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Charles Thévenin

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Ecole doctorale Sciences de la Nature et de l'Homme : Ecologie & Evolution

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*Centre d'Ecologie et des Sciences de la Conservation – CESCO*

*Equipe Conservation et Restauration des Populations*

## **Contribution of reintroduction strategies to the conservation of biodiversity at large scale.**

*Analysis of bird and mammal restorations in Europe*

Par **Charles THÉVENIN**

Thèse de doctorat d'Ecologie

Dirigée par François Sarrazin, Alexandre Robert et Christian Kerbiriou

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# Résumé

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L'impact néfaste des activités humaines sur la diversité biologique s'intensifie et de nombreuses études suggèrent que nous entrons dans une sixième crise d'extinction. Parmi les actions possibles pour enrayer l'érosion de la biodiversité, les déplacements d'organismes dans un but conservatoire, les « translocations de conservation », sont de plus en plus utilisées pour restaurer des populations. En particulier, les réintroductions visent à rétablir une population viable d'une espèce au sein de son aire d'indigénat, suite à l'extinction locale de populations. Ces actions répondent souvent à des besoins de conservation à l'échelle locale ou nationale, et leur contribution à la préservation de la biodiversité à large échelle reste encore à déterminer. Cette thèse s'intéresse à la cohérence des efforts de réintroduction à large échelle, en questionnant trois aspects.

Le premier aspect se base sur un inventaire rétrospectif des efforts de réintroduction d'oiseaux et de mammifères afin de questionner la représentativité et l'originalité des espèces réintroduites. En effet les réintroductions sont souvent critiquées en raison de forts biais taxonomiques et du fait que les actions de conservation espèce-centrées se concentrent souvent sur des espèces charismatiques. Une partie de mes travaux a donc permis de réévaluer ces biais taxonomiques via un inventaire des efforts de réintroduction en Europe. J'ai ainsi pu explorer plus en détail la contribution des espèces réintroduites à la diversité phylogénétique et fonctionnelle des oiseaux et mammifères en Europe. Dans le chapitre 1 nous montrons que les espèces réintroduites de mammifères et d'oiseaux ne sont pas représentatives de la diversité phylogénétique des assemblages Européens et Nord-Américains, mais que l'allocation des efforts de réintroduction semble se concentrer sur des espèces originales phylogénétiquement, c'est-à-dire des espèces « uniques » du point de vue évolutif et dont l'extinction entraînerait une perte disproportionnée de diversité biologique. Dans le chapitre 2, nous montrons que les biais taxonomiques au sein des réintroductions sont également liés à une faible représentativité de la diversité fonctionnelle des assemblages européens chez les mammifères, mais pas chez les oiseaux. Les réintroductions de mammifères ont aussi concerné des espèces qui supportent des combinaisons de traits fonctionnels plus originales à l'échelle continentale.

Ces deux premiers chapitres s'intéressent aux efforts de réintroduction au sein des assemblages européens en cherchant à identifier et à caractériser les espèces réintroduites « au moins une

fois ». Dans le troisième chapitre nous présentons un examen plus approfondi de la distribution des efforts de réintroduction chez les mammifères européens en prenant en compte les différences dans le nombre de programmes implémentés par espèce. Nous montrons une très forte hétérogénéité dans le nombre de projets mis en place par espèce. Ces résultats suggèrent que certains biais, notamment en faveur des Carnivores, ne seraient pas aussi forts que perçus auparavant.

Le second aspect se concentre autour de l'efficacité de ces programmes. En effet, si la mise en œuvre de programmes de réintroduction n'a cessé d'augmenter sur les dernières décennies, leur efficacité est néanmoins remise en question. Une grande part de la recherche appliquée aux réintroductions vise à identifier les facteurs liés au succès ou à l'échec des programmes de restauration de population. Malheureusement l'absence de consensus autour de la définition du succès de ces opérations rend discutable la généralisation des estimations passées des taux de succès pour les réintroductions. Nous proposons un cadre conceptuel démographique pour définir des critères de succès pour les programmes de translocation de conservation, en insistant sur le fait que ce succès se mesure essentiellement au travers de la viabilité de la population réintroduite et de l'amélioration de son statut de conservation en cohérence avec les enjeux de restauration de biodiversité à plus large échelle. Les facteurs qui contribuent à l'échec ou au succès de ces programmes peuvent alors être évalués en fonction de leur impact sur les différentes phases de dynamique de la population réintroduite (installation, croissance et régulation).

Enfin, dans une dernière partie, nous explorons les bénéfices potentiels des projets de dé-extinction en questionnant leur capacité à restaurer des processus évolutifs. La dé-extinction correspond à la résurrection d'espèces éteintes, et peut être considérée comme une forme extrême de translocation de conservation. Les populations « ressuscitées » présentent néanmoins des particularités écologiques et évolutives qui risquent de limiter le succès de ces programmes à produire des populations viables. De plus, même si les de-extinctions parviennent à rétablir des populations d'espèces éteintes, leur capacité à contribuer à la conservation via la restauration des processus évolutifs reste à démontrer.

# Abstract

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The impact of human activities on biological diversity is intensifying, and many studies suggest that we are entering a sixth mass extinction. Among the possible actions to halt the erosion of biodiversity, the human-mediated movements of organisms for conservation purposes, i.e. "conservation translocations", are increasingly used to restore populations. In particular, reintroductions aim to restore a viable population of a species within its indigenous range, following local population extinction. These actions often address local or national conservation needs, and their contribution to large-scale biodiversity conservation has yet to be determined. This thesis focuses on the coherence of reintroduction efforts at large scale, by questioning three aspects.

The first aspect focuses on a retrospective inventory of bird and mammal reintroduction efforts in order to question the representativeness and originality of reintroduction targets. Indeed reintroductions have been criticized because of strong taxonomic biases and the fact that species-centred conservation actions often focus on charismatic species. Part of my research aimed to reassess these taxonomic biases through an inventory of reintroduction efforts in Europe. I was thus able to explore in more detail the contribution of reintroduced species to the phylogenetic and functional diversity of birds and mammals in Europe. In Chapter 1 we show that reintroduced species of mammals and birds are poorly representative of the phylogenetic diversity of European and North American assemblages. However, the allocation of reintroduction efforts seems to focus on evolutionarily distinct species, i.e. species that are "unique" from an evolutionary point of view and which extinction would lead to a disproportionate loss of biological diversity. In Chapter 2, we show that taxonomic biases in reintroductions are also linked to low representativeness of the functional diversity of the European assemblage in mammals, but not in birds. Mammal reintroductions have also involved species that support more original combinations of functional traits at the continental scale.

These first two chapters investigated reintroduction efforts within European assemblages through the identification and characterization of species reintroduced "at least once". In the third chapter, we provide a more in-depth examination of the distribution of reintroduction efforts among European mammals, taking into account the differences in the number of

programs implemented per species. We show a very strong heterogeneity in the number of projects per species, and our results suggest that Carnivores may not be as over-represented as previously perceived.

The second aspect focuses on the effectiveness of these programs. Indeed, although the implementation of reintroduction programs has continued to increase over the last decades, their effectiveness remains unclear. Much of the research applied to reintroductions aims to identify factors related to the success or failure of population restoration programs. Unfortunately, the lack of consensus around the definition of success for these operations makes the generalization of past estimates of reintroduction success rates questionable. We propose a conceptual and unifying demographic framework to define success criteria for conservation translocation programs, emphasizing that success is measured primarily through the viability of the reintroduced population and the improvement of its conservation status, coherently with the recovery of biodiversity at large scale. The factors that contribute to the failure or success of these programs can then be evaluated according to their impact on the different phases of the dynamics of reintroduced populations (establishment, growth and regulation).

Finally, in a final section, we explore the potential benefits of de-extinction projects by questioning their ability to restore evolutionary processes. De-extinction, the resurrection of extinct species, has raised substantial controversy. De-extinction can be considered as an extreme form of conservation translocation; however, ecological and evolutionary peculiarities of such "resurrected" populations may limit the success of these programs in producing viable populations. Moreover, even if de-extinctions succeed in restoring populations of extinct species, their capacity to contribute to conservation through the restoration of evolutionary processes remains to be demonstrated.

# Liste des publications

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**Thévenin, C.**, Mouchet, M., Robert, A., Kerbiriou, C., & Sarrazin, F. (2018). Reintroductions of birds and mammals involve evolutionarily distinct species at the regional scale. *Proceedings of the National Academy of Sciences*, 115(13), 3404-3409.

Robert, A., **Thévenin, C.**, Princé, K., Sarrazin, F., & Clavel, J. (2017). De-extinction and evolution. *Functional Ecology*, 31(5), 1021-1031.

**Thévenin, C.**, Mouchet, M., Robert, A., Kerbiriou, C., & Sarrazin, F. Functional representativeness and distinctiveness of reintroduced birds and mammals in Europe. In preparation

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**Thévenin, C.**, Robert, A., Kerbirou, C., Mouchet, M., Hasnaoui, S., & Sarrazin, F., (2015). Translocations in Europe: What kind of wildness do we restore? ICCB: 27th International Congress for Conservation Biology; August 2-6 2015; Montpellier, France. (Oral)

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Sarrazin, F., Ferjani, S., Morin, A., **Thévenin, C.**, Mihoub, J-B., Robert, A., & Colas, B., (2018). Sharing translocations outputs: toward a webdatabase on Conservation Translocations of Flora and Fauna in the Western Palearctic. 2<sup>nd</sup> International Wildlife Reintroduction Conference. November 13-16, 2018, Lincoln Park Zoo, Chicago, Illinois, USA. (Oral, co-author)







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# Introduction

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## **Reversing the loss of biological diversity through population restoration**

The world is facing a massive loss of biological diversity, as evidence accumulates suggesting that Earth is currently entering a 6<sup>th</sup> mass extinction, with current and projected rates of species loss being higher than what would be expected from fossil records (Barnosky et al., 2011; Ceballos et al., 2015). Over 320 species of terrestrial vertebrates have become extinct since 1500 AD (Dirzo et al., 2014), and more than 25,000 species of animals and plants are now considered to be threatened by extinction according to the International Union for Conservation of Nature Red List (IUCN Red List, version 2018-1). Overexploitation, habitat destruction and degradation, pollutions, invasive species and Human-induced climate change are among the main threats to species worldwide (Maxwell et al., 2016), and the dramatic growth of Human activities and resource use are accelerating biodiversity loss. Analysis of the consequences of biodiversity loss generally focuses on species extinction; however, it likely underestimates the magnitude of the depletion of Earth's biota. In fact, this biodiversity crisis is even more severe if we account for the dramatic declines in both the numbers and sizes of populations globally, even for common and "least concern" species (Ceballos et al., 2017; Gaston and Fuller, 2008). The Living Planet Index, an indicator of the current state of biodiversity based on trends in vertebrate populations, estimated a 58% decline in population size of vertebrates worldwide in the past 40 years (McRae et al., 2016). The disappearance of populations and associated shrinkage in species' geographic range leads to changes in community composition and thus affects the functioning of natural ecosystems. Beyond the loss of species, this ecological crisis is expected to have substantial detrimental societal and economic consequences, due to the loss of ecosystem services or reduction of nature's contribution to people (Díaz et al., 2018; Secretariat of the Convention on Biological Diversity, 2014).

In order to tackle the erosion of biodiversity, conservation biology emerged as a synthetic, multidisciplinary science, which aims to provide management strategies for supporting the preservation and restoration of complex natural systems and favour their evolution (Soulé, 1985). International initiatives have attempted to halt and reverse the erosion of biodiversity

though coordinated action, such as the Convention on Biological Diversity which set up the Aichi Biodiversity targets meant to reduce the pressures on biodiversity by 2020 ([www.cbd.int](http://www.cbd.int)). One of the simplest ways to preserve biodiversity is to ensure the protection of species or to set aside areas in order to protect ecosystems, species assemblages and populations from all processes threatening their persistence in the wild. This “preventive” approach seeks to preserve native species in their natural habitats. However, human activities have led to the massive degradation and destruction of some ecosystems, which sometimes require direct human intervention for assisting the recovery of species. Reintroduction is a population restoration technique that aims to re-establish a population in the indigenous range of a species where it has been extirpated (IUCN/SSC, 2013). Reintroductions are part of the conservation translocation spectrum (Box 1), and generally occur when all other management strategies have failed and when the species will not be able to re-colonize some parts of its indigenous range without human intervention.

Translocations of organisms had occurred for millennia, often involving economically or culturally favoured species. The Human-mediated movement of species for addressing conservation issues has occurred for over a century, and one of the first attempt to restore extirpated populations can be attributed to the reintroduction of the bison (*Bison bison*) in North American landscapes in 1907. Reintroduction was revealed as a viable conservation tool in the second half of the 20<sup>th</sup> century thanks to several outstanding programs, such as the reintroduction of peregrine falcons in North America (Cade and Burnham, 2003) or the return of the Arabian Oryx in Oman after the species was catalogued as extinct in the wild (Spalton et al., 1999). As reintroductions became more popular, the number of implemented project increased but the success rate was low (Griffith et al., 1989), because of the implementation of numerous ill-conceived projects with poorly planned releases and little to no investment in post-release monitoring. In 1987, the IUCN published a position statement on reintroduction and other translocation practices, and in 1988, the Reintroduction Specialist Group (IUCN/SSC) was formed with the objective of designing guidelines to promote a better practice for conservation translocations (IUCN/SSC, 2013, 1998). Over the years reintroduction biology emerged as an applied science, with the purpose of providing knowledge that facilitates decision-making and improve management strategies (Armstrong and Seddon, 2008; Ewen et al., 2012; Sarrazin and Barbault, 1996; Seddon et al., 2007; Taylor et al., 2017).

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**Box 1. The conservation translocation spectrum**

Translocations, the Human induced movement and release of organisms, have been increasingly used in the past decades to address conservation issues. In order to avoid confusion related to the proliferation of new terms and concepts, Seddon (2010) provided a standard framework to develop a common terminology for defining conservation translocations.

**Conservation translocations** are defined as the human-mediated movement and release of organisms where the main purpose is to yield a measurable conservation benefit. This framework does not include some common types of translocations such as the release of rehabilitated individuals or the mediated movement of species to alleviate Human-wildlife conflicts. Mitigation translocations, i.e. economically driven translocations initiated when Human development and land-use conflict with population persistence at a local scale, are also not considered in this spectrum (Germano et al., 2015). This *conservation translocation spectrum* was later included in the latest IUCN Reintroduction Guidelines and Other Conservation Translocations (IUCN/SSC, 2013), and considers four types of conservation translocations. The first distinction to be made is whether the individuals are released within the indigenous range of the species. Releases within the documented distribution of the species are classified as **population restoration** projects, where the goal is to support the recovery of the focal species into parts of its range through reintroduction or reinforcement. **Reintroduction** is the release of an organism into an area that was once part of its range but from which it has been extirpated. The objective of a reintroduction is to re-establish a viable population, with a high probability of persistence with minimal to no human intervention (IUCN/SSC, 2013; Seddon, 1999). **Reinforcement** is the release of individuals into an existing population of conspecifics, and aims to increase population size, avoid potential genetic issues and ultimately increase the probability of persistence of the population.

Moving along the translocation spectrum, **conservation introductions** involve the release of individuals outside their indigenous range through assisted colonization or ecological replacement. **Assisted colonization** is the intentional release of individuals into favourable habitat outside the historical range of the species because there is evidence that the species cannot persist in its indigenous range due to climate change or other unmanageable threats. This pro-active type of translocation has generated a debate focusing on the risk of impacts of introduced (and hence potentially invasive) species on native species (Ricciardi and Simberloff,

2009), but is seen as a promising conservation tools, particularly in insular systems (Seddon, 2010). **Ecological replacement** is the release of a species outside its indigenous range in order to fulfil an ecological function that is no longer supported due to the extinction of another species. Because of species extinction, reintroduction is no longer an option and ecological replacement proposes to re-establish a viable population of a species known to fill a similar ecological niche. This type of translocation relies on finding functionally equivalent taxa to fill the vacant niche, yet the most acceptable approach should involve closely related species, and help improve the conservation status of the translocated species.

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Reintroduction can be an effective conservation tool, but it requires rigorous justification and planning. The likeliness of species recolonization and the need for direct human intervention must be assessed before managers and stakeholders can conclude that translocation is the most adapted conservation measure (IUCN/SSC, 2013). Other conservation alternatives such as habitat restoration or the design of protected areas can sometimes be more cost-effective and less risky than translocations. If reintroduction is deemed to be an acceptable option, it is of first importance to conduct feasibility studies and risk assessments in order to maximize the chance of success. Information on the biology and ecology of the species needs to be collected in order to predict how released individuals will perform in the recipient area. This background biological and ecological knowledge is key to develop efficient release strategies, and should cover as many aspects as possible, such as the life cycle of the species, its dispersal abilities and its biotic and abiotic habitat requirements. Habitat assessment is also essential in order to evaluate if the current environmental conditions suit the habitat requirements of the focal species. Threats that caused the previous extinction of the population need to be identified and significantly removed before releasing individuals. Reintroducing a species can involve several risks that need to be properly addressed to avoid translocation failure or unintended consequences. Reintroductions can affect the source population (when relocated individuals are removed from wild populations), have undesirable ecological effects (e.g., hybridization, disease transmission) and economic impacts (e.g., depredation on livestock). These potential risks for the translocated species, the recipient environment and the local human population, must be balanced against the expected conservation gain (improvement of the conservation status of the species from local to global scale, restoration of ecological function).

Conservation translocations are now conducted in wide range of ecosystems (Jourdan et al., 2018; Soorae, 2018; Swan et al., 2016), and involve a variety of stakeholders with different values, interests and objectives (Chauvenet et al., 2016; Ewen et al., 2014). As for any single species conservation action, priority might be accorded to species based on a variety of criteria such as their ecological role or their degree of endangerment. General public awareness and political support are key to ensure a sustainable reintroduction effort (Kleiman et al., 1994), and reintroductions can be promoted by focusing on flagship species (i.e., iconic or charismatic species that easily gather support and funding for conservation), or on species that are valued on grounds of cultural heritage. Motivations for reintroduction are thus likely complex and the justification is situation- and species-specific. Reintroductions mostly rely on a parochial approach to conserving species (Hunter and Hutchinson, 1994), and reintroduction projects generally focus on local or national conservation needs, which do not necessarily conflate with global conservation priorities.

Considering the high rate of biodiversity loss, and the lack of adequate funding for conservation, the assessment of the effectiveness of current conservation strategies is of paramount importance in order to maximize conservation gains globally. Over the past decades, the management of protected areas have benefited from the development of a structured systematic approach to conservation planning to evaluate how protected areas fulfill their role and protect biodiversity (Margules and Pressey, 2000). Systematic conservation planning recognizes two main objectives for protected areas: representativeness and persistence. Representativeness refers to the need to represent or sample the variety of biological diversity, and persistence refers to the need to promote the long-term survival of species by maintaining ecological processes and viable populations. Gap analyses have been used to explore the extent to which a protected area system effectively covers various elements of biodiversity at national, regional and even global scales (Jennings, 2000; Rodrigues et al., 2004; Scott et al., 1993; Thuiller et al., 2015; Veron et al., 2016). This approach identifies elements of biodiversity that are not sufficiently represented in conservation areas, which will in turn serve as a guidance for optimizing the expansion of the current network (Pollock et al., 2017).

Reintroduction practice also benefits from a vast and increasing production of peer-reviewed publications (Bajomi et al., 2010; Seddon et al., 2007). Reintroduction biology is now recognized as a field of applied science (Ewen et al., 2012), and several authors have urged the need for reintroduction biology to address a broader range of scientific questions that need to be answered to gain the knowledge required to assist decision-making and improve



reintroduction outcomes (Armstrong and Seddon, 2008; Sarrazin and Barbault, 1996). However, recent assessment of the literature suggests that reintroduction-related publications remain scattered and largely consist of descriptive accounts of reintroduction programs and retrospective analyses that aim to address questions on population establishment (Taylor et al., 2017). It seems that reintroduction biology is not completely fulfilling its role in providing the evidence base to support management decisions, but some promising trends are visible as more studies address clearly defined *a priori* questions. Current directions in reintroduction biology aim to improve the success of reintroduction practice in order to ensure that reintroductions contribute to species recovery and ecosystem restoration. However, there are still few studies in reintroduction research that have questioned a strategic approach in the assessment and optimization of the allocation of reintroduction efforts at large scale. Therefore, the extent to which population restoration projects may assist the conservation of biodiversity at regional, continental or global scale remains unclear. Reintroductions are intricate operations that involve a variety of ecological, sociological and economic aspects, and managers often need to make numerous decisions under uncertainty. Therefore, any assessment of the contribution of reintroductions to the conservation of biodiversity at large scales needs to consider that the observed patterns reflect a bottom up accumulation of locally implemented conservation actions that are rarely designed to tackle conservation priorities at larger spatial or organizational scales. With this thesis, I aimed to propose a way to assess the emerging conservation properties of the sum of local conservation translocations, and I explored how representativeness and persistence can be assessed in the context of reintroduction practice.

## **Aim of the thesis: assessing the relevance of the allocation of reintroduction efforts**

Reintroductions can represent a major financial and human commitment, and following releases, populations often need to be continually managed and monitored over several years. Given the debates regarding the economic and human cost of reintroduction programs (Lindburg, 1992), the underlying ethical and environmental questions raised by reintroduction practices, and their integration into wider environmental management schemes (e.g., rewilding), it is of first importance to provide evidence based arguments to describe how reintroductions may contribute to the conservation of biodiversity at larger scales.

One way to assess if reintroduction targets represent relevant conservation units is to question if reintroduction practitioners have focused on globally threatened species. The IUCN Red List of Threatened Species is a widely recognized and objective approach for evaluating the conservation status of species and identifying which species are threatened with extinction globally. Some outstanding recovery programs including reintroduction have saved species from the brink of extinction, that would otherwise only exist in captivity (such as the California condor, *Gymnogyps californianus*) (Alagona, 2004). However, using the IUCN Red List categories, studies have showed that on average reintroductions do not particularly focus on globally threatened species (Seddon et al., 2005), but rather on species that are at risk at national or provincial levels (Brichieri-Colombi and Moehrensclager, 2016). The study of how the conservation status of species can justify the implementation of reintroduction projects is challenging because it must acknowledge spatial and temporal constraints. For example the European Hamster (*Cricetus cricetus*) is considered Least Concern both globally and regionally (Europe), but has suffered severe declines and population extirpations in the Western limit of the species' range (IUCN, 2016a). This led to the implementation of reintroduction programs in France and the Netherlands and in this case, the reintroduction effort is justified by the species' conservation status at a local/national scale. Recent and available IUCN Red List assessments may also not illustrate the conservation status of the species at the time the reintroduction has occurred: the European beaver (*Castor fiber*) is now Least Concern both globally and regionally (Europe) (IUCN, 2016b). Beavers have been reintroduced in many parts of Europe after being reduced to less than 1200 individuals by the beginning of the 20<sup>th</sup> century (Halley and Rosell, 2002). Management limitations must also be considered, as species that are critically endangered at a global scale do not necessarily represent good candidates for reintroduction, because of the potential risk for the source population, or the financial cost of *ex situ* conservation in captive breeding programs.

In this thesis I did not further assess the conservation status of reintroduction targets, because the question of whether reintroductions involve (or should involve) globally threatened species has been thoroughly investigated. By definition, reintroductions will always focus on species that have suffered from population extirpation, and further studies are needed to investigate how restorations of locally extinct species improve not only their local status, but also their status at larger scales.

**With this thesis, I aimed to 1) investigate the allocation of reintroduction efforts at a continental scale and appraise how reintroduction programs can assist the conservation of various facets of biological diversity, 2) develop a demographic framework to define conservation translocation success criteria.**

*Revisiting taxonomic biases in reintroductions: representativeness and originality of reintroduction targets*

Part of the work presented here proceeds from the findings that reintroductions often focus on charismatic species, and show a taxonomic bias towards certain orders of mammals and birds. Carnivores and Ungulates are over-represented in reintroductions of mammals, while reintroductions of birds favour raptorial or game species (Seddon et al., 2005). Taxonomic bias, also referred to as taxonomic chauvinism (Bonnet et al., 2002), has long been acknowledged in science and is pervasive in conservation biology (Clark and May, 2002; Fazey et al., 2005). More than half of the records from the Global Biodiversity Information Facility (GBIF, [www.gbif.org](http://www.gbif.org)) are bird occurrences, even though birds account for less than 1% of the total number of species indexed in GBIF. Plants and vertebrates are overrepresented in several scientific fields and are more likely to raise funds for research and conservation action (Leather, 2009). Although taxonomic bias is well documented, its causes are less clear. Scientific productivity and conservation action face taxon-specific limitations that may lead to some groups being more studied (Pawar, 2003). This is based on differences in species' tractability, i.e. how easy it is to locate, obtain and manipulate some organisms. However, methodological challenges and species characteristics alone cannot fully justify the fact that studies on biodiversity only focus on a small subset of species. Two hypotheses have been put forward to understand taxonomic biases. The "societal preference" hypothesis suggests that public interests orientate the way data on biodiversity are gathered, while the "taxonomic research" hypothesis implies that scientific research will lead biodiversity data gathering. Societal interests seem to play a substantial role, and positive links exist between the general public opinion, scientific production and conservation policies (Troudet et al., 2017). Focusing on a few, often charismatic species, may prevent developing efficient conservation strategies and may offer little conservation benefits in the long term. Reintroduction programs are often criticized for being a species-centred approach biased toward charismatic species, and the

contribution of these programs to the restoration of different biodiversity components remains unclear.

Assessing the extent to which reintroductions can assist the conservation of biodiversity depends on how we measure and value biodiversity. So far, the study of taxonomic bias in reintroductions has investigated if reintroduction projects within different taxa are proportional to their prevalence in nature (i.e., number of species per taxa). This approach aims to assess if reintroduction targets are representative of the taxonomic diversity within some groups. However, there is now evidence that taxonomic diversity may not sufficiently capture other facets of biodiversity (Mazel et al., 2014). Furthermore, this approach only considered the diversity of reintroduced targets as a subset of species, and did not account for the originality of each individual species, i.e. the contribution of each individual species to the diversity of features in a set (Pavoine et al., 2005). In the first two chapters of this thesis, I revisited taxonomic biases in reintroductions, by evaluating the capacity of reintroduction programs to capture the phylogenetic and functional facets of biodiversity at a continental scale. I explored the distribution of reintroduction efforts for terrestrial mammals and terrestrial breeding birds in Europe because it is a region where, along North America and Oceania, most of reintroductions have been implemented. I focused on birds and mammals because these groups are among the most studied groups of organisms for which complete phylogenies and functional trait datasets are available (Bininda-Emonds et al., 2007; Jetz et al., 2014; Wilman et al., 2014). I conducted a comprehensive search of the reintroduction academic and grey literature in order to identify mammal and bird species that have been reintroduced at least once in Europe. Birds and mammals are also disproportionately studied in the reintroduction literature (Bajomi et al., 2010), which facilitated data collection when studying the distribution of reintroduction efforts at a continental scale.

In the first chapter, I assessed the potential contribution of reintroductions to the conservation of the diversity of evolutionary histories at a continental scale (i.e., Europe, North and Central America). Since the 1990s, scientists have argued that focusing on species richness might not be ideal, because it assumes that all species have the same conservation value even though the loss of a species with no close relative would represent a disproportionate loss of evolutionary history (Vane-Wright et al., 1991). Including information on the evolutionary relationships between organisms in conservation assessments have received increasing consideration and is now commonplace in the academic world (Brum et al., 2017; Jetz et al., 2014; Mazel et al., 2014; Pollock et al., 2017; Veron et al., 2017), and reasons for preserving evolutionary history

are many. The rationale behind this approach is that the branching pattern and branch lengths on a phylogenetic tree reflect the accumulation of genetic, phenotypic or behavioural differences between lineages, so that conservation strategies aiming to maximize the coverage of the phylogenetic tree of life will preserve the diversity of biological ‘features’, both measured and unmeasured (Faith, 1992). Measuring evolutionary diversity also provides a way to catch a sight of Earth’s evolutionary “heritage”, which can be considered to have intrinsic value (Mooers et al., 2005). Some authors suggest that preserving evolutionary diversity also preserves option values, i.e. benefits provided by biodiversity in ensuring options for future generations (Faith, 2016; Forest et al., 2007). Multiple indices have been developed to quantify evolutionary history, and can be categorised in two types (Vellend et al., 2011). One approach focuses on measuring the evolutionary distinctiveness (ED) of each taxon on a phylogenetic tree in order to identify which species support larger portions of independent evolutionary history (i.e., not shared with close relative taxa) (Isaac et al., 2007; Vane-Wright et al., 1991). The other approach is to quantify the phylogenetic diversity (PD) of a subset of focal species and assess their contribution to the whole phylogenetic tree (Faith, 1992). ED- and PD-based approaches in conservation differ conceptually (Redding et al., 2014). A species’ evolutionary “uniqueness” is primarily estimated by the length of the terminal branch connecting it to the phylogenetic tree. Preserving evolutionarily distinct species is a way to preserve unshared evolutionary information in the terminal branches of the phylogenetic tree, while maximizing PD in a subset of species will likely preserve evolutionary history represented by deep phylogenetic branches. Using up to date phylogenies I measured the phylogenetic diversity (Faith, 1992) encompassed by reintroduction targets, and the evolutionary distinctiveness (Isaac et al., 2007) of each individual species.

In Chapter 2, I assessed the range of functional traits covered by reintroduction targets in the European assemblage. It is increasingly recognized that biodiversity has multiple components, and that the quantification of biodiversity should include the diversity of form and function, often measured from functional traits (Violle et al., 2007). Functional traits are measurable features of an organism that influence their performance and thus ecosystem functioning (Díaz and Cabido, 2001; McGill et al., 2006). Functional diversity (FD) has emerged as a useful biodiversity component that quantifies trait variation between species to represent the diversity of species’ niches or functions (Petchey and Gaston, 2006, 2002a). FD has proven useful to explain variations in ecosystem functioning, because functional diversity can relate to ecological patterns and processes that affect community assembly and function (Cadotte et al.,

2011). Quantifying the amount of functional trait space that is encapsulated by a set of species is increasingly used to develop or assess conservation strategies (Mouillot et al., 2014; Petchey and Gaston, 2002b; Thuiller et al., 2015). Using the same European avian and mammalian assemblages, and the list of reintroduced species, I used data on body mass, foraging behavior and activity to quantify the functional diversity of reintroduction targets, i.e. the breadth of ecological niches filled by reintroduction targets. As of phylogenetic diversity, multiple measures of functional diversity have been developed (Schleuter et al., 2010; Villéger et al., 2008). In this thesis I chose to use dendrogram-based indices with similar mathematical properties as PD and ED. Dendrograms employ hierarchical clustering techniques to represent variation in trait space by a tree figure, with nodes and branch lengths representing ecological differences between species. Among dendrograms indices, Functional Diversity allows to assess the functional representativeness of a subset of species (Petchey and Gaston, 2002a), and Functional Distinctiveness measures the originality of a species' association of functional traits (Mouillot et al., 2013).

Because reintroductions of birds and mammals are taxonomically clustered in some orders (Seddon et al., 2005), we expected each subset of reintroduced species (e.g., reintroduced mammals in Europe) to be poorly representative of the phylogenetic and functional diversity of the associated continental assemblage. However, it was more difficult to make predictions with respect to the originality of reintroduction targets because even though conservationists tend to favour charismatic species, how the features defining such attractiveness, which depend on culture and local contexts (Bowen-Jones and Entwistle, 2002), relate to evolutionary or functional distinctiveness has not been investigated.

In the first two chapters, I explored the distribution of reintroduction efforts by comparing reintroduced species to non-reintroduced species. Similarly, other reviews have discussed the distribution of reintroduction "projects" using lists of reintroduced species (e.g., Seddon et al., 2014). However, it is unlikely that all reintroduction targets have benefitted from the same restoration effort and more comprehensive assessments need to account for differences between reintroduction targets. In the third chapter, I performed a more in-depth search of the reintroduction-related literature in order to gather data on implemented programs for European terrestrial mammals. I explored the spatial and temporal distribution of reintroduction efforts, using both the number of implemented programs and the number of associated publications as proxies.

*Persistence: a proposed unified framework for reintroduction success assessments*

In the previous chapters, I investigated the allocation of reintroduction efforts through the representativeness of reintroduction targets. However these studies only inform us on the potential contribution to biodiversity conservation, and further studies need to account for failures and success to quantify the actual contribution of reintroductions. Distinguishing between success and failures is essential to evaluate the effectiveness of reintroductions as a conservation tool.

Quantifying the level of success of a reintroduction program remains complicated and there is still no general definition of success. Some studies have tried to estimate the rate of success of translocations, and tried to determine associated factors (Brichieri-Colombi and Moehrensclager, 2016; Germano and Bishop, 2009; Griffith et al., 1989; Wolf et al., 1998, 1996). However, most of these studies relied on surveys and subjective appreciations from managers. Even when success was defined as the re-establishment of “a viable, self-sustaining population in the wild” (Griffith et al., 1989), it remained vague and did not provide quantitative and objective thresholds to determine success. The IUCN Re-introduction Specialist Group’s (RSG) *Global Reintroduction Perspectives* is a project that aims to inventory and publish reintroduction case studies from around the world (Soorae, 2018, 2016, 2013, 2011, 2010, 2008). Each project is associated with a measure of success, but here again this approach relies on the managers of each project indicating the goals of the project and the associated indicators of success. The number and type of specified goals is different from one project to another (Ewen et al., 2014), and the outputs they relate to vary in scales (e.g., the difference between achieving captive breeding and releases, and quantifying a confirmed increase in population vital rates).

The definition of reintroduction success is still debated and has yielded a substantial scientific production over the years (Griffith et al., 1989; Miller et al., 2014; Moehrensclager et al., 2013; Robert et al., 2015; Sarrazin, 2007; Sarrazin and Barbault, 1996; Seddon, 1999). Based on this important bibliographic corpus, and on recent contributions on how to measure conservation success (Akçakaya et al., 2018), we propose a unifying demographic framework for success assessment which is centred on the notion of population viability but accounts for the transient dynamics of any reintroduction.

