moving migrants up the stress gradient in the case of stressed communities. In the global dispersal treatments, the pool contained equal contributions from all wells of the metacommunity, and 2 μL of this was distributed to all wells of the metacommunity. In the no dispersal treatment, each well was inoculated exclusively with 1% from the corresponding well on the old plate, so that no cross-well transfer occurred.

Phase 2 of the experiment started 24 h after the seventh transfer. We diluted the grown communities to 10^5 cells/mL in KB (matching densities of 10^5 cells/mL for which we had assayed the tolerance of *P. fluorescens* SBW25 to streptomycin) supplemented with 500 $\mu\text{g}/\text{mL}$ streptomycin, a concentration that was lethal to the great majority of ancestral cells (Supplementary Figure 2). Bacteria were incubated at 28°C for 4 days, with no transfer or dispersal events. After the transfer, the abundance of each community was recorded by absorbance readings (OD_{590}) after 24 h (day 8), 30 h, 48 h (day 9), 72 h (day 10), and 120 h (day 12). Morphological diversity was scored after plating cells on KB-Agar on two occasions: on day 8 (24 h after the beginning of Phase 2) and on day 12 (at the end of Phase 2).

Measuring Morphological Diversity

Counts of morphotypes were scored every day during Phase 1 and on two instances during Phase 2, by plating on KB-Agar after dilution in KB. Each community was sampled and grown on two replicate Petri dishes. The morphotypes of all colonies were scored visually after 3 days of growth at 28°C; this corresponded to 50–500 colonies per replicate community. The two values obtained from replicate Petri dishes were then averaged to give the composition of each community. In some cases, when colonies failed to grow or when colonies grew very quickly and fused into a continuous biofilm, morphotype composition could not be estimated reliably. Thus, some replicates had to be discarded in analyses of composition and diversity (see below).

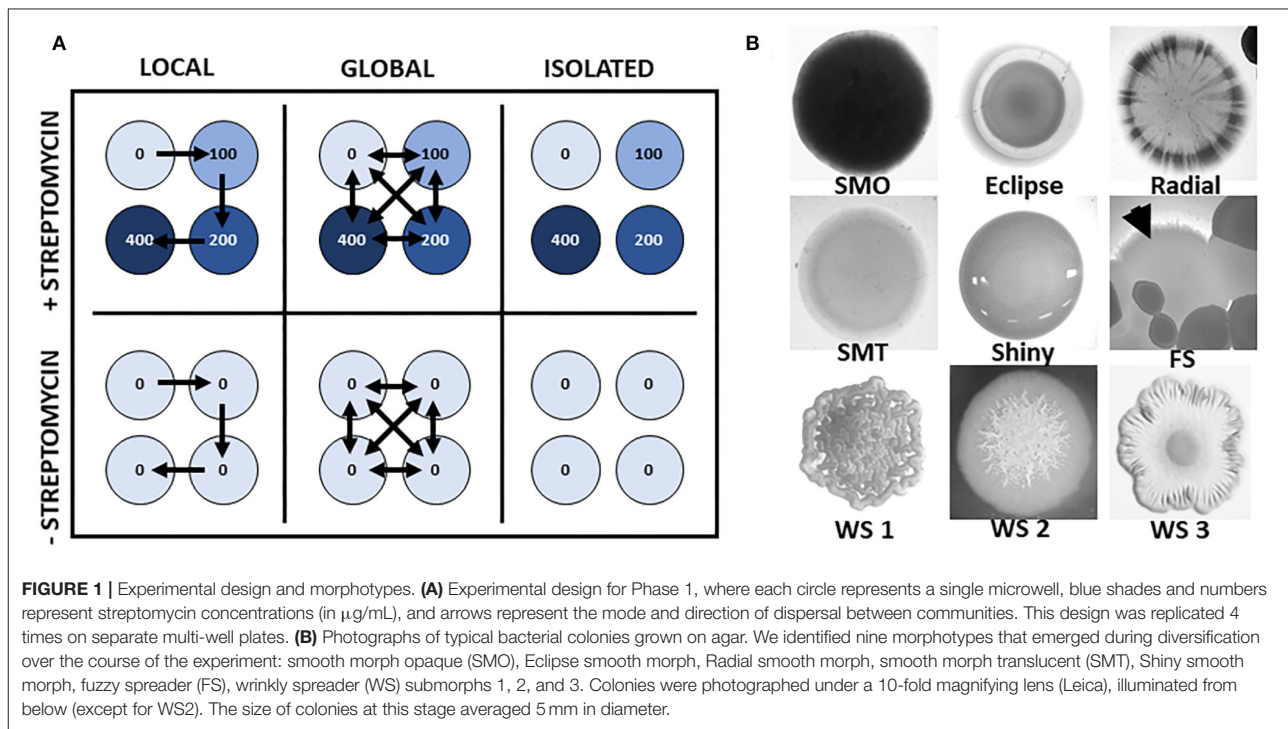
In keeping with previous work (Rainey and Travisano, 1998), we identified three morphs: smooth morph (the planktonic, ancestral morph), wrinkly spreader (which colonizes the air-liquid interface by forming a biofilm within 1 to 2 days) and fuzzy spreader (which colonizes the bottom of the wells after 4 days). We further divided the smooth morphotype into five subclasses – all had a smooth appearance but differed in opacity and pattern: “smooth morph translucent,” “smooth morph opaque” (Figure 1B); “shiny smooth morph;” “eclipse smooth morph;” and “radial smooth morph.” We also divided the wrinkly spreader morphotype into three subclasses – all contained “wrinkles” (distinctive asperities on the surface of the colony), but differed in the extent to which these wrinkles covered them: “wrinkly spreader 1” colonies were completely covered in wrinkles, “wrinkly spreader 2” colonies had a wrinkly center and smooth edge, and “wrinkly spreader 3” colonies had a smooth center and a wrinkly edge. This diversity observed within the wrinkly spreader morph is consistent with previous work with *P. fluorescens* (Hodgson et al., 2002; Massin and Gonzalez, 2006; Bantinaki et al., 2007). Finally, fuzzy spreader colonies displayed a distinctive blurry edge. Diversity counts thus included a total pool of nine morphological types (Figure 1B). Diversity in a local community was computed as the exponent of the Shannon index:

$$H = -\sum_{i=1}^S p_i \log(p_i)$$
, where S is the number of morphotypes and p_i is the relative abundance of morphotype i in the community. The exponent of Shannon is known as the effective number of species (Jost, 2006) – or in this case the effective number of morphotypes (henceforth diversity).

Statistical Analyses

All statistical analyses were conducted in R version 3.4.3 (R Core Team, 2017). We used linear models (ANOVAs) to test the effect of dispersal mode (three levels), streptomycin concentration (four levels, in the case of exposed metacommunities only), and their two-way interaction on the abundance (OD_{590}) and diversity of communities at key time points of the experiment: at the end of Phase 1 (day 7), the beginning of Phase 2 (day 8) and the end of Phase 2 (day 12). We evaluated the response of control metacommunities separately from exposed metacommunities. We also included experimental replicates (the 4 micro-well plates) as a blocking factor in all models. The number of replicates for each day of the experiment is referenced in the Supplementary Material (Supplementary Table 1 for abundances and Supplementary Table 2 for morphological diversity replicates). When main effects were statistically-significant, we conducted *post hoc* pairwise comparisons of factor levels using Tukey’s “Honest Significant Difference” method (function “TukeyHSD” in R). Response variables were log-transformed when it improved the normality and homogeneity of model residuals.

To visualize differences in morphotype composition among treatments, we performed non-metric multidimensional scaling (NMDS) analyses separately at the end of Phase 1 and Phase 2, combining control and exposed metacommunities (R-package “vegan” version 2.5-6, function “metaMDS”). These NMDS ordinations and all other multivariate analyses



used the Bray-Curtis dissimilarity index and proportional (relative abundance) data when calculating distance matrices. We tested whether morphotype composition varied among treatments using permutational multivariate analysis of variance (pMANOVA) implemented with the function “Adonis” in vegan. Separate pMANOVA models were fitted for control and streptomycin-treated metacommunities, using as a grouping factor “dispersal” (for both exposed and unexposed metacommunities) or “streptomycin concentration” (for exposed metacommunities only). We also conducted two analyses to reveal treatment effects on beta diversity, the variance in morphotype composition among local communities. We first used permutation-based tests of multivariate homogeneity of groups dispersions (the “PERMDISP” procedure implemented in function “betadisper” in vegan) to compare beta diversity at the “treatment” scale (e.g., variation in composition among all communities grown in concentrations of 100 vs. 200 $\mu\text{g}/\text{mL}$ of streptomycin). These tests used “plate” and “dispersal” as grouping factors (for control metacommunities), or “plate,” “dispersal,” “streptomycin concentration,” and their two-way interaction as factors (for exposed metacommunities). We then computed a metacommunity-scale measure of beta diversity, calculating, for each metacommunity of four microwells, the mean multivariate distance of the four local communities to their group centroid. Metacommunity-scale beta diversity was analyzed with ANOVA using “dispersal” (local vs. global vs. isolated), “metacommunity type” (control vs. streptomycin-treated), their two-way interaction, and “plate” as factors. This analysis only included the subset of metacommunities in which

morphotype composition could be reliably estimated for all four local communities.

Finally, to test the hypothesis that treatment effects on community composition and alpha diversity affected the trajectory and outcome of evolutionary rescue, we used independent linear regressions to link alpha diversity and community composition on day 7 (end of Phase 1) with OD_{590} on day 8 and day 12. OD_{590} on day 8 indicates the initial potential of communities to grow at a dose of stress lethal to the ancestral cells, while OD_{590} on day 12 indicates final community abundance at this lethal dose of stress, i.e., the outcome of evolutionary rescue of multiple morphs. The measure of community composition used in this analysis were scores on the first axis of the NMDS ordination described above.