Technological advances in genetic engineering and selective breeding have opened the possibility for resurrecting globally extinct species. De-extinction, the process of (re)creating an organism to restore a species lost to extinction, has rapidly captured the imagination of the general public, but this new conservation initiative has received mixed enthusiasm from the scientific community (Sherkow and Greely, 2013). While some view de-extinction as a “moral imperative” to repair the damages caused by Human activity and development, others argue that de-extinction projects might divert scarce resources for conserving extant species, and that the general public might lose the sense of urgency toward the current biodiversity crisis if we consider that extinct species could simply be resurrected. Resurrecting species has raised some ethical debates, but in any case, if de-extinctions were to assist conservation efforts then the primary objective for species resurrection should be the restoration of free-ranging populations (Seddon et al., 2014b). De-extinction thus appears as a translocation issue and can be treated as an extreme form of reintroduction, in which the source stock for releases does not come from wild or captive populations, but from genetically engineered individuals. While applying the IUCN Reintroduction Guidelines (IUCN/SSC, 2013) will ensure the objective selection of de-extinction candidate by carefully planning the translocation process, the actual conservation benefit of de-extinction remains unclear. De-extinction has raised some debates on the definition of historical targets in restoration, and the ecological and evolutionary processes that this practice aims to restore are not clearly defined (Jones, 2014). In the last chapter we questioned the expected conservation benefit of de-extinction projects from an evolutionary point of view.

## **Collecting data on reintroduction projects in Europe: comprehensive searches of the reintroduction-related literature**

Incentives for documenting reintroduction projects at large scale exist (e.g., Soorae, 2018), but most of the information on reintroduction projects remains scattered in academic publications, institutional reports, books, conference proceedings, etc... In this thesis, I developed and applied two literature search protocols in order to collect data on reintroduction projects from both grey and academic literatures. We described our literature searches as “comprehensive searches”



(*sensu* Swan et al., 2016), because they do not classify as systematic reviews *per se*, although each reviewing process is based on a clearly defined and repeatable protocol.

The first step of our literature research was to identify which species, among the mammalian and avian European assemblages, have been reintroduced *at least once* in Europe. I retrieved the lists of all native extent terrestrial mammals and terrestrial breeding birds in Europe. I used the IUCN Red List website for mammals (202 species, [iucnredlist.org](http://iucnredlist.org)), and the Birdlife database for birds (378 species, [datazone.birdlife.org](http://datazone.birdlife.org)). For each species, and with the help of two interns, I searched the ISI Web of Knowledge database and Google Scholar, using the Latin name of the species and a set of keywords (the search protocol is described in the Materials and Methods and Supplementary Materials of Chapter 1). For each species, I looked for at least one reference that would provide evidence that the species has been involved in at least one movement-and-release event that satisfies the IUCN definition of a reintroduction (IUCN/SSC, 2013). I may have missed some articles in this search, but the literature I reviewed is a good and representative proxy. For those species that have been reintroduced many times (e.g., *Castor fiber*), this identification process was rapidly achieved considering the large amount of associated publications. For species reintroduced less frequently, this identification process was longer, although based on the same protocol. The published literature may not reflect all mammal and bird reintroductions in Europe, yet we wanted to provide an objective and repeatable search protocol, so that our results can be compared with other reviews of reintroduction efforts. These searches allowed us to differentiate between reintroduced and non-reintroduced species within the avian and mammalian European assemblages, and the collected data have been used to perform analyses of representativeness in Chapters 1 and 2. Thirty-seven species of terrestrial breeding birds have been reintroduced at least once, representing 10% of the 378 native birds in Europe (Table 1). Twenty-eight species of terrestrial mammals have been reintroduced at least once, representing 15% of the 202 native terrestrial mammals in Europe (Table 2).

In a second time, I investigated the differences in the number of implemented reintroduction programs among the previously identified reintroduced species. I focused on reintroduced mammals in Europe (28 species) and performed a more in-depth search of the grey and academic literature (described in Chapter 3), with the inclusion of more generic terms that may relate to reintroductions (e.g., “release”, “relocation”). The objective was to inventory independent reintroduction programs in order to study the distribution of reintroduction efforts among reintroduced mammals in Europe. The search yielded more than 1600 references, from

which 413 references were used to describe 375 programs implemented in 28 European countries between 1910 and 2013.

Table 1: List of the 37 species of native European terrestrial breeding birds that have been reintroduced at least once in Europe.

Order	Species	English name	French name
Accipitriformes	<i>Accipiter gentilis</i>	Northern Goshawk	Autour des palombes
Accipitriformes	<i>Aegypius monachus</i>	Cinereous vulture	Vautour moine
Accipitriformes	<i>Aquila adalberti</i>	Spanish imperial eagle	Aigle ibérique
Accipitriformes	<i>Aquila chrysaetos</i>	Golden eagle	Aigle royal
Accipitriformes	<i>Circus pygargus</i>	Montagu's harrier	Busard cendré
Accipitriformes	<i>Gypaetus barbatus</i>	Bearded vulture	Gypaète barbu
Accipitriformes	<i>Gyps fulvus</i>	Griffon vulture	Vatour fauve
Accipitriformes	<i>Haliaeetus albicilla</i>	White-tailed eagle	Pygargue à queue blanche
Accipitriformes	<i>Milvus milvus</i>	Red kite	Milan royal
Accipitriformes	<i>Pandion haliaetus</i>	Osprey	Balbusard pêcheur
Anseriformes	<i>Anser anser</i>	Greylag goose	Oie cendrée
Anseriformes	<i>Anser erythropus</i>	Lesser white-fronted goose	Oie naine
Anseriformes	<i>Aythya nyroca</i>	Ferruginous duck	Fuligule nyroca
Anseriformes	<i>Oxyura leucocephala</i>	White-headed duck	Erismature à tête blanche
Ciconiiformes	<i>Ciconia ciconia</i>	White stork	Cigogne blanche
Falconiformes	<i>Falco cherrug</i>	Saker falcon	Faucon sacre
Falconiformes	<i>Falco naumanni</i>	Lesser kestrel	Faucon crécerellette
Falconiformes	<i>Falco peregrinus</i>	Peregrine falcon	Faucon pèlerin
Falconiformes	<i>Falco tinnunculus</i>	Common kestrel	Faucon crécerelle
Galliformes	<i>Alectoris graeca</i>	Rock partridge	Perdrix bartavelle
Galliformes	<i>Alectoris rufa</i>	Red-legged partridge	Perdrix rouge
Galliformes	<i>Bonasa bonasia</i>	Hazel grouse	Gélinotte des bois
Galliformes	<i>Coturnix coturnix</i>	Common quail	Caille des blés
Galliformes	<i>Perdix perdix</i>	Grey partridge	Perdrix grise
Galliformes	<i>Tetrao tetrix</i>	Black grouse	Tétras lyre
Galliformes	<i>Tetrao urogallus</i>	Western capercaillie	Grand Tétras
Gruiformes	<i>Grus grus</i>	Common crane	Grue cendrée
Gruiformes	<i>Crex crex</i>	Corn crake	Râle des genêts
Gruiformes	<i>Fulica cristata</i>	Red-knobbed coot	Foulque à crête
Gruiformes	<i>Porphyrio porphyrio</i>	Western swamphen	Talève sultane
Otidiformes	<i>Otis tarda</i>	Great bustard	Grande outarde
Passeriformes	<i>Corvus corax</i>	Common raven	Grand corbeau
Passeriformes	<i>Emberiza cirrus</i>	Cirl bunting	Bruant zizi
Strigiformes	<i>Bubo bubo</i>	Eurasian eagle-owl	Hibou grand-duc
Strigiformes	<i>Glaucidium passerinum</i>	Eurasian pygmy owl	Chevêchette d'Europe
Strigiformes	<i>Strix uralensis</i>	Ural owl	Chouette de l'Oural
Strigiformes	<i>Tyto alba</i>	Western barn owl	Chouette effraie

Table 2: List of the 28 species of native European terrestrial mammals that have been reintroduced at least once in Europe.

<b>Order</b>	<b>Species</b>	<b>English name</b>	<b>French name</b>
Carnivora	<i>Felis silvestris</i>	Wild cat	Chat sauvage
Carnivora	<i>Lynx lynx</i>	Eurasian lynx	Lynx d'Europe
Carnivora	<i>Lynx pardinus</i>	Iberian lynx	Lynx pardelle
Carnivora	<i>Lutra lutra</i>	Eurasian otter	Loutre d'Europe
Carnivora	<i>Martes martes</i>	European pine marten	Martre des pins
Carnivora	<i>Meles meles</i>	European badger	Blaireau européen
Carnivora	<i>Mustela lutreola</i>	European mink	Vison d'Europe
Carnivora	<i>Ursus arctos</i>	Brown bear	Ours brun
Artiodactyla	<i>Bison bonasus</i>	European bison	Bison d'Europe
Artiodactyla	<i>Capra ibex</i>	Alpine ibex	Bouquetin des Alpes
Artiodactyla	<i>Capra pyrenaica</i>	Iberian ibex	Bouquetin d'Espagne
Artiodactyla	<i>Rupicapra pyrenaica</i>	Pyrenean chamois	Isard
Artiodactyla	<i>Rupicapra rupicapra</i>	Chamois	Chamois
Artiodactyla	<i>Alces alces</i>	Elk	Elan
Artiodactyla	<i>Capreolus capreolus</i>	Roe deer	Chevreuril
Artiodactyla	<i>Cervus elaphus</i>	Red deer	Cerf élaphe
Artiodactyla	<i>Rangifer tarandus</i>	Reindeer	Renne
Lagomorpha	<i>Oryctolagus cuniculus</i>	European rabbit	Lapin de garenne
Rodentia	<i>Castor fiber</i>	European beaver	Castor d'Europe
Rodentia	<i>Arvicola amphibius</i>	European water vole	Grand campagnole
Rodentia	<i>Cricetus cricetus</i>	European hamster	Hamster d'Europe
Rodentia	<i>Glis glis</i>	Edible dormouse	Loir gris
Rodentia	<i>Muscardinus avellanarius</i>	Hazel dormouse	Muscardin
Rodentia	<i>Micromys minutus</i>	Eurasian harvest mouse	Rat des moissons
Rodentia	<i>Marmota bobak</i>	Bobak marmot	Bobak
Rodentia	<i>Marmota marmota</i>	Alpine marmot	Marmotte des Alpes
Rodentia	<i>Sciurus vulgaris</i>	Red squirrel	Ecureuil roux
Rodentia	<i>Spermophilus citellus</i>	European ground squirrel	Souslik d'Europe



# **Chapter 1: *Reintroduction of birds and mammals involve evolutionarily distinct species at the regional scale***

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## **Context:**

Taxonomic biases have been described in reintroductions, however we do not know to which extent conservation actions addressing population extirpations can contribute to the preservation of evolutionary history. In this study we searched the grey and academic literature to identify species of bird and mammal that have been reintroduced at least once in Europe, and used published data on conservation translocations in North America to assess the phylogenetic representativeness and the evolutionary isolation of reintroduced species considering the regional pool of species.

## **Key findings:**

Our results show that, because of taxonomic clustering, reintroduction targets are poorly representative of the regional phylogenetic diversity, but seem to involve more evolutionarily distinct species than expected by chance.

Our study sheds new light on the link and complementarity between species-centered and phylogenetic approaches to the conservation of biological diversity. Evolutionary considerations seem unlikely to have prevailed in setting priority target in reintroductions, however this phylogenetic framework provides a more in-depth evaluation of the allocation of reintroduction efforts than the characterization of taxonomic biases.





# Reintroductions of birds and mammals involve evolutionarily distinct species at the regional scale

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**Reintroductions offer a powerful tool for reversing the effects of species extirpation and have been increasingly used over recent decades. However, this species-centered conservation approach has been criticized for its strong biases toward charismatic birds and mammals. Here, we investigated whether reintroduced species can be representative of the phylogenetic diversity within these two groups at a continental scale (i.e., Europe, North and Central America). Using null models, we found that reintroduced birds and mammals of the two subcontinents tend to be more evolutionarily distinct than expected by chance, despite strong taxonomic biases leading to low values of phylogenetic diversity. While evolutionary considerations are unlikely to have explicitly driven the allocation of reintroduction efforts, our results illustrate an interest of reintroduction practitioners toward species with fewer close relatives. We discuss how this phylogenetic framework allows us to investigate the contribution of reintroductions to the conservation of biodiversity at multiple geographic scales. We argue that because reintroductions rely on a parochial approach of conservation, it is important to first understand how the motivations and constraints at stake at a local context can induce phylogenetic biases before trying to assess the relevance of the allocation of reintroduction efforts at larger scales.**

conservation translocations | conservation priorities | phylogenetic diversity | evolutionary isolation

**W**hen looking at population declines and losses rather than focusing only on species extinctions, Earth's biological diversity is under more severe threats than initially perceived (1). Therefore, effective conservation actions are required to sustain evolutionary trajectories in biological systems and to ensure ecosystem functioning and services (2). In this context, population restoration offers a tool to mitigate or reverse the consequences of local population extinctions; thus, population restoration promotes species persistence and counters the dramatic shrinkage in a species' geographical range (3).

Conservation translocations are human-mediated movements and releases of organisms, where the primary objective is to yield a measurable conservation benefit (4). Reintroductions are part of the conservation translocation spectrum, and reintroductions aim to reestablish a population in the species' indigenous range following local extinction or extirpation. Reintroductions have been used for over a century, and the number of programs, as well as the number of targeted species, have increased over recent decades (3, 5, 6). Except for some rare projects included in ecosystem restoration (7), reintroductions are primarily case-by-case initiatives that are locally designed population-centered conservation approaches. By definition, reintroductions follow the local extinction of a population, but they do not necessarily involve globally threatened species (8). In fact, reintroduction implementations are usually driven by national conservation targets, the ability to garner public and political support, or the technical feasibility of translocation releases. All of these factors are non-neutral with respect to taxonomy, with studies showing that mammals and birds are overrepresented in reintroduction

programs (5, 8). Reintroductions offer a powerful conservation tool. However, the fact that conservation goals are being set at the local scale should not hamper their ability to contribute to the conservation of biodiversity at large scales. If a bias toward birds and mammals is likely to persist, the focus of reintroductions should be on, when possible and with respect to national priority targets, species that are the most likely to contribute to the persistence of the diversity of the Tree of Life (9).

With scarce resources available for conservation, the objective prioritization among taxa and regions is required to maximize conservation returns (10, 11). Since the 1990s, scientists have promoted the incorporation of information on shared and nonshared evolutionary history between species into conservation prioritization. Based on the assumption that not all species contribute equally to biodiversity, additional value should be granted to evolutionarily distinct species, that is, those that lack close relatives, because the loss of a species in an old clade would result in a greater loss of biodiversity (9, 12). Based on the assumption that closely related taxa are more likely to share similar features, conservation strategies that aim to preserve high levels of evolutionary diversity should capture the value of biodiversity as variation (13) and potentially provide unanticipated benefits in the future (14–17). Some studies suggest that the rate of loss of evolutionary information could even be much higher than the rate of species loss, as the extinction threat is not randomly distributed in phylogeny (18). Thus, the consideration of evolutionary history in conservation decision making is a way to set relevant and objective conservation goals while also using easily communicable metrics, such

## Significance

**There are general acknowledgements that Earth's sixth mass extinction event is more severe than perceived when looking at population extirpations (rather than focusing only on species extinctions) and that species extinctions are associated with the rapid loss of evolutionary history. In this study, we investigate how population reintroductions, a major conservation tool used to reverse population extirpations, can contribute to the preservation of evolutionary diversity within birds and mammals. Using data on reintroductions of terrestrial birds and mammals in Europe and North America, we show that, despite strong taxonomic biases leading to a poor representativeness of the regional phylogenetic diversity, reintroduction practitioners seem to have focused on highly evolutionarily distinct species.**

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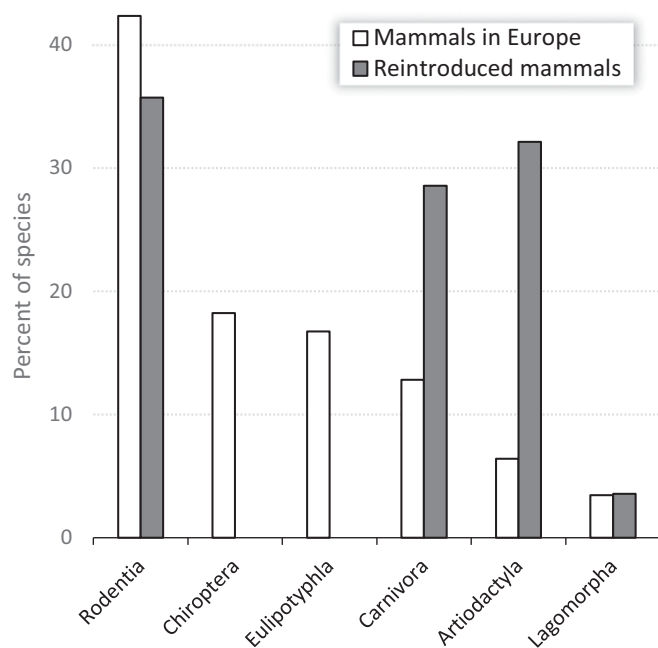
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**Fig. 1.** Taxonomic distribution of reintroduced species within the different orders of the terrestrial mammals of Europe. Unshaded bars are the proportions of mammals out of the 202 species of Europe, and shaded bars are the proportions of mammals out of the 28 reintroduced species.

as the duration of species' evolutionary histories in terms of millions of years of evolution (19).

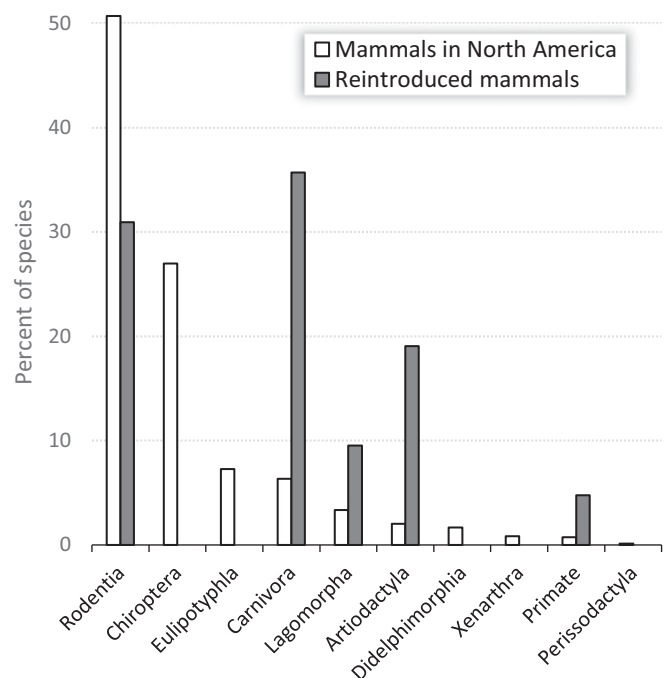
Methodological developments and the increasing amount of phylogenetic data available should foster the implementation of conservation projects based on evolutionary considerations (20–23). However, it also remains necessary to assess whether current management strategies are relevant to the conservation of evolutionary diversity. While gap analyses have examined the efficiency of current protected area networks on the protection of evolutionary diversity (24–26), the contribution of species-centered conservation measures [for example, translocations (3)] on the preservation of broad-scale evolutionary diversity is largely unknown.

Here, we investigated how the allocation of reintroduction efforts could contribute to biodiversity conservation at a continental scale, focusing on the phylogenetic dimension of biodiversity rather than on taxonomy. We focused on reintroduced terrestrial birds and mammals in Europe as well as in North and Central America (including Mexico and the Caribbean, but hereafter called North America) (*Materials and Methods*). We investigated the phylogenetic richness (i.e., quantity of phylogenetic differences) (27) expected for our focal subsets of reintroduced species (e.g., reintroduced European mammals) given the regional pool of species. First, we calculated the phylogenetic diversity (PD) (14) of each subset of reintroduced species, that is, their total amount of independent evolutionary history, to assess whether a focal subset of reintroduced species is representative of the regional phylogenetic diversity. Second, we quantified the evolutionary isolation of reintroduced species using the evolutionary distinctiveness (ED) index (20), which estimates the conservation value of each individual species based on its unique evolutionary history. We constructed null models to test the deviation of our two metrics from the value expected when species were randomly drawn in the associated regional phylogeny. Reintroduced species are not expected to collectively contribute to high PD because they are taxonomically clumped, but they might be more evolutionarily distinct than species drawn

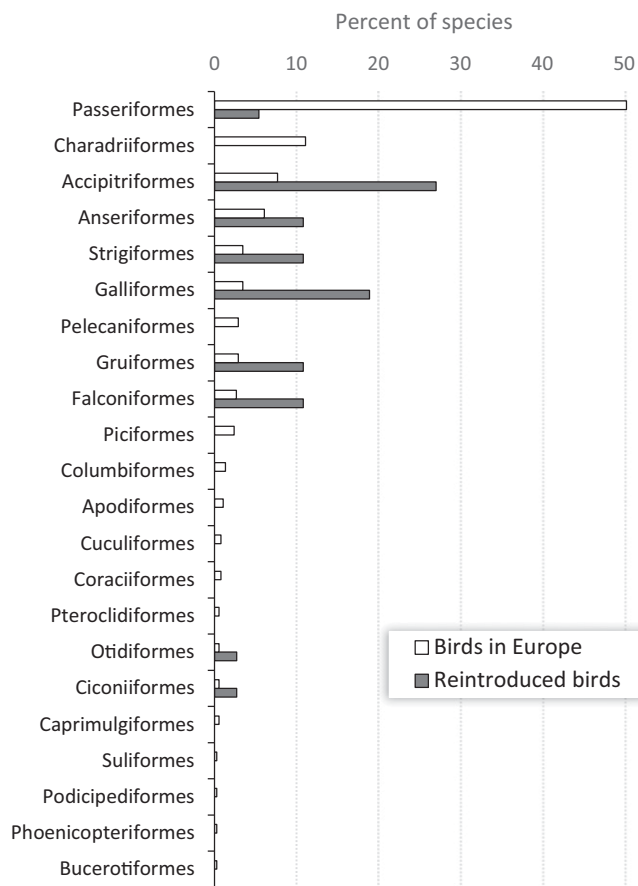
at random if they come from less diverse clades (8). While our results confirmed these general expectations on PD, they indicated that the distribution of ED scores for reintroduced species vary according to the region or group considered. Overall, our work shows that the selection of species for reintroduction, which is mostly driven by conservation needs at local scales, either contrasts or converges with broad-scale, evolutionary-based conservation priorities depending on the metric being considered.

## Results and Discussion

**Evolutionary Diversity and Reintroductions.** Twenty-eight mammalian species have been reintroduced at least once in Europe (i.e., 14% of the 202 terrestrial mammalian species), and these species are distributed among four orders: 10 rodents, 9 ungulates, 8 carnivores, and 1 lagomorph (Fig. 1). This taxonomic pattern is consistent with the results of North America (28), with the only difference being the reintroduction of two primates (*Alouatta pigra* and *Ateles geoffroyi*) in Central America. More than 50% of reintroduced mammals on both subcontinents are members of the orders Carnivora or Artiodactyla (Fig. 2). Thirty-seven bird species have been reintroduced at least once in Europe (i.e., 10% of the 378 terrestrial breeding bird species). The order Accipitriformes includes the highest number of reintroduced species of birds in Europe, followed by the order Galliformes (Fig. 3). We can see differences in the taxonomic distribution of reintroduced bird species between the two subcontinents, with the order Passeriformes accounting for 25% of the reintroduced birds in North America (Fig. 4); in contrast, Passeriformes account for only 1% of the reintroduced birds in Europe. Our results are consistent with previous studies showing that reintroduction efforts are strongly taxonomically biased within birds and mammals (8). In both regions, avian and mammalian reintroductions seem to favor large charismatic species (e.g., *Bison bonasus*, *Lynx pardinus*, *Gypaetus barbatus*), which easily garner



**Fig. 2.** Taxonomic distribution of reintroduced species within the different orders of the terrestrial mammals in North America (including Mexico, Central America, and the Caribbean). Unshaded bars are proportions of mammals out of the 838 species of North America, and shaded bars are the proportions of mammals out of the 42 reintroduced species.

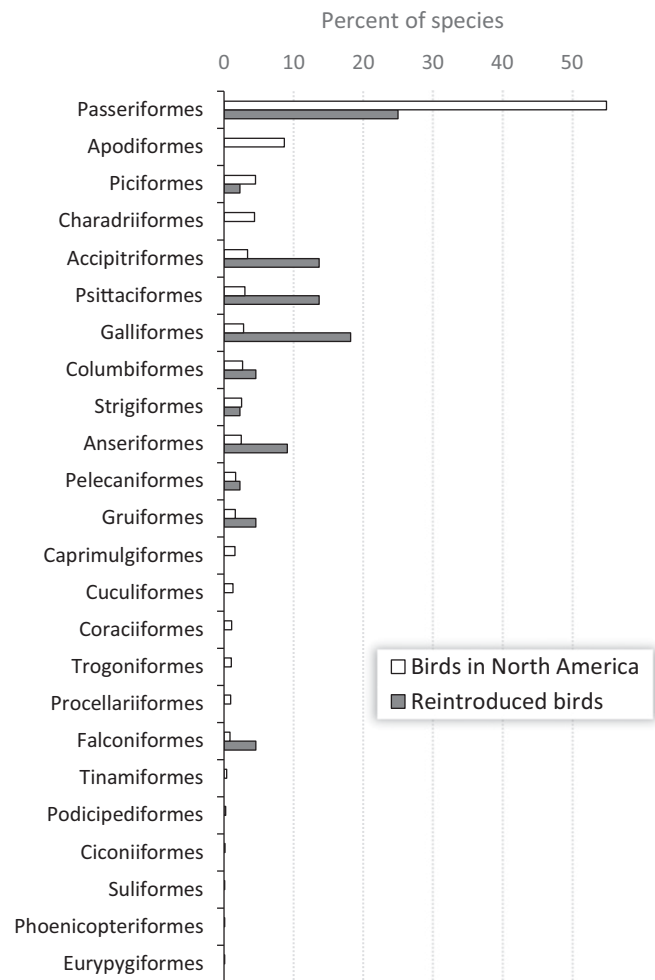


**Fig. 3.** Taxonomic distribution of reintroduced species within the different orders of the terrestrial birds of Europe. Unshaded bars are proportions of birds out of the 378 species of Europe, and shaded bars are the proportions of birds out of the 37 reintroduced species.

public support and funds for conservation, or exploited species (e.g., *Cervus elaphus*, *Capra ibex*, *Tetrao urogallus*), for which overharvesting could have led to local extinction.

Because of this taxonomic clustering in the allocation of reintroduction efforts, reintroduced birds and mammals in Europe and North America are poorly representative of the associated regional phylogenetic diversity. The PD measured for reintroduced mammals in North America is significantly lower than expected by chance ( $PD_{reint} = 1,387.4$  My;  $\mu = 1,747.61$  My;  $SD = 145.36$ ;  $P$  value = 0.015) (Table 1), and the three remaining subsets of reintroduced species (i.e., European mammals, North American birds, and European birds) showed PD values lower than random expectations but did not significantly depart from our null model (i.e., associated  $P$  values ranged from 0.063 to 0.114) (Table 1). Low PD values observed for reintroduction target species might be caused by shared causes of extirpation, at least for mammals. Within mammals, extinction threats caused by hunting pressure are more strongly phylogenetically clumped than threats caused by habitat loss or invasive species (29). Reintroduction feasibility requires the identification and eradication of past threats and causes of extirpation (4); thus, the possibility of both identification and eradication of these threats may affect the selection of reintroduction candidate species. Overexploitation is likely to be the easiest threat to identify in the past extinction of vertebrates, and it is also likely to be easier to mitigate through strict protection and hunting regulations than the control of invasive species or the restoration of degraded habitat.

The concept of evolutionary distinctiveness appears only once in the International Union for Conservation of Nature (IUCN) *Guidelines for Reintroductions* (4). Managers undertaking reintroductions face multiple decisions, which can rely on competing objectives and uncertainty (30). Therefore, evolutionary considerations are not expected to ultimately influence the allocation of reintroduction efforts. However, our results show that there is a significant trend in the reintroduction of mammals and birds toward species with few close relative taxa at the continental scale. When considering the median ED score of reintroduced species, we found that reintroduced mammals in Europe and North America are more evolutionarily distinct than expected by chance, as the median ED is significantly higher than the random expected value (median  $ED_{reint} = 20.84$  My and 13.46 My;  $P$  value = 0.018 and  $P$  value < 0.001, respectively) (Table 2). In Europe, the median ED score of reintroduced bird species is higher than expected by chance (median  $ED_{reint} = 19.81$  My;  $P$  value = 0.047), while the median ED of reintroduced birds in North America is not significantly different from the random expected value (median  $ED_{reint} = 8.76$  My;  $P$  value = 0.99) (Table 2). Reintroduced birds with the highest ED value tend to be large-bodied species from less diverse clades (Accipitriformes, Strigiformes, Gruiformes) in both subcontinents. Because ED



**Fig. 4.** Taxonomic distribution of reintroduced species within the different orders of the terrestrial birds out of the 1,748 species of North America (including Mexico, Central America, and the Caribbean). Unshaded bars are proportions of birds out of the 1,748 species of North America, and shaded bars are the proportions of birds out of the 44 reintroduced species.

**Table 1. PD scores of reintroduced birds and mammals and the associated expected value and SD of PD for a given subset size and a regional phylogenetic tree**

Group	Subcontinent	No. of native terrestrial species	No. of reintroduced species	PD of reintroduced species	Expected PD	SD of PD	<i>P</i> value
Mammals	Europe	202	28	1,080.42	1,259.96	96.49	0.063
	North America	838	42	1,387.4	1,741.61	145.36	<b>0.015</b>
Birds	Europe	378	37	1,422.62	1,592.57	107.54	0.114
	North America	1,748	44	1,592.11	1,818.95	131.98	0.086

Deviation from the null model is presented as a *P* value, which was computed using the *pnorm* function in R. Bold values indicate  $P < 0.05$ .

scores are negatively related to the size of a clade, the different patterns observed between the two regions can be explained by the prevalence of members of the order Passeriformes in North American-reintroduced birds. Within mammals, while reintroduced species with the highest ED in North America come from less diverse clades (as for birds), the high median ED observed for reintroduced European mammals was largely driven by highly evolutionarily distinct species of rodents (Table S3).

Overall, our results suggest that, while reintroduced species tend to be more evolutionarily distinct, the overall contribution of the focal subset of reintroduced species to the regional phylogenetic diversity is low because the species composing these focal subsets are less phylogenetically complementary than expected under a random model (see discussions in refs. 13 and 31).

#### Decision Processes and Phylogenetic Patterns of Reintroductions.

Our null model was built to evaluate the departure of the observed process from a basic random process. Such a random process implies that every terrestrial species in the regional assemblage has the same chance of being selected for reintroduction, which constitutes a reference model but not a realistic expectation. Indeed, although it has been suggested that reintroductions of mammals and birds target a minority of globally threatened species (8, 28), local extirpation biases may exist with respect to phylogeny (32–34). Furthermore, logical decision processes about which species to reintroduce not only necessarily consider the priority of the species for recovery (of which evolutionary history is only one component) but also consider the probability that management will be successful and the likely economic and ecological costs of the program (e.g., translocation and ongoing management costs, demographic cost to the source population) (22, 35, 36). While any locally extinct species can benefit from a reintroduction effort, these competing interests and practical limitations can impose constraints on the combinations of traits of reintroduced species. For example, body size can be hypothesized as a trait that influences the ability to garner public and political support (e.g., large-bodied species are more emblematic), the ability to successfully breed in captivity (e.g., facilitated with small-bodied species) or the ability to plan translocations (e.g., large-bodied species require large home

ranges). In that context, reintroduced species could encompass a nonrandom combination of traits, and characterizing the various constraints imposed on the implementation of reintroduction programs would allow researchers to build more relevant null models to investigate the phylogenetic structure expected for reintroduced species. This would be the first step required if we want reintroduced species to be representative of the phylogenetic diversity within an assemblage.

**Geographic Scales of Decisions.** Identifying gaps between the optimized allocation of conservation resources and the current allocation levels requires the consideration of the potential mismatch between global priority setting and actual implementations of conservation actions that largely depend on local practitioners and decision makers reaching consensus (37, 38). This spatial implication of conducting conservation planning at different scales has been well studied in the context of managing protected areas under the systematic conservation planning framework (10, 39, 40), but it remains relatively unexplored in the context of population restorations. Evolutionary distinctiveness measures and PD approaches in conservation prioritization differ conceptually, even if they both rely on information on evolutionary relationship between species (41). Whether PD- or ED-based approaches for conservation prioritization will ensure the best preservation of the Tree of Life under current management practice is beyond the scope of our paper. However, it is important to consider which prioritization scheme can be more easily implemented at the management level. Reintroduction practitioners designing species-specific programs are more likely to integrate “evolutionary value” through evolutionary isolation measures as these are more flexible and can be compared with other individual measures of species value (e.g., cost of recovery or probability of success) that might influence decision-making processes. However, actual reintroduction practices rely on a parochial approach to conserving species, and while opportunities to restore locally extirpated species should always merit our concern and action, incentives for restoring local diversity will not guarantee the preservation of overall regional/global diversity (13, 42). International coordination might operate at the European level (e.g., the Life Program funded by the European Commission) but is less likely to be achieved across North

**Table 2. Median ED scores of each focal subset of reintroduced mammal and bird species in Europe and North America**

Group	Subcontinent	No. of reintroduced species	Median ED of reintroduced species	Expected median ED	SD of median ED	<i>P</i> value
Mammals	Europe	28	20.84	16.6	1.74	<b>0.018</b>
	North America	42	13.46	9.25	1.05	<b>&lt;0.0001</b>
Birds	Europe	37	19.81	15.48	1.9	<b>0.047</b>
	North America	44	8.76	8.75	1.1	0.99

Expected median ED and SD were obtained after drawing 10,000 random sets of species of the same size from the associated phylogeny. The deviation from the null model is presented as a *P* value, computed as  $2 * (\text{Number of sampled median ED values} > \text{Median ED of reintroduced species}) / (\text{Number of samples drawn})$ . Bold values indicate  $P < 0.05$ .

America, Central America, and the Caribbean. Here, our aim was not to advocate for a systematic allocation of reintroduction efforts toward the broad-scale maximization of phylogenetic diversity. Rather, our objective was to emphasize how this phylogenetic framework can help evaluate the potential conservation benefit of reintroductions at any spatial scale. This framework simply relies on estimating the relative contribution of a single species or a subset of species (e.g., reintroduced species) to the diversity of features within any given assemblage (13); thus, the framework can be applied at local, national, regional, or global scales (43).

The development of reintroduction biology over recent decades was built on the combination of knowledge from locally implemented programs to produce insights that inform the worldwide practice of reintroduction (6, 44, 45). In addition, the recent exponential increase in the number of implemented programs provides opportunities to assess the relevance of the allocation of reintroduction efforts at different spatial scales. Reintroduction is primarily an attempt to restore locally extirpated species and, in turn, contributes to limiting the loss of feature diversity at local and global scales. Reintroduction can also be used as a powerful tool to restore the spontaneous dynamics of genes and the functional traits of the focal species that could shape community and ecosystem dynamics, thus supporting evolutionary processes. Incorporating evolutionary considerations into reintroduction planning allows us to ponder the type of diversity we are trying to restore and reminds us that conservation translocations fundamentally aim to restore evolutionary trajectories for the target species and its biotic environment (2).

## Materials and Methods

**Study Area and Reintroduced Species.** We focused on birds and mammals because these groups benefit from the best coverage in the peer-reviewed and gray reintroduction literature, leading to the substantial availability of data (5, 46). Our study area covered the European peninsula and North and Central America (including Mexico and the Caribbean, but hereafter called North America), which are two regions where nearly 40% of worldwide translocation programs have been implemented (3). In each subcontinent, we considered the lists of terrestrial breeding bird species established by BirdLife (i.e., Europe: 378 species; North America: 1,748 species; [datazone.birdlife.org/species/search](http://datazone.birdlife.org/species/search)), and the IUCN lists of terrestrial mammal species (i.e., Europe: 202 species; North America: 838 species; [www.iucnredlist.org](http://www.iucnredlist.org)). We built four regional phylogenetic trees based on these lists and from global phylogenies of all extant birds and mammals. We used updated phylogenies for mammals (47, 48), where polytomies were resolved (49), and where the Carnivora clade was replaced with a highly resolved supertree that was published more recently (24, 50). For birds, we used the global bird phylogenies built and published by Jetz et al. (51), available at [www.birdtree.org](http://www.birdtree.org).

Species were included in reintroduction efforts, and thereafter called “reintroduced species,” if they had been involved in any past or ongoing documented release of individuals that satisfies the reintroduction definition provided by the IUCN *Guidelines for Reintroductions*, which was published in 2013 (4), regardless of the success of the reintroduction. Bird and mammal species that have been reintroduced at least once in Europe were identified through a comprehensive search of translocation-related publications. We conducted our research using both the ISI Web of Science database and Google Scholar, as the latter can provide references from the gray literature, which contains a substantial amount of information regarding reintroduction projects. We used the keywords “reintroduc\*,” “re-introduc\*,” “translocat\*,” and the species’ Latin name, and we checked independently for each European bird and mammal species (Table S1). For each query, we looked for at least one reference that would provide evidence that the species had been involved in at least one movement-and-release event that satisfied the IUCN definition of a reintroduction. Although this is not a systematic review (52, 53), we applied the same methods to locate and use information from scientific and nonscientific sources and used a rigorous, transparent, and repeatable protocol. Our results provide a detailed picture of the taxonomic distribution of reintroduction efforts of terrestrial mammals and birds in Europe that can be compared with other reviews on this topic (54). Acknowledging that we only

used English sources and that publication biases may exist (with respect to taxa, country, etc.), our literature search might have led to an underestimation of the number of reintroduced species in Europe. We extracted the list of reintroduced terrestrial breeding birds and mammals in North America from the review published by Brichieri-Colombi and Moehrenschrager (28) on animal conservation translocations. We did not consider subspecies separately in our analyses since our phylogenetic trees did not provide relationships between taxa at the subspecies level. Consequently, species were considered as reintroduced as long as one of their subspecies had been reintroduced at least once. In our final analyses, we considered 67 reintroduced terrestrial mammals (i.e., 25 in Europe, 39 in North America, 3 in both) and 79 reintroduced terrestrial breeding birds (i.e., 35 in Europe, 42 in North America, 2 in both) (Table S2).

**Phylogenetic Diversity of Reintroduced Species.** The phylogenetic diversity quantifies the cumulated amount of independent evolutionary histories of a subset of species in a tree (14). Given one phylogenetic tree, the PD of a subset of species is measured as the sum of the length of the branches in the minimal subtree connecting all of the taxa of the subset:

$$PD(\text{tree}) = \sum_j L_j,$$

with  $L_j$  representing the length of branch  $j$ . For a given number of species, the higher the value of PD for a subset of species, the more evolutionarily distant the species are within the subset. For each taxonomic group in each region, we calculated the total unrooted PD of the subset of reintroduced species [ $PD_{\text{reint}}$ ] using the *pd.query* function from the package *PhyloMeasures* (55). We compared this value to the PD value expected for a random subset of species of the same size in the associated regional species pool (e.g., European birds, North American mammals). For that purpose, we used the *pd.moments* function, which provides optimized algorithms to compute the exact expressions of the expectation [ $\mu PD$ ] and the SD [ $sdPD$ ] of the PD for a given number of species in a specific phylogenetic tree. A subset of reintroduced species can be considered as representative of the regional phylogenetic diversity if the  $PD_{\text{reint}}$  value does not significantly depart from the associated 95% confidence interval calculated as  $\mu PD \pm 1.96 * sdPD$ .

**Evolutionary Distinctiveness of Reintroduced Species.** We measured the evolutionary isolation of individual species using the ED, which is based on the fair-proportion index that quantifies how few relatives a species has and how phylogenetically distant those relatives are (20). The ED score of species  $i$  is the total branch length between each node connecting the tip (species) to the root of the tree, each time divided by the number of species subtending that branch:

$$ED_i = \sum_{j \in P(i, \text{Root})} \frac{L_j}{n_j},$$

with  $P(i, \text{Root})$  being the set of branches connecting species  $i$  to the root of the tree, and  $n_j$  being the number of species subtending branch  $j$ . We used the *evol.distinct* function from the *ape* package (56) to calculate the ED scores for mammals and birds in each regional phylogeny. We assessed whether reintroduced species were more or less evolutionarily distinct than expected if species were randomly drawn from the regional pool. We used the median ED of the subset of reintroduced species rather than the mean given the skewness of the distribution of ED scores, and compared the median ED to the 95% confidence interval of the null distribution obtained by drawing 10,000 random samples of species of the same size in the associated regional phylogeny. The departure from the expected median ED produced by our null model was expressed as a  $P$  value and was calculated as the number of random median ED values that were superior to the median ED of reintroduced species and divided by the number of randomly drawn subsets.

We tested the deviation from our null model for both metrics of each set of reintroduced species (i.e., terrestrial mammals or terrestrial breeding birds) on each subcontinent (i.e., Europe or North America). In each case, the analyses were run using 100 fully resolved regional phylogenetic trees. All results provided are the median of the values taken across the 100 phylogenetic trees. All analyses were compiled with R 3.2.2.

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# Supporting Information

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We searched independently for each European species by adding the Latin name provided by the IUCN or BirdLife taxonomic referential to the list of search terms described above. Species of birds and mammals in our lists were considered native to Europe or North America if they were present or naturalized in these areas before the 1500 AD benchmark. We did not set any temporal restrictions, and we considered all manuscripts written in English that were available online. For Web of Science, we considered all records matching our query. For Google Scholar, we considered the first 50 records. This search was performed in the spring of 2015.

We focused on past or current reintroduction projects, and we did not include planned reintroductions, for example, ongoing projects where we could not find evidence that individuals had been released yet. The term “reintroduction” itself has been largely employed to address any attempt to reinject individuals within an area, and we only selected records that satisfied the definition provided by the IUCN/SSC *Guidelines for Reintroductions* (2013). One example of the misuse of this term is the reappearance of wild boars in England. The species has been driven to extinction in United Kingdom due to direct persecution and habitat loss, yet some populations have been maintained because of individuals escaping from stocks imported by farmers in the 1970s, which subsequently interbred with feral or domestic pigs (1). The wild boar is then cited as a “reintroduced” species in the United Kingdom in some records, and while several feasibility studies for actual reintroduction of wild boars in Scotland have been published (2), we did not find evidence supporting the intentional release of individuals in our research.

There are several other translocation types that we did not account for as reintroduction programs. Experimental translocations were not considered as reintroduction projects, as the primary goal of the release of individuals was not set toward the establishment of a viable population, but rather to provide insight and a better understanding of particular translocation-related mechanisms. A significant part of mammal and bird reintroductions involve game species (3), and sometimes it can be difficult to disentangle the hunting objective from the conservation objective. In these cases, we retained reintroduction projects if there was no doubt about the expected benefit being aimed toward species conservation rather than toward hunting purposes. Species rehabilitations, where injured, sick, or orphaned individuals were treated and released back into the wild, were not included. Finally, we did not include mitigation translocations, where the objective was to reduce animal mortality induced by human activities and development (4).

Nine reintroduced species belong to the top 5% most evolutionarily distinct species in each region: the European beaver (*Castor fiber*), the edible dormouse (*Glis glis*), the hazel dormouse (*Muscardinus avellanarius*), and the barn owl (*Tyto alba*) in Europe; and the North American beaver (*Castor canadensis*), the burrowing owl (*Athene cunicularia*), the California condor (*Gymnogyps californianus*), and the brown pelican (*Pelecanus occidentalis*) in North America. The osprey (*Pandion haliaetus*) is the only species that is highly evolutionarily distinct and that has been reintroduced in both regions.

1. Yalden DW (1986) Opportunities for reintroducing British mammals. *Mamm Rev* 16: 53–63.
2. Montgomery WI, Provan J, McCabe AM, Yalden DW (2014) Origin of British and Irish mammals: Disparate post-glacial colonisation and species introductions. *Quat Sci Rev* 98:144–165.

3. Griffith B, Scott JM, Carpenter JW, Reed C (1989) Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.
4. Germano JM, et al. (2015) Mitigation-driven translocations: Are we moving wildlife in the right direction? *Front Ecol Environ* 13:100–105.

**Table S1. List of the terms used to identify reintroduced mammal and bird species in Europe**

Category	Search term
Translocation	reintroduc* OR re-introduc* OR translocat* AND
Motive	population* OR conserv* OR restorat*

Terms were used in the ISI Web of Science database and Google Scholar search engine to identify which terrestrial mammals and breeding birds have been reintroduced at least once.

\*Indicates the use of a wildcard; for example, reintroduc\* can refer to reintroduction OR reintroductions OR reintroduce OR reintroduces OR reintroduced OR reintroducing.

**Table S2. List of terrestrial bird and mammal species that have been reintroduced at least once in Europe or North America**

Group	Order	Family	Species	Europe	North America	Refs.
Aves	Accipitriformes	Accipitridae	<i>Haliaeetus leucocephalus</i>	0	1	1
Aves	Accipitriformes	Accipitridae	<i>Harpia harpyja</i>	0	1	1
Aves	Accipitriformes	Accipitridae	<i>Ictinia mississippiensis</i>	0	1	1
Aves	Accipitriformes	Accipitridae	<i>Pandion haliaetus</i>	1	1	1, 2
Aves	Accipitriformes	Accipitridae	<i>Parabuteo unicinctus</i>	0	1	1
Aves	Accipitriformes	Accipitridae	<i>Accipiter gentilis</i>	1	0	3
Aves	Accipitriformes	Accipitridae	<i>Aegypius monachus</i>	1	0	4
Aves	Accipitriformes	Accipitridae	<i>Aquila adalberti</i>	1	0	5
Aves	Accipitriformes	Accipitridae	<i>Aquila chrysaetos</i>	1	0	6
Aves	Accipitriformes	Accipitridae	<i>Circus pygargus</i>	1	0	7
Aves	Accipitriformes	Accipitridae	<i>Gypaetus barbatus</i>	1	0	8
Aves	Accipitriformes	Accipitridae	<i>Gyps fulvus</i>	1	0	9
Aves	Accipitriformes	Accipitridae	<i>Haliaeetus albicilla</i>	1	0	10
Aves	Accipitriformes	Accipitridae	<i>Milvus milvus</i>	1	0	11
Aves	Accipitriformes	Cathartidae	<i>Gymnogyps californianus</i>	0	1	1
Aves	Anseriformes	Anatidae	<i>Anas laysanensis</i>	0	1	1
Aves	Anseriformes	Anatidae	<i>Branta canadensis</i>	0	1	1
Aves	Anseriformes	Anatidae	<i>Branta sandvicensis</i>	0	1	1
Aves	Anseriformes	Anatidae	<i>Cygnus buccinator</i>	0	1	1
Aves	Anseriformes	Anatidae	<i>Anser anser</i>	1	0	12
Aves	Anseriformes	Anatidae	<i>Anser erythropus</i>	1	0	13
Aves	Anseriformes	Anatidae	<i>Aythya nyroca</i>	1	0	14
Aves	Anseriformes	Anatidae	<i>Oxyura leucocephala</i>	1	0	15
Aves	Ciconiiformes	Ciconiidae	<i>Ciconia ciconia</i>	1	0	16
Aves	Columbiformes	Columbidae	<i>Patagioenas inornata</i>	0	1	1
Aves	Columbiformes	Columbidae	<i>Zenaida graysoni</i>	0	1	1
Aves	Falconiformes	Falconidae	<i>Falco femoralis</i>	0	1	1
Aves	Falconiformes	Falconidae	<i>Falco peregrinus</i>	1	1	1, 17
Aves	Falconiformes	Falconidae	<i>Falco cherrug</i>	1	0	18
Aves	Falconiformes	Falconidae	<i>Falco naumanni</i>	1	0	19
Aves	Falconiformes	Falconidae	<i>Falco tinnunculus</i>	1	0	20
Aves	Galliformes	Cracidae	<i>Crax rubra</i>	0	1	1
Aves	Galliformes	Odontophoridae	<i>Colinus virginianus</i>	0	1	1
Aves	Galliformes	Phasianidae	<i>Bonasa umbellus</i>	0	1	1
Aves	Galliformes	Phasianidae	<i>Lagopus muta</i>	0	1	1
Aves	Galliformes	Phasianidae	<i>Meleagris gallopavo</i>	0	1	1
Aves	Galliformes	Phasianidae	<i>Tympanuchus cupido</i>	0	1	1
Aves	Galliformes	Phasianidae	<i>Tympanuchus pallidicinctus</i>	0	1	1
Aves	Galliformes	Phasianidae	<i>Tympanuchus phasianellus</i>	0	1	1
Aves	Galliformes	Phasianidae	<i>Alectoris graeca</i>	1	0	21
Aves	Galliformes	Phasianidae	<i>Alectoris rufa</i>	1	0	22
Aves	Galliformes	Phasianidae	<i>Bonasa bonasia</i>	1	0	23
Aves	Galliformes	Phasianidae	<i>Coturnix coturnix</i>	1	0	24
Aves	Galliformes	Phasianidae	<i>Perdix perdix</i>	1	0	25
Aves	Galliformes	Phasianidae	<i>Tetrao tetrix</i>	1	0	26
Aves	Galliformes	Phasianidae	<i>Tetrao urogallus</i>	1	0	27
Aves	Gruiformes	Gruidae	<i>Grus americana</i>	0	1	1
Aves	Gruiformes	Gruidae	<i>Grus canadensis</i>	0	1	1
Aves	Gruiformes	Gruidae	<i>Grus grus</i>	1	0	28
Aves	Gruiformes	Rallidae	<i>Crex crex</i>	1	0	29
Aves	Gruiformes	Rallidae	<i>Fulica cristata</i>	1	0	30
Aves	Gruiformes	Rallidae	<i>Porphyrio porphyrio</i>	1	0	31
Aves	Otidiformes	Otididae	<i>Otis tarda</i>	1	0	32
Aves	Passeriformes	Corvidae	<i>Aphelocoma coerulescens</i>	0	1	1
Aves	Passeriformes	Corvidae	<i>Aphelocoma insularis</i>	0	1	1
Aves	Passeriformes	Corvidae	<i>Corvus hawaiiensis</i>	0	1	1
Aves	Passeriformes	Corvidae	<i>Corvus corax</i>	1	0	33
Aves	Passeriformes	Emberizidae	<i>Emberiza cirius</i>	1	0	34
Aves	Passeriformes	Fringillidae	<i>Loxops coccineus</i>	0	1	1
Aves	Passeriformes	Fringillidae	<i>Pseudonestor xanthophrys</i>	0	1	1
Aves	Passeriformes	Laniidae	<i>Lanius ludovicianus</i>	0	1	1
Aves	Passeriformes	Sittidae	<i>Sitta pusilla</i>	0	1	1

Table S2. Cont.

Group	Order	Family	Species	Europe	North America	Refs.
Aves	Passeriformes	Turdidae	<i>Myadestes obscurus</i>	0	1	1
Aves	Passeriformes	Turdidae	<i>Myadestes palmeri</i>	0	1	1
Aves	Passeriformes	Turdidae	<i>Sialia mexicana</i>	0	1	1
Aves	Passeriformes	Vireonidae	<i>Vireo bellii</i>	0	1	1
Aves	Pelecaniformes	Pelecanidae	<i>Pelecanus occidentalis</i>	0	1	1
Aves	Piciformes	Picidae	<i>Picoides borealis</i>	0	1	1
Aves	Psittaciformes	Psittacidae	<i>Amazona leucocephala</i>	0	1	1
Aves	Psittaciformes	Psittacidae	<i>Amazona vittata</i>	0	1	1
Aves	Psittaciformes	Psittacidae	<i>Ara ararauna</i>	0	1	1
Aves	Psittaciformes	Psittacidae	<i>Ara macao</i>	0	1	1
Aves	Psittaciformes	Psittacidae	<i>Ara militaris</i>	0	1	1
Aves	Psittaciformes	Psittacidae	<i>Rhynchopsitta pachyrhyncha</i>	0	1	1
Aves	Strigiformes	Strigidae	<i>Athene cucularia</i>	0	1	1
Aves	Strigiformes	Strigidae	<i>Bubo bubo</i>	1	0	35
Aves	Strigiformes	Strigidae	<i>Glaucidium passerinum</i>	1	0	36
Aves	Strigiformes	Strigidae	<i>Strix uralensis</i>	1	0	37
Aves	Strigiformes	Tytonidae	<i>Tyto alba</i>	1	0	38
Mammals	Artiodactyla	Antilocapridae	<i>Antilocapra americana</i>	0	1	1
Mammals	Artiodactyla	Bovidae	<i>Bison bison</i>	0	1	1
Mammals	Artiodactyla	Bovidae	<i>Oreamnos americanus</i>	0	1	1
Mammals	Artiodactyla	Bovidae	<i>Ovibos moschatus</i>	0	1	1
Mammals	Artiodactyla	Bovidae	<i>Ovis canadensis</i>	0	1	1
Mammals	Artiodactyla	Bovidae	<i>Bison bonasus</i>	1	0	39
Mammals	Artiodactyla	Bovidae	<i>Capra ibex</i>	1	0	40
Mammals	Artiodactyla	Bovidae	<i>Capra pyrenaica</i>	1	0	41
Mammals	Artiodactyla	Bovidae	<i>Rupicapra pyrenaica</i>	1	0	42
Mammals	Artiodactyla	Bovidae	<i>Rupicapra rupicapra</i>	1	0	43
Mammals	Artiodactyla	Cervidae	<i>Alces americanus</i>	0	1	1
Mammals	Artiodactyla	Cervidae	<i>Cervus elaphus</i>	1	1	1, 44
Mammals	Artiodactyla	Cervidae	<i>Rangifer tarandus</i>	1	1	1, 45
Mammals	Artiodactyla	Cervidae	<i>Alces alces</i>	1	0	46
Mammals	Artiodactyla	Cervidae	<i>Capreolus capreolus</i>	1	0	47
Mammals	Carnivora	Canidae	<i>Canis lupus</i>	0	1	1
Mammals	Carnivora	Canidae	<i>Vulpes velox</i>	0	1	1
Mammals	Carnivora	Felidae	<i>Lynx canadensis</i>	0	1	1
Mammals	Carnivora	Felidae	<i>Lynx rufus</i>	0	1	1
Mammals	Carnivora	Felidae	<i>Panthera onca</i>	0	1	1
Mammals	Carnivora	Felidae	<i>Puma concolor</i>	0	1	1
Mammals	Carnivora	Felidae	<i>Felis silvestris</i>	1	0	48
Mammals	Carnivora	Felidae	<i>Lynx lynx</i>	1	0	49
Mammals	Carnivora	Felidae	<i>Lynx pardinus</i>	1	0	50
Mammals	Carnivora	Mustelidae	<i>Enhydra lutris</i>	0	1	1
Mammals	Carnivora	Mustelidae	<i>Lontra canadensis</i>	0	1	1
Mammals	Carnivora	Mustelidae	<i>Martes americana</i>	0	1	1
Mammals	Carnivora	Mustelidae	<i>Martes pennanti</i>	0	1	1
Mammals	Carnivora	Mustelidae	<i>Mustela nigripes</i>	0	1	1
Mammals	Carnivora	Mustelidae	<i>Neovison vison</i>	0	1	1
Mammals	Carnivora	Mustelidae	<i>Taxidea taxus</i>	0	1	1
Mammals	Carnivora	Mustelidae	<i>Lutra lutra</i>	1	0	51
Mammals	Carnivora	Mustelidae	<i>Martes martes</i>	1	0	52
Mammals	Carnivora	Mustelidae	<i>Meles meles</i>	1	0	53
Mammals	Carnivora	Mustelidae	<i>Mustela lutreola</i>	1	0	54
Mammals	Carnivora	Ursidae	<i>Ursus americanus</i>	0	1	1
Mammals	Carnivora	Ursidae	<i>Ursus arctos</i>	1	1	1, 55
Mammals	Lagomorpha	Leporidae	<i>Brachylagus idahoensis</i>	0	1	1
Mammals	Lagomorpha	Leporidae	<i>Sylvilagus aquaticus</i>	0	1	1
Mammals	Lagomorpha	Leporidae	<i>Sylvilagus bachmani</i>	0	1	1
Mammals	Lagomorpha	Leporidae	<i>Sylvilagus palustris</i>	0	1	1
Mammals	Lagomorpha	Leporidae	<i>Oryctolagus cuniculus</i>	1	0	56
Mammals	Primate	Atelidae	<i>Alouatta pigra</i>	0	1	1
Mammals	Primate	Atelidae	<i>Ateles geoffroyi</i>	0	1	1
Mammals	Rodentia	Capromyidae	<i>Geocapromys brownii</i>	0	1	1



Table S2. Cont.

Group	Order	Family	Species	Europe	North America	Refs.
Mammals	Rodentia	Castoridae	<i>Castor canadensis</i>	0	1	1
Mammals	Rodentia	Castoridae	<i>Castor fiber</i>	1	0	57
Mammals	Rodentia	Cricetidae	<i>Neotoma floridana</i>	0	1	1
Mammals	Rodentia	Cricetidae	<i>Neotoma fuscipes</i>	0	1	1
Mammals	Rodentia	Cricetidae	<i>Neotoma magister</i>	0	1	1
Mammals	Rodentia	Cricetidae	<i>Peromyscus maniculatus</i>	0	1	1
Mammals	Rodentia	Cricetidae	<i>Peromyscus polionotus</i>	0	1	1
Mammals	Rodentia	Cricetidae	<i>Arvicola amphibius</i>	1	0	58
Mammals	Rodentia	Cricetidae	<i>Cricetus cricetus</i>	1	0	59
Mammals	Rodentia	Gliridae	<i>Glis glis</i>	1	0	60
Mammals	Rodentia	Gliridae	<i>Muscardinus avellanarius</i>	1	0	61
Mammals	Rodentia	Heteromyidae	<i>Dipodomys merriami</i>	0	1	1
Mammals	Rodentia	Heteromyidae	<i>Dipodomys nitratooides</i>	0	1	1
Mammals	Rodentia	Muridae	<i>Micromys minutus</i>	1	0	62
Mammals	Rodentia	Sciuridae	<i>Cynomys gunnisoni</i>	0	1	1
Mammals	Rodentia	Sciuridae	<i>Cynomys ludovicianus</i>	0	1	1
Mammals	Rodentia	Sciuridae	<i>Marmota flaviventris</i>	0	1	1
Mammals	Rodentia	Sciuridae	<i>Sciurus niger</i>	0	1	1
Mammals	Rodentia	Sciuridae	<i>Marmota bobak</i>	1	0	63
Mammals	Rodentia	Sciuridae	<i>Marmota marmota</i>	1	0	64
Mammals	Rodentia	Sciuridae	<i>Sciurus vulgaris</i>	1	0	65
Mammals	Rodentia	Sciuridae	<i>Spermophilus citellus</i>	1	0	66

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**Table S3. Top five highest ED species among reintroduced species in each region (Europe/North America) for each group (Mammals/Birds)**

Group	Region	No. of species	Order	Family	Species	Rank*
Mammals	Europe	202	Rodentia	Castoridae	<i>Castor fiber</i>	2
			Rodentia	Gliridae	<i>Glis glis</i>	6
			Rodentia	Gliridae	<i>Muscardinus avellanarius</i>	9
			Lagomorpha	Leporidae	<i>Oryctolagus cuniculus</i>	16
			Rodentia	Sciuridae	<i>Sciurus vulgaris</i>	17
	North America	838	Rodentia	Castoridae	<i>Castor canadensis</i>	2
			Artiodactyla	Antilocapridae	<i>Antilocapra americana</i>	44
			Artiodactyla	Bovidae	<i>Bison bison</i>	45
			Lagomorpha	Leporidae	<i>Brachylagus idahoensis</i>	58
			Primate	Atelidae	<i>Ateles geoffroyi</i>	62
Birds	Europe	378	Strigiformes	Tytonidae	<i>Tyto alba</i>	2
			Accipitriformes	Accipitridae	<i>Pandion haliaetus</i>	10
			Otidiformes	Otididae	<i>Otis tarda</i>	21
			Ciconiiformes	Ciconiidae	<i>Ciconia ciconia</i>	24
			Gruiformes	Rallidae	<i>Porphyrion porphyrio</i>	28
	North America	1,748	Accipitriformes	Accipitridae	<i>Pandion haliaetus</i>	7
			Pelecaniformes	Pelecanidae	<i>Pelecanus occidentalis</i>	32
			Accipitriformes	Cathartidae	<i>Gymnogyps californianus</i>	47
			Strigiformes	Strigidae	<i>Athene cunicularia</i>	69
Accipitriformes	Accipitridae	<i>Harpia harpyja</i>	124			

\*Species' rank among the associated regional pool of species, based on highest ED scores.



# Chapter 2: *Functional representativeness and distinctiveness of reintroduced birds and mammals in Europe*

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## **Context:**

Functional Diversity is increasingly used as an important facet of biodiversity which aims to represent dissimilarities in ecological niches between species in natural communities or large scale assemblages. We focused on reintroduced birds and mammals in Europe and used information on body mass, foraging activity, diet types and foraging height to represent the range of functional traits supported by species at the continental scale. Using an approach similar to the previous chapter, we tested if reintroduction targets are representative of the functional diversity of the continental assemblage, and measured the functional distinctiveness of reintroduced species in the continental species pool.

## **Key findings:**

Our results show different patterns between reintroduced birds and reintroduced mammals. In Europe, reintroduced mammals are poorly representative of the regional functional diversity, but seem to involve more functionally species than expected by chance. However reintroduced birds support a wider range of functional trait combinations and are representative of the regional assemblage. The analysis showed that, contrary to reintroduced mammals, the level of functional distinctiveness of reintroduced birds is similar to random expectations.

This analysis provide complementary insights on the representativeness and distinctiveness of reintroduction targets. However, the limited number of traits considered, and the large spatial scale of the study hinder the interpretation of our findings, and further studies are needed to assess the contribution of reintroduction to the conservation of key ecological processes.



# Functional representativeness and distinctiveness of reintroduced birds and mammals in Europe

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## Abstract

Reintroductions, the human-mediated movement of organisms to re-establish locally extinct populations, have become a popular conservation tool. Because the implementation of reintroductions often focus on local or national conservation issues, their contribution to the conservation of biodiversity at large scale remains unclear. Taxonomic bias in reintroductions have been described, however several studies have stressed the need to account for the different components of diversity when assessing the relevance of the allocation of conservation efforts. As available resources for conservation are scarce, additional value can be granted to species that are performing more singular functions than others. Here we investigate the diversity of functional traits supported by reintroduced species of birds and mammals in Europe. For each taxonomic group, we tested if reintroduction targets are representative of the functional diversity of the continental assemblage, and measured the functional distinctiveness of reintroduced species. We found that reintroductions of birds did not focus on functionally distinct species, and that reintroduced birds are representative of the functional diversity at a continental scale. However, reintroductions of mammals involved more functionally distinct

species than expected, even though reintroduced mammals are not collectively representative of the diversity of functional traits within the continental assemblage.

## **Introduction**

How species diversity relates to ecosystem functioning is one of the core debates in ecology (Cardinale et al., 2002; Gagic et al., 2015), and one critical issue is the extent to which ecosystem functioning is buffered against species loss (Cadotte et al., 2011; Oliver et al., 2015a, 2015b; Petchey and Gaston, 2002a; Wardle, 2016). In ecosystems with high levels of functional redundancy, i.e. the fact that several species can support the same function (Rosenfeld, 2002), it was assumed that a high proportion of species could be lost before inducing the disappearance of functional groups in natural communities (Fonseca and Ganade, 2001). However this assumption has been challenged, even in species rich systems where many functions are left highly vulnerable and supported by a few species only (Mouillot et al., 2014). One way to indirectly assess the individual roles of species in assemblages is by studying functional trait diversity. Functional traits are well-defined and quantifiable morphological, behavioral or phenological features of an organism, related to an ecological processes that can potentially influence fitness and performance (Violle et al., 2007). Trait based-approaches can be used to address a variety of ecological questions, including assembly rules in biological communities, and can also provide meaningful conservation targets in ecological restoration (Laughlin, 2014; Laughlin et al., 2017).

Trait-based approaches provide a way to measure functional diversity by summarizing the variation in trait values between organisms (Petchey and Gaston, 2002b). Functional diversity is a multi-faceted concept that can be considered at multiple ecological scales, from populations and communities to regions and continents (Carmona et al., 2016). Because of its great potential to describe ecological processes, the characterization of functional diversity provides a compelling framework to develop conservation priorities. For example, one assumption of this trait-based approach is that species with more distinct combinations of functional traits are more likely to support functions that may not be delivered by species with more common associations of traits (Gagic et al., 2015; Jain et al., 2014). Furthermore, highly distinct combinations of traits seem to be supported by rare species, thus the functions they support might be more

vulnerable to extinction (Leitão et al., 2016; Mouillot et al., 2013). If the conservation of species with more distinct combinations of functional traits (i.e. functional distinctiveness) conflates with the maintenance of ecosystem processes and services, then the measure of species' functional distinctiveness would provide a solid basis for guiding both protection and restoration strategies. Studies have investigated the congruence of protected areas networks and how they contribute to the preservation of functional diversity (Guilhaumon et al., 2015; Thuiller et al., 2015), but the representativeness of single species conservation targets has received little attention.

Among single species conservation strategies, reintroduction aims to re-establish a population within the indigenous range of the focal species following local extinction, through the release of a limited number of individuals. For this reason, reintroductions are generally case by case initiatives that are not collectively designed to tackle global or continental conservation issues related to the preservation of taxonomic, phylogenetic or functional diversity. The principal objective of reintroduction projects is to improve the conservation status of the focal species, however, restoring lost ecological functions or services may also drive the implementation of population restoration projects (IUCN/SSC, 2013). In such cases, the primary focus of the translocation shift from single-species conservation to the inclusion of whole ecosystem management targets. For example, reintroduction of apex predators can be expected to have substantial impact at the landscape level through the restoration of top-down interactions that structure ecosystem dynamics (Estes et al., 2011; Ritchie et al., 2012). The study of the distribution of reintroduction efforts at larger scale is thus required in order to explore how population restorations may assist the conservation of global ecosystem functioning. The well documented taxonomic bias in reintroductions (Seddon et al., 2005) not only influences the diversity of evolutionary histories involved in reintroduction efforts (Thévenin et al., 2018), but may also shape the diversity of species characteristics and niche differences if reintroduction practitioners have focused on particular functional groups. How these patterns will translate in terms of functional trait diversity has yet to be documented. If reintroductions target some particular groups of species (e.g., raptorial bird species), then we expect the breadth of ecological functions involved, as depicted by the combination of functional traits supported by reintroduced species, to be narrow.

Here, we explored the association of functional traits of reintroduced terrestrial mammals and birds in Europe, and assessed the extent to which reintroductions may have contributed to the conservation of the European functional diversity for these two groups. We used data on



behavioral traits reflecting the way species acquire resources from their environment (feeding behavior and foraging activity), and information on body mass and diet traits which reflect the resource use requirements of species (Devictor et al., 2010). These traits represent how a given organism impacts the community structure and ecosystem functioning, and can hence be considered as “effect” traits, which differ from “response” traits, i.e. traits that determine the response of organisms to environmental change (Lavorel and Garnier, 2002; Luck et al., 2012). For each taxa, we used dendrograms to represent the differences in trait values between species in each European assemblage. We measured the functional diversity of each set of reintroduced species (Petchey and Gaston, 2002b) and calculated the functional distinctiveness of each individual species (Mouillot et al., 2013). We compared the obtained values to a null model where reintroduced species were randomly sampled from the European assemblage, in order to investigate the complementarity among reintroduced species’ trait values and to determine if reintroduced species support more distinct combinations of functional traits.

## **Materials and Methods**

We focused on 28 terrestrial mammal species (15% of the 202 European species), and 37 terrestrial breeding bird species (10% of the 378 European species), which have been reintroduced at least once in Europe. Reintroduced species were identified through a comprehensive search of the reintroduction-related literature, and details of the literature research protocol and complete lists of reintroduced species can be found in Thévenin et al. (2018). For functional traits, we used the dataset published by Wilman et al. (2014) who compiled functional trait values for all 9,993 and 5,400 extant bird and mammal species derived from the literature. These traits are relevant to the “Eltonian niche”, i.e. a multidimensional space describing biotic interactions and resource-consumer dynamics related to the acquisition of energy and nutrients. This dataset provides information on body mass, diet type, foraging behavior along a vertical gradient (foraging stratum) and foraging activity (e.g. nocturnal, diurnal). Body mass is a continuous variable given in grams. A species’ diet is described as a multichoice nominal variable representing whether the species’ diet includes one or several of the following eight categories: Invertebrate, Vertebrate, Fish, Carrion, Nectar, Seed, Fruit and Plant (e.g. grass, ground vegetation, seedlings, weeds...). For birds, the foraging stratum is also

given as a multichoice nominal variable with seven different discrete levels from below the water surface to aerial foraging. For mammals this variable is categorical, with species assigned to only one category (ground level including aquatic foraging; ground foraging; scansorial; arboreal; aerial). Finally the foraging activity is given as a multichoice nominal variable for mammals (diurnal, nocturnal and/or crepuscular), while it is a binary variable for birds (nocturnal vs diurnal). Functional trait values for reintroduced birds and mammals are presented in Supplementary Materials (Table S1 and S2).