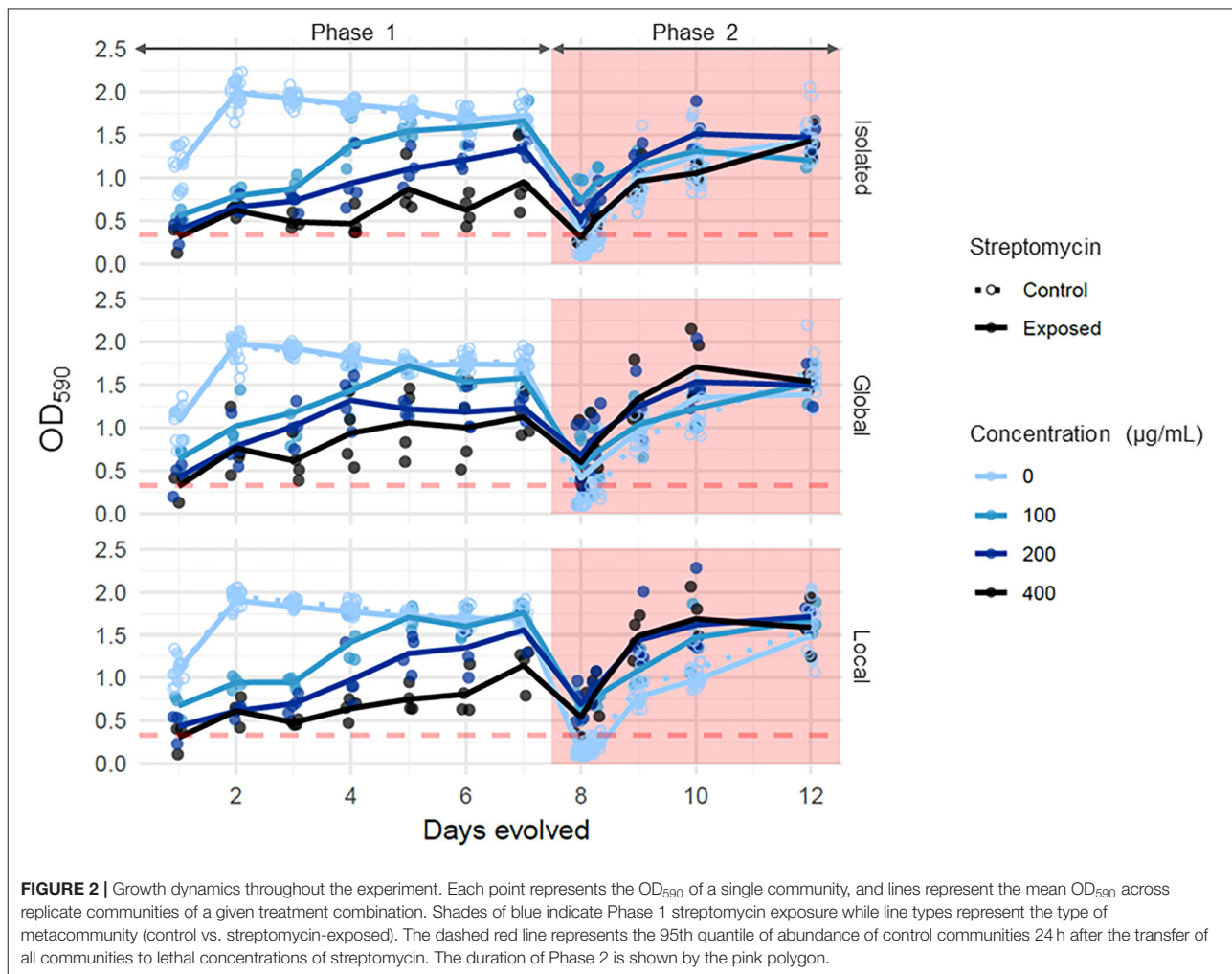
RESULTS

Ancestral Organisms

The ancestral bacterial culture was isomorphic and composed of Smooth Morph Opaque (SMO) exclusively. In these bacteria, growth was impeded by streptomycin concentrations as low as 50 $\mu\text{g}/\text{mL}$ (ANOVA: $F = 2,680$, $p < 0.0001$), and no growth was recorded for concentrations of 400 $\mu\text{g}/\text{mL}$ or more after 24 h (Supplementary Figure 2).

Phase 1

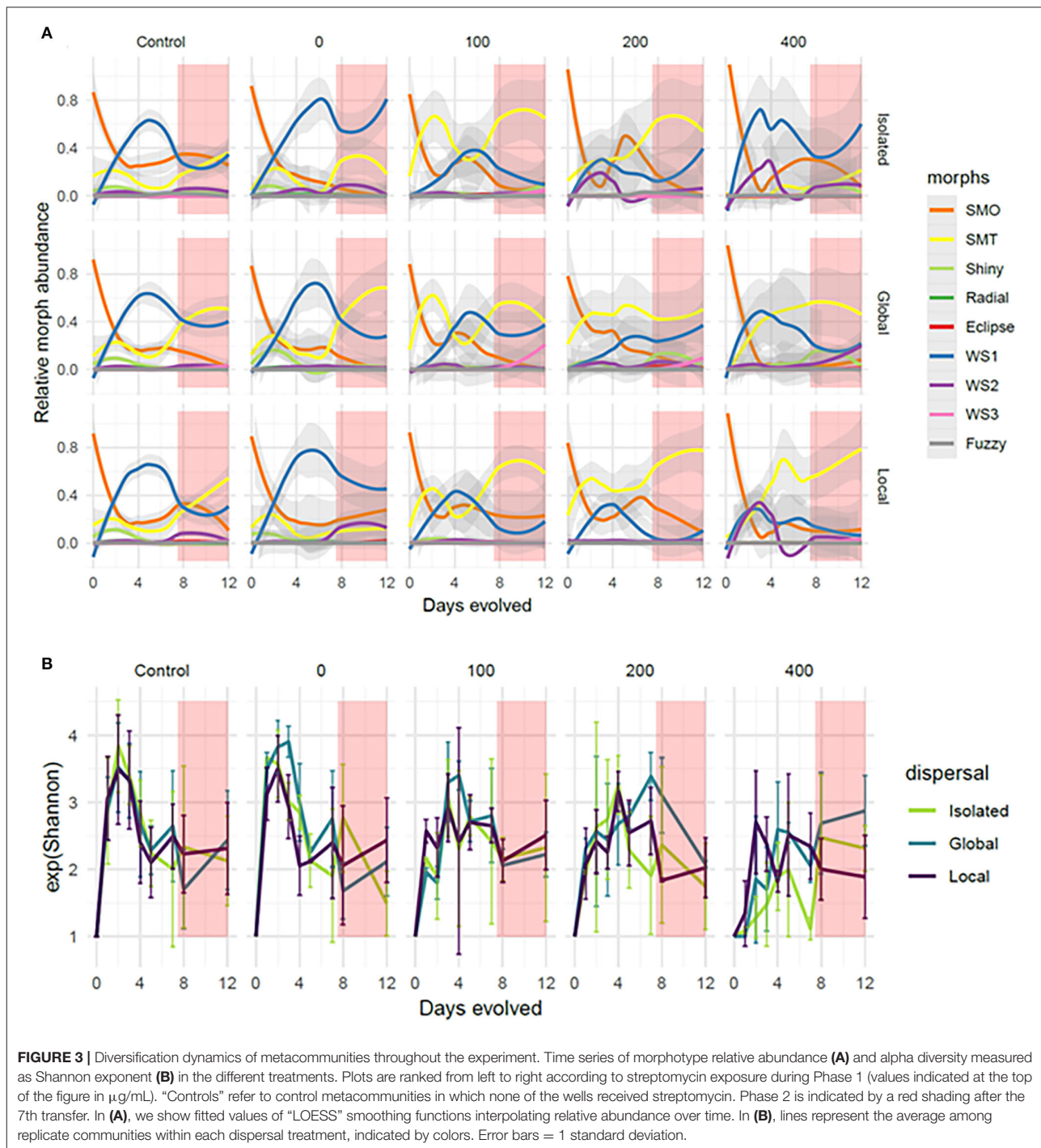
Growth was initially negatively affected by streptomycin, but communities displayed rapid adaptation to streptomycin during Phase 1 (Figure 2). During the first 24 h (~ 30 generations



in benign conditions), cultures of *P. fluorescens* reacted to streptomycin in the same way as the ancestral cells: growth was significantly lower in cultures with higher concentrations of streptomycin in the environment (ANOVA: $F = 238.6$, $p < 0.0001$). However, by the end of Phase 1, while streptomycin still negatively affected growth at the highest concentrations (Tukey HSD between 0 vs. 200 or 400 $\mu\text{g/mL}$: $p < 0.0001$), communities that had evolved in concentrations of 100 $\mu\text{g/mL}$ grew to abundance levels that were not significantly different than in benign environments (Tukey HSD: $p = 0.91$). By the end of Phase 1, OD₅₉₀ of communities exposed to streptomycin at 200 and 400 $\mu\text{g/mL}$ were increased by 2 or 3-fold compared with the beginning of Phase 1. In contrast to streptomycin exposure, the dispersal treatment did not significantly affect Phase 1 abundance in neither control metacommunities (ANOVA: $F = 0.812$, $p = 0.451$), nor streptomycin-exposed metacommunities ($F = 2.386$, $p = 0.108$). The interaction between dispersal mode and

streptomycin concentration was not significant in streptomycin-exposed metacommunities ($F = 1.151$, $p = 0.356$).

Streptomycin exposure also influenced the dynamics of diversification. Starting from isomorphic, clonal cells, bacteria diversified into nine different morphotypes during the experiment (Figures 1B, 3A). In benign conditions, communities displayed a repeatable diversification pattern where SMO first dominated the community, coexisting with shiny smooth morph and SMT in lower abundances, followed by a rise within the first 2 days in the abundance of wrinkly spreader 1 (WS1), which replaced SMO as the dominant morph throughout the rest of Phase 1. As a result, the effective number of morphotypes increased in the first few days of Phase 1, reaching a maximum of 3.6 at the end of the 2nd day (averaged across control communities, s.d. = 0.72), and subsequently decreased as WS1 then dominated the community (Figure 3B). These repeatable diversification dynamics were altered in



communities exposed to streptomycin. In environments supplemented with streptomycin in concentrations of 100 and 200 $\mu\text{g}/\text{mL}$, communities displayed a consistently different diversification pattern where SMT rapidly became dominant, replacing SMO as the dominant morph within the first 2 days, and subsequently co-occurring with SMO and WS1

(and WS2 in highly stressful environments) throughout the rest of Phase 1. Communities exposed to streptomycin in concentrations of 400 $\mu\text{g}/\text{mL}$ did not display such a consistent trend in morphological diversification, in part because the dispersal treatment modulated the increase in the relative abundance of SMT (Figure 3A): SMT was

abundant in concentrations of 400 μg/mL only in spatially connected communities.

Dispersal clearly influenced diversification dynamics and the generation of alpha diversity during Phase 1 (Figure 3). By the end of Phase 1, morphotype diversity was significantly higher in communities connected through dispersal, in both control metacommunities (ANOVA: $F = 3.82, p = 0.0337$) and exposed metacommunities (ANOVA: $F = 5.24, p = 0.0148$). However, the spatial structure of dispersal did not influence final Phase 1 diversity, as communities linked by global and local dispersal had comparable diversity, in both control metacommunities (Tukey HSD: $p = 0.97$) and exposed metacommunities (Tukey HSD: $p = 0.73$). In exposed metacommunities, streptomycin exposure had a weak but non-significant effect on diversity (ANOVA: $F = 2.78, p = 0.068$), while the interaction between streptomycin and dispersal was not significant ($F = 0.75, p = 0.62$).

The dispersal and streptomycin treatments influenced both the mean composition of communities and the variance in composition among local communities (Figure 4). In control metacommunities, dispersal did not have a statistically significant effect on morphotype composition (pMANOVA: $p = 0.06$), but had a very strong effect on heterogeneity among local communities receiving the same dispersal treatment (Figure 4A; PERMDISP: $p < 0.0001$). Local dispersal reduced heterogeneity more than global dispersal. In streptomycin-exposed metacommunities, the antibiotic gradient had a much stronger influence on composition than did dispersal. Indeed, while streptomycin exposure influenced the mean composition of communities (Figure 4B; pMANOVA: $p = 0.002$), the main effect of dispersal on composition and the two-way interaction between dispersal and streptomycin concentration were not statistically-significant (pMANOVA: $p = 0.26$ and 0.66 , respectively). Nonetheless, as in control metacommunities, dispersal reduced heterogeneity among local communities (PERMDISP: $p = 0.03$). Streptomycin exposure had the opposite effect of increasing heterogeneity among communities at higher doses (Figure 4B; PERMDISP: $p = 0.0003$). At the metacommunity-scale, variance in community composition among the four local communities forming a metacommunity was highly reduced by dispersal (Figure 4C; ANOVA, main effect of dispersal: $F = 24.95, p = 0.001$). This effect however disappeared in exposed metacommunities (Figure 4C; ANOVA, main effect of metacommunity-scale streptomycin treatment: $F = 8.96, p = 0.02$; two-way interaction effect of streptomycin and dispersal: $F = 5.87, p = 0.04$).

In summary, dispersal and streptomycin exposure over Phase 1 jointly affected the diversification of evolving *Pseudomonas* metacommunities, resulting in a gradient of morphotype diversity, composition, and history of stress across treatments, all of which were hypothesized to influence subsequent recovery of abundance and diversity in Phase 2.