We built up functional trees from functional traits distances between each pair of species (Petchey and Gaston, 2002b). We calculated pairwise functional distances using a mixed-variable coefficient that allows various types of variables to be included. Euclidean distance was used for body mass (log-transformed), which is generally defined as:

$$EucD_{ab} = \sqrt{(x_a - x_b)^2}$$

with  $x_a$  and  $x_b$  being the values of body mass (continuous variable) of species  $a$  and  $b$  respectively. For other type of data (e.g., multichoice nominal), we used the Gower distance, which general formula is given by:

$$GowD_{ab} = \frac{1}{N} \sum_{i=1}^N d_{iab}$$

where  $d_{iab}$  measures the dissimilarity between species  $a$  and  $b$  for the trait  $i$ :

$$d_{iab} = \frac{|x_{ia} - x_{ib}|}{\max(x_i) - \min(x_i)}$$

The pairwise distances were calculated using the *dist.ktab* function in the *ade4* R-package. We then applied hierarchical classification methods to synthesize the multidimensional trait space into a dendrogram, or functional tree. Representing a functional multidimensional space (each functional trait being an axis of this space) using a dendrogram can result in a loss of information because the distances between species are based on the lengths of the branch connecting the tips in the functional tree (i.e. the cophenetic distances), instead of the aggregation of the pairwise distance on each trait in multidimensional functional space. Following Mouchet et al. (2008), we selected the clustering method which led to the lowest amount of distortion between the initial and cophenetic pairwise distance matrix. The

Unweighted Pair Group Method with Arithmetic Mean (UPGMA) provided the most robust trees, which is consistent with results of other studies (Podani and Schmera, 2006).

We used the fair-proportion index to estimate the distinctiveness of species in terms of functional traits (hereafter Functional Distinctiveness, FDist). Similar to the Evolutionary Distinctiveness index (Isaac et al., 2007), FDist scores are the sum of the lengths of the branches of the functional tree, from the root to the tip (species), each length being divided by the number of species supported by the given branch (Mouillot et al., 2013). The FDist scores of each species in a subset sum up to the Functional Diversity of the whole subset (sum of the lengths of the branches of a given functional tree) (Petchey and Gaston, 2002b). Functional Diversity (hereafter FD) measures the complementarity among species' trait values in a particular species assemblage through the estimation of the dispersion of species in trait space. The higher the FD for a given subset of species, the more functionally dissimilar the species are within the subset.

We used the *pd.query* function from the *PhyloMeasures* R-package (Tsirogiannis and Sandel, 2016) to calculate the FD of each set of reintroduced species. For each taxa, we compared the FD values of reintroduced species to the FD value expected under a null model assuming that species are sampled randomly from the continental functional tree. For that purpose we computed the expected value (i.e.,  $\mu\text{FD}$ ) and standard deviation (i.e.,  $sd\text{FD}$ ) of FD describing the distribution of FD values for a given number of species ( $n = 28$  for mammals and  $n = 37$  for birds) in the associated functional tree (*pd.moments* function, *PhyloMeasures* package). Reintroduced species were considered to be representative of the diversity of functional traits if the FD value was included in the 95% confidence interval, calculated as  $\mu\text{FD} \pm 1.96 * sd\text{FD}$ .

We calculated the Functional Distinctiveness of reintroduced species using the *evol.distinct* function from the *ape* package (Paradis et al., 2004). For birds and mammals separately, we compared the median FDist score to the distribution expected if reintroduction targets were randomly drawn from the continental pool of species. We used the median FDist instead of the mean because of the skewness of the distribution of FDist scores. For that purpose, we built a null distribution by calculating the median FDist scores of 10,000 randomly drawn samples of species of the same size ( $n = 28$  species for mammals and  $n = 37$  species for birds) in the associated functional tree, and compared the median FDist of reintroduced species to the 95% confidence interval of the null distribution. The departure from the expected median FDist produced by our null model was expressed as a p-value and was calculated as the number of

random median FDist values that were superior to the median FDist of reintroduced species and divided by the number of randomly drawn subsets.

## Results

The functional diversity of the 28 reintroduced species of mammals is lower than expected under our null model ( $FD_{reint} = 3.857$ ,  $p\text{-value} = 0.03$ ) (Table 1). Our data show that several reintroduced species are among the most functionally distinct species of the terrestrial mammal assemblage in Europe (Supplementary Materials, Table S1). The most functionally distinct reintroduced mammal in our data is the European pine marten (*Martes martes*,  $FDist = 0.2388$ ,  $rank = 4/202$ ). The other highly functionally distinct reintroduced mammals are the edible dormouse (*Glis glis*,  $FDist = 0.2065$ ,  $rank = 9/202$ ), the hazel dormouse (*Muscardinus avellanarius*,  $FDist = 0.1893$ ,  $rank = 13/202$ ) and the red squirrel (*Sciurus vulgaris*,  $FDist = 0.1884$ ,  $rank = 14/202$ ). Our results also show that the median FDist of the 28 reintroduced mammals is higher than expected under our null model (median  $FDist_{reint} = 0.0505$ ,  $p\text{-value} < 0.001$ ) (Figure 1).

Reintroduced birds show more diverse combinations of functional traits than reintroduced mammals. Our results show that there is no significant deviation from the distribution of FD values expected if reintroduced bird species were randomly sampled from the continental assemblage of terrestrial breeding birds ( $FD_{reint} = 8.364$ ,  $p\text{-value} = 0.59$ ) (Table 1). The most functionally distinct reintroduced bird is the common raven (*Corvus corax*,  $FDist = 0.2807$ ,  $rank = 5/378$ ), with its highly diverse diet comprising almost all categories except nectar. Reintroduced birds are not more functionally distinct than expected, and the median FDist of reintroduced birds was close to the random expectation (median  $FD_{reint} = 0.0976$ ,  $p\text{-value} = 0.79$ ) (Figure 2).

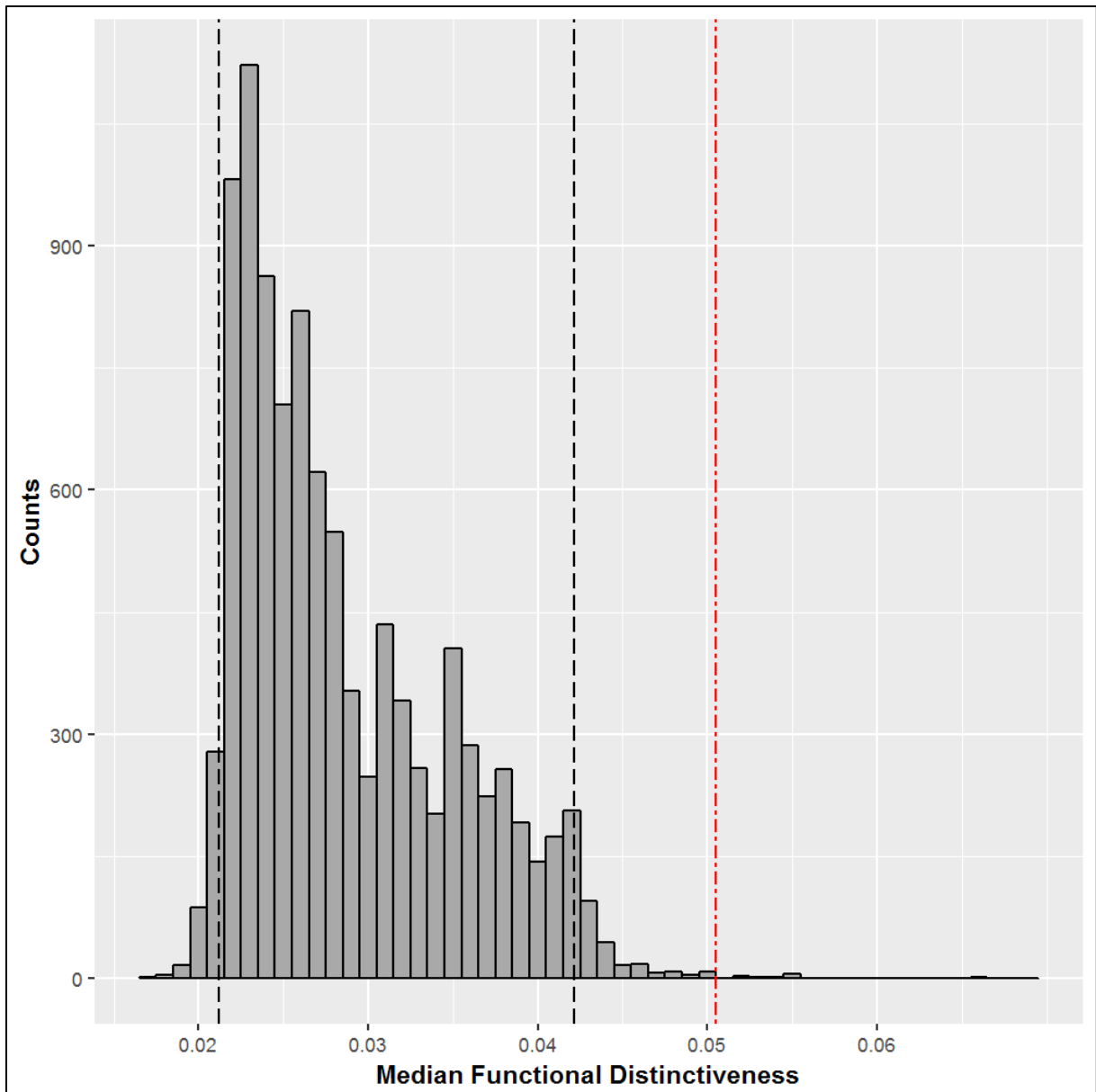


Figure 1: The null distribution of the median Functional Distinctiveness for 28 mammal species randomly drawn from the functional tree of European terrestrial mammals (10000 samples). Black dashed lines represent the 95% CI interval (i.e. [0.0212, 0.0421]), and the red-dashed line represent the observed median FDist value for reintroduced mammals (median  $FDist_{reint} = 0.0505$ ,  $p$ -value  $< 0.001$ ).

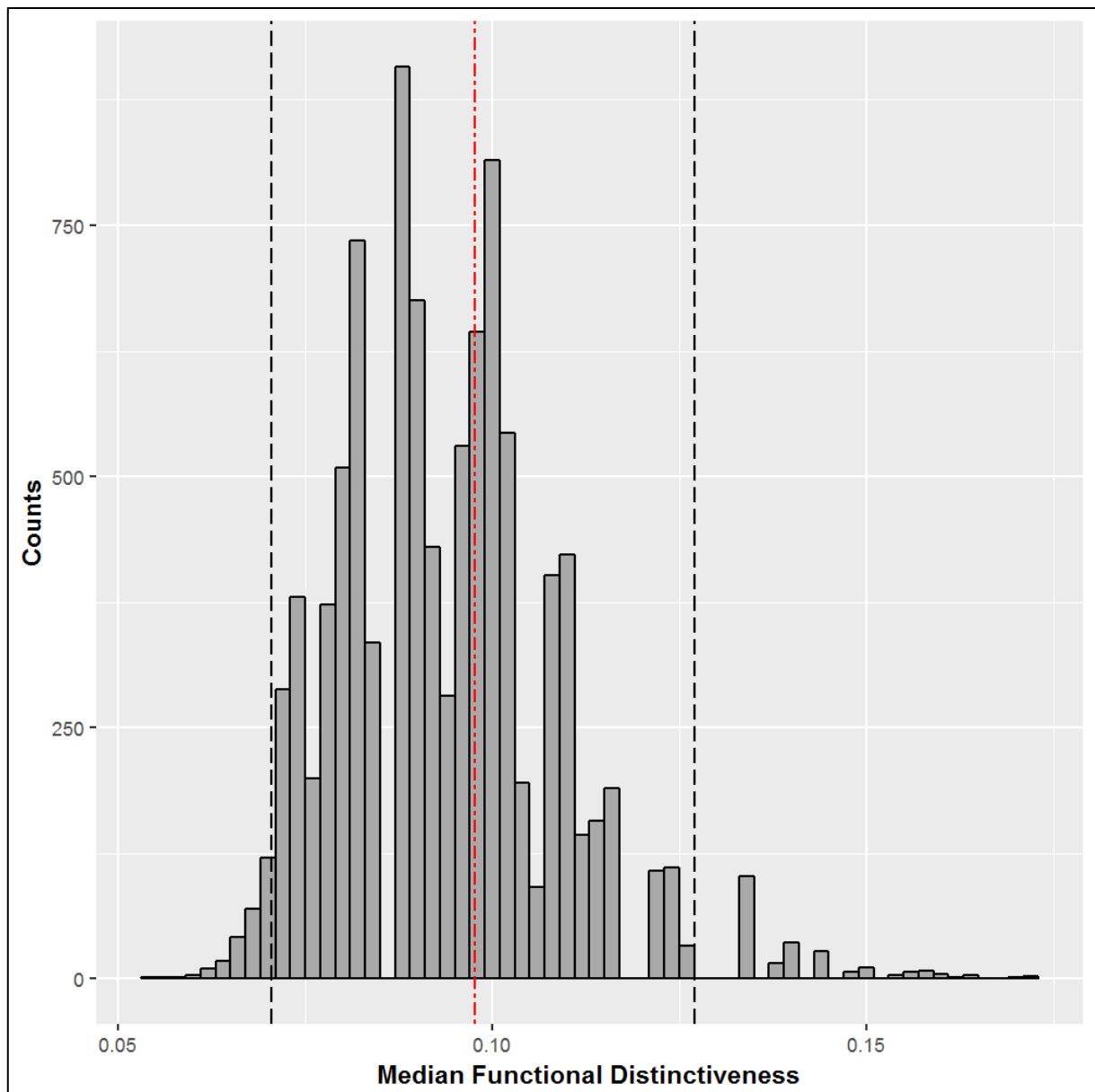


Figure 2: The null distribution of the median Functional Distinctiveness for 37 species randomly drawn from the functional tree of European terrestrial breeding birds (10000 samples). Black dashed lines represent the 95% CI interval ([0.0715, 0.1331]), and the red-dashed line represent the median FD value for reintroduced birds (median  $FD_{reint} = 0.0976$ ,  $p$ -value = 0.79).

*Table 1: Functional Diversity (FD) for each subset of reintroduced birds and mammals in Europe, and the associated expected value  $\mu FD$  and  $sdFD$  for the associated subset size (number of reintroduced species in each group) under our null model. Deviation from the null model is presented as a  $p$ -value from a Z-test statistics. Bold values indicate  $p < 0.05$ .*

GROUP	No. of native terrestrial species	No. of reintroduced species	FD of reintroduced species	Expected FD	SD of FD	$p$ -value
MAMMALS	202	28	3.857	4.807	0.443	<b>0.03</b>
BIRDS	378	37	8.364	8.611	0.458	0.59

## Discussion

While phylogenetic diversity informs us on the evolutionary and biogeographic histories of taxa, functional trait-based ecology provides a framework that can link species' characteristics with ecosystem functions and services (Cadotte et al., 2011). Functional diversity has been advocated as a biodiversity measure that account for dissimilarities in species' forms and functions, and here we provide new insights on how reintroduction targets can be representative of the diversity of a continental assemblage of species and thus contribute to the conservation of biodiversity at large scales. Our results show that reintroductions of birds in Europe mainly involve raptorial and game species, which are poorly representative of the phylogenetic diversity of the European assemblage, but remain representative of the functional diversity of European terrestrial breeding birds. Our findings also suggest that reintroduction programs involve species of terrestrial mammals in Europe that are individually more functionally distinct than if drawn at random from the continental assemblage, but that, collectively, these species carry less functional diversity than expected.

Functional trait diversity provides a promising way to assess the ecological roles of species, but the outputs may be more meaningful when considering species that share the same conditions and resources or that co-evolved under similar biogeographical regions and historical processes (Hidasi-Neto et al., 2015). These conditions might not be met here, because running such analysis at the continental scale comes with the assumption that all species can potentially interact, as we did not take into account species' geographic range overlapping. In this case,

some species might not appear as ecologically distinct in the continental pool of species, but could occur in areas where other functionally similar species do not. Our analysis showed that, when considering the whole continental assemblage of European terrestrial mammals, large herbivores are not particularly functionally distinct, because all members of the Artiodactyla order in Europe (except the wild boar, *Sus scrofa*) share the same diet types (plant material), foraging strategy (ground feeder) and, to some extent, have similarly large body masses. Our data show that reintroduction projects within mammals have involved many ungulates, hence an analysis at the continental scale will consider these associations of functional trait as relatively redundant, as these species differ only when considering their period of activity. Considering differences in functional trait values at the scale of continental assemblages might not be appropriate to apply community assembly concepts, however the species supporting the most distinct associations of functional traits at such large scale will likely remain among the most functionally distinct species wherever they might occur. In addition to identifying which reintroduced species are functionally distinct at large scale, we need to locate where they might also be distinct at the local scale by considering where the reintroduction has been implemented (release site) and assess the local assemblage of species with which the reintroduction target is likely to interact.

Here we used functional dendrograms and the fair-proportion index (Isaac et al., 2007; Mouillot et al., 2013), so functionally distinct species are those that contribute to the functional diversity of the assemblage because they support a combination of trait values (diet, activity, body mass and foraging height) that is not supported by other species on the functional tree. The extent to which such distinctiveness relate to key ecological functions or other ecological concepts is ambiguous. For example the continuum between functionally distinct and functionally redundant species is not straightforwardly consistent with other concepts such as the continuum between specialist and generalist species. Therefore the question whether reintroduction practitioners have focused on functionally distinct species might not reflect the fact that ecological processes are given increased attention in the reintroduction literature and practice (Macdonald et al., 2000; Wilmers et al., 2003). For example, three out of the four European species of vultures have been reintroduced in Europe. Among other aspects, incentives for reintroducing large vultures are based on their specialized scavenger diet. Here, the fact that these four species share similar trait values and are considered altogether in the same continental pool of species led to reintroduced vultures not being particularly functionally distinct (*Gypaetus barbatus*,  $FDist = 0.1005$ , rank = 175/378; *Aegypius monachus* and *Gyps fulvus* were



closely related sharing the same values of  $FDist = 0.0975$ , and  $rank = 181/378$ ). The study of functional diversity allows to explore the value and dissimilarity of morphological, ecological and behavioral traits in biological assemblages, but its ability to describe a species ecological function is highly constrained by the type and number of traits considered (Petchey and Gaston, 2006). The type of functional traits considered, and the way they are weighted in calculating species' dissimilarities largely influence the measure of functional diversity and species' rankings based on functional distinctiveness. While the idea of prioritizing species based on their functional originality is promising, it remains challenging in practice because we have imperfect knowledge about which, and how many traits and function must be integrated. The functional differences described here mostly concern species' resource use patterns. Resource use may not reflect finer divisions in some functional groups and may be less appropriate to describe accurately some ecosystem processes. It may thus overlook the important role of some individual species (Petchey and Gaston, 2006). Information on functional traits has been made increasingly available for animals but the number of traits considered, and the extent to which they relate to an ecological function is still limited compared to plants (Díaz et al., 2016; Lavorel and Garnier, 2002). One central argument for the restoration and conservation of apex predators is the direct and indirect impacts they have at the landscape level. Top-down effects of top predators in ecosystem can have tremendous effects for the entire ecosystem, through the alteration of herbivory and further effects on the abundance and composition of plant communities (Smith and Bangs, 2009). In the dataset we used, diet types and body mass provided a proxy for the trophic level of a species, but will mostly help differentiate herbivores from carnivores. One major element that could be integrated in such analyses is information on the type and number of species' trophic interactions.

Alongside with the improvement of the conservation status of the focal species, reintroductions can be designed to restore lost ecological functions and processes in degraded ecosystems (IUCN/SSC, 2013). The study of functional diversity patterns could play a substantial role in reintroduction planning. Before implementing releases, managers are advised to conduct feasibility studies and assess the potential risks associated with translocating the focal species. These risks can be sociological (e.g. Human-wildlife conflicts associated with the reintroduction of apex predators), but also ecological because the re-integration of a species in a trophic network can have potential deleterious effects on other species in the ecosystem. Some systems may have undergone profound change in community composition, depending on the time elapsed between the extirpation and the return of the species. Feasibility studies must

address biotic interactions (competition, predation), to predict the impact of the return of the focal species to the community, which could have reached a different equilibrium since extirpation (Osborne and Seddon, 2012). However managers may lack the tools to do so, and trait-based approaches could help foreseeing these negative impacts, both for the species, but also for the recipient community. Indeed, in some case, the reduction or local eradication of competitors or predators prior to the rerun of the focal species has generated technical and ethical debates. Such approaches could contribute to identify reintroduction targets that will enhance functional complementarity at the scale of the communities and, hopefully, improve ecosystem functioning. Unfulfilled functional roles can be viewed as opportunities for species reintroduction, and in some cases population restoration projects may improve both the conservation status of the focal species along with the functioning and resilience of restored ecosystems (Lipsey et al., 2007). Reintroductions can also represent a way to experiment at large scale in ecology (Sarrazin and Barbault, 1996). Reintroduction could be used to further explore the impact of functionally distinct species in natural communities, or investigate competition in niche dimensions induced by the return of the focal species.

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## **Supplementary Materials**

Table S1: Functional trait values and Functional Distinctiveness scores for each of the 28 reintroduced terrestrial mammals in Europe. FDist ranks are given in decreasing order out of the 202 species of European terrestrial mammals.

Table S2: Functional trait values and Functional Distinctiveness scores for each of the 37 reintroduced species of terrestrial breeding birds in Europe. FDist ranks are given in decreasing order out of the 378 species of European breeding birds.



Table S1

ORDER	SPECIES	FDist score	FDist rank	DIET								FORAGING STRATUM	ACTIVITY			BODY MASS (grams)
				Invertebrate	Vertebrate	Fish	Scavenge	Fruit	Nectar	Seed	Plant		Nocturnal	Crepuscular	Diurnal	
CARNIVORA	<i>Martes martes</i>	0.238832794	4	0	1	0	0	1	0	0	0	Scansorial	1	0	0	1300
RODENTIA	<i>Glis glis</i>	0.206522667	9	0	0	0	0	1	0	1	0	Arboreal	1	1	0	128.09
RODENTIA	<i>Muscardinus avellanarius</i>	0.189294398	13	1	0	0	0	1	1	0	1	Arboreal	1	0	0	27.5
RODENTIA	<i>Sciurus vulgaris</i>	0.188397252	14	0	0	0	0	1	0	1	1	Arboreal	0	0	1	333
CARNIVORA	<i>Meles meles</i>	0.147896969	23	1	1	0	0	1	0	1	1	Ground	0	0	1	13000
CARNIVORA	<i>Ursus arctos</i>	0.136855926	25	1	1	0	0	1	0	0	1	Ground	0	1	1	180520.42
RODENTIA	<i>Cricetus cricetus</i>	0.114850042	31	1	1	0	0	0	0	0	1	Ground	0	1	0	510
RODENTIA	<i>Marmota bobak</i>	0.098233068	33	0	0	0	0	1	0	1	1	Ground	0	0	1	5500
RODENTIA	<i>Marmota marmota</i>	0.098233068	34	0	0	0	0	1	0	1	1	Ground	0	0	1	2010
CARNIVORA	<i>Lutra lutra</i>	0.092911515	35	1	1	1	0	0	0	0	0	Ground	1	1	1	8785.14
CARNIVORA	<i>Felis silvestris</i>	0.088401213	36	1	1	0	0	0	0	0	0	Ground	1	1	0	5099.99
CARNIVORA	<i>Lynx lynx</i>	0.058520458	47	0	1	0	0	0	0	0	0	Ground	1	0	0	17950
CARNIVORA	<i>Mustela lutreola</i>	0.056250954	49	1	1	0	0	0	0	0	0	Ground	1	1	0	440
CARNIVORA	<i>Lynx pardinus</i>	0.054509062	51	0	1	0	0	0	0	0	0	Ground	1	0	0	9400
RODENTIA	<i>Arvicola amphibius</i>	0.046419018	57	0	0	0	0	1	0	0	1	Ground	1	1	1	120
ARTIODACTYLA	<i>Cervus elaphus</i>	0.041755672	72	0	0	0	0	0	0	0	1	Ground	1	1	0	165015.85
RODENTIA	<i>Micromys minutus</i>	0.037740575	80	1	0	0	0	0	0	1	1	Ground	1	1	1	6
ARTIODACTYLA	<i>Alces alces</i>	0.034714593	88	0	0	0	0	0	0	0	1	Ground	1	1	0	356998.16
ARTIODACTYLA	<i>Bison bonasus</i>	0.034714593	89	0	0	0	0	0	0	0	1	Ground	1	1	1	5.00E+05
LAGOMORPHA	<i>Oryctolagus cuniculus</i>	0.029495848	93	0	0	0	0	0	0	0	1	Ground	1	0	0	1832.22
RODENTIA	<i>Spermophilus citellus</i>	0.024280665	109	1	0	0	0	0	0	1	1	Ground	0	0	1	290
ARTIODACTYLA	<i>Capreolus capreolus</i>	0.022112803	126	0	0	0	0	0	0	0	1	Ground	1	1	1	22500
RODENTIA	<i>Castor fiber</i>	0.022112803	127	0	0	0	0	0	0	0	1	Ground	1	1	0	19000
ARTIODACTYLA	<i>Capra ibex</i>	0.022023684	128	0	0	0	0	0	0	0	1	Ground	0	1	1	85166.51
ARTIODACTYLA	<i>Rangifer tarandus</i>	0.022023684	129	0	0	0	0	0	0	0	1	Ground	0	0	1	86033.98
ARTIODACTYLA	<i>Capra pyrenaica</i>	0.020851917	135	0	0	0	0	0	0	0	1	Ground	0	1	1	50000
ARTIODACTYLA	<i>Rupicapra rupicapra</i>	0.020819234	139	0	0	0	0	0	0	0	1	Ground	0	1	1	26100
ARTIODACTYLA	<i>Rupicapra pyrenaica</i>	0.019787324	145	0	0	0	0	0	0	0	1	Ground	0	1	1	30000

Table S2

ORDER	SPECIES	FDist score	FDist rank	DIET								FORAGING STRATUM							ACTIVITY (Nocturnal = 1)	BODY MASS (grams)
				Invertebrate	Vertebrate	Fish	Scavenge	Fruit	Nectar	Seed	Plant	Water below surface	Water around surface	Ground	Understory	Midhigh	Canopy	Aerial		
Passeriformes	<i>Corvus corax</i>	0.280656623	5	1	1	1	1	1	0	1	1	0	0	1	0	1	0	1	0	927.97
Accipitriformes	<i>Pandion haliaetus</i>	0.255171574	14	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1483.2
Otidiformes	<i>Otis tarda</i>	0.246832616	17	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	6759.92
Accipitriformes	<i>Haliaeetus albicilla</i>	0.233258201	21	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	0	4729.27
Anseriformes	<i>Anser anser</i>	0.194543784	48	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	3302.41
Gruiformes	<i>Porphyrio porphyrio</i>	0.181552062	73	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	773.88
Galliformes	<i>Bonasa bonasia</i>	0.174734147	88	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	429
Gruiformes	<i>Grus grus</i>	0.172764602	90	1	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0	5499.99
Galliformes	<i>Tetrao urogallus</i>	0.171875192	92	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	2716.61
Falconiformes	<i>Falco naumanni</i>	0.166226024	100	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	152.06
Gruiformes	<i>Crex crex</i>	0.156178319	113	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	154.91
Anseriformes	<i>Anser erythropus</i>	0.150217646	117	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1755.5
Strigiformes	<i>Bubo bubo</i>	0.137059581	127	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2668.51
Strigiformes	<i>Glaucidium passerinum</i>	0.133055064	133	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	57.87
Falconiformes	<i>Falco tinnunculus</i>	0.115031204	145	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	183.21
Falconiformes	<i>Falco cherrug</i>	0.114680583	146	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	961.21
Galliformes	<i>Alectoris graeca</i>	0.108082256	160	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	594.11
Accipitriformes	<i>Gypaetus barbatus</i>	0.100464098	175	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	5694.98
Gruiformes	<i>Fulica cristata</i>	0.097645772	179	1	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	826
Accipitriformes	<i>Aquila adalberti</i>	0.097581941	180	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2958.03
Accipitriformes	<i>Aegypius monachus</i>	0.097529354	181	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	9320.55
Accipitriformes	<i>Gyps fulvus</i>	0.097529354	182	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	7435.99
Accipitriformes	<i>Milvus milvus</i>	0.096220203	185	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1071.77
Strigiformes	<i>Strix uralensis</i>	0.090361651	194	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	780.56
Strigiformes	<i>Tyto alba</i>	0.090361651	195	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	403.32
Anseriformes	<i>Aythya nyroca</i>	0.083975601	204	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	574
Falconiformes	<i>Falco peregrinus</i>	0.080626931	219	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	759.95
Accipitriformes	<i>Aquila chrysaetos</i>	0.07718719	224	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	4247.97
Anseriformes	<i>Oxyura leucocephala</i>	0.073666105	231	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	661.09
Accipitriformes	<i>Accipiter gentilis</i>	0.072562924	238	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	866.04
Galliformes	<i>Alectoris rufa</i>	0.066852209	258	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	527.86
Ciconiiformes	<i>Ciconia ciconia</i>	0.066652881	259	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	3445.8
Galliformes	<i>Perdix perdix</i>	0.062266745	276	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	405.3
Galliformes	<i>Tetrao tetrix</i>	0.053843881	298	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	1068.66
Galliformes	<i>Coturnix coturnix</i>	0.047042809	313	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	96.28
Accipitriformes	<i>Circus pygargus</i>	0.045276175	318	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	310.75
Passeriformes	<i>Emberiza cirius</i>	0.022252314	377	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	25.6



# Chapter 3: *Heterogeneity in the allocation of reintroduction efforts: review of the implementation of mammalian reintroductions in Europe*

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## **Context:**

Studies investigating taxonomic biases in the allocation of reintroduction efforts at large scale generally consider taxonomic bias within and among higher taxa (e.g. vertebrates, plants), and compare the number of reintroduced species within a taxa to its prevalence in nature. This approach is likely to underestimate biases because the number of implemented projects may greatly vary between species in a given taxonomic group. Here we focused on 28 previously identified reintroduced species of mammals, and performed a more in-depth search of the academic and grey literature in order to inventory past and current reintroduction projects in Europe. We assess the variation in reintroduction effort between species using the number of implemented programs and the number of publications as proxies.

## **Key findings:**

Our search of the literature yielded more than 1600 references. We found 413 relevant publications, from which we described 375 reintroduction programs of mammals implemented in 28 European countries from the early 20<sup>th</sup> century to 2013. More than 60% of all identified reintroduction programs of European mammals involved the beaver (*Castor fiber*), the Alpine ibex (*Capra ibex*) or the European bison (*Bison bonasus*).

We show a striking heterogeneity in reintroduction efforts among reintroduced mammals. Our results show that Carnivores are not over-represented when accounting for the number of implemented programs, although reintroductions of Carnivores seem to be associated with more publications.



# Heterogeneity in the allocation of reintroduction efforts among terrestrial mammals in Europe

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Key words: Conservation translocations | Reintroductions

## Abstract

Reintroductions offer a powerful tool to reverse adverse anthropogenic impacts on biodiversity by restoring extirpated populations within the indigenous range of species. Reintroductions have become popular, and have been increasingly used over the last decades. However this species-centred conservation approach has been criticized for being taxonomically biased and for focusing on large and charismatic species. Studies investigating taxonomic biases in the allocation of reintroduction efforts at large scale generally consider taxonomic bias within and among higher taxa (e.g. vertebrates, plants), by comparing the number of reintroduced species within a taxa to its prevalence in nature. Here, we show that the bias is even more striking when accounting for the differences in the number of implemented programs among reintroduced species. We conducted a comprehensive search of the peer-reviewed and grey literature to inventory reintroduction programs of European terrestrial mammals. Based on previous work, we identified 28 species that have been reintroduced a least one time. For each reintroduced mammal, we extensively searched two literature search engines (ISI Web of Science database and Google Scholar) and found 413 relevant publications, which described 375 distinguishable reintroduction projects implemented in Europe from the early 20<sup>th</sup> century to 2013. We used the number of implemented programs and the number of associated publications to investigate the distribution of reintroduction efforts among species. Our results show a substantial heterogeneity in the allocation of reintroduction efforts, with 68% of implemented

reintroductions in Europe involving beavers (*Castor fiber*), Alpine ibex (*Capra ibex*) and European bison (*Bison bonasus*) (164, 54 and 39 projects respectively).

## Introduction

Biodiversity is under more severe threats than perceived when considering population declines and losses at a global scale, rather than focusing only on species extinction (Ceballos et al., 2017). Effective conservation strategies are therefore required to reverse the dramatic shrinkage in species' geographical ranges, in order to support evolutionary trajectories in biological systems, as well as sustainable ecosystem functioning and services (Sarrazin and Lecomte, 2016). Reintroduction, the process of re-establishing a population in the indigenous range of a species where it has been extirpated, is a popular conservation tool, as it goes beyond the traditional approach aiming at reducing adverse anthropogenic impacts on biodiversity, and moves forward to the proactive return of species in the wild where they have disappeared. Reintroductions have been used for over a century, and the number of implemented programs, as well as the number of species involved have increased exponentially over the past decades.

Besides issues related to the success of local reintroduction programs (Robert et al. 2015), an important concern of reintroduction biology is whether the accumulation of local reintroduction efforts have the potential to benefit to a wide array of biodiversity at large taxonomic scale, which is not possible if most programs focus on e.g. a few charismatic species. Using a database of reintroduction projects worldwide, yielding a total of 699 reintroduced species of plants and animals, Seddon et al. (2005) showed that vertebrate projects were over-represented with respect to their prevalence in nature. Among them, the reintroduced species were mostly mammals and birds, whereas fish were under-represented. More recently, we showed similar biases within reintroduced mammals in Europe, with a disproportionate list of reintroduced Carnivores and Ungulates relative to their prevalence in the European assemblage of terrestrial mammals (Thévenin et al., 2018). While these studies brought important insights into taxonomic and phylogenetic patterns of reintroductions, which are necessary to appreciate potential biases in reintroduction efforts, they did not consider the differences in the implementation of individual population restoration projects.