Phase 2

In Phase 2, all communities were transferred to a concentration of streptomycin lethal to the ancestral cells (500 μg/mL). In the 24 h following exposure to 500 μg/mL of streptomycin, communities that had never been exposed to streptomycin in

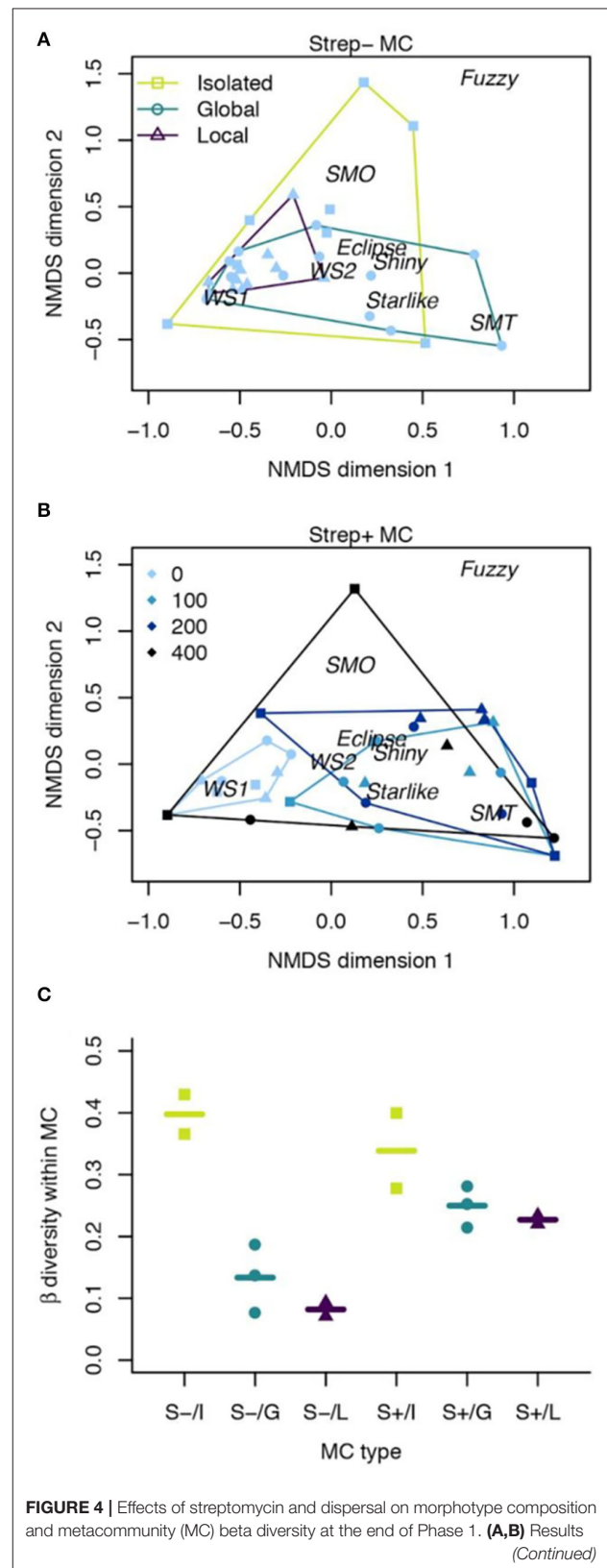


FIGURE 4 | Effects of streptomycin and dispersal on morphotype composition and metacommunity (MC) beta diversity at the end of Phase 1. (A,B) Results (Continued)

FIGURE 4 | of NMDS ordination of community composition, indicating the location of local communities (points) and morphotypes (words) in multivariate space. For visualization purposes, results are shown separately for control metacommunities (**A**) and streptomycin-exposed metacommunities (**B**). Symbols denote dispersal treatments while colors indicate streptomycin exposure. Convex hulls regroup communities having received the same dispersal (**A**) or streptomycin (**B**) treatment. Morph acronyms are defined in **Figure 1**. (**C**) Metacommunity-scale beta diversity (mean distance to group centroid of 4 local communities comprising a metacommunity) as a function of metacommunity type and dispersal treatment. Symbols represent metacommunities while horizontal lines correspond to treatment means. S-, control metacommunities. S+, streptomycin-exposed metacommunities. I, Isolated; G, global dispersal; L, local dispersal.

Phase 1 underwent a 5-fold decline in abundance compared with the end of Phase 1 (**Figures 2, 5A**), confirming that this dose of streptomycin is highly stressful to the majority of cells even after *in vitro* diversification. In contrast, local communities that had been exposed to at least 100 $\mu\text{g}/\text{mL}$ of streptomycin during Phase 1 recovered an abundance two to three times higher than naïve communities in the first 24 h of Phase 2 (**Figure 5A**; ANOVA, main effect of streptomycin exposure: $F = 14.8$, $p < 0.0001$). However, dispersal altered this general trend (**Figure 5A**; ANOVA, interaction effect of streptomycin exposure and dispersal: $F = 2.97$, $p = 0.02$), as the beneficial effect of exposure to a high dose of streptomycin in Phase 1 was diminished in isolated communities. The spatial structure of dispersal did not influence these responses (Tukey HSD between global vs. local dispersal: $p > 0.1$ at all Phase 1 streptomycin concentrations).

Contrary to our hypothesis, diversity levels achieved at the end of Phase 1 did not have a significant effect on the abundance recovered by communities at the onset of Phase 2 (**Figure 5B**; linear regression: $R^2 = 0.002$, $p = 0.71$). Community composition at the end of Phase 1 did however have a significant effect on the abundance recovered in the first 24 h of Phase 2 (**Figure 5C**; linear regression: $R^2 = 0.25$, $p = 0.0028$). More specifically, communities where SMT occurred in higher abundances at the end of Phase 1 recovered a significantly higher abundance following the first 24 h of Phase 2 ($p < 0.0001$). This morph eventually came to dominate most communities throughout Phase 2 (**Figure 3A**), while SMO, WS1 and WS2 occurred at lower abundances, and other rare morphotypes that existed in Phase 1 were lost entirely. For example, “radial” smooth morph was only detected in one of 143 communities throughout Phase 2, and “fuzzy spreader” in only five communities. Conversely, one morph (“wrinkly spreader 3”) that had never been detected in Phase 1 was detected in 17 of 143 communities throughout Phase 2. However, in contrast to Phase 1 where differences in diversity were noted across treatments, in the first 24 h of Phase 2, communities displayed similar levels of morphological diversity with no significant effect of the treatment they had received during Phase 1 (ANOVA: $F = 1.05$, $p = 0.4215$). Importantly, all communities lost a large fraction of their cells at the onset of Phase 2 regardless of which morphs they contained (even communities dominated by SMT), suggesting that no morph was

fully resistant to this dose of antibiotic and that within-morph evolutionary rescue was required for persistence in Phase 2.

Eventually, by the end of Phase 2, all communities recovered similar levels of abundance and diversity, with no significant effect of their history of stress and dispersal on final abundance and diversity (**Figures 2, 3B**; ANOVA for OD₅₉₀: $F = 1.07$, $p = 0.3997$; for diversity: $F = 0.91$, $p = 0.5544$). Effects of Phase 1 treatments on community composition had also vanished by the end of Phase 2 (pMANOVA: $p > 0.05$ for all factors).

In sum, evolutionary rescue of multiple morphs occurred in all communities, allowing abundance and diversity to be maintained at a dose of antibiotic lethal to the majority of the ancestral, isomorphic cells. Thus, dispersal and the history of streptomycin exposure influenced the trajectory of evolutionary rescue (i.e., the initial decline in abundance and growth following lethal stress) but not the final outcome of rescue.

DISCUSSION

Since the original formulation of evolutionary rescue theory for isolated populations of single species (Gomulkiewicz and Holt, 1995), extending the theory to conditions closer to those at play in natural communities has been a major challenge in the study of evolutionary rescue (Fussmann and Gonzalez, 2013; Osmond and de Mazancourt, 2013). This challenge is now being addressed through careful experimentation (Low-Décarie et al., 2015; Fugère et al., 2020; Scheuerl et al., 2020). Here we studied evolutionary rescue in metacommunities undergoing adaptive diversification across a gradient of environmental stress. We have shown that the history of exposure to stress, and the presence and spatial structure of dispersal in metacommunities of the rapidly evolving bacterium *P. fluorescens* SBW25 can affect adaptation, diversification and evolutionary rescue following severe environmental degradation caused by antibiotic stress.

During the experiment, the isomorphic ancestral cells diversified *in vitro* into a total of nine morphotypes, forming phenotypically diverse communities that recovered both abundance and diversity following exposure to initially lethal levels of stress, demonstrating evolutionary rescue in these metacommunities. Mutations are the source of this phenotypic variation, allowing bacteria to colonize different ecological niches, in particular the surface of the liquid medium (Spiers et al., 2002; McDonald et al., 2009). Despite extensive genetic and phenotypic variation, however, the bacteria still belong to the same species, *P. fluorescens* SBW25. The species concept is blurry in bacteria (Rosselló-Mora and Amann, 2001; Riley and Lizotte-Waniewski, 2009) and challenging to quantify (Staley, 2006), and the case of rapid diversification in *P. fluorescens* is no exception. Nonetheless, asexual growth combined with niche specialization and morphological diversity supports the analogy between the different morphotypes and different species in a community, and ultimately allows us to interpret the recovery of diverse and abundant populations of morphotypes in terms of evolutionary rescue of multiple species forming a metacommunity. Our results show that: (1) dispersal and antibiotic stress jointly influenced diversification dynamics. At the end of this diversification

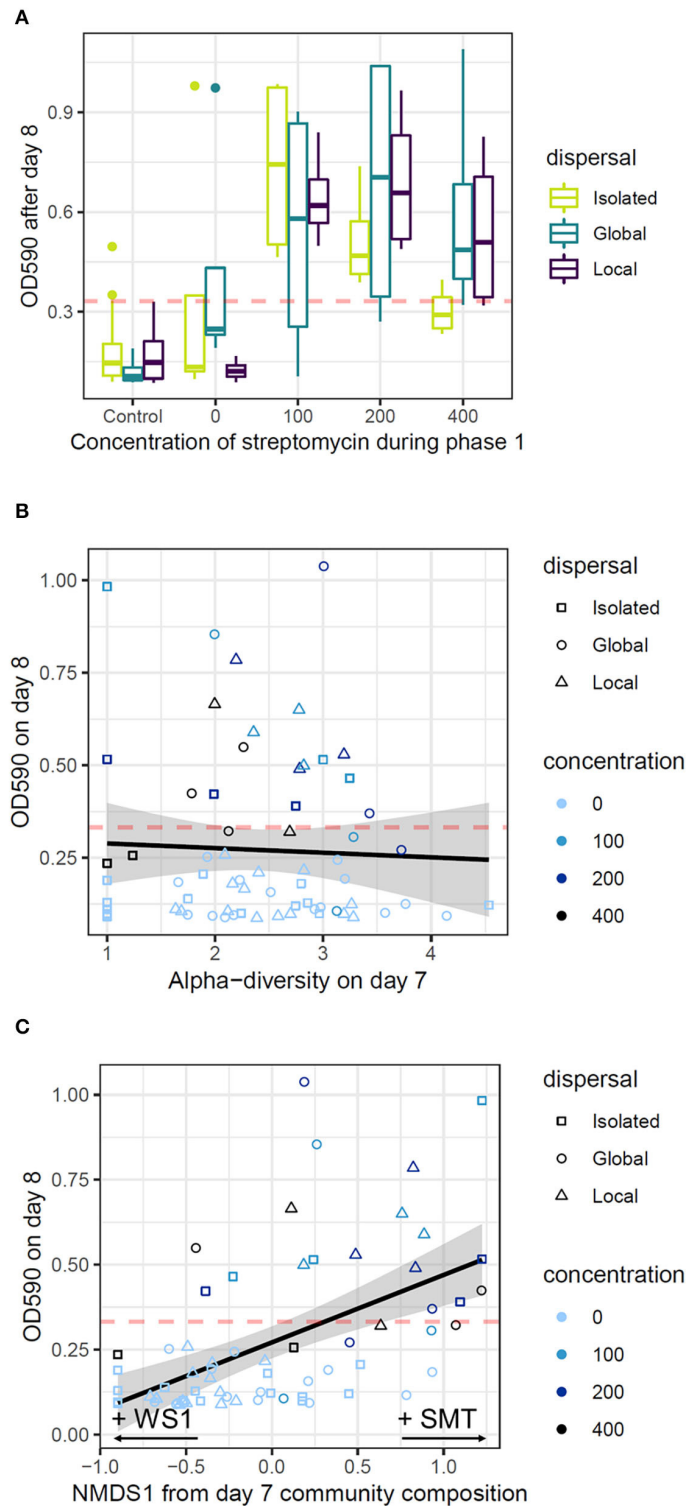


FIGURE 5 | Drivers of initial growth at a lethal dose of streptomycin. Panels represent the OD₅₉₀ of communities after 24 h of Phase 2 as a function of streptomycin concentrations during Phase 1 **(A)**, diversity (Shannon exponent) at the end of Phase 1 **(B)**, and community composition (NMDS 1st axis) at the end of Phase 1 **(C)**. In each panel, the dashed red line represents the 95th percentile of the OD₅₉₀ of control communities, representing the threshold for evolutionary rescue. In **(A)**, boxplots *(Continued)*