Here we provide a more in-depth look at the distribution of the number of implemented reintroduction programs per species. We focused on a list of 28 species of European terrestrial

mammals that we identified as reintroduced at least once (Thévenin et al. 2018). For each species, we searched the ISI Web of Knowledge database and used Google Scholar search engine to identify reintroduction projects implemented over the past century. We describe the heterogeneity in the implementation of population restoration projects and their reporting among European reintroduced mammals. The dataset we compiled allows to explore the temporal and geographic distribution of reintroduction efforts in Europe.

## Materials and Methods

Our primary objective here was to make an inventory of reintroduction “programs” and considered that a “program” should correspond to one re-established population or meta-population. We performed a comprehensive search (Swan et al., 2016) of the reintroduction and translocation-related literature to identify past and ongoing reintroduction programs implemented in the European subcontinent, including the western part of Russia and excluding Turkey. Using a list of 28 previously identified reintroduced species among the IUCN list of 202 native European terrestrial mammals (Thévenin et al., 2018), we performed independent queries for each species using the ISI Web of Science database, including all indexed literature. Because substantial information about translocation projects can be found in the grey literature, we also run each query on Google Scholar and searched for additional references in the 50 first records. We performed this search in the spring of 2016, and took into account all published records available online up to May 1<sup>st</sup> 2016. Our search terms were selected to maximize specificity at the expense of sensitivity, in order to focus on reintroductions and avoid publications relating to supplementations of existing populations or mitigation translocations used to manage human-wildlife conflicts (Table 1). To account for potential taxonomic revisions over time and the fact that the species’ name used by the authors at the time of publication may no longer correspond to the current name, the species search terms included both the Latin name and English common name along with all relevant synonyms available on the “Taxonomy” tab of the Species Fact Sheet provided by the IUCN Red List website (available at [www.iucnredlist.org](http://www.iucnredlist.org)). For example the species search terms used for identifying translocations of Water voles (*Arvicola amphibius*) included the following terms: “European Water Vole” OR “Eurasian Water Vole” OR “Water Vole” OR “*Arvicola amphibius*” OR “*Arvicola terrestris*” OR “*Mus amphibius*”.



*Table 1: List of the terms used to identify reintroduction programs for native terrestrial mammals in Europe*

<b>Category</b>	<b>Search Term</b>
<b>Species</b>	Latin name OR synonym(s) OR Common name(s)
<b>Translocation</b>	reintroduc* OR re-introduc* OR translocat* OR re-establish* Or releas* OR relocat*
	AND
<b>Motive</b>	population* OR conserv* OR restorat*
	AND
<b>Location</b>	Europe*

*Terms were used in the ISI Web of Science database and Google Scholar search engine to identify documented reintroduction programs. \*Indicates the use of a wildcard; for example, reintroduc\* can refer to reintroduction OR reintroductions OR reintroduce OR reintroduces OR reintroduced OR reintroducing.*

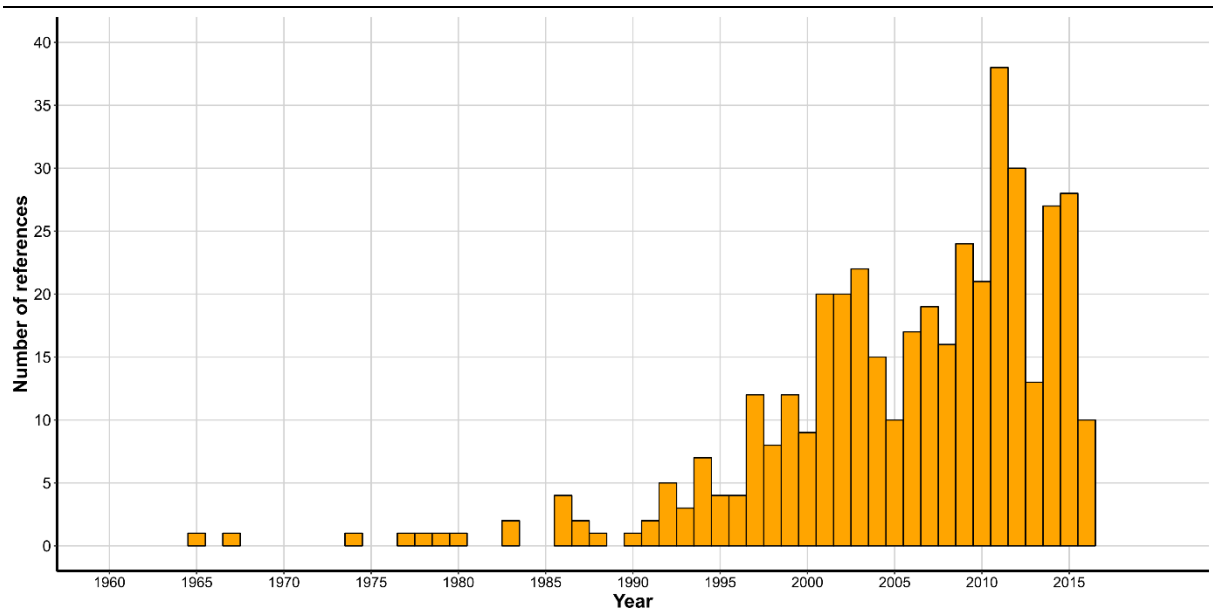
We accurately screened each publication to determine which publications were relevant, that is, which described at least one program of translocation and release of individuals that we considered to be a reintroduction based on the intent and location of releases, i.e. the attempt to re-establish a free-ranging population in the former range of the species where it has been extirpated (IUCN/SSC, 2013). Sometimes the full text was not accessible, but we included the publication if we could unambiguously extract all relevant and necessary information from the abstract. If a publication describing a reintroduction failed to provide the basic information (e.g., approximate year of first release) but explicitly mentioned other publications containing complementary information regarding the project, we extended our search to such cited literature. Some publications mentioned or described multiple reintroductions programs for a single species, usually reviewing the recovery of the focal species through time (e.g., Biebach & Keller, 2012). In that case we considered the list of programs as described in such publication. Most of the publications we screened focused on a single species, with only seven publications mentioning or describing reintroduction projects for more than one species. Reintroductions of mammals often involve game species (Griffith et al., 1989), and it was sometimes difficult to fully grasp whether the main purpose of the translocation would lean towards species exploitation rather than long-term conservation. Such cases where conservation did not seem

to be the primary objective of releases were considered as restocking translocations and not integrated in our data. Some reintroductions of potential game species were included when they clearly aimed at restoring a viable population in the wild.

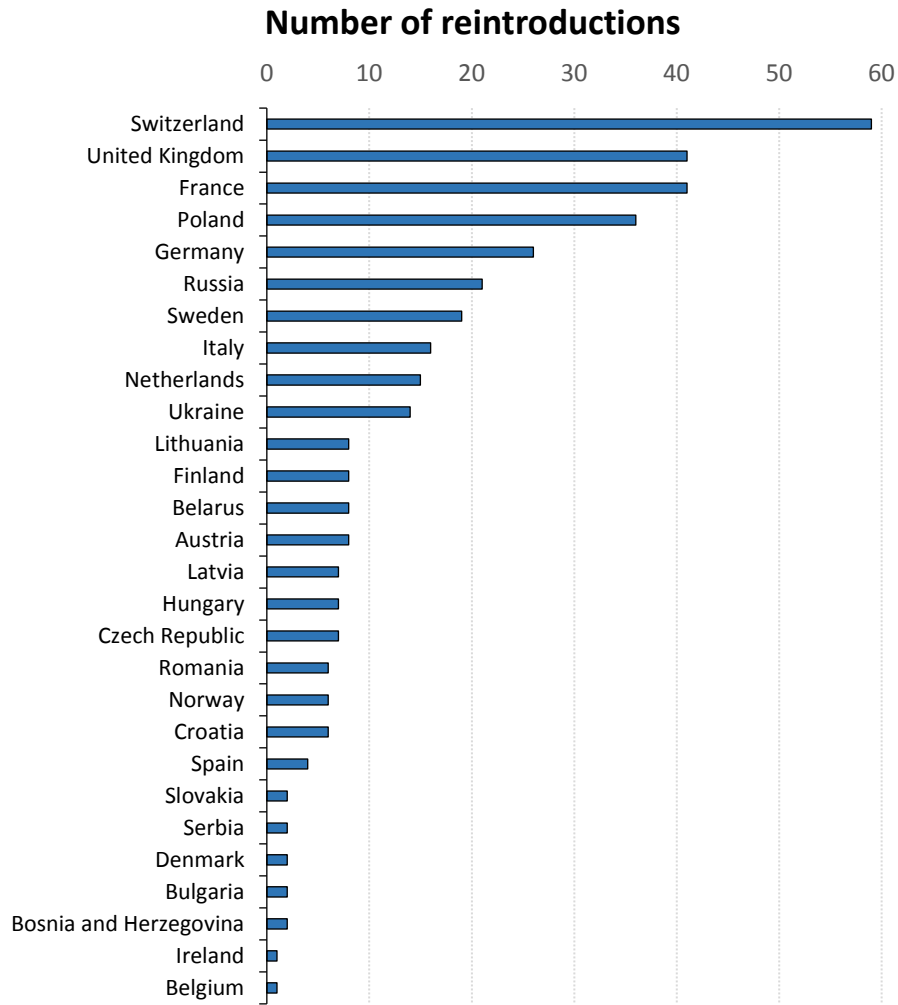
For each relevant publication, we extracted the year of publication, type of conservation translocation, species translocated, approximated year of first release, country and location of releases. The location of releases refers to the most precise sub-national geographic area encompassing the translocation site, and the precision varied substantially between publications (e.g., province, national park, nearest town). Some publications did not provide a precise date of first release, but rather a time interval, for which in the absence of additional information, we deduced the year of first release as the middle of the given period (e.g., if individuals were “released in the 1970s”, we considered the first year of release to be 1975). In some cases multiple releases were clustered into a single reintroduction program if we deemed the different release events to contribute to the same population unit, based on the location of releases and expected home range of the species.

## **Results**

Our searches on Web of Science yielded 1665 unique references, and we found 318 relevant references that described reintroduction projects precisely enough (year of first release, country and location of release site). We found 96 additional relevant references through our search on Google Scholar, or by extending our search to the cited references of some articles. These 413 publications, published between 1965 and March 2016, described 375 distinguishable reintroduction projects implemented in 28 European countries between 1910 and 2013. The number of relevant publications increased over the past 30 years (Figure 1). Reintroductions projects were implemented in 28 European countries, and most of these programs were undertaken in Switzerland (61), France (41), the United Kingdom (41) and Poland (36) (Figure 2).



*Figure 1: Temporal distribution of the 413 relevant publications used to describe reintroduction projects for native European terrestrial mammals. The number of references in 2016 only accounts for publications between January and March.*



*Figure 2: Number of reintroduction projects by countries in the European subcontinent.*

The allocation of reintroduction efforts per species is highly heterogeneous, with the number of programs ranging from only one reintroduction up to 164 (Figure 3). Only six out of 28 species were involved in more than ten reintroduction attempts, and the median number of reintroduction programs per species is three. The beaver is the most reintroduced mammal in Europe, and has been involved in more than 40% of all the reintroduction attempts we identified, followed by the Alpine ibex (54 programs, 14%) and the European bison (39 programs, 10%). The reporting effort per species was evaluated by considering the ratio of the number of publications over the number of programs for each species. Low values of this ratio indicate that relatively few publications described numerous reintroduction programs. This is the case for the 5 most reintroduced species in our dataset (*Castor fiber*, *Capra ibex*, *Bison bonasus*, *Muscardinus avellanarius*, *Arvicola amphibius*), with the lowest ratio being the Alpine ibex with 54 reintroduction attempts described using only 15 publications (ratio = 0.28).

In contrast, some species have generated a substantial amount of publications relative to the number of releases, as exemplified with 5 reintroduction projects of brown bears being described in 27 publications (ratio = 5.4). When considering the taxonomic distribution of reintroduction programs within the different orders of terrestrial mammals of Europe, we found that Rodents and Ungulates are over-represented, totalling 60% and 30% of reintroduction projects, respectively, while representing 42% and 6% of native European terrestrial mammal species (Figure 4).

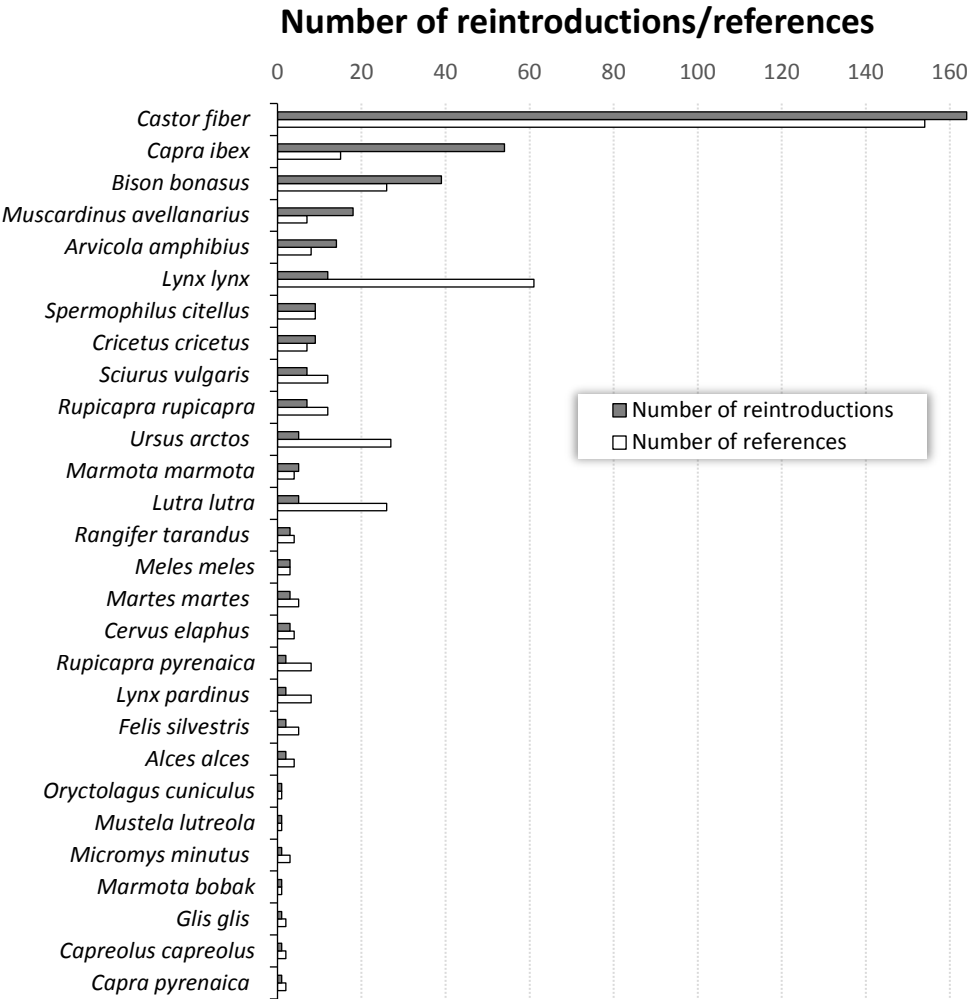


Figure 3: Number of reintroduction projects (dark grey bars) and associated references (white bars) for the 28 terrestrial mammals reintroduced in Europe. Because some publications described reintroductions for different species, the total number of references here is larger than the number of unique references.

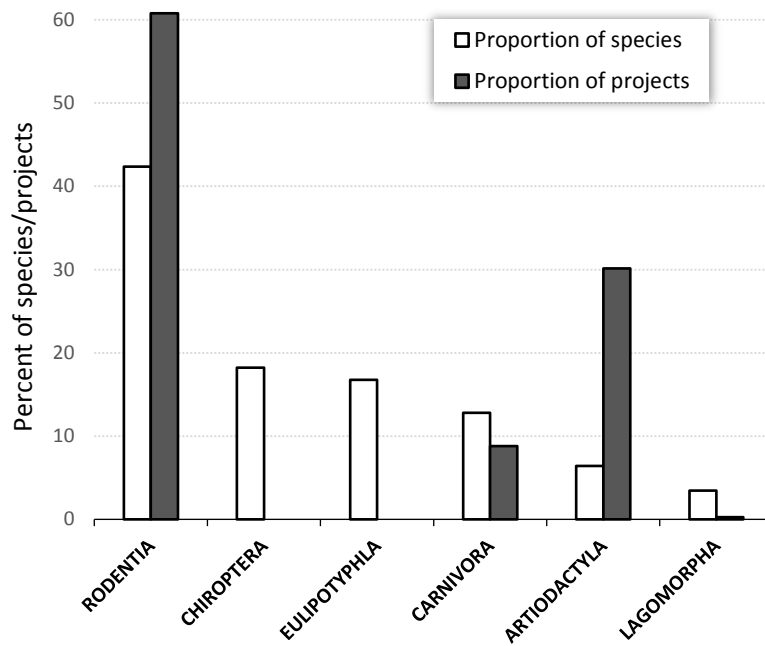


Figure 4: Proportion of reintroduction projects per taxonomic order of terrestrial mammals (dark grey bars) compared to the proportion of species out of the 202 European terrestrial mammals (white bars).

The two oldest programs in our data are the reintroduction of the red squirrel (*Sciurus vulgaris*) into Epping Forest, Ireland, in 1910 (MacKinnon, 1978), and the reintroduction of the Alpine ibex (*Capra ibex*) in Graue Hoerner, Switzerland, which started in 1911 (Biebach and Keller, 2012; Stüwe and Nievergelt, 1991). The number of reintroduction programs has increased throughout the time period (Figure 4), and the apparent diminution in the number of reintroduction programs from 2006 onward can be attributed to a time lag between releases, data collection and any associated publication (Fazey et al., 2005; Swan et al., 2016). For most of the first half of the 20<sup>th</sup> century (up to the late 1950s), reintroductions of terrestrial mammals in Europe essentially involved beavers or Alpine ibex (51 and 28 programs respectively, out of 86). The other species reintroduced in this time period are the above mentioned red squirrel, the elk (*Alces alces*; Schönfeld, 2009; Świsłocka et al., 2013), the brown bear (*Ursus arctos*; Buchalczyk, 1980) and the reindeer (*Rangifer tarandus*; Røed et al., 2014). When considering the 3 mostly reintroduced species in our data, we can see that beavers have benefited from a consistent and continuous reintroduction effort throughout the entire time period considered (Figure 5). Reintroductions of Alpine ibex are more clustered in the first half of the time period considered (the last release in our dataset occurred in 1995) and most of the restoration of free-

ranging populations of the European bison has taken place in the past 60 years (Kraśńska and Kraśński, 2013).

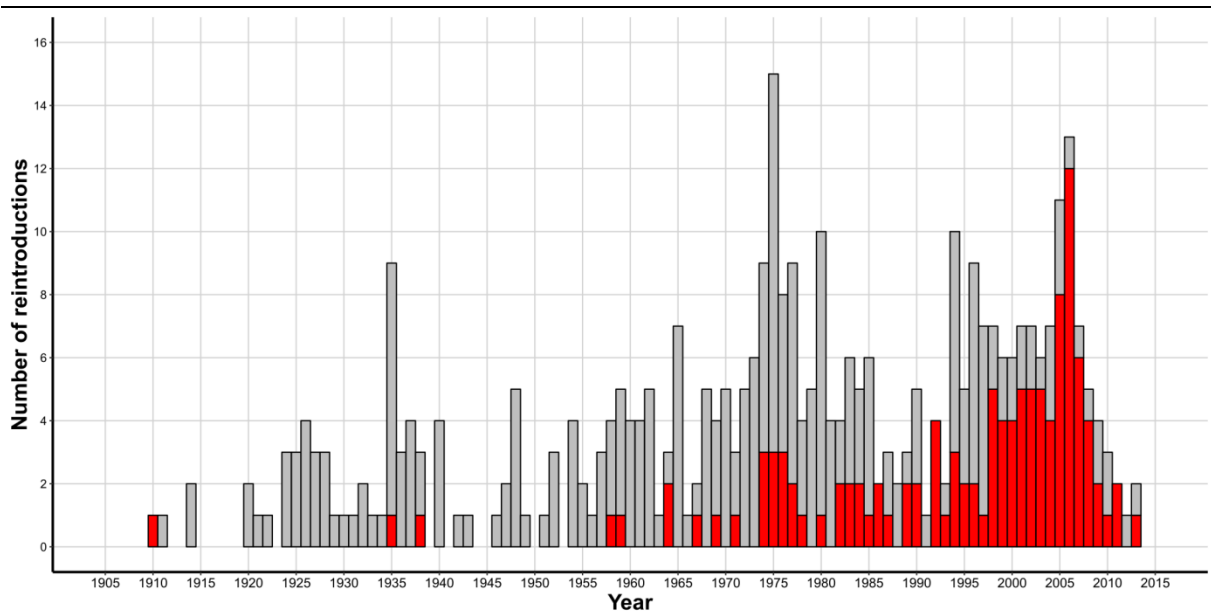


Figure 5: Stacked histogram of the temporal distribution of the 375 reintroduction projects for native European terrestrial mammals, based on approximate date of first release. Grey bars represent reintroductions of beavers, European bison or Alpine ibex ( $n = 257$ ). Red bars represent reintroduction projects for the remaining 25 species ( $n = 118$ ).

During our search we identified 144 additional translocations for which the ultimate objective was not clearly leaning toward conservation, but rather toward hunting purposes. Because of the uncertainty we did not integrate these programs as reintroductions in our dataset. These translocations mostly involved the red deer (*Cervus elaphus*, 69 translocations) and the roe deer (*Capreolus capreolus*, 54 translocations).

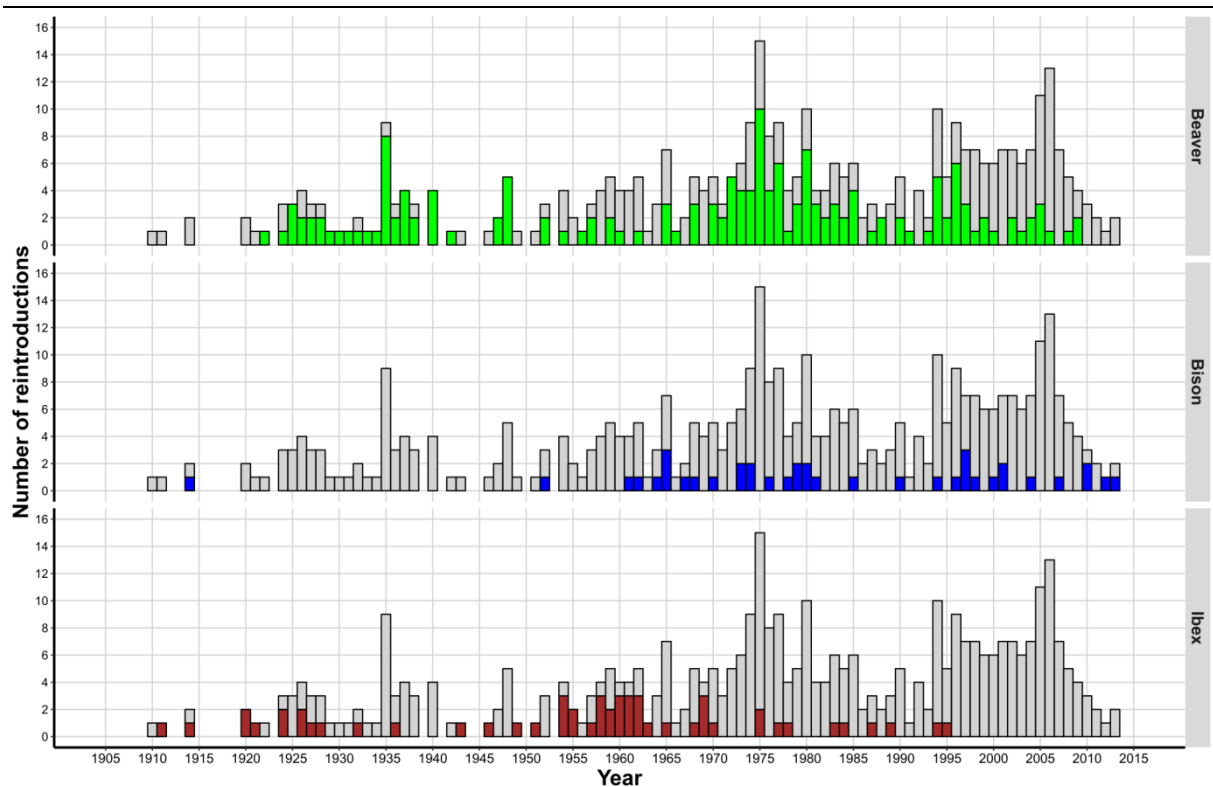


Figure 6: Stacked histograms of the temporal distribution of reintroduction projects of the beaver (green bars,  $n = 164$ ), European bison (blue bars,  $n = 39$ ) and Alpine ibex (brown bars,  $n = 54$ ), based on approximate date of first release.

## Discussion

Our results show that the heterogeneity in the allocation of reintroduction efforts is more striking when accounting for the number of implemented projects among reintroduced species. The most reintroduced species in our dataset are the beaver, the Alpine ibex and the European bison, for which the main cause of population extirpation was overhunting. Of all reintroduced mammals, the remarkable recovery of European beavers undeniably benefited from widespread reintroductions. At the end of the 19<sup>th</sup> century, the species was reduced to about 1200 individuals scattered in 8 small relict populations and would have been listed then as critically endangered (Halley et al., 2012). Reintroductions started in 1922 in Sweden and were later implemented in 20 other European countries. Early successes with remarkably little planning or monitoring confirmed the beaver as a reliable candidate for reintroductions, and may have triggered a self-reinforcing feedback for more implementations of programs over the years (Halley and Rosell, 2002). Incentives for restoring populations of beavers were initially related



to fur-harvesting, and later reintroductions became more motivated by ecosystem management reasons. The beaver is considered to be a key-stone species, which will substantially impact the structure and dynamics of aquatic ecosystems at the landscape level. Beaver's dams will influence the hydrology of surrounding areas, thus altering nutrient cycles and will subsequently modify the structure of invertebrate and plant communities (Macdonald et al., 1995). Such prominent and well-documented functional role of the species in its recipient ecosystem may have played a role in the disproportionate, large scale effort that was invested into its restoration.

Considering the number of implemented programs allows to reinterpret reintroduction biases between mammalian orders in Europe. Previous studies have shown that, among mammals, Carnivores and Ungulates are over-represented in reintroduction efforts (Seddon et al., 2005). More than half of the reintroduced species of mammals in Europe are members of the Artiodactyla or the Carnivora orders, although these orders represent less than 20% of species in the European assemblage of native mammals (Thévenin et al. 2018). However, when accounting for the number of implemented programs, the pattern is clearly maintained for Ungulates (30% of implemented programs), but Carnivores are no longer over-represented (8% of implemented programs). On the other hand, Rodents account for 42% of all native European terrestrial mammals, and here we found that 60% of reintroduction projects of European terrestrial mammals targeted rodents.

High numbers of reintroduction projects are associated with relatively similar numbers of publication, but our results suggest that some reintroduced species are relatively more reported in the literature. The species with the most imbalanced ratio of the number of publications over the number of associated publications are the Eurasian lynx (*Lynx lynx*), the brown bear (*Ursus arctos*) and the otter (*Lutra lutra*). Predators are charismatic species that are often employed in conservation because they can easily gather public interest (i.e., “flagship species”, *sensu* Simberloff 1998), and such societal preferences may influence the choice of study species and lead to more publications. Even though large carnivores are now recovering throughout Europe thanks to favourable legislation and increases in prey availability (Chapron et al., 2014), the reintegration of such large predators comes with many challenges that may require making adjustments to the practices of some sectors like agriculture, forestry or hunting (Boitani and Linnell, 2015; Breitenmoser et al., 2010). Restoring populations of large predators where they have been extirpated constitutes a major challenge if adaptations to coexistence have been lost and if husbandry practices have evolved. Reintroductions of top predators can have economic

costs (e.g., predation on livestock) and trigger social conflicts. This human aspect needs to be carefully addressed and managed (Stahl et al., 2001), which is likely to generate additional research and publications.

Our search of the literature is certainly not exhaustive, but we believe that our data provide a good and representative proxy of the allocation of reintroduction efforts for European terrestrial mammals. Publication biases in conservation and reintroduction research have been documented (Bajomi et al., 2010; Clark and May, 2002; Fazey et al., 2005; Fischer and Lindenmayer, 2000; Miller et al., 2014; Troudet et al., 2017), and show that some species receive disproportionate attention, and that successful translocations are more likely to be published than failed ones or those with uncertain outcomes. While our results provide a highly indicative description of reintroduction efforts for native European terrestrial mammals, we acknowledge that our data mostly reflect publication effort, and are likely to underestimate the number of programs implemented throughout Europe. Another issue lies in the access to past publications, and how terminology evolved over the years. Some documentation of reintroduction attempts implemented several decades ago may have yet to be digitalized and indexed, and programs that have been recently implemented might not have yet been described in the literature. Additionally, reporting of reintroduction efforts at a continental scale is challenged by gaps and heterogeneity in the collection and compilation of information related to restoration attempts. First, language may greatly influence the spatial distribution of our European data. We only considered sources written in English, and we suspect that we might have missed a substantial amount of information written in the native language of the reintroduction team. For example our search yielded 4 reintroduction programs in Spain over the last century, while Perez et al., (2012), who conducted an extensive review of translocations projects in Spain, taking into account Spanish language documentation, found 9 translocation projects implemented from 1996 onwards. Studies have shown that the availability of information on biodiversity is unevenly distributed around the world (Boakes et al., 2010), and that the wealth of a country as well as the proportion of English speakers are positively associated with data availability (Amano and Sutherland, 2013). The high number of reintroductions found in the United Kingdom can also be explained by insularity, as species will have lower probabilities of natural recolonization after extinction, so that reintroduction becomes a valuable conservation option. The spatial distribution of our data is also greatly influenced by previous compilations and reviews of reintroduction projects in some areas. For example, 48 out of the 59 reintroductions identified in Switzerland involved the Alpine ibex,

and 40 of these were mentioned in Biebach & Keller (2012). Similarly, 23 out of the 36 reintroduction projects we identified in Poland involved the beaver, which were all mentioned in a study on the expansion of the species in Europe by Kasperczyk (1987).

Over the past thirty years, the development of reintroduction biology has advocated for an improvement of reintroduction practice and implementation, and managers need to collect and use all available information to improve reintroduction design and benefit from knowledge accumulated through past attempts to restore populations (Armstrong and Seddon, 2008; Ewen and Armstrong, 2007; IUCN/SSC, 2013; Sarrazin and Barbault, 1996). One important challenge is therefore to enhance the documentation and transmission of knowledge from past reintroduction programs. Some species, or groups of species (e.g. carnivores) of mammals have benefited from reviewing efforts describing and inventorying reintroduction projects in Europe (Clark et al., 2002; Halley and Rosell, 2002; Krasieńska and Krasieński, 2013; Stüwe and Nievergelt, 1991). Our data constitute a core contribution to the development of a webdatabase inventorying conservation translocation projects in Europe and the Mediterranean basin which will promote standardization in reintroduction reporting to improve their adaptive management (TRANSLOC webdatabase project, <http://translocations.in2p3.fr/>).

In this study we used the number of implemented programs and the number of associated publications to estimate the reintroduction effort per species. This is only one way to assess how resources are distributed in population restoration projects, and further studies are needed to explore other aspects such as the financial costs of programs, information on release strategies (number of individuals and number of release events), or how much effort was invested to insure habitat quality before release.

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# Chapter 4: *A unified demographic approach of reintroduction success assessment*

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**Context:**

Reintroduction is a popular tool for conservation; however, it lacks a shared, univocal, quantitative and operational framework for the definition of reintroduction success. Nevertheless, any improvement of reintroduction outcomes relies on our ability to identify correlates of success and failure considering a variety of reintroduction scenarios. This requires the development of a clear definition of success criteria, applicable to the largest range of species, life histories, management techniques, environmental conditions and conservation contexts.

**Aim:**

Our purpose here is to present a general demographic framework to identify key processes involved in reintroduction dynamics and viability, and to define metrics to assess reintroduction outcome and outputs.

Here, we argue that a unified demographic framework that accounts for establishment, growth and regulation phases that shape translocated population's dynamics and viability may provide a strong theoretical basis for developing a coherent and comprehensive set of reintroduction success criteria and metrics. We also argue that beyond assessing the actual achievement of each phase, the *a priori* definition of the practitioner's expectations for their realisation is of first importance to evaluate the efficiency of any reintroduction program.

We do not aim to propose a new or alternative view on the issue, but rather we show that a demographic framework based on population viability may allow using a shared language and unifying current views on reintroduction success assessments in the larger context of species conservation and recovery.



# A unified demographic approach of reintroduction success assessment

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## Abstract

Defining the success of reintroduction is an endless debate due to the intrinsically transient and non-equilibrated dynamics of any translocated population. Additionally the time, spatial and abundance scales to measure this success are necessarily idiosyncratic according to taxa and environment. It is however of crucial importance locally and globally, firstly to put reintroduction practice in an adaptive management context, secondly to improve the understanding of key processes underlying reintroduction success and finally to actually reconnect reintroduction projects to the recovery of threatened biodiversity through their contribution to the improvement of the conservation status of focal species. According to the numerous literature on reintroduction monitoring and success assessment, we propose a unified framework to share a common language among reintroduction practitioners. This framework aims i) to define potential reintroduction expectations based on a priori data and scenarios of outputs and outcomes; ii) to structure milestones of reintroduction monitoring; iii) to classify levels of reintroduction achievements that account for establishment, growth and regulation of reintroduced populations; and iv) to propose metrics of reintroduction efficiency. Beyond reintroduction, this framework appears relevant for a large range of conservation translocations.