FIGURE 5 | represent the median and quartiles of the OD₅₉₀ of replicate communities, colored by their mode of dispersal during Phase 1. In **(B,C)**, each dot represents a single local community and the line represents the linear response of OD₅₉₀ on day 8 to diversity and community composition on day 7, respectively. Shapes represent the mode of dispersal, and shades of blue represents the concentrations of streptomycin communities were exposed to during Phase 1 (in $\mu\text{g}/\text{mL}$).

process, variation in community composition, but not diversity, subsequently influenced evolutionary rescue; (2) the history of exposure to stress was a strong predictor of the trajectory of evolutionary rescue, but not the outcome of rescue. Communities with a history of antibiotic exposure had greater fitness at the onset of severe stress than naive communities, even though all communities eventually rescued; and (3) the presence of dispersal, but not its spatial structure, modulated diversification in Phase 1 and evolutionary rescue in Phase 2. We further elaborate on each of these results below.

Effect of Antibiotic Stress and Dispersal on Diversification and Adaptation

During the selection phase, growth, diversity and community composition changed over time but followed different dynamics depending on local environmental conditions, corroborating results from previous studies with this model system (Rainey and Travisano, 1998; Kassen et al., 2000; Massin and Gonzalez, 2006). At the beginning of the selection phase, both growth and diversity were reduced in higher concentrations of streptomycin. This effect on diversity could relate to the nature of the system. Diversification is driven by competition for oxygen in rapidly growing cultures of the aerobic bacteria *P. fluorescens*, but because streptomycin hampers growth, lower densities at sublethal concentrations could lead to greater oxygen availability, reduced competition, and slower diversification rates. For example, SMT rapidly dominates harsh environments in Phase 1 only in spatially connected communities, while its emergence is much slower in highly stressed, isolated communities. By the end of the selection phase, stressed communities evolved and grew to abundances and diversity levels close to that of benign environments, demonstrating a striking adaptation to high doses of streptomycin within just a few days.

Further, we have shown that streptomycin markedly altered community dynamics and dominance patterns among morphotypes. For example, while rare in benign environments, the morph SMT was dominant at intermediate doses of streptomycin (100 or 200 $\mu\text{g}/\text{mL}$) and at the highest dose of streptomycin (400 $\mu\text{g}/\text{mL}$) when communities were also linked by dispersal, potentially indicating a mass effect (Leibold et al., 2004). Other morphotypes such as SMO and WS1, which were dominant in benign environments, occurred in lower abundances in streptomycin-exposed environments, while yet other rare morphs (e.g., fuzzy spreader) went locally extinct after exposure to lethal levels of streptomycin.

These shifts in dominance patterns during the experiment suggest that the potential for resistance evolution is different among morphs. Alternatively, streptomycin might alter the relative competitive abilities of the different morphs as they simultaneously evolve within patches (Rainey and Travisano, 1998) and across the gradient of antibiotic stress between

patches (Osmond and de Mazancourt, 2013). Streptomycin normally kills bacteria by binding to the 30S ribosomal subunit, inhibiting mRNA translation and thus protein synthesis (Biswas and Gorini, 1972). Mutations conferring resistance to streptomycin may trade-off with growth potential in benign environments, making resistant individuals less abundant in the absence of streptomycin. Yet another hypothesis for the differences in diversification dynamics concerns the mechanisms by which different morphs emerged in different environments. For example, the transition from SMO-dominated communities to SMT-dominated communities with streptomycin exposure could be the result of both genetic evolution (streptomycin-induced selection on standing variation or novel mutations) and phenotypic plasticity. Antibiotic application is known to alter other phenotypes (e.g., biofilm formation) in populations of the closely related *Pseudomonas aeruginosa* that also acquire antibiotic resistance (Drenkard and Ausubel, 2002). Nonetheless, a strong genetic contribution to phenotypic differentiation has previously been shown for some *P. fluorescens* morphs, where the emergence of a wrinkly spreader morph from a monoclonal isogenic population of smooth morphs was driven by novel mutations and selection (Rainey and Travisano, 1998; Spiers et al., 2002; McDonald et al., 2009). Further analyses would be necessary to distinguish plastic (e.g., expression of cellulose polymer forming biofilm, Spiers et al., 2002) from genetic influences on morphological diversification and antibiotic resistance in our experimental design, bearing in mind that it is also possible, and perhaps more realistic, that both processes could be involved (Chevin et al., 2013; Kovach-Orr and Fussmann, 2013; Lind et al., 2018; Carja and Plotkin, 2019).

At the metacommunity level, dispersal and streptomycin had opposing effects on both alpha and beta diversity generated during the selection phase. While streptomycin greatly lowered local (alpha) diversity, the effect of streptomycin on community composition also translated into greater compositional difference between local communities. This is expected as the antibiotic gradient creates habitat heterogeneity, promoting beta diversity within metacommunities (Veech and Crist, 2007; Matthiessen et al., 2010). However, dispersal countered the effects of streptomycin, as it increased local diversity in harshly stressed (200 or 400 $\mu\text{g}/\text{L}$) and otherwise depauperate communities, while at the same time homogenizing community composition within metacommunities. Even in control metacommunities without an antibiotic gradient, dispersal increased mean local diversity and reduced metacommunity beta diversity. Both of these effects (higher local diversity, lower beta diversity) of the intermediate rate of dispersal that we used (1%) are consistent with the metacommunity theory (Leibold et al., 2004; Howeth and Leibold, 2010) and with experimental evidence (Matthiessen et al., 2010). Despite these strong effects of dispersal on diversification, the spatial structure of dispersal did not have

a consistent effect on diversity; both local and global dispersal resulted in similar patterns of alpha and beta diversity at the end of the selection phase.

Increased diversity through dispersal has the potential to be selected upon in the case of environmental change (Schiffers et al., 2013). We therefore predicted faster or more complete adaptation to the antibiotic stress in metacommunities linked by dispersal. Our results do not support this prediction: neither the presence nor the spatial structure of dispersal influenced community abundance reached by the end of Phase 1. However, the presence of dispersal clearly influenced how fast communities with a history of streptomycin exposure recovered their abundance during the rescue trial of Phase 2.

Drivers of Evolutionary Rescue

We observed repeated and consistent evolutionary rescue in *P. fluorescens* metacommunities exposed to harsh levels of streptomycin. By the end of Phase 2, viable and diverse communities grew in conditions that were lethal to the ancestral, isomorphic cells, which demonstrates evolutionary rescue of multiple morphs. Because the ancestral population lacked variation, this rescue process was ultimately driven by evolution. Adaptive evolution occurred both during Phase 1 as isomorphic bacteria underwent adaptive radiation driven by competition and modulated by antibiotic exposure, and during the rescue trial in Phase 2 when communities adapted quickly to the high dose of antibiotic. Past exposure to streptomycin was the main cause of the difference in the trajectory of recovery following exposure to severe stress, confirming previous findings from experimental studies of evolutionary rescue in microbial systems (Gonzalez and Bell, 2013; Low-Décarie et al., 2015; Bell et al., 2019; Fugère et al., 2020).

Evolutionary rescue can arise from standing variation or from mutations arising early (i.e., first few cell divisions) in the selection treatment. Our design was focused on the study of the net outcome in the race between the decline in abundance and the rate of recovery by rare resistant cells, or individuals, among different morphotypes of *P. fluorescens*. Evolutionary rescue is above all a question of whether the rate of adaptation to environmental change occurs on the same time scale as the demographic decline (Gienapp et al., 2013; Lindsey et al., 2013). If all communities eventually recovered similar levels of abundance and diversity, they did so at varying rates.

Following exposure to harsh dose of streptomycin in Phase 2, communities that had been exposed to at least 100 µg/mL of streptomycin in Phase 1 had greater fitness (i.e., population growth averaged across morphotypes) than communities naive to the antibiotic. This effect likely arose because genetic and plastic changes conferring increased resistance at an intermediate dose of stress also provided a correlated advantage at a higher dose of stress. This result supports the conclusion that historical selection facilitates adaptation to a deteriorating environment (Gonzalez and Bell, 2013; Samani and Bell, 2016).

By the end of Phase 2, all communities recovered similar levels of abundance and diversity, perhaps owing to the evolved diversity that was absent in the ancestral cells. Indeed, communities that were allowed to evolve for 7 days even in

benign conditions had a much higher morphological diversity than the ancestral cells, variation upon which natural selection could act in Phase 2. However, we did not find a significant effect of diversity on either the trajectory or the outcome of evolutionary rescue. Instead, our results suggest that community composition, rather than diversity, determined the trajectory of evolutionary rescue. Indeed, the abundance of SMT at the end of the selection phase significantly increased the abundance in communities 24 h after the onset of Phase 2 – although only in communities that had also experienced streptomycin in Phase 1. That is, both historical selection and a high relative abundance of SMT were necessary for a swift recovery in Phase 2 (Figure 5C), suggesting that ecological processes (morphotype sorting in favor of the relatively more resistant SMT morph) and evolutionary processes (past adaptation of the SMT morph to streptomycin) both promoted community recovery. Higher abundance of SMT before the rescue trial of Phase 2 was a result of both past exposure to streptomycin and presence of dispersal. Some isolated communities exposed to high doses in Phase 1 had a low relative abundance of SMT, while some control communities with dispersal had a high abundance of SMT – and both these types of communities collapsed to low abundances at the onset of Phase 2. Therefore, our results suggest that community composition influenced the speed of community recovery, as a result of the interplay between past dispersal events and previous exposure to stress. However, as for diversification, the presence of dispersal mattered most, not its spatial structure.

Here, we quantified the outcome of rescue based on the recovery of abundance following exposure to severe stress. By the end of Phase 2, communities recovered abundance and diversity in levels comparable to the end of the selection phase, indicating that evolutionary rescue of multiple morphs occurred in all communities by the end of Phase 2 of the experiment. Abundance or diversity are both aggregate measures of community recovery. Our analysis of community composition showed that communities at the end of Phase 2 were very different in composition compared with Phase 1 communities, indicating a shift to different compositional states despite the recovery of similar levels of abundance and diversity.