## **Reintroductions need standardized success criteria**

Conservation translocations are the human-mediated transfer of individuals from one area to another where the main goal is to yield a quantifiable conservation benefit (IUCN/SSC, 2013). Reintroductions are part of the conservation translocation spectrum, and aim to re-establish a population within the indigenous range of the focal species following local extinction, through the release of a limited number of individuals. Reintroductions have been widely used for over a century and in many parts of the world (Brichieri-Colombi and Moehrensclager, 2016; Jachowski et al., 2016; Seddon et al., 2014a; Thévenin et al., 2018), and the number of implemented programs has increased exponentially over the past decades (Seddon and Armstrong, 2016). Reintroduction is an emblematic proactive tool of the conservation arsenal. However its efficacy is subject to debate since costs are generally high (Helmstedt and Possingham, 2017) and conservation gains are suspected to be limited due to a potentially high rate of failure (Seddon and Armstrong, 2016). Over the last decades, numerous authors have advocated for improved implementation, monitoring and evaluation of reintroductions (Armstrong and Seddon, 2008; Gitzen et al., 2016; Parker et al., 2013; Sarrazin and Barbault, 1996; Sutherland et al., 2010). However, while ecological restoration has generated a well-structured framework to identify the attributes of restored ecosystems relying on six criteria (absence of threats, physical conditions, species composition, structural diversity, ecosystem functionality, external exchanges; (McDonald et al., 2016), there is currently no similar unified framework for restored populations. The Reintroduction Specialist Group of the International Union for the Conservation of Nature (RSG /IUCN) proposed significant guidelines to carefully design programs and achieve successful operations (IUCN/SSC, 2013, 1998). However, it did not provide a shared, univocal, quantitative and operational framework for the definition of reintroduction success and let it under the responsibility of each reintroduction practitioners and the pressure of their local context.

The fundamental purpose of developing a standardized definition of reintroduction success is to avoid case-specific rules of thumb that prevent cross-taxa applicability and comparison between programs, as well as potential bias in reintroduction publications (Miller et al., 2014). Incentives for measuring reintroduction success are diverse, whether it focuses on case-study evaluations, the measure of success rates among multiple projects, or the identification of shared underlying mechanisms. Therefore, it seems that there is a multitude of conflicting

approaches to the definition of reintroduction success (Chauvenet et al., 2016; Moseby et al., 2011). Nevertheless, any improvement of reintroduction outcomes relies on our ability to identify correlates of success and failure considering a variety of reintroduction scenarios. This requires the development of a clear definition of success criteria, applicable to the largest range of species, life histories, management techniques, environmental conditions and conservation contexts.

First, it is a prerequisite to setting the conservation translocation cycle (IUCN/SSC, 2013) into an adaptive management approach (IUCN/SSC, 2013; McCarthy et al., 2012; McCarthy and Possingham, 2007; Sarrazin and Barbault, 1996). Indeed, the assessment of each step of this cycle – i.e. evaluation of conservation situation, definition of goal, evaluation of alternatives, decision to translocate, design, implementation, monitoring, outcome assessment and dissemination - requires clear definitions, not only of the ultimate outcome, but also of step by step outputs to drive efficiently each reintroduction on the short and long terms.

Second, on a wider scale, defining reintroduction success is essential to make reintroduction biology relevant (Armstrong and Seddon, 2008; Taylor et al., 2017). It would help to set up reintroductions as experiments (Armstrong et al., 1995; Armstrong and Seddon, 2008), for both conservation priorities and “acid tests” in basic ecology (Sarrazin and Barbault, 1996). It would facilitate meta-analyses by improving comparability across translocation programs, studies and species. Currently, meta-analyses often suffer from some noise arising from *ad hoc* definitions of success, impeding rigorous inter-program comparisons (Dalrymple et al., 2012). While unified standard for reintroduction monitoring is crucial (Gitzen et al., 2016; Sutherland et al., 2010), adopting a unified definition of reintroduction success based on standardized criteria is prior key to understand the basic processes involved in reintroduction dynamics as well as to assess the efficiency of management practices within an evidence-based conservation approach (Pullin et al., 2004; Pullin and Knight, 2003; Sutherland et al., 2004).

Third, and most importantly, it is crucial to truly reconnect reintroductions to large scale conservation issues (Robert et al., 2015a). Indeed, the actual impact of reintroductions to species conservation and recovery must be assessed in a sort of global adaptive management loop embracing the choice of candidate species. Recently, Akçakaya et al. (2018) proposed a global definition of species recovery and conservation success that emphasizes viability, ecological functionality and representation. This definition relies on the use of four metrics including conservation legacy, conservation dependence, conservation gains and recovery

potential. If reintroductions aspire to contribute to large-scale species conservation and recovery, we must define reintroduction success coherently with these ultimate aims. Some reintroduction programs support the whole representation of a given species (e.g. California condors; Conrad, 2018) whereas many others intrinsically contribute to restore a small portion of this representation. The comparison of the level of reintroduction success should thus not rely on representation *per se*. However, in any case, viability and functionality need to be considered even at local levels. Since functionality largely depends on population abundance, which in turn affects population viability, restoring viable populations constitutes a primary objective for any successful reintroduction. Although this principle was advocated in the reintroduction arena far before the global recovery proposal by Akcakaya (2018), and most authors now agree upon the fact that the fundamental aim of any reintroduction should be to establish a viable population (IUCN/SSC, 2013), its implementation remains largely challenging due to intrinsically transient dynamics of reintroduced populations.

Throughout the paper, we make an important distinction between reintroduction outputs and outcomes. Outputs refer to what the program has achieved in the short-term, and provide tools to track and quantify change in order to assess the progress of a given program in real time. They can indicate whether a program has met its specific objectives, which is the fundamental basis for the application of an adaptive management framework (Chauvenet et al., 2016). Reintroduction outcomes refer to the long-term conservation benefits of the program, and focus on the improvement of the conservation status at population, metapopulation and species levels, i.e. to conservation legacy (Akçakaya et al., 2018). Our purpose is to present a general demographic framework to identify key processes involved in reintroduction dynamics and viability, and define metrics of outcome and outputs relevant for reintroduction monitoring and success assessment whatever the translocated taxon.

## **Towards a unified framework for the demographic assessment of reintroduction success**

Similarly to species recovery (Akçakaya et al., 2018), there is a consensus to diagnose a reintroduction failure when the expected reintroduced population is actually extinct. Yet, the

definition of the extent to which a program is successful is often weak and this weakens the robustness of reintroduction assessment and understanding. There have been numerous attempts to define reintroduction success criteria or proxies (Chauvenet et al., 2016; Fischer and Lindenmayer, 2000; Miller et al., 2014; Ostermann et al., 2001; Parlato and Armstrong, 2018; Pavlik, 1996). The evaluation of success has generally relied upon surveys or subjective assessments from managers based on specific objectives and indicators (Brichieri-Colombi and Moehrenschrager, 2016; Ewen et al., 2014). The former IUCN Guidelines for Reintroductions (IUCN/SSC, 1998) recommended restoring a “self-sustaining population”. In the seminal papers by Griffith et al. (1989), and Wolf et al. (1998, 1996), project managers themselves answered questionnaires on their local assessment of “the creation of a self-sustaining population” and the quality of the target environment. However, this criterion did not rely on sharply defined indices and a manager that considered his reintroduced population as self-sustaining was likely prone to declare that habitat quality was good or excellent there. Other reviews tried to combine the information available within papers, (i.e., managers’ perception of population sustainability) with other indicators of population establishment (Cochran-Biederman et al., 2015; Godefroid et al., 2011). Self-sustainability was often inconclusive since it did not provide clear sustainability thresholds and it was often unclear if the persistence of the population no longer relied on any form of management (Seddon and Armstrong, 2016), i.e. without conservation dependence (Akçakaya et al., 2018). To cope with the first argument, Sarrazin and Barbault (1997, 1996) proposed to reconnect reintroduction to the population viability framework that benefited early from massive theoretical and empirical approaches in population biology (Beissinger and McCullough, 2002; Morris and Doak, 2002; Soulé, 1987). They acknowledged that a common agreement of extinction risk or minimum population size had to be found for reintroductions and suggested to take inspiration from the IUCN Red List criteria for threatened species that are largely applied across taxa (Mace and Lande, 1991). Thereafter Sarrazin (2007) advocated for a demographic framework and the use of IUCN red list criteria once reintroduced population is regulated. Moehrenschrager et al. (2013) made recommendation for assessing the contribution of reintroductions to species conservation through such criteria, and their relevance was assessed through modelling (Robert et al., 2015a). The recent framework by Akçakaya et al. (2018) is consistent with this proposal since they build a Green list of recovered species based on Red list criteria for population viability.

However, the use of standardized criteria to regularly reassess the success of one reintroduction or compare several projects remains a challenge for various reasons. Seddon (1999) pointed out



that variation in life history traits between target species limits the general usefulness of any one criterion, and that, by any criteria, the definition of a successful program is limited in time. Much of the disagreements in the development of standardized criteria thus lies in the definition of the key concepts underlying reintroduction success criteria. Clearly, any simple quantitative criteria linked to absolute values of population size or population growth rate is taxon, environment and management dependant. However, if the actual realizations of any population dynamics are idiosyncratic, the demographic processes involved and the way they drive these dynamics are largely shared among taxa and environments. In the same way, accounting for the time scale of success assessment must be at the core of any standardization of reintroduction success (Miller et al., 2014). Looking for a unique success criterion is thus pointless and a set of complementary criteria is necessary to embrace this intrinsic complexity.

Here, we argue that a unified demographic framework that accounts for the disequilibria that shape translocated population's dynamics and viability may provide a strong theoretical basis for developing a coherent and comprehensive set of reintroduction success criteria and metrics. We also argue that beyond the assessment of each success criterion, the *a priori* definition of reintroduction practitioner's expectations is of first importance to evaluate the efficiency of any reintroduction program along its path. We mostly focus on the biological success of reintroductions, i.e. the progress toward the ultimate improvement of the reintroduced population conservation status, which can be discriminated from project success, i.e. the project's achievements in terms of, e.g., local community involvement, policy or education independently of biological success (Pavlik, 1996). Indeed, analysing and modelling the dynamics and viability of the reintroduced populations is a powerful approach that actually integrates the positive or negative consequences of such project achievements on the survival, reproduction and dispersal of released individuals and their following generations (Sarrazin, 2007). Our approach is congruent to the analogy made by Caswell (2001) between population conservation modelling and medical approaches. He argued that the main tasks of managers and scientists engaging in a population modelling are i) the assessment of the current status of the population, ii) the diagnosis of the causes of problems, iii) the prescription of the best target for management intervention and iv) the prognosis of the likely fate of the population under such management. This prognosis provides in turn quantifiable and achievable targets against which performance can later be evaluated, in agreement with the core concept of structured decision modelling and adaptive management (Chauvenet et al., 2016; Nichols and Armstrong, 2012).

The ability to fulfil these tasks for reintroduced populations critically depends on the demographic data we can collect. However, our demographic framework allows identifying the key points of the processes where such evaluations are needed, the limits of the assessment that can be made depending on the type of data available and, consequently, the priorities for reintroduction monitoring. Structuring success criteria thus entails the structuration of both milestones toward success and the required monitoring to implement such assessment.

Our aim here is not to create a new or alternative view of reintroduction assessment. On the contrary, we aim at unifying previous proposals from numerous authors in a stabilized standard of comprehensive framework accounting for the obvious trade-off between robustness, relevance, generality and operability of these criteria.

## **Transient dynamics of reintroduced populations**

### ***Establishment, growth and regulation processes***

The most optimistic prediction in any reintroduction is that the translocated individuals will survive, settle locally, breed and generate a population that will grow and remain large enough to be viable on the long-term. The expected dynamics of any successfully reintroduced population can be schematically split into three basic phases: population establishment, population growth and population regulation (IUCN/SSC, 2013; Sarrazin, 2007) (Figure 1a).

Starting from initially small numbers in an environment with sufficient resources to support the return of the species, a fundamental expectation is the potential of reintroduced populations for exponential growth. Theoretically, in the absence of environmental pressures and considering that density dependence is negligible, the population should converge to a stable rate of asymptotic growth and a stable stage or age distribution (Caswell, 2001). However, released individuals may struggle to settle, and the observed population growth rate may be highly variable and lower than expected in the early stages of the reintroduction. The establishment phase encompasses this early period of slower and potentially highly variable population growth, due to the combined effects that transient dynamics (Stott et al., 2011), potential Allee effects (Deredec and Courchamp, 2007) and potential post-release effects on demographic

parameters of released individuals (Sarrazin and Legendre, 2000) will have on population growth rate. This is also a period where population size will generally be small, hence highly sensitive to demographic stochasticity.

When these factors no longer threaten population growth, it may exhibit a phase of exponential growth. During the growth phase, demographic rates are expected to be maximal and the growth rate may reach the maximal intrinsic rate of increase in the absence of environmental perturbation, as the population converges to the stable structure. For some species, and particularly short lived ones, environmental stochasticity may entail fluctuations of the population growth rate and reduce its actual mean value even in non-limiting environments.

As the population grows, regulating processes whatever their nature will come into effect, reducing demographic parameters and limiting population growth. This may result from intraspecific competition for any resource (e.g., food, nesting sites) inducing a density-dependent negative feedback on population growth rate, but also from interspecific interactions (e.g., competition, predation, parasitism...), as well as Human activities, including direct or indirect destruction or exploitation and habitat limitations. The population may then enter some dynamics that exhibit steady state, cycles or quasi cycles, chaos etc. We hereafter refer to “regulated populations” when the reintroduced population size seems to have reached an upper limit (assuming that there is no further spatial expansion), and is showing no more increasing trend (i.e. the mean population growth rate converges to 1, Figure 1a and 1b). The regulating processes likely to operate below the ultimate limit that entails regulation will differ from one reintroduction project to another, within and between taxa, and may vary over time. It is thus possible that regulation process occur before any significant effect on population growth rate.

### ***Key factors shaping reintroduced population dynamics***

Numerous mechanisms shape the dynamics of reintroduced populations. The factors acting on the viability of reintroduced populations can be schematically split in three groups: i) the species' life history traits, biology and ecology, ii) the environmental conditions and iii) the reintroduction strategy. The species biology and ecology include all life cycle parameters, as well as physiological, behavioural, reproductive, social, functional traits or processes likely to play a role in the translocated population viability. These intrinsic characteristics are those that shape population dynamics, help quantify the position of a population along a fast-slow

continuum of life histories (which partly determines the relationship between initial population size and extinction risk; Legendre et al., 1999), and determine the relationships between the reintroduced population and its recipient environment (Monnet et al., 2015). The environmental conditions largely account for all the environmental factors that will affect population growth rate including climatic conditions, the availability and quality of resources, pathogens, etc. The initial causes of extirpation and the level of their management or mitigation prior to releases also fall into this category. The reintroduction strategy involves all the parameters of the project itself and its implementation, including the number, age, stage, origin of the translocated individuals, hard vs soft release tactics etc. These three main groups of factors generate interactions between genotypes, phenotypes and environments that shape the basic demographic rates of survival, reproduction and dispersal of translocated individuals and following generations (Robert et al., 2007, 2004; Sarrazin and Barbault, 1996; Sarrazin and Legendre, 2000).

A well-designed reintroduction strategy is thus critical to avoid failure in the early stages of the reintroduction dynamics, as post-release effects will induce perturbations in vital rates that can impede the establishment of the reintroduced population. For example, previous theoretical and empirical works suggest that the release method (e.g., number of released individuals, age or stage structure of releases and period of release) can influence survival (Sarrazin et al., 1994) and reproduction (Sarrazin and Barbault, 1996). The release strategy can also interact with dispersal behaviour (Le Gouar et al., 2008; Mihoub et al., 2011) and environmental variation (Hardouin et al., 2014) to shape demographic rates in translocated populations. The origin of founders (e.g. wild or captive-born) can affect the movement behaviour and survival of released individuals (Bright and Morris, 1994; Ginsberg, 1994; Mathews et al., 2005), and how the initial population structure differs from the expected stable state will largely determine population growth during the establishment phase. Genetic issues can arise throughout the dynamics. For example, inbreeding, drift load or ill-adaptation favoured by captive breeding can lead to failures during the establishment phase or at longer time horizons (Frankham, 2008; Robert, 2009).

The focal species' life history, the political and social context, as well as the management strategies and constraints all interact to create unique reintroduction challenges. Identifying correlates of success seems therefore highly difficult when all these interacting factors are considered together. Nevertheless, some of the mechanisms acting on reintroduction dynamics are not expected to have the same impact throughout the entire process of reintroduction (Figure

Id). Cochran-Biederman et al. (2015) suggested that species intrinsic characteristics such as spawning guild, temperature guild and age of maturity were not particularly correlated with project failure, even though these were expected to influence success in freshwater fish reintroductions. However, their review did not account for differences in monitoring periods, and whether a project had failed in the early phase of establishment, or later on. This highlights a major challenge, which is the ability to distinguish between the phases, because the main correlates of project failure may differ during establishment, growth or regulation. The tempo of life histories influences the dynamics of the population, especially during the early phase of establishment (Legendre et al., 1999), and the consequences of demographic stochasticity may be negligible once the population has reached a sufficient size (Komers and Curman, 2000). On the other hand, some species characteristics can have potential indirect effects on the long-term, for example, the reintroduction of top predators may induce Human-wildlife conflicts as abundance increases, leading to possible arguments about what population size would be considered manageable, thus influencing the carrying capacity.

## **A robust design of reintroduction success assessment**

### ***Structuring reintroduction success: shared temporal outcome and outputs to measure reintroduction achievements and efficiency***

As for any measure of conservation success, attempts to define reintroduction success need to distinguish outputs from outcomes (Howe and Milner-Gulland, 2012). Because most reintroduction projects span over several years or even decades, their adaptive management cannot rely only on the assessment of reintroduction outcomes and require making inferences on progress in each stage preceding the regulation phase. Measuring progress requires the formulation of clear objectives and associated relevant indicators in the beginning. Some studies have shown that objectives set by practitioners can be very diverse, and need ranking. Because the fundamental aim is the establishment of a viable population, objectives should represent crucial steps toward population growth and persistence, i.e. be rooted in demography. We propose to view the achievement of establishment, growth and regulation phases as

common milestones for any reintroduction program. By adopting a common demographic framework, the succession of such milestones can help designing objectives as major progress points to reach throughout population establishment and population growth. They differ in each stage and require different monitoring and modelling methods (Converse and Armstrong, 2016).

Measuring reintroduction success must consider both long-term conservation outcomes and management efficiency i.e., performance and target achievement throughout the project. The assessment of reintroduction outcomes focuses on the re-establishment of a viable population (or metapopulation, see next sections). Since some reintroductions will require management over many years, active adaptive management has been appraised in the context of reintroductions to support better decisions in face of uncertainty (McCarthy and Possingham, 2007). In this context, the measure of reintroduction success cannot only rely on long-term conservation outcomes, but should also evaluate the performance of the project in meeting the goals and objectives that must have been specified by practitioner's expectations prior to releases.

To embrace the complexity of reintroduction success we thus propose to discriminate milestone achievements from efficiency in each step of the reintroduction dynamics. We do not aim at putting a quotation on past or ongoing projects. On the contrary, we want to allow all reintroduction practitioners speaking a common language to share their good or bad experiences, their outstanding progress as well as their deepest difficulties since we are convinced that a well-documented failure may be more fruitful than a non-documented success, for evidence based reintroduction and global conservation.

### ***Metrics of expected reintroduction outputs and outcome***

A minimum set of data (Table 1) are required to define the scenarios of reintroduction as well as the expected outcome and outputs of reintroduction (Table 2) during the feasibility period that should be set up prior to any reintroduction implementation (IUCN/SSC, 2013). These data concern the life history traits of the focal species, the potential habitat suitability and the planned reintroduction strategy. In order to account for uncertainty inherent with any ecological prediction, the values of these parameters should include minimal, medium and maximal

expectations. Of course, better standards can be reached in many programmes but they should not be downgraded.

The minimum requirements for the species life history traits are the expected values of generation time ( $T_{exp}$ ), asymptotic growth rate ( $\lambda_{exp}$ ) and age or stage at first reproduction ( $a_{exp}$ ). They may be obtained from the literature or demographic databases (e.g., Salguero-Gómez et al., 2016) as well as the comparison with close surrogates of the focal species. It is highly recommended that an explicit structured life cycle be drawn to get a direct access of age or stage structure population dynamics.

The minimum requirement for the potential habitat suitability of the focal population is an estimate of the future habitat extent ( $HE_{exp}$ ) that can be obtained from the species past distribution and expected size of habitat patch. Together with an estimate of the potential maximum density of the species in this future habitat ( $MD_{exp}$ ), it becomes possible to evaluate the potential carrying capacity ( $K_{exp}$ ). Beyond crude estimates of  $HE_{exp}$  and  $MD_{exp}$ , the use of up to date habitat suitability modelling (e.g. Osborne & Seddon 2012) may provide more relevant predictions of  $K_{exp}$ .

The minimum requirements concerning the planned reintroduction strategy include logically the number of released individuals ( $NR_{exp}$ ), the expected date of first ( $DFR_{exp}$ ) and last ( $DLR_{exp}$ ) releases, and the age or stage distribution of first releases ( $ASR_{exp}$ ). Ideally, scenarios of the full distribution of age/stage released through time would be helpful to predict precisely the potential outputs of these releases.

Once these data are assembled, the expected values for reintroduction outputs and outcome can be quantified (Table 2). Once again, all values of these milestones are minimal, medium and maximal expectations according to the combinations of minimal, medium and maximal values of the parameters previously defined. At each step, we define a minimum set of parameters and expected outcome or output for all reintroduction and many additional milestones could potentially be listed that have been proposed in the past alternatively for different species or reintroduction context.

Here we identify a set of expected primary outputs and outcomes that define the reintroduction achievements (Table 3) in each phase of any reintroduction dynamics. The first level of achievement is the end of the establishment phase. It is defined by the autonomous increase of the population and the convergence of its growth rate ( $GAE_{exp}$ ) toward the expected asymptotic growth rate for the species or the best expectation of the mean stochastic growth rate. The

minimum delay between the last release and this convergence ( $MDT_{exp}$ ) depends on the life cycle of the species since it is inherent to damping ratio (Caswell 2001, Ezard et al. 2010). The expected date of establishment end ( $DC\lambda_{exp}$ ) allows defining the potential population size at this date ( $NC\lambda_{exp}$ ). The discrepancy between the expected population size once regulated ( $K_{exp}$ ) and  $NC\lambda_{exp}$  entails the estimation of the potential duration of the growth phase when combined with  $GAE_{exp}$  (see table 2). Finally, the expected outcome of the reintroduction is defined as the IUCN red list status of the species within  $HE_{exp}$  ( $RLS_{exp}$ ).

A secondary set of expected secondary outputs is relevant to show progress particularly during the establishment phase. It includes the expected date of first reproduction in the wild ( $DFB_{exp}$ ), which constitutes one of the first milestones towards population establishment, and the expected level of population growth during establishment above the cumulative sum of releases ( $GDE_{exp}$ ).

### ***Monitoring reintroduction achievements and efficiencies***

Numerous authors have called for a standardization of the monitoring and publication of reintroduction outcomes and extensive literature on such monitoring is now available from case studies to general recommendations (Ewen and Armstrong, 2007; Gitzen et al., 2016; Parker et al., 2013; Sarrazin and Barbault, 1996; Seddon et al., 2007; Sutherland et al., 2010). The IUCN guidelines on conservation translocations (IUCN/SSC, 2013) emphasized the importance of post-release monitoring as being one of the irreducible components of the reintroduction process.

The efficiency of our framework relies on the necessity of monitoring reintroduced population on the short and long term. The collection of data is driven by the requirements to fill in the parameters and milestones defined during prior to reintroduction (Tables 1 and 2). It mostly concerns the observed values of the parameters defining the reintroduction implementation, the actual population dynamics through the establishment growth and regulation phases and the actual habitat quality (Table 3).

The monitoring period required before population regulation largely depends on the life history strategy of the species and the environmental conditions. Furthermore, the precision of post-release monitoring is likely to vary among different programs, depending on the human and



economic investment, as well as the difficulty of monitoring individuals that can be challenging for some taxa. The type of data collected determines the ability to make predictions, and whether progress can be measured prospectively or retrospectively. Individual monitoring through capture-mark-recapture methods allows estimating accurately demographic parameters (Armstrong et al., 2017). They provide a robust framework to analyse the mechanisms involved and the influence of many intrinsic and extrinsic factors on population dynamics (Figure 1). A vast majority of reintroduction programs have been dealing with abundance or density estimates (absolute or relative), which limits the understanding of the underlying processes of reintroduction dynamics. Nevertheless, studying the mean, trend and variability over time of the population growth rate provides a powerful way to assess progress in the early stages of the reintroduction dynamics (Komers and Curman, 2000). The degree of precision in the definition of reintroduction milestones and their associated indicators depends on the investment that can be made in monitoring, and the type of data collected. It is thus important to evaluate the limits associated with the kind of data that will be actually gathered, to design monitoring relevant enough to address the ultimate questions of reintroduction success assessment.

### ***Categories of reintroduction achievements***

To clarify the endless debate about reintroduction success we propose a simple grid to classify any reintroduced population according to its actual achievements at the date of evaluation. The three phases of reintroduction dynamics are the direct basis of these achievements (Table 4). According to the parameters defined during the feasibility period (Tables 1 and 2), and the data gained during monitoring (Table 3) it is possible to put any reintroduction in one of these categories. A reintroduction can be planned but not implemented yet, all achievement criteria are then obviously “non-applicable”. Once releases start, the establishment phase may be “ongoing”, or “failed” if full extinction occurs before the predicted end of establishment. It is “achieved” when population growth is observed after the end establishment phase ( $DS\lambda_{obs}$ , Table 3). During establishment, achievement in growth phase and regulation are “not applicable”. Once the establishment phase is “achieved”, the growth phase is “ongoing”, as long as the population grows without significant regulation. If extinction occurs, the growth phase achievement is “failed”. The process of regulation is likely to differ strongly among species and environment. This may entail a sharp or slow reduction of  $\lambda_{obs}$  during that period

that indeed will exhibit some transience due to changes in at least one demographic parameter. In that context the detection of regulation requires a sufficient period. This period will be also necessary to evaluate the actual outcome of the reintroduction through red list criteria ( $RLS_{obs}$ ; Table 3). We thus propose to define the regulation phase as “suspected” when the population is still growing but shows an apparent reduction of population growth rate or change in some demographic parameter (reduced survival or reproduction, increased dispersal) that may be due to increasing negative density dependence. The regulation is “ongoing” when the population is regulated and the assessment of the long term population viability is being implemented. It is “achieved” once the population is regulated and no extinction occurred during the monitoring period necessary to project population viability and assign the red list category of the restored population. The regulation is “failed” whenever the population shows regulation but extinction occurs before any assessment of population viability. For each phase the achievement may be “not estimated” when data are potentially available but no assessment has been run yet, or “not estimable” when no data is available to evaluate this achievement. We illustrate this proposal with the example of a set of eleven reintroduction programmes dedicated to the restoration of three species of vultures in southern France (Box 1). These reintroductions have been implemented from the early 1980s and the comparison of their achievements must account for the time since first and last releases. The diagnosis of transition can be explored from time series of abundance (Supplementary Materials) but more accurate individual-based monitoring is required to identify the key processes of these transitions.

### ***Metrics of reintroduction efficiency***

Once milestone achievement is assessed (Table 4) the outputs and outcome observed through monitoring (Table 3) can be compared to the initial recovery expectations that were set up during the feasibility period (Tables 1 and 2). A large diversity of efficiency measures could be recommended and, once again, they could strongly vary depending on species, locations, reintroduction managers, as well as the political, social and economic context. Clearly, good survival, philopatry and reproduction of released individuals are examples of generic reintroduction outputs that can act as short term measures of performance for reintroduction projects. However, our purpose is to identify the primary efficiency measurements that directly address short- and long-term population dynamics that shape the ultimate viability of the

regulated population. The metrics of efficiency mostly concern the population size and population growth rate (Table 5). They allow the assessment of the efficiency of the reintroduction implementation, population establishment, growth and regulation through the comparison of the actually observed parameters that characterize these processes with the initial expectations of reintroduction managers. This can result from continuous metrics showing the percentage of gain or loss compared to expectations, as well as categories that underline high, medium or low realisation of output and outcome compared to their initially expected values. High or low realisation of red list status of the regulated population (*RLS*), or population growth rate after establishment (*GAE*) are logical indicators of high or low efficiency of the reintroduction. However, other parameters such as released number (*NR*), or duration of release (*DLR-DFR*) may give a signal of strong or poor efficiency depending on the actual outputs and outcome of the project.

It is clear that any discrepancy between reintroduction practitioner's expectation and observed recovery values may result from challenges in prediction and/or challenges in implementation. However, sharing common metrics on efficiency may be crucial to identify weaknesses and improve collectively our ability to predict, set up and achieve successful reintroductions. The strong time lag between time of prediction and time of validation poses also the question of the progress in ecological sciences reminding that reintroductions are large scale experiments in ecology (Sarrazin and Barbault, 1996). Additionally it will not be easy to define accurately the initial expectations for projects-initiated decades ago independently from the actual outcome of these projects (Box 1). Our framework for reintroduction efficiency is thus mostly dedicated to recent and new projects. The temptation might be to downgrade expectations during feasibility in order to secure a low discrepancy with future realisation and thus an apparent high efficiency. However, we predict some equilibria in practitioner's expectations since they may ultimately result from a trade-off between reasonable prudence and necessary ambition to gain public, political and economic support for long-term reintroduction projects.

## **Potential of population viability analyses for reintroduction planning and assessment**

Defining demographic measures of reintroduction success may seem data demanding. This is true during the feasibility period to formulate the potential recovery expectations. Whenever data are actually missing, planning reintroduction requires to build up reasonable scenarios on these potential expectations. Nevertheless, their implementation benefits from the numerous development of evidence based knowledge in population ecology and conservation. Indeed, population viability analyses have generated a huge diversity of modelling approaches and modelling tools with numerous trade-offs between generality and precision, idiosyncrasy and forecasting power. Several reviews have extensively explored the richness of the concepts and tools available for a reintroduction practitioner to set up prospective and retrospective modelling and define relevant monitoring (Armstrong and Reynolds, 2012; Converse and Armstrong, 2016; Nichols and Armstrong, 2012). Matrix population models are a powerful starting point to provide a mathematical framework to describe prospectively structured population dynamics by accounting for the species' life cycle (Caswell, 2001). Simple matrix projection analyses offer substantial insights regarding both the equilibrium properties and the transient dynamics of a population (Ezard et al., 2010). Asymptotic analyses provide informative quantities regarding the equilibrium properties of the population (e.g. the asymptotic growth rate and the stable population structure), that can be used as quantifiable objectives to evaluate performance during the Growth phase. On the other hand, the evaluation of the expected performance during the Establishment phase can benefit from the study of the transient properties of population matrix models. Reintroduced populations are rarely released at the stable structure and thus present particular cases of disturbance (i.e. changes in the initial demographic structure compared to the stable state), and release costs induce perturbations to vital rates (i.e. changes in the stable demographic distribution). Consequently, a very conservative prediction of the duration of establishment may be the length of the transient period, i.e. the period of time in which the population exhibits transient dynamics before settling to the stable state. Convergence rates, such as the damping ratio (Caswell, 2001) describe how quickly a perturbed population settles back to the stable state. The quantification of convergence time, however, is more difficult and highly depends on initial conditions. Moreover, because each new release event may disturb the demographic structure of the population and divert it from the stable state, any estimation of the minimal time to convergence, in the absence of release effects, requires assessing the structure of the population only after the last release event (Figure 1c).

In the same way, the definition of the reintroduction recovery potential as the red list category of the regulated population is at the core our framework that recognizes long-term viability as the fundamental aim of any reintroduction. Viability assessments rely on the estimation of the extinction risk for the population, which itself needs to be described specifically enough in time and space (Beissinger and McCullough, 2002; Morris and Doak, 2002). The IUCN Red List provides the most comprehensive assessment of species extinction risk, based on quantitative analysis of viability or proxies of viability including decline rate, range, and population size (Akçakaya et al., 2018; IUCN/SSC, 2017). This system is flexible and has been applied globally to a variety of species and life cycles (Mace et al., 2008; Maxwell et al., 2016). The IUCN Red List Categories and Criteria were initially designed to consider the extinction risk of species globally, but can be used without modification at a local scale if the population is isolated from conspecific populations outside the geographically defined area (IUCN, 2012; IUCN/SSC, 2017). The extinction risk of such an isolated population is considered to be identical to that of an endemic taxon (Mace et al., 2008).

As suggested by Sarrazin and Barbault (1996) and Sarrazin (2007), Moehrenschrager et al. (2013) proposed to measure reintroduction success by assigning a Red List-equivalent status to the reintroduced population at the regional scale, which was defined as a sub-global geographic area that should represent a “meaningful spatial scale that encompasses the potential expanse of a small but growing reintroduced population”. Reintroduction ‘success’ was then quantified as the degree to which the population improves in threat category, starting from the “regionally extinct” status. The authors suggested that the reintroduced species status could be regularly evaluated throughout the project, starting after at least 5 years of monitoring. In their framework, a single metric was used and therefore the evaluation of progress and target achievement was indivisible from the assessment of long-term persistence. Using the IUCN Red List categories, complete reintroduction failure in any stage was described as the return of the reintroduced population to a Regionally Extinct category, as there is no longer evidence of the species occurrence. In contrast, if we consider that the fundamental objective of any reintroduction is to produce viable populations, then the most favourable conservation outcome for the project should be attained if the projected viability do not put the population in one of the threatened categories of the IUCN Red List (e.g. quantitative analyses yielding a probability of extinction of less than 10% over 100 years). Different levels of success were thus given if the reintroduced population falls into one of the three threat categories (Critically Endangered, Endangered and Vulnerable).

However, if the long-term viability of the reintroduced population is quantified through quantitative analysis (criterion E), i.e. population viability analyses, it is strategic to underline that although establishment and growth phases constitute crucial steps toward success, the data collected during these phases cannot be used to make predictions about long-term persistence due to the partial vision they provide on the actual dynamics of the reintroduced population (Sarrazin 2007, Robert et al. 2015a). Indeed estimating the long-term viability of the reintroduced population from the data collected during the establishment phase is likely to produce very pessimistic results due to the potentially negative impacts of releases costs, Allee effects and demographic stochasticity (Armstrong et al., 2017). On the contrary, the growth phase is likely to show the best demographic parameters and any population viability analysis is likely to be overly optimistic since there might be no consideration for any population regulation processes at this stage (Niel and Lebreton, 2005). Reliable projections of long-term population dynamics and viability require full integration of the intrinsic population properties (estimated during the growth phase) and the environment. Such integration can be conducted once there is evidence of regulation, e.g., by explicitly modelling the relationship between population density and demographic parameters in a population viability analysis framework (Zabel et al., 2006), and using all relevant available information on life history, habitat requirements, threats and management options to estimate extinction risk.