CONCLUSIONS AND IMPLICATIONS

Here, we studied the dynamics of evolutionary rescue occurring in evolving communities. We found that the history of stress and dispersal promotes the incidence of evolutionary rescue (Low-Décarie et al., 2015; Bell et al., 2019; Fugère et al., 2020). Our results have management implications, although a few caveats should be acknowledged before extrapolating to natural systems. While dispersal could in theory increase the likelihood of adaptation and subsequent recovery in communities across a fragmented, heterogeneous landscape, other ecological factors such as population size and generation time are crucial to the recovery of populations. Here, the very large populations responsible for striking evolutionary rescue in *P. fluorescens* may be common for microbial species but are rarely so for metazoan species that typically exist at much lower densities or have slower

generation times and lower reproductive rates (vander Wal et al., 2013) although cases of evolutionary rescue in metazoans have been observed (Ozgo, 2014; Reid et al., 2016). This suggests that evolutionary rescue may be less likely in conservation contexts but more likely in agroecosystems or clinical settings where microbes respond to high doses of biocides (Alexander et al., 2014).

We found that dispersal fosters evolutionary rescue following environmental degradation, which corroborates previous findings (Perron et al., 2007; Bell and Gonzalez, 2011; Low-Décarie et al., 2015; Gokhale et al., 2018). For pathogens and invasive species, globalization is increasing the potential for dispersal to contribute to the evolution of resistance across common selective environments, including the widespread application of common antibiotics and pesticides (Thanner et al., 2016; Hudson et al., 2017). For example, streptomycin is used in agriculture worldwide for the control of plant pathogenic bacteria (e.g., in orchards). Resistance is often observed in multiple bacterial pathogens, including *Pseudomonas* sp. in these orchard settings (Vanneste and Voyle, 2002; Sundin and Wang, 2018), although this may not influence the abundance and diversities of major bacteria taxa soil communities or cause convergence in community similarity (McManus, 2014; Walsh et al., 2014). It remains unclear whether the dispersal of micro-organisms between exposed sites may engender resistance across a microbial metacommunity.

Evolutionary rescue theory is also relevant for conservation biology, where the focus is not the eradication of species but their protection and restoration. Widespread habitat loss is decreasing the potential of already vulnerable populations and communities to disperse across habitat patches and entire landscapes to adapt to new disturbances such as climate change (Norberg et al., 2012). Our results suggest that, especially for depauperate communities, isolation of habitat patches or dispersal barriers could hinder the recovery of communities following severe environmental deterioration (Cheptou et al., 2017). Although we used a simple laboratory model system that lacks some of the complex dynamics and interactions that

characterize natural ecosystems exposed to human impacts, our results support the conclusions from theory that spatial connectivity through dispersal is an important determinant of eco-evolutionary dynamics and persistence of diversity across changing and degraded landscapes (Crooks and Sanjayan, 2006; Norberg et al., 2012; Thompson and Fronhofer, 2019).

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

AG designed research. LO'C carried out the experiment. LO'C and VF performed statistical analysis and prepared the figures. All authors contributed significantly to interpreting the results and writing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.517434/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Quantifying the impact of vegetation-based metrics on species persistence when choosing offsets for habitat destruction

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Abstract: Developers are often required by law to offset environmental impacts through targeted conservation actions. Most offset policies specify metrics for calculating offset requirements, usually by assessing vegetation condition. Despite widespread use, there is little evidence to support the effectiveness of vegetation-based metrics for ensuring biodiversity persistence. We compared long-term impacts of biodiversity offsetting based on area only; vegetation condition only; area \times habitat suitability; and condition \times habitat suitability in development and restoration simulations for the Hunter Region of New South Wales, Australia. We simulated development and subsequent offsetting through restoration within a virtual landscape, linking simulations to population viability models for 3 species. Habitat gains did not ensure species persistence. No net loss was achieved when performance of offsetting was assessed in terms of amount of habitat restored, but not when outcomes were assessed in terms of persistence. Maintenance of persistence occurred more often when impacts were avoided, giving further support to better enforce the avoidance stage of the mitigation hierarchy. When development affected areas of high habitat quality for species, persistence could not be guaranteed. Therefore, species must be more explicitly accounted for in offsets, rather than just vegetation or habitat alone. Declines due to a failure to account directly for species population dynamics and connectivity overshadowed the benefits delivered by producing large areas of high-quality habitat. Our modeling framework showed that the benefits delivered by offsets are species specific and that simple vegetation-based metrics can give misguided impressions on how well biodiversity offsets achieve no net loss.

Keywords: biodiversity offsets, biodiversity metrics, population viability analysis, simulation tool, species persistence

Cuantificación del Impacto de las Medidas Basadas en la Vegetación sobre la Persistencia de las Especies cuando se Eligen las Compensaciones por la Destrucción del Hábitat

Resumen: Con frecuencia se requiere por ley que los desarrolladores compensen los impactos ambientales por medio de acciones de conservación. La mayoría de las políticas de compensación especifican medidas para calcular los requerimientos de cada compensación, generalmente mediante la evaluación de las condiciones de la vegetación. A pesar del uso extenso de estas medidas basadas en la vegetación, existe muy poca evidencia que respalde su efectividad para asegurar la persistencia de la biodiversidad. Comparamos los impactos a largo plazo de las compensaciones de biodiversidad basadas solamente en el área; solamente en la condición de la vegetación; la idoneidad del área \times hábitat; y la idoneidad condición \times hábitat en las simulaciones de desarrollo y restauración para la Región Hunter de Nueva Gales del Sur, Australia. Simulamos el desarrollo y las compensaciones

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subsecuentes mediante la restauración dentro de un paisaje virtual, conectando las simulaciones con los modelos de viabilidad poblacional para tres especies. Las ganancias del hábitat no aseguraron la persistencia de las especies. No hubo pérdida neta cuando el desempeño de las compensaciones se evaluó en relación con la persistencia. El mantenimiento de la persistencia ocurrió más seguido cuando se evitaron los impactos, lo que proporciona un mayor respaldo para mejorar la aplicación de la fase de prevención de la jerarquía de mitigación. Cuando el desarrollo afectó a las áreas con una alta calidad de hábitat para las especies, no se pudo garantizar la persistencia. Por lo tanto, las especies deben considerarse más explícitamente en las compensaciones, en lugar de sólo considerar a la vegetación o al hábitat. Las declinaciones causadas por la falta de consideración directa de las dinámicas poblacionales de las especies y de la conectividad opacaron los beneficios producidos por las grandes áreas de hábitat de alta calidad. Nuestro marco de trabajo para el modelado demostró que los beneficios producidos por las compensaciones son específicos para cada especie y que las medidas simples basadas en la vegetación pueden brindar impresiones mal informadas sobre qué tanto influyen las compensaciones de biodiversidad en la no pérdida neta.

Palabras Clave: análisis de viabilidad poblacional, compensaciones de biodiversidad, herramienta de simulación, medidas de la biodiversidad, persistencia de la especie

摘要: 法律经常要求开发商通过有针对性的保护行动来抵消对环境的影响。大多数生物多样性补偿政策明确规定了计算补偿量需求的指标, 通常都是基于对植被条件的评估。这类基于植被的指标虽然已经得到广泛使用, 但在其确保生物多样性续存方面的有效性却几乎没有证据支持。本研究模拟了澳大利亚新南威尔士州猎人区的开发和恢复情况, 并分别从面积、植被条件、地区及生境的适宜性、植被条件及生境的适应性这几个方面比较了生物多样性补偿措施的长期影响。我们在一个虚拟景观中模拟了开发及随后通过恢复得到的补偿, 并将模拟情况与 3 个物种的种群生存模型进行整合。结果显示, 如果以恢复生境的数量来评价补偿效果, 则可以实现无净损失; 但如果以物种续存来进行评价, 则不能实现。在避免影响的情况下, 物种更有可能续存, 这一结果为更好地执行减缓影响层级结构中的避免影响阶段提供了进一步支持。当发展影响到物种高质量生境的区域时, 不能保证物种续存。因此, 必须更明确地将物种纳入补偿机制中, 而不仅仅是考虑植被或生境。因未能直接考虑物种种群动态和连接度而导致的种群数量下降的影响, 会超出制造大面积高质量生境带来的好处。我们的模型框架表明, 生物多样性补偿带来的好处是物种特有的, 而简单的基于植被的指标可能会误导人们, 使其对生物多样性补偿在多大程度上实现了无净损失产生错误印象。【翻译: 胡怡思, 审校: 聂永刚】

关键词: 生物多样性补偿, 生物多样性指标, 种群生存力分析, 模拟工具, 物种续存

Introduction

Biodiversity offsetting is used around the globe to deliver conservation gains aimed at achieving no net loss or net gain of biodiversity to compensate for impacts caused by development (Bull et al. 2016a). However, lack of consistency in offsetting policies at different levels of governance (e.g., state vs. federal) and different stages of offset implementation make it difficult to consistently define what achieving no net loss requires (Maron et al. 2018). Moreover, it is unclear whether offsets achieve their claimed conservation outcomes under current frameworks (zu Ermgassen et al. 2019). The ineffectiveness of biodiversity offsets has been attributed to inconsistent and unclear biodiversity metrics (Gibbons et al. 2018) and inadequate postimplementation monitoring and compliance at offset sites (Theis et al. 2019).

Accurately measuring biodiversity is challenging, and popular offsetting metrics assign habitat condition or area scores to a site by assessing, scoring, and weighting several vegetation attributes (Oliver et al. 2014; Marshall et al. 2020; zu Ermgassen et al. 2019). With habitat condition scores varying across an area of impact, it is common to simply sum scores such that, for example, 25 ha of perfect-condition vegetation would receive the same

overall offset score as 50 ha of vegetation that scores 50% less (Marshall et al. 2020).

Reliance on habitat- and vegetation-based offsetting metrics (Gibbons et al. 2018) can be problematic when such metrics do not strongly correlate with the ecological features that an offsetting program seeks to conserve (Kujala et al. 2015). Often, habitat attributes and vegetation-based surrogates fail to capture the extent of biodiversity that is claimed (Cristescu et al. 2013; Hanford et al. 2016). Moreover, current offsetting metrics are likely to result in undervaluation of degraded or smaller patches, even when these are of high ecological importance (Wintle et al. 2019).

The premise of many offset policies is to ensure persistence of populations, species, ecosystems, and communities (Maron et al. 2012). However, this goal is not currently supported by relevant metrics. No-net-loss policies require that offset sites deliver the same or higher vegetation-condition scores relative to impact sites but achieving this target alone may not ensure sites will deliver long-term benefits or ensure persistence of populations or species (Gardner et al. 2013). Therefore, assessment of the ability of vegetation condition to act as a surrogate for species persistence appears to be a necessary first step in offset-policy evaluation. Combining vegetation condition measures with explicit species

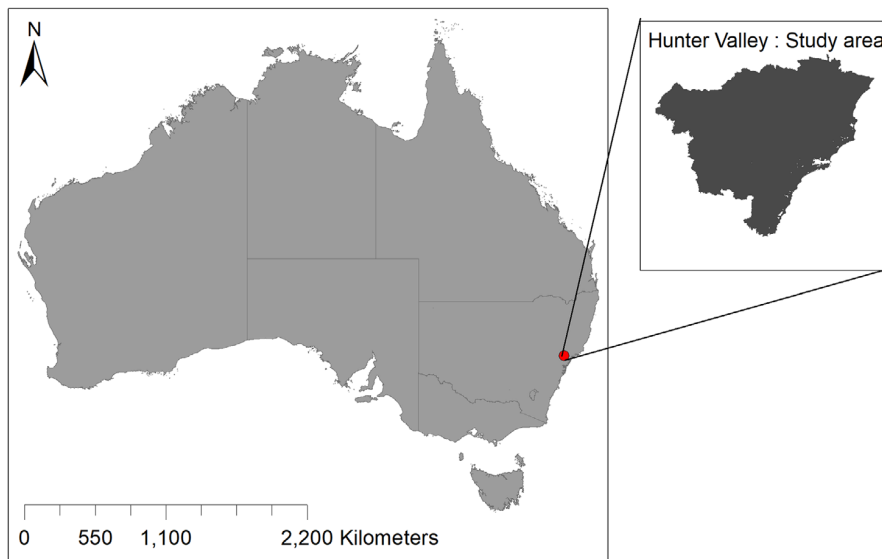


Figure 1. Hunter Valley region, New South Wales, Australia.

assessments in an adaptive management framework can be an effective approach to offset management (Drielsma et al. 2016). However, there has been little quantitative research on how vegetation-based offset metrics truly function in relation to species-persistence targets (Gelcich et al. 2017).