The spatial scale of reintroduction implementation must also be considered. Although there is no theoretical limitation to the application of IUCN criteria at the scale of reintroduced populations, some criteria may need to be refined to account for the differences between reintroduced and remnant populations (Robert et al., 2015a). Usually, a reintroduction focuses on the fate of one re-established population, but it can be potentially included in a network of populations interacting through dispersal at a larger scale. If the projected viability of the reintroduced population cannot be dissociated from the fate of neighbouring populations (especially for species capable of long distance dispersal), then the IUCN quantitative thresholds used to categorize population into threat categories should be applied at wider organizational and spatial scale (e.g. metapopulations). In such cases, Moehrensclager et al. (2013) proposed to assess the success of the reintroduction as the contribution of reintroduced population to the improvement in threat category assessed at a wider organizational scale. Our framework makes a link between the local conservation legacy of a given reintroduction and the global impact on species conservation and recovery (Akçakaya et al., 2018).

In some cases, reintroduction may remain the best management option (e.g. when natural recolonization is unlikely) even though the re-establishment of a fully viable population may not be possible (e.g. habitat availability is low). This demonstrates the importance of formulating the goal of the project, which is a statement of the intended result of the reintroduction (IUCN/SSC, 2013). This goal will often be expressed in terms of the desired size or spatial distribution of the population. In order to facilitate comparability, we argue that this desired level of performance should be defined in terms of population viability and set as an IUCN red list category (criteria B or D, see *RLS<sub>exp</sub>* Table 2).

## Perspectives

The shortcomings associated with our framework mirror those of any framework aiming at providing generic guidelines and criteria in conservation biology, notably the IUCN Red List approach. The universality of concepts and criteria is intrinsically problematic in ecology and conservation biology, and has been extensively discussed in the fields of viability assessments (Brook et al., 2011; Flather et al., 2011), conservation status (Cardoso et al., 2012, 2011) and reintroduction biology (Haskins, 2015; Robert et al., 2015b). Here, we provide a demographic framework to standardize outcomes and outputs, which constitute the two major components of reintroduction success assessments. We argue that the definition of a shared demographic framework is the first step required that allows guiding management decisions, setting achievable targets and developing standardized criteria of success. However, we advocate that such standardized criteria and more project- or taxa-specific success criteria should not be mutually exclusive. They complement each other to put the full process of reintroduction in a renewed and enlarged adaptive management process. Our framework aims at increasing the number and length of adaptive management loops in reintroduction biology, from the strategic decisions to launch reintroductions among a large variety of threatened taxa and environments, up to the short-term drive of a local release strategy. It constitutes the basis of a common language among reintroduction practitioners on the strategic and controversial subject of reintroduction success assessment. We focused here on reintroduction but at this stage, we do not see significant counterarguments that would prevent us using this framework for other conservation translocations such as assisted colonization's or even de-extinction independently

of the necessary ethical and ecological debates about their conservation relevance (Chauvenet et al., 2013; Robert et al., 2017; Seddon, 2010; Seddon et al., 2014b).

Some authors have questioned the development of a standardized definition of reintroduction success, because each reintroduction attempt is unique and that such operations rely on so much uncertainty that the oversimplification of such complex processes might not be practical (Haskins, 2015). Since our assessment involve the input of researchers and managers engaged in the program, it allows going beyond subjective expert opinion and will further improve reviews of reintroduction success. Such success assessment is necessarily demanding. It requires time, data and thus monitoring efforts but no robust inference can be obtained otherwise. It also requires transparency and collaborative skills on shared principles. However, the preservation and restoration of biodiversity requires such robust assessment of reintroduction contribution to species conservation and recovery.



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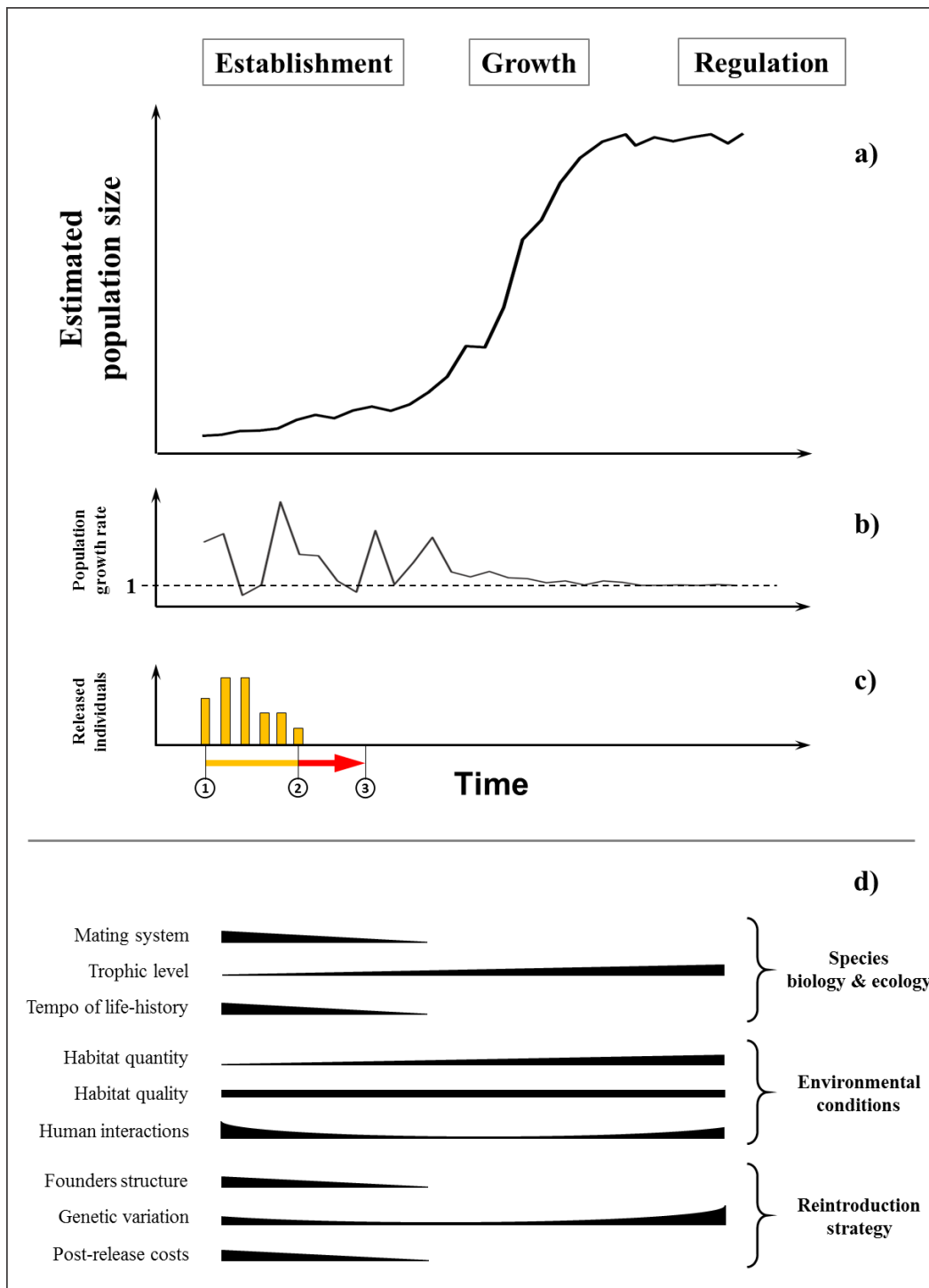


Figure 1: Schematic representation of the dynamics of a monitored reintroduced population. a: Hypothetical time series of population size (or density) depicting the different phases of the dynamics of reintroduced populations (Establishment, Growth and Regulation), and b: the temporal variation in the realized population growth rate. c: Each release event of individuals (starting at ①) will act as perturbations and divert the population from the theoretical stable state. A conservative estimate of the length of the Establishment phase is the length of the transient period (③) which integrates the population structure after the last release event (②). d: Examples of factors and processes that affect the population growth rate. The thickness of the line represents the potential sensitivity of population growth rate to each factor.

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**Box 1.**

Defining reintroduction success has been an endless debate that prevents the comparison of many translocation programs. Using a neutral grid of achievement allows appreciating the actual progress of a reintroduction programme at a given date or since its implementation. From the early 1980s, three species of vultures have been reintroduced in different places in southern France (Table 1a) by a group of institutions that have shared experiences and monitoring standards (Table 1b). Table 1 provides a brief summary of their level of achievement in 2018 together with a simple description of their implementation. This grid allows structuring the analyses and comparisons of these programs for e.g. post-release effects on survival and dispersal (Prog. A, B, C, D; Le Gouar et al., 2008), genetics of release stocks (Prog. A, B, C, D, E ; Le Gouar et al., 2006), habitat suitability (Prog. F, Mihoub et al., 2014; Prog. I, J, K, King Gillies et al. in prep), or competition for food resources (Prog. A, Bosé et al., 2007; Monsarrat et al., 2013).

Table 1: Example of actual level of achievement assessed in 2018 for 11 programmes of vulture's reintroduction in France. Gf: Griffon vulture, *Gyps fulvus*; Am: Black vulture, *Aegypius monachus*; Gb: Bearded vulture, *Gypaetus Barbatus*. Prog.: reintroduction programme; Spec.: Species;  $DFR_{obs}$ : date of first release ;  $DLR_{obs}$ : date of last release  $NR_{obs}$ : Number of individuals released; n/a : not applicable

a)

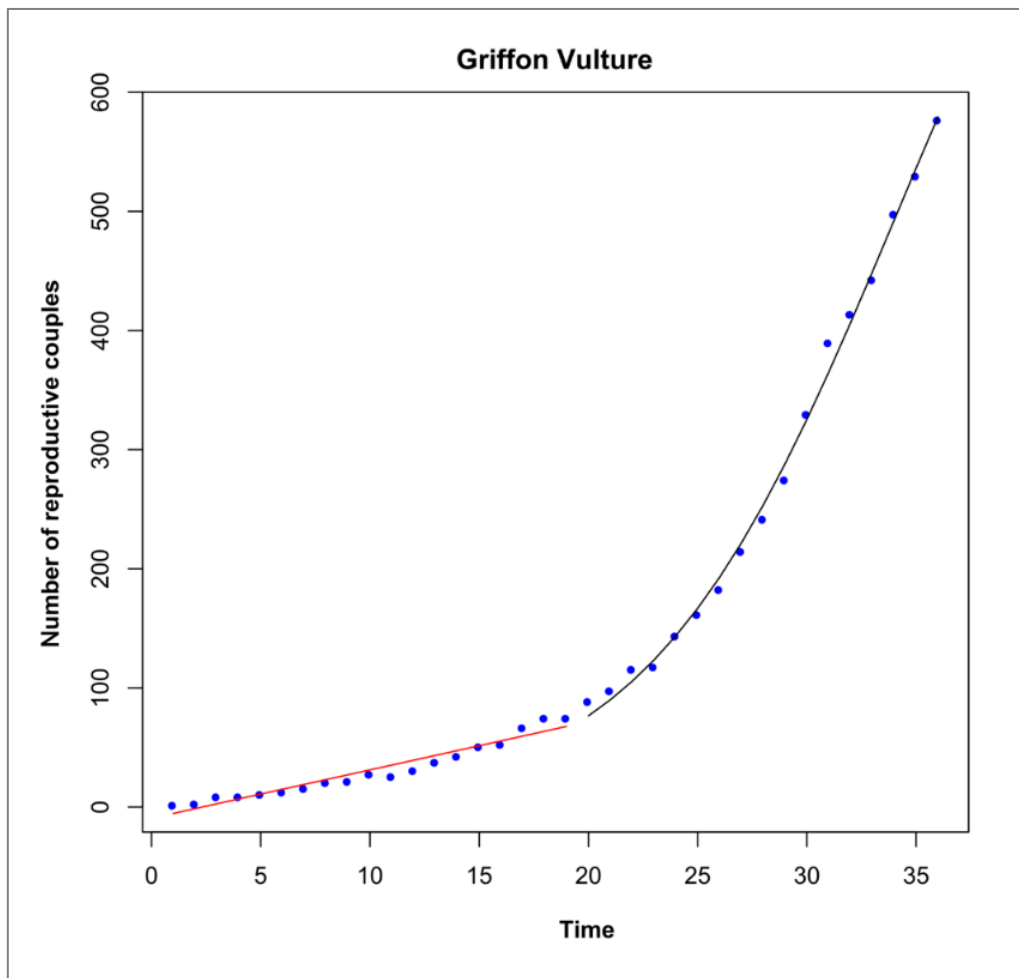
Prog.	Spec.	Area	Release period			Level of achievement in 2018		
			$DFR_{obs}$	$DLR_{obs}$	$NR_{obs}$	Establishment	Growth	Regulation
A	Gf	Grands Causses	1981	1986	61	achieved	ongoing	suspected
B	Gf	Navacelles	1993	1997	50	failed	n/a	n/a
C	Gf	Baronnies	1996	2001	53	achieved	ongoing	n/a
D	Gf	Diois	1999	2010	96	achieved	ongoing	n/a
E	Gf	Verdon	1999	2004	91	achieved	ongoing	n/a
F	Am	Grands Causses	1992	2004	53	achieved	ongoing	suspected
G	Am	Baronnies	2004	n/a	46	ongoing	n/a	n/a
H	Am	Verdon	2005	n/a	31	ongoing	n/a	n/a
I	Gb	Diois	2010	n/a	11	ongoing	n/a	n/a
J	Gb	Grands Causses	2012	n/a	15	ongoing	n/a	n/a
K	Gb	Baronnies	2017	n/a	7	ongoing	n/a	n/a

b)

**Reintroduction practitioner' for each project**

A, F, J : Ligue pour la Protection des Oiseaux Grands Causses, Parc national des Cévennes ; C, G, K : Vautours en Baronnies ; D, I : Parc naturel régional du Vercors ; E, H, : Ligue pour la Protection des Oiseaux PACA ; B : Grive.

We applied a piecewise modeling approach (Supplementary Materials) to time series of population abundance estimates for a reintroduced population of Griffon vulture in the Grands Causses region of France (Figure 2). We used the number of breeding pairs estimated through nest monitoring between 1982 and 2017. The best fitting model suggests that the population has gone through a phase of establishment during the first 19 years ( $t_{\text{est}} = 19$ ), before exhibiting logistic growth (estimated  $r = 0.18$ ,  $K = 988$ ).



*Figure 2: Time series of the number of breeding pairs in the reintroduced population of Griffon vultures in the Grands Causses. Time is given in year with  $t_0 = 1982$ . The red line is the linear portion of the piecewise model, and the black curve corresponds to a logistic growth model.*

Table 1: Data required to set up expected outcome and outputs of reintroduction (see table 2 and 3). All values for species life history traits, habitat suitability and reintroduction strategy are minimal, medium and maximal expectations defined during feasibility prior to implementation.

<b>Data required</b>	<b>Notation</b>	<b>Scenarios</b>	<b>Potential source or computation</b>
<i>Species life history traits</i>			
Minimum requirement			
Generation time	$T_{exp}$	min. / med. / max.	Literature or IUCN Red list on Generation time
Asymptotic growth rate	$\lambda_{exp}$	min. / med. / max.	Literature or databases e.g. COMADRE /COMPADRE
Age / stage at first reproduction	$a_{exp}$	min. / med. / max.	Literature or databases e.g. COMADRE /COMPADRE
Recommended			
Explicit Life cycle			Literature or databases e.g. COMADRE /COMPADRE
Values of demographic parameters		min. / med. / max.	Literature or databases e.g. COMADRE /COMPADRE
<i>Habitat suitability for the focal population</i>			
Minimum requirement			
Habitat extent	$HE_{exp}$	min. / med. / max.	Species past distribution and expected size of habitat patch.
Maximum density	$MD_{exp}$	min. / med. / max.	Literature on species ecology
Carrying capacity	$K_{exp}$	min. / med. / max.	$K_{exp} = HE_{exp} * MD_{exp}$
Recommended			
$HE_{exp}$ , $MD_{exp}$ , $K_{exp}$		min. / med. / max.	Estimate through up to date habitat suitability modelling
<i>Reintroduction strategy</i>			
Minimum requirement			
Number released	$NR_{exp}$	min. / med. / max.	Local expectation during feasibility
Date of first release	$DFR_{exp}$	min. / med. / max.	Local expectation during feasibility
Date of last release	$DLR_{exp}$	min. / med. / max.	Local expectation during feasibility
Age/stage of first releases	$ASR_{exp}$	min. / med. / max.	Literature on reintroduction biology
Minimum duration of transience	$MDT_{exp}$	min. / med. / max.	Based on damping ratio, $T_{exp}$ and $\lambda_{exp}$ and releases excluding effects or releases
Recommended			
Full distribution of age/stage released through time.			

Table 2: Expected milestones and reintroduction outcome. All values are minimal, medium and maximal expectations defined during feasibility prior to reintroduction implementation.

a) Expected primary outputs and outcome defining reintroduction achievement in each phase

<b>Primary output/outcome</b>	<b>Notation</b>	<b>Scenario</b>	<b>Potential source or computation</b>
<i>Expected end of establishment phase</i>			
Date of convergence toward $\lambda_{exp}$ :	$DC\lambda_{exp}$	min. / med. / max.	$DC\lambda_{exp} = DLR_{exp} + MTD_{exp}$
Population size at $DC\lambda_{exp}$ :	$NC\lambda_{exp}$	min. / med. / max.	Population size or proxy of population size
<i>Expected end of growth phase</i>			
Growth rate after establishment	$GAE_{exp}$	min / med. /max	$GAE_{exp} = \lambda_{exp}$ or the best expectation of mean growth rate in unlimited stochastic environment
Duration of growth until regulation	$DER_{exp}$	min. / med. / max.	$DER_{exp} = \ln(K_{exp}) - \ln(NC\lambda_{exp}) / \ln(GAE_{exp})$
<i>Expected outcome for regulated population</i>			
IUCN red list status within $HE_{exp}$	$RLS_{exp}$	min. / med. / max.	Red list criteria E, or conservative use of criteria D and/or B

b) Expected secondary outputs showing progress towards establishment

<b>Secondary output</b>	<b>Notation</b>	<b>Scenario</b>	<b>Potential source or computation</b>
<i>During establishment phase:</i>			
Date of first breeding in the wild	$DFB_{exp}$	min. / med. / max.	According to $a_{exp}$ , $DFR_{exp}$ , $ASR_{exp}$
Growth during establishment	$GDE_{exp}$	min. / med. / max.	Mean growth rate of population above the cumulated number of individuals released

Table 3: Monitoring of the reintroduction process including the parameters of the actual reintroduction implementation. Population dynamics and habitat suitability.

<b>Monitoring data</b>	<b>Notation</b>	<b>Method</b>
<i>Reintroduction implementation</i>		
Minimum requirement		
Number released	$NR_{obs}$	Recorded during releases
Date of first release	$DFR_{obs}$	Recorded during releases
Date of last release	$DLR_{obs}$	Recorded during releases
Age/stage of first releases	$ASR_{obs}$	Recorded during releases
Recommended		
Time distribution of released age/stage		Recorded during releases.
<i>Population dynamics</i>		
Minimum requirement		
Population size at time $t$	$N_{obs t}$	Population size estimate or proxy of abundance up to population regulation
Population growth rate at time $t$	$\lambda_{obs t}$	$N_{obs t+1} / N_{obs t}$
Date of convergence of $\lambda_{obs}$	$DS\lambda_{obs}$	Date of convergence of $\lambda_{obs}$ toward stability
Duration of transience	$DT_{obs}$	$DT_{obs} = DS\lambda_{obs} - DLR_{obs}$
Recommended		
Estimate of demographic parameters for released and wild born generations		Estimated from field data through e.g. CMR
Generation time	$T_{obs}$	Estimated from field data through e.g. CMR and matrix modelling
Age / stage at first reproduction	$a_{obs}$	Estimated from field data through e.g. CMR
<i>Habitat suitability for the focal population</i>		
Minimum requirement		
Habitat extent	$HE_{obs}$	Estimated once population is regulated.
Maximum density	$MD_{obs}$	Estimated once population is regulated
Carrying capacity	$K_{obs}$	$K_{obs} = HE_{obs} * MD_{obs}$



Table 4: Categories of achievement in each reintroduction phase

<b>Achievement category</b>	<b>Criterion</b>
<i>Establishment phase</i>	
Achieved	Population growth observed after the end of establishment phase
Failed	Population extinction before the actual end of the establishment phase
Ongoing	No extinction but the actual end of the establishment phase is not observed
Not estimated	Data potentially available but no assessment yet.
Not estimable	No data available
Not applicable	No release yet
<i>Growth phase</i>	
Achieved	Population regulation following population growth after the end of establishment phase
Failed	Population extinction following population growth after the end of establishment phase
Ongoing	Population growth after the end of establishment phase, but no regulation detected
Not estimated	Data potentially available but no assessment yet.
Not estimable	No data available
Not applicable	No release yet, or establishment not achieved
<i>Regulation phase</i>	
Suspected	Population growth with a suspected reduction of growth rate that may entail regulation
Achieved	Population regulated without extinction during the assessment of population viability
Failed	Population regulated but extinction occurs during the assessment of population viability
Ongoing regulation phase	Population regulated and the assessment of population viability is being implemented
Not estimated	Data potentially available but no assessment yet.
Not estimable	No data available
Not applicable	No release yet, or growth not achieved

Table 5: Metrics of reintroduction realisation to be combined with reintroduction achievements to measure reintroduction efficiency. The list of parameters is available in Table 1, 2 and 3. Observed values can also be compared to minimal, medium or maximal scenarios (expected values, see Table 1 & 2).

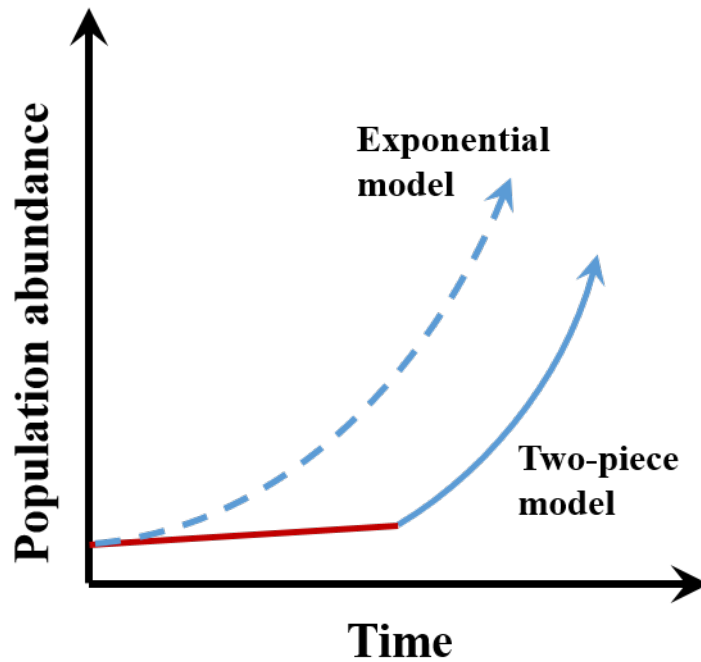
<b>Step of the reintroduction dynamics</b>	<b>Deviation from expectation</b>
<i>Programme implementation</i>	
Number release	$(NR_{obs} - NR_{exp}) / NR_{exp}$
Delay in release start	$(DFR_{obs} - DFR_{exp}) / DFR_{exp}$
Delay in last release	$(DLR_{obs} - DLR_{exp}) / DLR_{exp}$
Duration of release	$(DLR_{obs} - DFR_{obs}) - (DLR_{exp} - DFR_{exp})$
<i>Establishment phase</i>	
Delay of first breeding in the wild	$(DFB_{obs} - DFB_{exp}) / DFB_{exp}$
Growth during establishment	$(GDE_{obs} - GDE_{exp}) / GDE_{exp}$
<i>Growth phase</i>	
Delay of convergence toward $\lambda_{exp}$	$(DC\lambda_{obs} - DC\lambda_{exp}) / DC\lambda_{exp}$
Population size at $DC\lambda_{exp}$	$(NC\lambda_{obs} - NC\lambda_{exp}) / NC\lambda_{exp}$
Growth rate after establishment	$(\lambda_{obs} - GAE_{exp}) / GAE_{exp}$
<i>Regulation phase</i>	
Delay of entry in regulation	$(DER_{obs} - DER_{exp}) / DER_{exp}$
<i>Reintroduction outcome (regulated population)</i>	
IUCN red list status within $HE_{obs}$	$RLS_{obs}$ versus $RLS_{exp}$

## SUPPLEMENTARY MATERIALS

Many reintroduction projects have now been underway for several years (Tarszisz et al., 2014), making time series of population abundance potentially available to study the long-term effect of reintroduction projects. However, without additional demographic data, the diagnosis of the establishment, growth and regulation phases from time series remains challenging.

The study of exotic species provides a framework that can be adapted, to some extent, to reintroductions, as exotic and reintroduced populations share some aspects of a colonization process (e.g. translocated population starting from initially small numbers) (Blackburn and Cassey, 2006; Cassey et al., 2008). Similar to what has been documented for exotic populations, reintroduced populations can exhibit periods of “lags” between the time when the individuals are introduced and the time when the population starts to grow substantially. Crooks (2005) made a distinction between the “inherent lag” and the “unexpected lag”. The “inherent” lag phase is what should be congruous to the early steps of an exponential or a logistic growth population model, which produces initial phases of apparent slow growth followed by rapid increases. On the other hand, the “unexpected” lag corresponds to a period of limited/slower population growth that is longer than what we could expect from exponential/logistic growth models. Slow-growth exhibited by reintroduced populations after release can be due to environmental factors, demographic post-release effects, demographic/environmental stochasticity and possible Allee effects. Here we consider that the establishment phase occurs when these additional post-release effects cause “unexpected” lags in the early stages of reintroduction projects.

We assume here that, in the absence of post-release effects, the null expectation would be a single stage process of exponential growth, or logistic-type growth if the population experiences regulating processes. We consider that if the reintroduced population actually suffers a discrete phase of establishment (similar to the lag phase described in the biological invasion literature Crooks 2005, Aikio et al. 2010), then the observed pattern will diverge from these expectations, and will be best represented by two separate processes (Figure S1).



*Figure S1: Starting from initially small numbers, populations are expected to grow slowly in the early stages of reintroduction, as exemplified by an exponential model (dashed lines). Populations that went through establishment phases can exhibit periods of null or linear growth rate followed by non-linear growth that can be approximated using piecewise models.*

With sufficient data, time series of estimates of population abundance can help identifying the different phases of the reintroduction dynamics. We can fit 5 classes of models to the population growth trajectory in order to identify which populations can be best represented by a two-stage process (i.e., including an establishment phase prior to the growth or growth/regulation phase). First as a (silly) null hypothesis we fit a linear growth model: if the population analyzed was released recently enough, it may have not emerged from the establishment phase and may exhibit a near-linear growth (Crooks, 2005). We can fit the following model:

$$N_{t,Lin} = a * t + N_0 \quad (1)$$

Where  $N_t$  is the size of the population at a given time  $t$ ,  $N_0$  is the initial population size,  $a$  is the linear rate of increase. Then we fit an exponential and a logistic model to approximate a non-linear growth trajectory. The exponential model is the basic expectation for population growth after release, and the logistic model to test whether the population the population exhibits regulating processes:

$$N_{t,Expo} = e^{rt} * N_0 \quad (2)$$

$$N_{t,Log} = \frac{N_0 * K}{N_0 + (K - N_0) * e^{-rt}} \quad (3)$$

Where  $r$  is the population intrinsic exponential growth rate and  $K$  (eq. 3) is the carrying capacity for the population. Finally, we consider two last classes of models by combining the establishment phase (eq. 1) with the exponential and logistic growth models, respectively. We use the approach proposed by Aikio et al. (2010) and fit a piecewise model which combines two mathematical expressions. The first portion of the piecewise model is a linear model which represents the establishment phase of limited population growth. The second part of the piecewise model is an exponential or a logistic model, depending on whether the population is growing exponentially or exhibiting regulation processes. Because we use time series where time is discrete, we allow the two portions of the piecewise models to be disconnected. We establish  $t_{est}$  as the time where the establishment phase ends:

$$N_t = \begin{cases} N_{t,Lin} & , t \leq t_{est} \\ N_{t,Expo} \text{ or } N_{t,Log} & , t > t_{est} \end{cases} \quad (4)$$

For each piecewise model, we determine the length of the establishment phase by varying the value of  $t_{est}$  in one-year steps over the monitoring period and find the value of  $t_{est}$  that minimizes the total least square error (sum of the least square errors of the linear and non-linear parts of the model). Then, for each class of model, we use the Akaike Information Criterion corrected for small sample sizes (AICc, Anderson and Burnham, 2002). The best fitting model allows us to identify the best underlying model for the population growth trajectory, according to whether the reintroduced population exhibits regulating processes or not, and goes through a phase of establishment or not.

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# Chapter 5: *De-extinction and Evolution*

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**Context:**

Technological advances have now raised the possibility for resurrecting extinct species. While de-extinction can be viewed as a form of conservation translocation, there is much debate about the potential conservation benefits associated with its practice. So far, the controversy surrounding de-extinction projects have focused on ecological, societal and economic issues. Here we discuss the potential evolutionary benefits of de-extinction projects, and show that although de-extinction is a stimulating idea, its capacity to restore evolutionary trajectories is not guaranteed.

**Aim:**

In this paper, we apply an evolutionary framework to understand how evolutionary processes can influence the dynamics and ecology of resurrected species, and to put de-extinctions into a wider macro-evolutionary conservation perspective. Resurrected populations show some eco-evolutionary peculiarities (discontinuity of biological processes, small initial genetic diversity, and the divergence between evolutionary and environmental trajectories) that impose constraints on the local success of de-extinction projects. De-extinction, by essence, is not antagonistic with the reinstatement of functions or the conservation of evolutionary processes, however, it is questionable whether de-extinction has the potential to restore the evolutionary values of lost biodiversity.





## THE ECOLOGY OF DE-EXTINCTION

# De-extinction and evolution

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### Summary

1. De-extinction, the process of resurrecting extinct species, is in an early stage of scientific implementation. However, its potential to contribute effectively to biodiversity conservation remains unexplored, especially from an evolutionary perspective.
2. We review and discuss the application of the existing evolutionary conservation framework to potential de-extinction projects. We aim to understand how evolutionary processes can influence the dynamics of resurrected populations and to place de-extinction within micro- and macro-evolutionary conservation perspectives.
3. In programmes aiming to revive long-extinct species, the most important constraints to the short-term viability of any resurrected population are (i) their intrinsically low evolutionary resilience and (ii) their poor eco-evolutionary experience, in relation to the absence of (co)adaptation to biotic and abiotic changes in the recipient environment.
4. Assuming that some populations of resurrected species can persist locally, they have the potential to bring substantial benefits to biodiversity if the time since initial extinction is short relative to evolutionary dynamics. The restoration of lost genetic information could lead, along with the reinstatement of lost ecological functions, to the restoration of some evolutionary patrimony and processes, such as adaptation and diversification.
5. However, substantial evolutionary costs might occur, including unintended eco-evolutionary changes in the local system and unintended spread of the species. Further, evolutionary benefits are limited because (i) the use of resurrected populations as 'evolutionary proxies' of extinct species is meaningless; (ii) their phylogenetic originality is likely to be limited by the selection of inappropriate candidate species and the fact that the original species might be those for which de-extinction is the most difficult to achieve practically; (iii) the resurrection of a few extinct species does not have the potential to conserve as much evolutionary history as traditional conservation strategies, such as the reduction of ongoing species declines and extinction debts.
6. De-extinction is a stimulating idea, which is not intrinsically antagonistic to the conservation of evolutionary processes. However, poor choice of candidate species, and most importantly, too long time scales between a species' extinction and its resurrection are associated with low expected evolutionary benefits and likely unacceptable eco-evolutionary risks.

**Key-words:** adaptation, biocentric conservation ethics, conservation phylogenetics, conservation translocation, de-extinction, evolutionary processes

### Introduction

De-extinction, the idea of bringing back extinct species using back breeding, or cloning and genomic engineering,

has generated excitement and controversy (Sherkow & Greely 2013). So far, debates surrounding de-extinction have focused on ecological, ethical, societal and economic issues, but rarely on evolutionary considerations. Evolution is nonetheless one of the most important frameworks with which to describe and understand the effects of

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human actions on biological processes and also the primary ethical postulate that justifies conservation research and practices (Soulé 1985). Evolutionary biology has been central to the science of conservation biology since its inception (Hendry *et al.* 2010) and many evolutionary biologists acknowledge that the current human-driven biotic crisis is likely to disrupt and deplete certain basic processes of evolution (Myers & Knoll 2001). Moreover, conservation biologists have developed theories to understand the evolutionary effects of the main drivers of biodiversity changes (such as habitat destruction, climate change or invasive species), as well as the expected benefits of conservation actions (such as protection or restoration). The fields of conservation genetics and evolutionary conservation biology address, for instance, short-term genetic deterioration (Coron *et al.* 2013), future evolutionary potential (Lynch & Lande 1998) and the designation of conservation units and management plans that seek to conserve both evolutionary processes and patterns (Moritz 2002). The application of this evolutionary framework to any de-extinction approach is essential, not only to understand how evolutionary processes can favour or constrain the dynamics and ecological consequences of resurrected species, but also to put de-extinction projects, with their potential risks and benefits, into the widest, macro-evolutionary, conservation perspective.

The most important eco-evolutionary peculiarities of resurrected populations will be (i) the discontinuity of biological processes at the scales of the resurrected organisms and populations; (ii) the small initial genetic diversity inherent to de-extinction pathways such as cloning; and (iii) the divergence of evolutionary and environmental trajectories potentially leading to the maladaptation of resurrected species to the rest of the world (biotic, abiotic, from local to global scale). Much of the excitement and controversy associated with de-extinction has focused on the first, qualitative, issue (discontinuity), because it is related to the very definition of de-extinction and what distinguishes it from all other types of conservation translocations (IUCN 2013, 2016). Yet, from an evolutionary perspective, the costs and benefits associated with de-extinction are also linked to the latter two, quantitative, issues. In particular, the divergence issue is critically related to the time elapsed between the extinction of the target species and its resurrection; the temporal scales envisaged for the de-extinction of the Saber-toothed cat (*Paramachairodus ogygia*) or the Woolly mammoth (*Mammuthus primigenius*) are perhaps the most challenging aspects of these programmes.