To address this gap, we developed a simulation framework to compare performance of commonly used vegetation-based offset metrics with alternative metrics that include more detailed species data. Our framework combines a model simulating development and offsetting with population viability analyses (PVAs) for 3 species in the Hunter Region, New South Wales (NSW), Australia. We aimed to improve understanding of how vegetation-based offset metrics capture development impacts on habitat and persistence of target species.

Methods

Target Species

The Hunter Region in NSW, Australia (Fig. 1), has a long history of agriculture and coal mining, and mine leases and applications occupy ~21% of the Hunter Valley (90,500 ha) (Kujala et al. 2015; NSW Government, Planning and Environment, 2016). This region is home to several susceptible species, including the 3 we considered: squirrel gliders (*Petaurus norfolcensis*), Powerful Owls (*Ninox strenua*), and northern brown bandicoots (*Isodon macrourus*). Squirrel gliders are hollow nesting, gliding marsupials widely distributed along the east coast of Australia (Sharpe & Goldingjay 2017). The Powerful Owl is a large owl with a wide home range in southeastern Australia (Soderquist & Gibbons 2007). Both species are considered vulnerable

in NSW. Northern brown bandicoots are medium-sized ground-dwelling marsupials with short life cycles, high population growth rates, and moderate dispersal (Ramalho et al. 2018). This species is not currently considered threatened. These species were selected primarily because they are sufficiently well studied to build spatially explicit population models.

Habitat and Species Data

We used two types of raster maps to conduct our simulations: a vegetation condition map and species habitat suitability maps (Kujala et al. 2015). The vegetation condition map was used to estimate the native vegetation condition for the Hunter Region at 100-m grid-cell resolution. Scores ranged from 0 to 1, depending on known land-use categories. Zero indicated areas containing no natural vegetation, whereas 0.5 could indicate agricultural land with remnant vegetation. One indicated extant and relatively undisturbed vegetation (Supporting Information). Species distribution models (SDMs) (100-m grid-cell resolution) were built for each species with MaxEnt (Elith et al. 2011; Kujala et al. 2015), again with values of 0–1 (Supporting Information). Being based on presence-only data, the SDMs represent only relative habitat suitability for each species in the region (Guillera-Aroita et al. 2015). We interpreted MaxEnt's logistic output values as roughly indicative of relative carrying capacity (Merow et al. 2013), giving the fraction of maximum carrying capacity attainable for each species (Supporting Information). Because MaxEnt outputs are not comparable between species, we examined relative changes in total habitat suitability between scenarios only within species.

We multiplied our vegetation condition layer and SDMs to produce a proxy of current habitat suitability (Supporting Information) for each species; values ranged

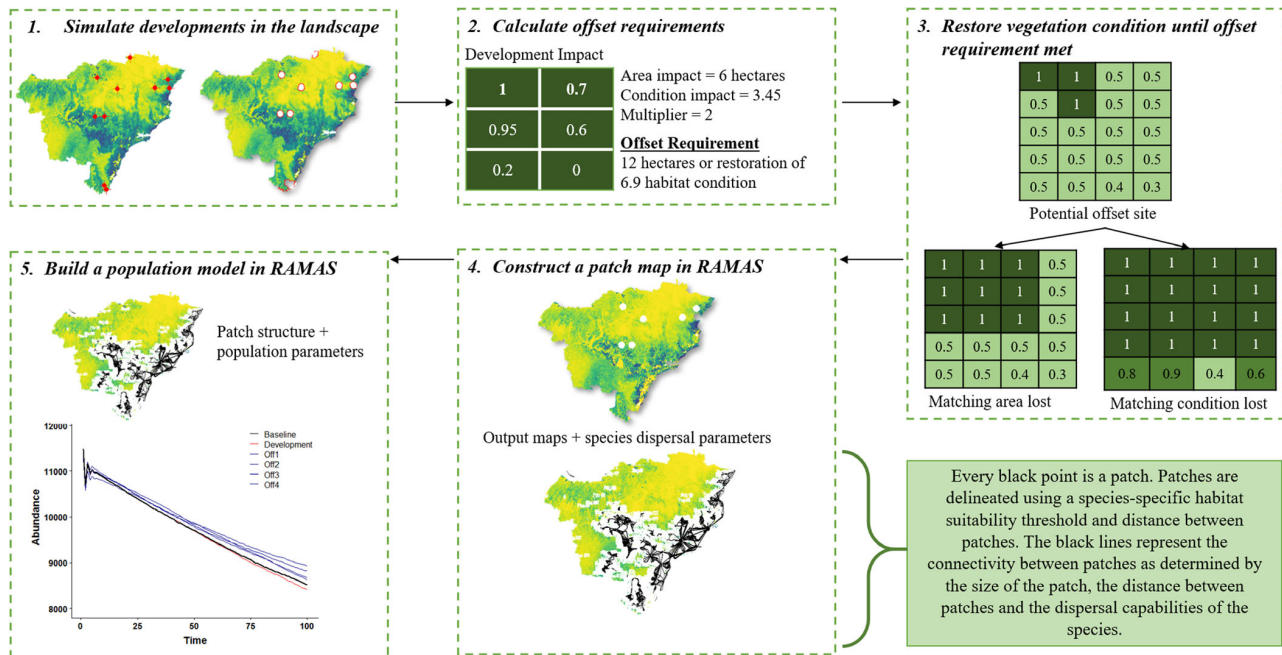


Figure 2. Simulation modeling framework conducted within R (steps 1 to 3) and RAMAS GIS (steps 4 and 5). The maps represent habitat suitability on a scale of 0–1 (yellow, not suitable; blue, highest quality habitat; green squares in steps 2 and 3, grid cells in the landscape and their condition values; red points in step 1, development sites chosen; white circles in step 1, sites cleared). The impacts of each development are calculated in terms of area and condition lost (step 2). Vegetation condition is restored until the requirement is met either in terms of area or condition (step 3). Each resulting map, including development without offsets and developments with offsets, is used in RAMAS GIS to build a patch map based on the resulting landscape structure and species dispersal parameters (step 4). The patch map is used in a spatially explicit population model that tracks abundance of the species through time (step 5).

from 0 and 1. The resulting habitat suitability map for each species represented the baseline used to compute the impacts of each development and its required offset. This was also the baseline map used to define landscape structure and determine carrying capacity in our spatially explicit PVAs.

Modeling Framework

We used the above raster layers as inputs to simulate development impacts and calculate offset requirements within R 3.6 (R Foundation for Statistical Computing 2017). For all development and offset simulations, we used our current habitat suitability map as a baseline for each species. Each subsequent raster generated by the simulations was then used to represent habitat changes within the PVAs for each species.

Our modeling framework involved five steps: simulate developments; calculate offset requirements; restore vegetation until offset requirements are met; construct a landscape patch structure for the species; and build population models for the species to predict population persistence (Fig. 2). We assumed consistently across all

metrics that restoration returns vegetation condition to the highest level immediately. Because we were interested in comparing relative performance of offset metrics, rather than providing realistic predictions about restoration success, it was deemed unnecessary to perfectly characterize variation in restoration outcomes. We acknowledge this is a coarse simplification of likely success of restoration efforts (Maron et al. 2012).

Development Impacts

We simulated 4 development scenarios for each species: S1, large developments with strict avoidance of high-quality habitats; S2, large targeted developments that remove high-quality habitat; S3, small developments with strict avoidance; and S4, small targeted developments. All 4 scenarios had a total development footprint of 100,000 ha (approximately 21% of the landscape). Large developments were each 10,000 ha and occurred 10 times in the landscape during one simulation (S1, S2). Small developments were 1,000 ha and occurred 100 times (S3 and S4). Scenario 1 and 3 represented our strict avoidance scenarios, where development was targeted toward the

least suitable habitat for each species, based on species current habitat suitability. This aligns with the avoidance stage of the mitigation hierarchy (Phalan et al. 2017). In targeted development scenarios S2 and S4, development was directed to high suitability areas to represent a worst-case scenario. We also simulated 2 additional development scenarios where impacts were allocated randomly (Supporting Information). Each scenario was repeated 50 times to account for spatial stochasticity. Development impacts reduced vegetation condition of affected grid cells to 0.

Offset Metrics and Simulation

We calculated offset exchanges based on area only (area); vegetation condition only (condition); area \times habitat suitability (areaXSDM), and condition \times habitat suitability (conditionXSDM). Area was based solely on the area lost due to development, and the offset simply restored the same area of habitat elsewhere. Condition was calculated by summing the current habitat condition lost due to development, and restoration was required to enhance habitat condition by an equivalent amount elsewhere. The metric areaXSDM, as with area, was based on the area lost due to development but differed in that offsets were restricted to an equivalent area in the landscape that was also suitable habitat for the species as modeled by the SDM (after applying a species-specific threshold to differentiate between habitat and non-habitat [Supporting Information]). The metric conditionXSDM, as with condition, offset the summed current habitat condition lost due to development, but restoration was again restricted to species' habitat as modeled by the SDM (Supporting Information).

These metrics were intended as coarse simplifications of offset metrics currently used in Australia. In NSW offset legislation relies on the biodiversity assessment method (BAM) which incorporates 30 measures of habitat and landscape to assess biodiversity (NSW Office of Environment & Heritage 2018). These are largely focused on habitat features. When species are accounted for in the BAM metric, measurements generally include species presence or absence and habitat suitability. These are measures accounted for in the above metrics, albeit simplistically. We used a multiplier of 2 for all offset targets, meaning that offsets needed to deliver gains of twice the amount lost. Large multipliers (e.g., >10) are more likely to ensure no net loss; however, relatively low multipliers (e.g., 2–3) are commonly used in practice (Bull et al. 2016b; Laitila et al. 2014). Multipliers in the BAM vary from 1 and 3 and depend on species' sensitivity to loss and to offset gains. Therefore, the multiplier of 2 we used accounts for a moderate-to-high sensitivity to loss and a moderate-to-high potential gain (NSW Office of Environment & Heritage 2018).

For all repetitions of our development scenarios, we restored impacts based on all four metrics. A starting point for restoration was randomly selected within a buffer zone around the development (Supporting Information). Each cell adjacent to the starting point was searched and restored until the total offset requirement was met. At the end of each simulation, an updated raster layer was generated with the simulated developments and offsets added to the species current habitat suitability layer.

Spatially explicit PVA

Population viability analyses estimate the probability of a species persisting in a landscape given its habitat requirements, dispersal ability, and demographic variables. We built spatially explicit PVAs for each species with the software RAMAS GIS 5.1 (Akçakaya & Root 2005). We used the current habitat suitability maps of the species to develop the baseline patch structure and to simulate population dynamics over a 100-year period prior to developments or offsets. Patch structure is delineated by RAMAS with a habitat suitability threshold and species-specific information on dispersal (Akçakaya & Root 2005) (Fig. 1). We used the species-specific maximum training sensitivity plus specificity (Cardador et al. 2018) as our threshold, which was extracted from the MaxEnt model outputs (Supporting Information). We derived species-specific dispersal and demographic parameters from the literature and tested them through sensitivity analyses (Supporting Information). We then re-ran the PVAs for each species, replacing the baseline patch structures with those generated from development and offset simulations.

Scenario Analyses

We ran 50 simulations per development scenario and 50 corresponding restorations for each metric, for all 3 species, for which PVAs were run for 1000 replicates over 100 years. We used two measures to evaluate metric effectiveness: percent change in total habitat suitability (HS) from baseline, calculated using the species' updated raster maps, and percent change in average estimated minimum abundance (EMA) from baseline, calculated from the PVAs. The EMA is the smallest population size that occurs across the duration of a simulation averaged across replicates (Wintle, 2013). We examined CIs around the 50 repeats to assess correlations between metric use and changes in HS and EMA from baseline. We also assessed changes in landscape structure by comparing mean number and size of suitable habitat patches in the landscape with minimum and maximum EMA values (Supporting Information).

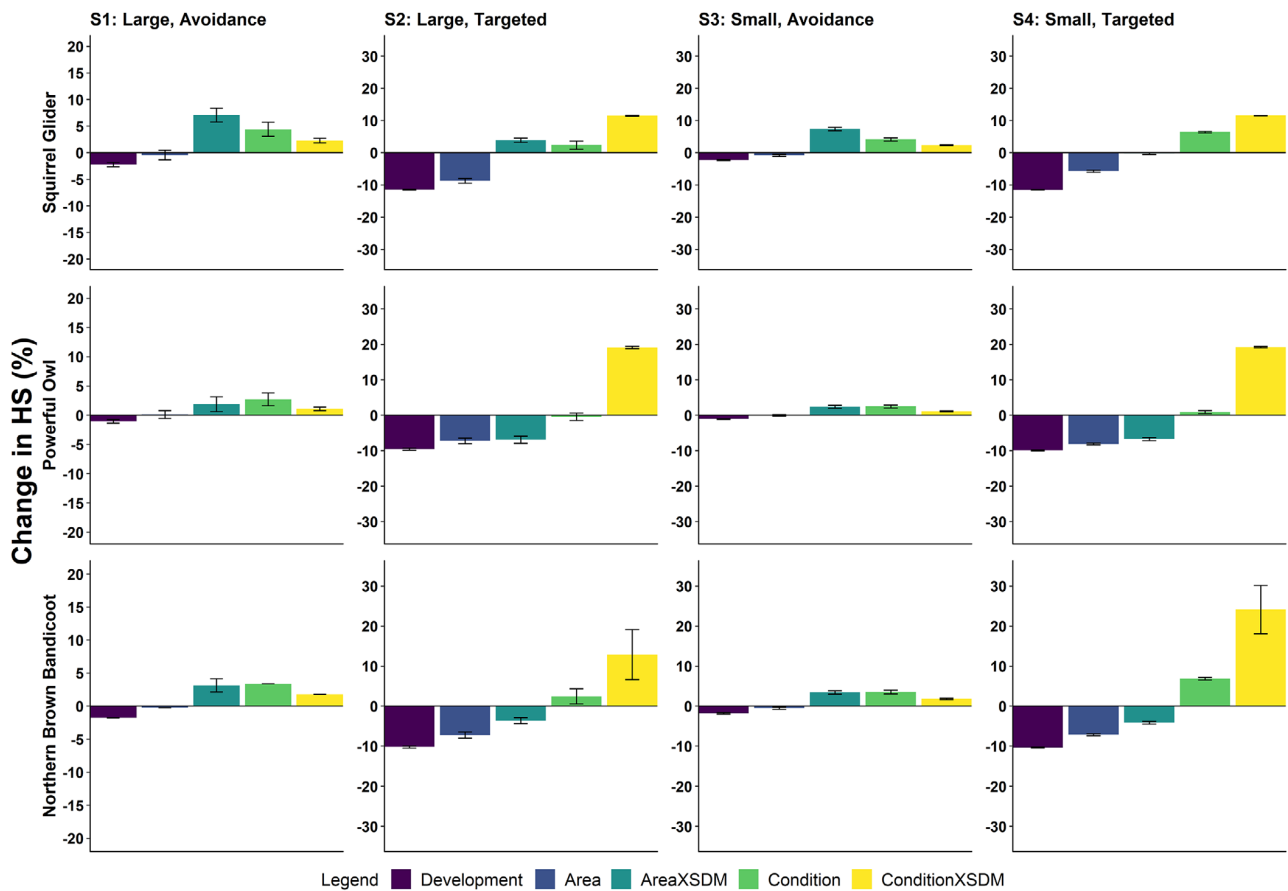


Figure 3. Percent change in habitat (HS) from baseline for 3 species under 4 development scenarios (S1, large development avoidance; S2, large targeted development; S3, small development avoidance; S4, small targeted development; error bars, SD generated from 50 repetitions of each simulation; dark blue, development impact; blue, area only; turquoise, area \times habitat suitability [SDM]; green, condition only; yellow, condition \times habitat suitability [SDM]).

Results

Change in Habitat Suitability

Impacts of development on the percent change in HS were consistent across species but varied between scenarios. Targeting developments to species' high-quality habitat (S2 and S4) caused a 10.5% (SD 0.8) decline in HS for our species (Fig. 3), whereas under strict avoidance (S1 and S3) species lost on average 1.7% (SD 0.5) of their habitat (Fig. 3).

The effectiveness of offset metrics in compensating for development impacts on HS varied among development scenarios and species. The area-only approach consistently failed to achieve no net loss of HS for all scenarios and species (Fig. 3). Thus, simply compensating for the area lost did not produce enough habitat to match development impacts. Under the avoidance scenarios (S1 and S3), the 3 remaining metrics achieved net gains in HS for all species (Fig. 3). However, when de-

velopments were targeted (S2 and S4), the benefits delivered by most metrics—except conditionXSDM—were smaller. The areaXSDM metric failed to achieve a no net loss for the Powerful Owl and northern brown bandicoot in S2 and for all 3 species in S4. This is likely because in high-impact development scenarios, even when offsets are targeted toward high suitability pixels (e.g., areaXSDM), simply matching area alone will not compensate for enough of the lost condition to return the overall HS back to the species baseline level.

The conditionXSDM metric produced net gains in all 4 development scenarios across all 3 species. Notably, when using the conditionXSDM metric, because offset requirements were extremely high, around 24% and 28% of offset requirements respectively for Powerful Owl and northern brown bandicoot were not met. In these scenarios the simulation ran out of habitat to restore and still resulted in large net gains in HS compared with baseline.

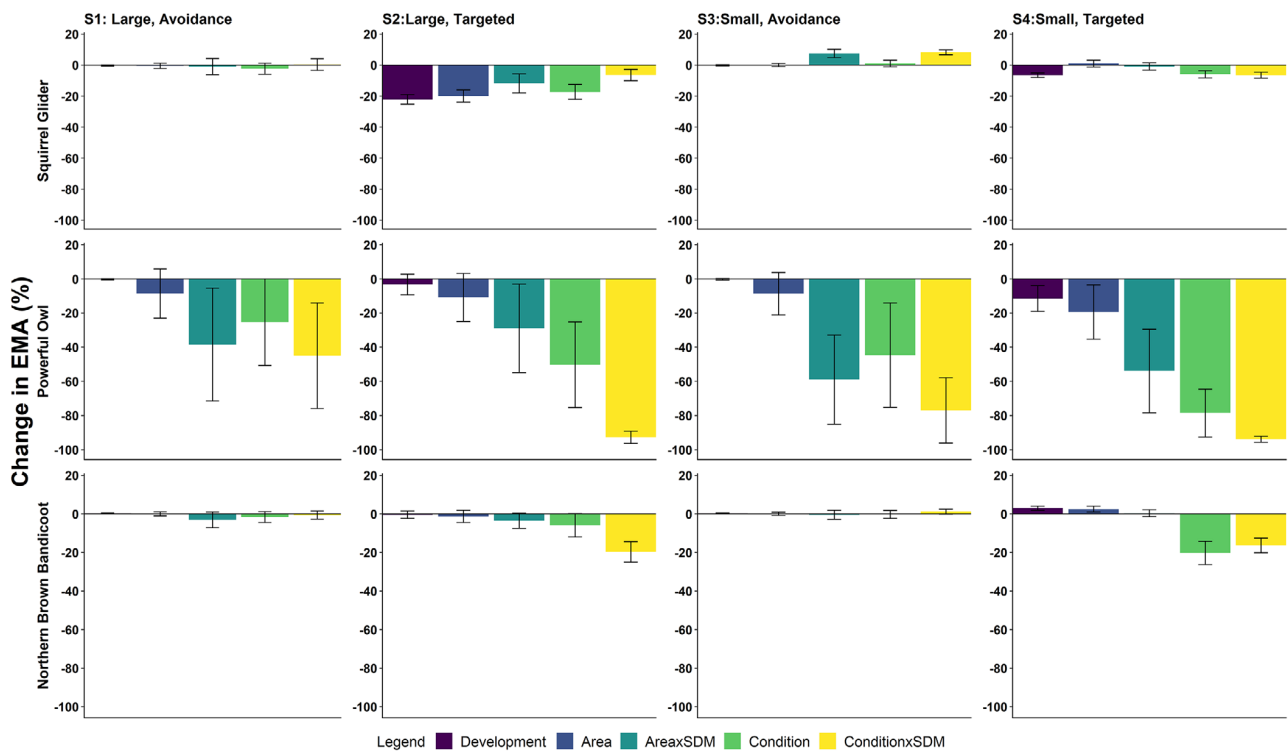


Figure 4. Percent change in estimated minimum abundance (EMA) (averaged across population viability replicates) from the species baseline for 3 species under 4 development scenarios (error bars, SD in EMA produced by the simulation runs; S1, large development avoidance; S2, large targeted development; S3, small development avoidance; S4, small targeted development; dark blue, the development impact; turquoise, area \times habitat suitability [SDM]; green, condition only; yellow, condition \times habitat suitability).

The condition-only approach also achieved no net loss and sometimes net gains in HS for all species and scenarios; however, gains were smaller than the conditionXSDM metric (Fig. 3). Compensating for condition, particularly when coupled with information on SDMs, resulted in larger offset areas than area-based metrics (Supporting Information). For all species the conditionXSDM metric resulted on average in patches 1.4 times larger than the other 3 metrics and 1.7 times larger than the species baselines patch structure (Fig. 5).

Change in EMA

Development impacts on EMA were not proportional to impacts observed on HS and varied among species and scenarios (Fig. 4). Declines in EMA were less dramatic when the size of the development was small (S3, S4) (Fig. 4), except for the Powerful Owl, for which highest declines were observed under S4. Development impacts on squirrel glider EMA were higher than the other two species, particularly when the developments were targeted (S2, S4) (Fig. 4). Under all 4 development scenarios, changes in northern brown bandicoot EMA were minimal and even showed a small net gain in S4

(Fig. 4). This could be due to the high reproduction rates of northern brown bandicoots and the influence of development on the landscape structure, which may have been more favorable for this species.

Benefits delivered to population persistence by offsets varied notably among metrics, species, and scenarios; generally, most of the metrics failed to achieve net gains. In our worst-case scenarios, S2 and S4, no net loss in EMA was only rarely achieved, only for the northern brown bandicoot and Powerful Owl in some replicates and only when using area only and areaXSDM (Fig. 4). Generally, all 3 species' abundance declined significantly across all metrics even when the metrics resulted in significant gains in HS (e.g., conditionXSDM) (Fig. 3).

Development impacts on squirrel glider EMA were best offset when using metrics that included species-specific information on habitat suitability (SDM) (Fig. 4). When development impacts were small and a strict avoidance approach was taken, the 2 SDM inclusive metrics achieved net gains for the squirrel glider. Comparatively, no net loss of EMA for Powerful Owls was only achieved in some simulations, generally when using the area metric (Fig. 4), even though this metric failed to achieve a no net loss in HS (Fig. 3). Similarly,

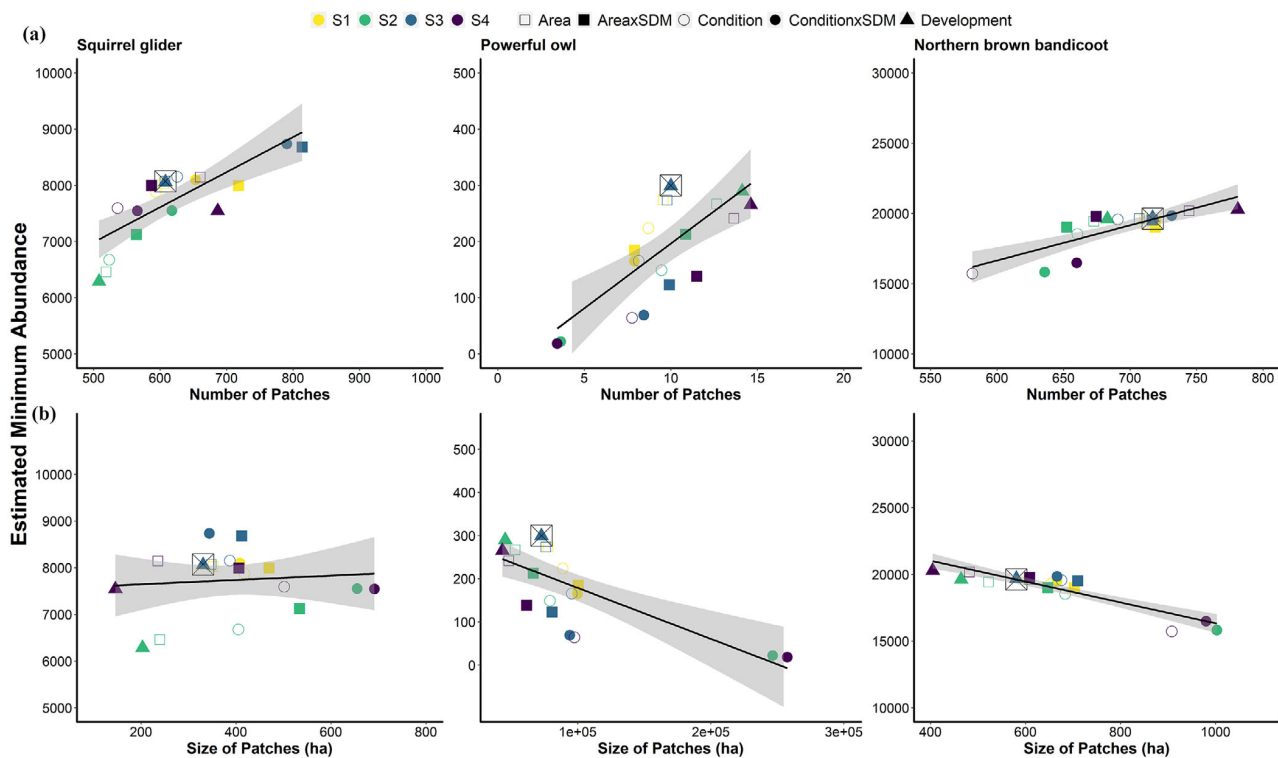


Figure 5. Comparison of the estimated minimum abundance (EMA) values with average (a) number of patches and (b) size of patches under 4 development scenarios (yellow, S1, large development avoidance; green, S2, large targeted development; blue, S3, small development avoidance; dark blue, S4, small targeted development) and 4 metrics (open square, area; solid square, area \times habitat suitability [SDM]; open circle, habitat condition; solid circle, condition \times habitat suitability [SDM], and solid triangle, development; black square with a cross, baseline value for number of patches relative to EMA; trend line, relationship between EMA and number or size of the patches as a linear regression; gray shading, variation around regression estimate).

not net loss was achieved for northern brown bandicoots in some replicates when using the two area-based metrics (Fig. 4). Condition-based approaches only resulted in no net loss for northern brown bandicoots in some simulations when the development impacts were untargeted (S1, S3) (Fig. 4). Across all three species, the conditionXSDM metric, which produced the largest gains in HS, frequently failed to compensate for declines in EMA. In Powerful Owls and northern brown bandicoots, the use of this metric resulted in larger declines than development on its own (Fig. 4).

Landscape Configuration and Population Declines

Scenarios that resulted in more patches generally resulted in higher EMA values for all species (Fig. 5). The largest declines in EMA occurred when the development or offsets reduced the number of patches available in the landscape. Furthermore, across all species, EMA was highest when patch size was small, although this relationship was not as clear for the squirrel glider (Fig. 5). It appears that in scenarios where patch size was large

(e.g., conditionXSDM metric [Supporting Information]) there was a corresponding decline in the number of patches available and overall lower EMA values relative to the species' baselines. This is clear in northern brown bandicoots and Powerful Owls for which conditionXSDM produced extremely large patches with fewer patches available overall (Fig. 5). This suggests that, at least for these species, producing large, continuous offset patches may not ensure population persistence. Instead, scenarios that resulted in maintaining multiple patches had overall the highest EMA (Fig. 5).

Discussion

We quantitatively demonstrated how habitat loss and mitigation of these losses translates to species persistence. When performance of offsetting was measured in terms of total habitat gains, achieving no net loss, and even net gains was feasible with the metrics we tested. This was particularly apparent when information on a species' habitat suitability was included in offset calculations. In

all four development scenarios, metrics that accounted for SDM values delivered the highest net gains in HS (Fig. 3). This may be important when developments are likely to affect core habitats and therefore require offsets to be strategically assigned to areas of high quality (Gordon et al. 2011). Conversely, offset trades based solely on area lost versus area gained failed in all cases to deliver a no net loss in HS for all three species (Fig. 3). Thus, simply accounting for area resulted in offsets that were too small to match development impacts in terms of lost HS. This is consistent with previous research showing that offset trades based on area only metrics are unlikely to achieve no net loss, particularly without significant multipliers (Bull et al. 2016b; Sonter et al. 2019).

Despite significant gains in HS, none of the metrics were consistently effective at offsetting development impacts on species' populations (Fig. 4). Our results highlight that relying on vegetation condition, or even changes in HS for target species, as a measure of offset success can be misleading. This was apparent in the vastly different outcomes we observed between HS and EMA (Figs. 3 & 4). Depending solely on HS could result in the false interpretation that offset actions are having long-term benefits for the target species. This could lead to exacerbated species declines and nudge species of least conservation concern toward a declining trajectory, even when every offset requirement is being met (Maron et al. 2015). This is also consistent with previous research demonstrating that restoration actions based on vegetation metrics alone do not effectively account for target species or populations (Cristescu et al. 2013; Hanford et al. 2016).

We also demonstrated the difficulty in achieving no net loss at a landscape scale (Peterson et al. 2018). Even when each individual offset action delivers a no net loss, this may not result in a landscape level benefit for the species. The metrics we tested all failed to support the structural and functional landscape characteristics necessary for the 3 species (Fig. 5). Although basic landscape metrics, such as patch size and distance, are usually incorporated into offset metrics (Gibbons et al. 2016), these basic structural connectivity measures still largely fail to capture development impacts on species or populations (Crouzeilles et al. 2015). There are benefits to accounting for functional connectivity in the planning stage of offsets, at least in terms of achieving no net loss targets (Bergès et al. 2020). Our results showed that the negative impacts of using only habitat-based metrics and ignoring species-specific connectivity may be significant, vary greatly among metrics, and, most alarmingly, are likely to go unnoticed unless changes in population dynamics are tested explicitly. These findings provide strong support for earlier calls that both structural (e.g., patch size and distance) and functional connectivity metrics (e.g., metapopulation connectivity and capacity [Moilanen et al. 2005; Bojkovic et al. 2015]) should

be accounted for in early stages of impact assessment and offset planning to avoid unexpected declines in populations and species (Tarabon et al. 2019).

This case study is a simplified version of current offset procedures, and we applied it to only 3 species. Commonly, practitioners have to design offsets to provide benefits for multiple target species simultaneously. We focused only on single-species outcomes to keep comparisons between metrics as transparent as possible. However, these results are naturally further complicated when considering how metric choice could interact with multiple species priorities (Whitehead et al. 2017). Exhaustive collection of data on ecology and demographic processes driving persistence is not possible for all species (Birkeland & Knight-lenihan 2016). However, increased availability of abundance and demographic data may fill this information gap over time. Failing to capture complex processes that drive changes in population persistence at a landscape level is likely to exacerbate biodiversity declines, such as we observed (Maron et al. 2016). Assessing species-specific metrics, such as abundance or density, that are generally driven by ecosystem processes (Otto et al. 2014), alongside vegetation condition metrics, may better enable offsets to capture the key species managers are aiming to protect and ensure long-term population persistence (Mckeeney & Kiesecker 2010; Schmeller et al. 2017). Inclusion of these data in offset approaches would likely improve offset outcomes for rare, low-density species with large home ranges, such as the Powerful Owl. Similarly, our use of HS information here, though largely ineffective at accounting for population persistence, did demonstrate benefits for delivering habitat gains in comparison to area or condition only metrics. For example, the net gains in HS delivered using the conditionXSDM metric resulted in some success for the squirrel glider populations so long as impacts were avoided where possible and ideally small (Fig. 4).

Recent shifts in policy requirements have promoted using HS information where possible and additional information on populations and abundance when required (Queensland Government 2014). Our use of species-specific HS was an attempt to reflect rapidly changing offset policies and increased interest in incorporating more species-specific information into offset calculations (Moilanen & Kotiaho 2018). Although SDMs do not capture population-level processes (Kujala et al. 2018), they provide a more accurate description of HS than simple vegetation-based metrics (Guisan & Thuiller 2005). Data required to build SDMs are becoming more prevalent and are relatively easy to access and collate at large scales (Boykin et al. 2012). Use of SDMs within biodiversity offsetting may also provide developers with information necessary to avoid areas where biodiversity impacts are likely to be significant (Houdet & Chikozho 2014). Moreover, SDMs can explicitly target restoration

efforts toward areas where habitat gains will be largest (Whitehead et al. 2017).

It is likely there is no single way of overcoming the challenges associated with offsetting for every scenario and species. Based on our results, 4 key conclusions and recommendations follow for offset policies. First, and reinforcing earlier calls (Phalan et al. 2017), avoidance of impacts through careful placement of new development is the most effective way of ensuring species persistence is maintained. Given challenges associated with increasing complexity in current offsetting metrics and the fact that some developments are not offsettable, avoiding and minimizing negative development impacts where possible is essential. Second, when developments affect areas of high suitability for species, it is essential that species, not only their habitat, be explicitly accounted for in offsets. We observed very different conservation outcomes when comparing habitat gains and species persistence. Ensuring the metrics accurately reflect the values we aim to conserve is crucial (Cristescu et al. 2013; Hanford et al. 2016). This is further dependent on policy frameworks under which an offset is required, highlighting the importance of explicitly stating biodiversity targets in the planning stage (Maron et al. 2018).

Third, although large offsets may have multiple benefits, our results demonstrate that more habitat does not necessarily translate into equal gains in persistence for all species. The implications of not accounting directly for species population dynamics and landscape structures may outweigh benefits delivered by producing large areas of suitable habitat (Fig. 5). Where data are available, abundance and demographic variables should be included in offset calculations to ensure populations are tracked and development impacts on populations are accountable. Finally, our results show that benefits delivered by offsets are nuanced and species specific. Therefore, impacts of metric choice should also be assessed for multiple species simultaneously to determine how these metrics align with achieving several persistence targets. These improvements may go some way toward mitigating development impacts on biodiversity and ensuring long-term conservation benefits.

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Supporting Information

- Appendix S1: Species and habitat data
- Appendix S2: Simulation framework and metrics
- Appendix S3: Population viability analyses (PVA)
- Appendix S4: Sensitivity analysis
- Appendix S5: Landscape results

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