Although some authors have recently emphasized that de-extinction projects raise new questions in conservation science, some important ecological and evolutionary processes relevant to resurrected species have been studied in other contexts. For example, the reintroduction literature (Seddon, Armstrong & Maloney 2007) has provided a rigorous examination of the eco-evolutionary processes driving the dynamics of (initially small) populations restored into their historic range (Robert *et al.* 2004; Robert 2009),

and some authors have recently argued that the fundamental criteria for selecting appropriate de-extinction candidates for conservation benefit should match selection criteria to those for reintroducing species that have been locally extirpated (Seddon, Moehrenschlager & Ewen 2014). On the other hand, the literature on invasive species has provided insights into populations that are completely exogenous to a given ecological recipient and evolutionary related questions of their success (Facon *et al.* 2006). Over the last few years, the debate on Pleistocene rewilding has raised the issue of restoration of long-extinct populations of extant species (Rubenstein & Rubenstein 2015) and conservation biologists have developed a feasibility and risk analysis framework for assisted colonization, the intentional movement of organisms outside their indigenous range (IUCN 2013). De-extinction is not simply an intermediate between reintroduction and invasion, but much can be learned from case studies on these topics.

In this paper, we review and discuss de-extinctions from an evolutionary perspective and address two questions:

1. Could de-extinction programmes result in long-term viable and self-sustainable populations despite potential ecological and evolutionary factors limiting their dynamics, and if so, would they have the evolutionary potential to locally re-establish lost ecological functions in their recipient ecosystem? In other words, does de-extinction have the potential to be successful at the local scale?
2. Assuming that some de-extinct species are locally successful, would they constitute a benefit to biodiversity at a global and macro-evolutionary scale?

## Evolutionary constraints on the local success of de-extinction projects

### DISCONTINUITY OF BIOLOGICAL PROCESSES

A first difference between de-extinctions and other types of conservation translocations (although shared with cloning of extant species) is the discontinuity or breakdown of some molecular, cellular, behavioural and ecological processes. Such discontinuity is mainly related to the non-genetic transmission of a proportion of the heritable biological and cultural information (Danchin *et al.* 2011), which might be disrupted by cloning protocols (Tsunoda & Kato 2002; Shapiro 2017). This includes epigenetic make-up, vertically transmitted symbionts, physiological effects and cultural transmission. Such discontinuities are potentially associated with demographic problems. For example, somatic cell nuclear transfer protocols can be associated with epigenetic drift of the embryonic genome, leading to developmental constraints on the clones, and potential post natal mortality (Loi, Galli & Ptak 2007). Recent ecological research also showed that imperfect vertical transmission of symbionts can affect population dynamics (Yule, Miller & Rudgers 2013). Other examples

include missing parental effects, such as antibodies transmission or behavioural care, which are likely to affect juvenile survival and, in turn, population dynamics.

#### INITIAL GENETIC DIVERSITY AND EVOLUTIONARY RESILIENCE

In most conservation translocations, the number of translocated individuals determines the extent of demographic stochasticity occurring during the establishment phase of the population's dynamics and thus influences success (Robert *et al.* 2015). From a genetic viewpoint, the initial number of individuals partly determines the initial genetic variation and subsequent short-term genetic deterioration and lack of adaptability (Robert, Couvet & Sarrazin 2007). Numbers of released individuals in reintroduction programmes typically range from a few tens to a few hundred individuals, and empirical reintroduction surveys suggest that there is a positive relationship between the number of released individuals and programme success (Wolf *et al.* 1996), yet the potential contribution of genetic effects to this pattern has not been clearly established.

One peculiarity of de-extinction with respect to initial genetic variation is that initial numbers of individuals and initial genetic variation can be completely decoupled in cases the operations are based on, for example multiple clones from a single source (see Steeves, Johnson & Hale 2017).

Although it has been suggested that new genomic editing techniques 'should be able to restore heterozygosity pretty easily in living genomes' (Brand 2014), the amount of initial genetic variation is likely to remain an important issue in de-extinctions. Evolutionary resilience refers to both the ability of populations to persist in their current state and to undergo evolutionary adaptation in response to changing environmental conditions (Sgró, Lowe & Hoffmann 2011). Low genetic variation can affect evolutionary resilience through reduction in population fitness due to increased inbreeding and drift loads (Keller & Waller 2002) and through reduced adaptability to future environmental changes (Lankau *et al.* 2011). A population founded with the genetic material from only one or a few individuals will experience similar genetic problems as any natural or captive population experiencing a severe bottleneck, in turn reducing its ability to adapt to changing environments (Frankham *et al.* 1999). Even assuming that genomic editing can be used, not only to fill gaps, but also to capture a significant fraction of the genetic variation of closely related, extant species, this would necessitate the use of hundreds of distinct individuals of the extant species to avoid such bottleneck effect.

On the positive side, although low genetic variation has been shown to increase the extinction risk, there are some documented cases of populations that have persisted over long periods of time at extremely small population sizes prior to recovery (e.g. Groombridge *et al.* 2000), and both conservation translocation and invasive species literatures provide examples of viable populations founded with very

few individuals (Taylor, Jamieson & Armstrong 2005). Furthermore, the science of conservation translocation provides concepts and tools (i) to minimize the loss of genetic variation of captive populations before release into the wild (Lacy 1989) and (ii) to maximize post-release survival and population growth through optimal release methods (Hardouin *et al.* 2014) and through continuing and adaptive management (Swaisgood 2010). Finally, the persistence of small populations is a general concern in conservation biology, and more research on this issue will provide benefits beyond the field of de-extinction. For example, rapid progress in breeding and genetic technologies associated with the de-extinction research may also be applied to the conservation of extant endangered species based on cloning, for example to target under-represented genetic lines (Holt, Pickard & Prather 2004) or mitigate the effects of demographic stochasticity.

#### EVOLUTIONARY DIVERGENCES

Like seed banks or cryogenic zoos, de-extinction raises the issue of evolutionary freezing (Simmonds 1962), which might imply strong divergence between the target species and its target environment. Such evolutionary divergence is primarily a matter of time. The times since extinction of the twenty de-extinction candidate species proposed following the TEDxDeExtinction conference (see Seddon, Moehrenschlager & Ewen 2014) range from a few years to more than 10 000 years, which means that, in some cases, several hundreds or thousands of generations might have elapsed since the original extinction (see Table 1). As a comparison, in the case of reintroductions, times between local extinction and the planned release range from a few years to a few 100 years (Fig. 1). Thus, although the time scales of de-extinction and reintroduction largely overlap, the temporal horizon envisaged for some 'deep de-extinction' projects (as coined by Sandler 2014) is likely to be several orders of magnitude longer than for any reintroduction project.

Although the effect of the time since local extinction on the success of reintroduction programmes has, to our knowledge, not been formally, empirically assessed, Osborne & Seddon (2012) recently pointed out that the longer this time, the greater the chance that suitable habitat will no longer be available. The environment is continually changing at different rates and scales, and humans are main drivers of these changes (Corlett 2015; Hofman *et al.* 2015). The main human drivers of rapid evolutionary responses are harvesting (Uusi-Heikkilä *et al.* 2015), invasive species (Mooney & Cleland 2001), habitat degradation (Macnair 1987) and ongoing climate change (Hof *et al.* 2011). Thus, in many regions of the world, conditions under which a 200-year-old tree established are likely to be quite different to those existing today (Sgró, Lowe & Hoffmann 2011), and the ecological context of a species that went extinct even only 100 years ago, such as the passenger pigeon (*Ectopistes migratorius*), has changed dramatically (Sherkow & Greely 2013; Peers *et al.* 2016).

**Table 1.** Generation length (GL) estimates for the 20 candidate species for de-extinctions. GL estimates for the Ivory-billed woodpecker, the Baiji and the Spanish Ibex (as the Bucardo is a subspecies) were taken from the BirdLife International (<http://www.birdlife.org>) and IUCN (<http://www.iucnredlist.org>) websites. For the rest of the candidate species, we used close relative living species as proxies to estimate GL values (see details and references in Table S1 of Supporting Information). The estimated number of generations since extinction is calculated as the time since extinction (in years) divided by GL

ID	Common name	Scientific name	Extinction	Time since extinction (years)	Generation length (years)	Reference (Generation length)	No. of generations since extinction
1	Passenger pigeon	<i>Ectopistes migratorius</i>	1914	101	6.9	BirdLife International (2015)	14.64
2	Carolina parakeet	<i>Conuropsis carolinensis</i>	1918	97	6.67	BirdLife International (2015)	14.54
3	Cuban red macaw	<i>Ara tricolor</i>	1864	151	12.7	BirdLife International (2015)	11.89
4	Ivory-billed woodpecker	<i>Campephilus principalis</i>	1944	71	6.5	BirdLife International (2015)	10.92
5	O'o	<i>Moho nobilis</i>	1934	81	5.6	BirdLife International (2015)	14.46
6	Elephant bird	<i>Aepyornis</i> sp./ <i>Mullerornis</i> sp.	1800s	215	10.5	BirdLife International (2015)	20.48
7	Moa	<i>Dinornis</i> spp.	1400s	615	10.5	BirdLife International (2015)	58.57
8	Huia	<i>Heteralocha acutirostris</i>	1907	108	12.5	BirdLife International (2015)	8.64
9	Dodo	<i>Raphus cucullatus</i>	1662	353	6.6	BirdLife International (2015)	53.48
10	Great auk	<i>Pinguinis impennis</i>	1852	163	13.6	BirdLife International (2015)	11.99
11	Auroch	<i>Bos primigenius</i>	1627	388	6	Murray <i>et al.</i> (2010)	64.67
12	Pyrenean ibex, Bucardo	<i>Capra pyrenaica pyrenaica</i>	2000	15	6.77	Pacifici <i>et al.</i> (2013)	2.22
13	Thylacine, Tasmanian tiger	<i>Thylacinus cynocephalus</i>	1936	79	4.67	Pacifici <i>et al.</i> (2013)	16.92
14	Woolly mammoth	<i>Mammuthus primigenius</i>	6400 years before present	6400	22	Pacifici <i>et al.</i> (2013)	500
15	Mastodon	<i>Mammuthus</i> spp.	10 000 years before present	10 000	22	Pacifici <i>et al.</i> (2013)	290.9
16	Saber-toothed cat	<i>Smilodon</i>	11 000 years before present	11 000	6	Pacifici <i>et al.</i> (2013)	1833.3
17	Steller's sea cow	<i>Hydrodamalis gigas</i>	1768	247	28.07	Pacifici <i>et al.</i> (2013)	9.51
18	Caribbean monk seal	<i>Monachus tropicalis</i>	1952	63	15	Pacifici <i>et al.</i> (2013)	4.2
19	Baiji, Chinese river dolphin	<i>Lipotes vexillifer</i>	2006	9	13.26	Pacifici <i>et al.</i> (2013)	0.68
20	Xerces blue butterfly	<i>Glaucopsyche xerces</i>	1941	74	1	Arnold (1987)	74

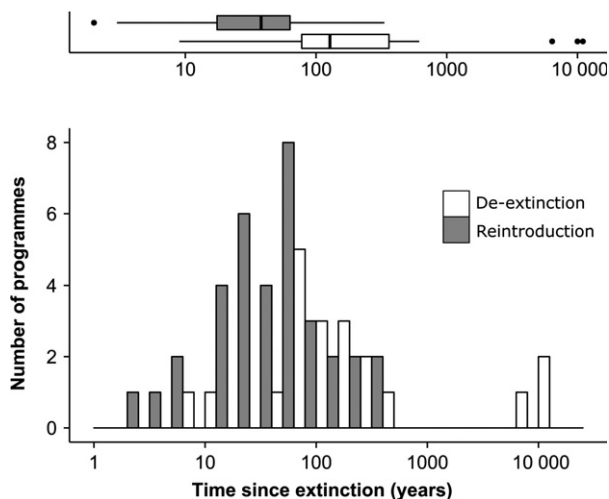
These dramatic environmental changes can be associated with particularly strong and rapid selection, as many populations have the capacity to respond to, for example, climate change within a time frame of tens of years (Hendry, Farrugia & Kinnison 2008). Such adaptive changes are generally considered much more rapid than non-adaptive changes (Stockwell, Hendry & Kinnison 2003), and most phenotypic differences observed among natural populations are likely adaptive (Hendry *et al.* 2010). Thus, recent temporal environmental changes and associated contemporary evolution are likely to generate strong levels of divergence between the environment and a de-extinct population that has not had the opportunity to adapt to (i) human-induced environmental changes, (ii) biotic changes in response to these changes, or (iii) biotic changes in response to the original extinction of the target species.

#### COMMUNITY PROCESSES

Evolutionary processes occurring at the level of the biological community further complicate patterns of divergence

between de-extinct populations and their recipient environment. There is abundant evidence that ecological interactions drive rapid evolution and can change the direction of evolution compared to adaptation in isolation (Liow, Van Valen & Stenseth 2011; Lawrence *et al.* 2012). Co-evolutionary processes occurring at the community level partly determine ecosystem functions (Bailey *et al.* 2009) and community response to climate (Reusch *et al.* 2005; Sgró, Lowe & Hoffmann 2011).

In the context of de-extinction, another potentially important factor of rapid evolutionary and ecological changes in the local community is the initial extinction of the target species itself, which is expected to affect eco-evolutionary feedbacks and in turn, community and ecosystem stability (de Mazancourt, Johnson & Barraclough 2008). Based on experiments, Lawrence *et al.* (2012) showed that, after the extinction of a species providing important functions, surviving species tended to restore (rather than further disrupt) those functions at relatively short time scales (70 generations). The ecological consequences of phenotypic change are expected



**Fig. 1.** Distribution of time since extinction (logarithmic scale) for de-extinction candidate species (white bars,  $n = 20$ ), compared to the time elapsed since local extinction for several reintroduction programmes in Europe (grey bars,  $n = 35$ , see Table S2 for details). Median time since extinction: 129.5 years (de-extinctions) and 38 years (reintroductions).

to be particularly important in species with large per capita ecological roles or those that are very abundant or rapidly evolving (e.g. some pathogens). For example, the loss of a predator can have manifold effects on the remainder of the community (Reznick, Ghalambor & Crooks 2008), such as the rapid growth of prey populations, changes in their age structure and population dynamics and a restructuring of the lower trophic levels (Pace *et al.* 1999). Predators can have a profound effect on the evolution of other species. Processes such as antipredator behaviour can develop over relatively short timescales (Blumstein & Daniel 2005) and thus disappear similarly quickly if they are costly (e.g. vigilance).

These ecology–evolution interactions can be formalized thanks to the concept of eco-evolutionary experience (Saul & Jeschke 2015), which emphasizes that (i) during evolution, species adapt to biotic interactions in their native environment and thereby accumulate eco-evolutionary experience, and (ii) this heritable experience might be applicable in new ecological contexts, for example when species are introduced to non-native environments. The degree to which a species can actually apply its experience in new ecological contexts depends on the ecological similarity between previous interactions and those in the new contexts and significantly influences a species' proficiency to persist with its new interaction partners (Cox & Lima 2006).

Thus, although there is some evidence that species reintroduction can lead to local community and ecosystem recovery (Ripple & Beschta 2012), in the cases of long-extinct populations, eco-evolutionary experience must be accommodated if the reconstruction of communities is to be successful.

## MALADAPTATION AND LOCAL SUCCESS

The most important and immediate cost of such divergence and maladaptation is likely to be a demographic cost: the re-extinction of the resurrected population (Steeves, Johnson & Hale 2017). Theory has demonstrated that the capacity of a population to survive an episode of selection will be determined more by whether or not the population can survive the initial increase in mortality rate than by whether or not it can evolve in response to selection (Gomulkiewicz & Holt 1995). In the case of invasive species, demographic costs of initial maladaptation are implied in the observation that introduced species (i) usually fail to become established (Sax & Brown 2000), (ii) do so only after a lag period, which is often accompanied by phenotypic changes (Facon *et al.* 2006) and that (iii) relatedness to native species can influence the success of invasive species (Strauss, Webb & Salamin 2006).

Phenotype plasticity tends to relax conditions under which such extinction is inevitable unless the costs of plasticity are high (Chevin, Lande & Mace 2010). However, both the discontinuity of biological and cultural processes and the loss of evolutionary and ecological histories might affect the effectiveness of plasticity in de-extinct populations. For example, at an individual level, organisms that evolved under variable climates tend to have much broader physiological tolerances for temperature than those that evolved in aseasonal zones (Tewksbury, Huey & Deutsch 2008). History might be especially important for phenotypically plastic responses, in which an individual uses specific environmental cues to elicit a phenotypic change (in morphology, behaviour, etc., Lankau *et al.* 2011). In de-extinction programmes, 'rapid' environmental changes can alter the relationship between cue and future condition, such that the normal phenotypic response to certain cues is no longer adaptive (Schlaepfer, Runge & Sherman 2002).

## Restoration of evolutionary trajectories

### PHYLOGENY OF DE-EXTINCT SPECIES

#### *Evolutionary history of de-extinct species*

Evolutionary history has been argued to capture the diversity of life better than simple measures of species richness (Purvis 2008). Since the 1990s, a phylogenetic approach to conservation has been proposed, in order to prioritize the protection of evolutionary distinct groups or of geographic areas. For example, at the level of a group of several species, a common measure used to quantify evolutionary history is phylogenetic diversity (Faith 1992), which is the minimum total length of all the phylogenetic branches required to connect the species in a phylogenetic tree. At the level of the individual species, indices of evolutionary distinctiveness quantify how few relatives a species has and how phylogenetically distant they are (Veron *et al.* 2015).

Phylogenetic diversity is sometimes used as a proxy of (integrative) functional diversity. It has been argued that, at the species level, evolutionarily distinct species exhibit rare functional traits (Pavoine, Ollier & Dufour 2005; but see Winter, Devictor & Schweiger 2012). Another important property is that both extinction rates and the prevalence of threatened species are non-neutral with respect to phylogenies (Diniz-Filho 2004). This knowledge of evolutionary history is increasingly used to set conservation priorities (Hendry *et al.* 2010; Lankau *et al.* 2011; Jetz *et al.* 2014), for example by identifying species which are at the same time both evolutionarily distinct and globally endangered (Isaac *et al.* 2007).

Can this framework be applied to the selection of de-extinction candidates? From the perspective of evolutionary conservation biology, one might consider that the 'moral imperative' (Seddon, Moehrenschrager & Ewen 2014) to reverse species extinction caused by humans should be translated into an imperative to reintroduce their extinct genomes into the global gene pool (Church & Regis 2012), or even to restore evolutionary trajectories interrupted by humans. Because de-extinction is primarily a species-based approach, the use of evolutionary distinctiveness measures to select candidates might seem pertinent. Restoring evolutionarily distinct extinct species should, in theory, maximize the restoration of evolutionary history. However, resurrections of long-extinct species raise problems that do not exist for other types of conservation translocation, related to DNA degradation and imperfect knowledge of evolutionary relationships between species. In this context, it has been suggested that the same next-generation DNA sequencing technologies that make de-extinction technologically feasible should be first applied to make new inferences on evolutionary relationships between species using ancient genomes (Shapiro & Hofreiter 2014), which offers promising potential to assess the evolutionary stakes of de-extinction initiatives.

#### *Unintended phylogenetic bias*

Despite the existence of an operational phylogenetical framework, the selection of candidate species for (classical) translocations is generally made without respect for phylogenetic considerations, although candidate selection can paradoxically (and unintentionally) lead to a reduced coverage of the phylogenetic tree of life. The decision and feasibility of translocating a particular extant species depends on multiple factors, including the conservation status of the species, the availability of individuals to be translocated, accurate translocation site, funds, public and political support, etc. Obviously, most of these constraints are non-neutral with respect to taxonomy. In the case of reintroductions, for example, Seddon, Soorae & Launay (2005) showed that vertebrate projects are over-represented with respect to their prevalence in nature. In the cases of rewilding programmes aiming at re-establishing ecological functions (IUCN 2013), strong functional biases are

expected. These taxonomic and functional biases will translate into phylogenetic biases.

The selection of candidate species for de-extinction projects is undoubtedly influenced by the biases that exist for other conservation translocations: a bias towards species with a supposedly important functional impact on ecosystems (such as grazers or predators), and more than ever a bias towards large, charismatic species. However, it is also very likely that these phylogenetic filters will differ, at least quantitatively in the case of de-extinction. First, because the list of known species extinctions since 1500AD is incomplete and biased (Purvis 2008), and, as the time scale increases, additional constraints on data and biological material availability are likely to amplify existing phylogenetic biases or engender new biases on candidate species (Alroy *et al.* 2001). Secondly, because the economic cost of de-extinction is intuitively far higher than for any other type of conservation translocation, any economic filter on the choice of candidate species (Tisdell & Nantha 2007) will be amplified.

Finally, the evolutionary benefit of any de-extinction programme relies on the phylogenetic distinctness of the target species. However, the technical feasibility of a programme is critically linked to the existence of organisms of phylogenetically closely related extant species to be used as egg donors, surrogates or references for genome reconstruction. This paradox questions the potential evolutionary benefits of de-extinction because evolutionarily distinct species might be those for which de-extinction is least feasible.

#### EVOLUTIONARY BENEFITS OF DE-EXTINCTIONS

##### *Evolutionary proxies?*

This is perhaps one of the biggest paradoxes about de-extinction: although primarily based on the manipulation of genetic information, the potential evolutionary benefit of these operations is non-trivial, unlike their ecological benefit. Many authors acknowledge that de-extinction could have potentially important ecological benefits (although these benefits are complex to characterize and should be balanced against potential ecological risks). These benefits rely on the concept of ecological proxy, that is, a substitute entity, which carries out similar ecological functions as the lost entity. Contrary to ecological proxy, the notion of 'evolutionary proxy' is meaningless. In other words, while nature's functions and services can be synthesized (Redford, Adams & Mace 2013), nature, by definition, cannot be. In contrast to functional diversity that can potentially be recovered through recurrent selection, historically isolated lineages cannot be recovered and historically isolated but ecologically exchangeable populations should be considered as distinct significant evolutionary units (Moritz 2002). Furthermore, one major component of biodiversity – that is both a component of the evolutionary history and the main driver of evolutionary

processes – is intraspecies genetic diversity, which is expected to be extremely low in most if not all species resurrected through cloning. Thus, while both the species as seen as a typological entity and its functional ecological role can indeed be resurrected (or at least be replaced by proxies), the evolutionary loss associated with the initial species decline and extinction is irreversible (Ehrlich 2014).

### *Balance of costs and benefits*

What might the evolutionary benefits of de-extinctions be? At the scale of the local biological system, assuming that a given programme (i) can reasonably be considered to be a short-term response to short-term human effects (see below), and (ii) can restore a significant fraction of lost genetic information of the extinct species, expected benefits are the same as those expected from any other type of translocation: the restoration of some evolutionary patrimony and processes, such as adaptation and diversification. Further assuming that local restoration leads to the reinstatement of lost ecological functions, this could contribute, at the global scale, to the improvement of functional and genetic diversity. Even assuming that de-extinction does not restore a significant fraction of lost genetic information, it has been suggested that it could also contribute to the global evolutionary resilience of current biodiversity: some programmes might directly benefit the conservation of particular phylogenetic groups by widening the ecological niche of the groups and their geographic ranges. For example, releasing elephants expressing mammoth genes into cold habitats can be seen as a means to extend the geographical distribution of elephants beyond their current declining, warm habitats (Shapiro 2015).

And what could be the evolutionary costs, assuming that the resurrected population is viable? Most, if not all evolutionary costs are probably mediated by ecological costs: (i) profound, unintended eco-evolutionary changes in the local system (including hysteretic phenomena, in which irreversible catastrophic shift occurs, see, for example Van Nes & Scheffer 2004), (ii) unintended spread of the species, which is likely in the case of mismatch between historic and current or future habitat suitability (Peers *et al.* 2016), (iii) sudden changes in local human pressures (e.g. increase of tourism following the resurrection of a highly charismatic species). These ecological costs, which are similar to some of the well-known consequences of invasive species and local environmental degradation, can have major unintended evolutionary consequences (Hendry *et al.* 2010).

## ALTERNATIVES TO DE-EXTINCTIONS

### *A restoration perspective*

Since most of the arguments in favour of de-extinction are linked to the concept of ecological proxy, the best alternative to the resurrection of extinct species could be the selection and release of extant ecological replacements (IUCN

2013). Using existing species as alternatives deserves to be considered (IUCN 2016), not only from an ecological perspective, but also from an evolutionary perspective (see an example in the Pyrenean wild goat (*Capra p. pyrenaica*) in Garcia-Gonzalez & Margalida 2014).

The functional arguments put forward to justify de-extinction projects apply to the translocation of both living and any potentially resurrected species. However, from an evolutionary viewpoint, the translocation of a resurrected species cannot be equivalent to the translocation of a living species, even in the case where the latter is exotic. Living species participate in the evolutionary process in the broad sense, for instance because they undergo speciation, because they engage in co-evolutionary arms race or trench warfare with their cohort of pathogens (Van Valen 1973) and because they continue to accumulate mutations, embedded in complex networks of gene flow. The eco-evolutionary factors that were driving the evolution of extinct species are just as extinct as the species themselves, and they can hardly be restored.

### *A conservation perspective*

A common reaction against de-extinction is to ask ‘why would we spend all this energy and effort to bring back ancient animals but let so many others just disappear?’ (Jamie Rappaport Clark, quoted in Gross 2013). Is this heuristic argument consistent with our knowledge on the potential respective benefits on evolutionary processes and patrimony of conserving extant species vs. resurrecting extinct species? It is estimated that one-fifth of vertebrate species are now threatened with extinction (Hoffmann *et al.* 2010). However, one important point is that the vast majority of species threatened with extinction are not extinct (Barnosky *et al.* 2011), and this is also true for phylogenetic diversity (review in Veron *et al.* 2015). Thus, the recent loss of species is dramatic and serious but does not yet qualify as a mass extinction in the paleontological sense of the Big Five (Barnosky *et al.* 2011); and there is still much of the world’s biodiversity left to save, but doing so will require the reversal of the well-known anthropogenic threats which are responsible for the ongoing declines (Ehrlich 2014). Thus, at a phylogenetic level, the potential benefits of saving threatened species and populations and reducing extinction debts is much more important than the likely benefits of resurrecting a few extinct species. This should be considered especially if one believes that there can exist a trade-off (e.g. economic) between de-extinction and other conservation approaches (see Iacona *et al.* 2016).

## EVOLUTIONARY VALUES

### *Ethics and values*

Assuming that a de-extinction programme results in a demographically viable population, and assuming that this population has led to the re-establishment of lost



ecological functions. Do the conservation benefits of this programme go beyond such functional aspects? The first functional aspect completed by de-extinction is a cultural service: the return of charismatic, popular species and a sort of reverence for the power of technology to resuscitate life. The second aspect completed by de-extinction is to restore functional services such as regulation, provisioning or supporting. In conservation sciences, biodiversity services are prominently associated with utilitarian conservation values. Do we intend to resurrect the species that we have led to extinction in the past in order only to benefit from associated biodiversity services? Would this be ethically acceptable?

Acknowledging that change is the basis of life (Dobzhansky 1973) implies a fundamental change from an anthropocentric to a biocentric philosophy in which biodiversity has its own participant role and history independently of human beings (Maris 2010). Thus, many biologists agree that maintaining evolutionary potential and processes is a primary concern of conservation science (Soulé 1985; Myers & Knoll 2001), and conserving evolutionary trajectories might constitute a challenging major evolutionary transition inducing a deliberate overcoming of the Anthropocene (Sarrazin & Lecomte 2016).

In agreement with these general principles, many ecological restoration approaches do not aim to return to some arbitrary historical state but instead focus on the reinstatement of functions to restore degraded ecosystems (IUCN 2013) and promote adaptation (Aitken & Whitlock 2013). De-extinction, by essence, is not antagonistic with these efforts aiming at restoring or maintaining functional variation. However, it is questionable whether de-extinction has the potential to restore the evolutionary values of lost biodiversity. Sandler (2014) recently argued that deep de-extinction does not restore the natural-history properties of species, nor their wildness or independence from humans, because it results only in organisms whose genetic make-up most resembles that of species that went extinct long ago, and for whom we have reconstructed the genome. We agree that the potential of de-extinctions to re-establish lost (evolutionary) value is questionable, and we advocate that Sandler (2014)'s reasoning be extended below and beyond the species level and be focused on the evolutionary processes themselves, rather than the products of these processes. Evolution operates through changes in the frequency of alleles across generations and not instant heritable changes in the properties of individuals themselves. Species traits or functions are not intrinsic drivers of evolution. Thus, although de-extinction has the potential to restore some historical patterns that might in turn influence future evolution, the impossibility of restoring past dynamics of co-evolution between the target organisms and their environments is the main limitation to the evolutionary value of de-extinct populations.

### *Saving species to restore evolutionary trajectories: time scale and ethical justifications*

Species are operational or ontological concepts useful to biologists rather than fixed categories within a continuum of biodiversity (Hey 2006). Although ultimate conservation goals are directed towards general processes, rather than products or entities (such as particular species), saving particular species from extinction is a pragmatic way to reduce the global rate of *untimely*, human-induced extinctions (Soulé 1985). This implies, however, that the strong and essential discrepancy between the time scale of macro-evolutionary processes and the time scale of human influence is clearly acknowledged. De-extinction makes sense only if it constitutes responses to short-term (at the evolutionary scale) human influence: a few tens or hundreds of generations since the extinction of the target species, which represents only a small fraction of the average longevity of species (Jenkins 1992). Moreover, this also implies that causes of extinction are identified as being anthropogenic, which might be ambiguous for distant extinctions (Stuart 2015). Archaeogenomics based on ancient DNA has an important role in helping resolve both the causes and effects of these distant extinction events (Hofman *et al.* 2015) and thus provide evolutionary and ethical justification to de-extinctions.

### **Conclusion**

De-extinction is a stimulating idea, which has raised, and will continue to raise debates among scientists. Focusing on ethical aspects, Sandler (2014) recently concluded that de-extinction is not intrinsically problematic, although it is in many respects a luxury. From an evolutionary viewpoint, we agree with Sandler's view and believe that critics from ecologists and evolutionary biologists do not need to focus on de-extinction *per se* but rather on its potential excesses, such as irrelevant choice of target species, potential of invasive impact on ecosystems, or unreasonable time scales. In particular, one of the most important scientific arguments against de-extinction could be an evolutionary one: extinct species do not evolve, but the rest of the world does. While some recent translocation practices aim at finding genotypes that can match future environments (Aitken & Whitlock 2013), de-extinction involves the risk that resurrected species are not adapted to the present, Anthropocene environment.

As the time elapsed since the extinction of the target species becomes longer, (i) the eco-evolutionary experience of the target species to its local environment will become lower and ecological functions provided by the target species will have more chance to have been fulfilled by evolutionary changes having occurred in the community; (ii) the technical difficulty will increase due to DNA degradation, in turn increasing the necessity of using phylogenetically closely related extant species for genome reconstruction (Shapiro 2017); (iii) our knowledge of the past ecological

context and evolutionary history of the target species becomes fragmentary and our responsibility in the initial extinction becomes uncertain.

Both feasibility assessment and selection of species for de-extinction programmes should include these considerations. Candidate species should have gone extinct recently, have high evolutionary distinctiveness and their original environment should be well described. Although species' traits are likely to influence de-extinction success, determining what life history or ecological traits can mitigate demographic problems associated with small population size, lack of genetic variation and maladaptation is not trivial. As in the case of invasive species, it is likely that barriers and filtering at various stages of de-extinction programmes will shape complex relationships between species traits and success (Capellini *et al.* 2015).

Feasibility assessments and comparisons should rely on thorough interdisciplinary modelling and comparative analysis. Within the last decades, an array of empirical and theoretical modelling techniques have been developed to project past and future environmental, ecological and evolutionary dynamics, such as niche modelling, (no-)analog ecosystem projection, predictive evolutionary modelling and population viability analysis. Embracing these techniques is essential to select best candidate species, optimize release methods and assess the chance of success and potential evolutionary benefits of de-extinction programmes.

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## Data accessibility

All data used in this manuscript are present in the manuscript and its supporting information.

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## Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

**Table S1.** List of the close relative living species used as proxies for the estimation of generation lengths for candidate species presented in Table 1.

**Table S2.** Reintroduction programs used in Fig. 1 to compare de-extinction and reintroduction time scales.

## **Supporting Information for the manuscript**

***De-extinction and evolution*, by Alexandre Robert, Charles Thévenin, Karine Princé, François Sarrazin & Joanne Clavel, for *Functional Ecology*.**

**Supporting Appendix 1. Supplementary information on de-extinction candidates and sample of reintroduced species considered in the article.**

**Table S1:** List of the close relative living species used as proxies for the estimation of generation lengths for candidate species presented in Table 1. a: complementary information is provided (i) if there is no close living relative species, or (ii) if the closest relative species cannot be used as a reliable proxy for generation length. b: when several close relative species were available, we used the average of their generation lengths.

**Table S2:** Reintroduction programs used in Figure 1 to compare de-extinction and reintroduction time scales. This information was retrieved from an animal translocation database under current development, focusing on translocation projects at the European scale (396 translocation programs throughout Europe). From this database, we sampled programs for which both the dates of local extinction and first release are known (n=35, all of these programs are reintroductions *sensu stricto*), allowing us to estimate the time elapsed since local extinction. For further information about the database, please contact François Sarrazin (sarrazin@mnhn.fr).

**Table S1**

<b>ID</b>	<b>Species used as a proxy</b>	<b>Complementary information<sup>a</sup></b>	<b>References</b>
1	<i>Patagioenas fasciata</i>	-	Johnson et al. 2010
2 <sup>b</sup>	<i>Aratinga nenday</i> <i>Aratinga solstitialis</i> <i>Aratinga auricapillus</i>	-	Kirchman et al. 2012
3	<i>Ara macao</i>	-	Wiley & Kirwan 2013
4	<i>Campephilus principalis</i>	The species is still listed as CR by the IUCN, and generation length estimates are available	BirdLife 2015
5 <sup>b</sup>	<i>Ptiligonys caudatus</i> <i>Phainoptila melanoxantha</i> <i>Phainopepla nitens</i> <i>Ptiligonys cinereus</i>	-	Fleischer et al. 2008
6, 7	<i>Dromaius novaehollandiae</i>	Moas and Elephant birds are close relative to the extant kiwis ( <i>Apteryx sp.</i> ), but considering the relatively small size of kiwis we used the Emu as a better proxy for generation length values	Mitchell et al. 2014
8 <sup>b</sup>	<i>Philesturnus carunculatus</i> <i>Callaeas cinereus</i>	-	Lambert et al. 2009
9	<i>Caloenas nicobarica</i>	-	Shapiro et al. 2002
10	<i>Alca torda</i>	-	Bengtson 1984
11	<i>Bos taurus</i>	-	Murray et al. 2010
12	<i>Capra pyreneica</i>	-	García-González & Margalida 2014
13	<i>Sarcophilus harrisi</i>	Miller et al. 2009 show that the Tasmanian tiger is more closely related to the Numbat ( <i>Myrmecobius fasciatus</i> ) rather than the Tasmanian devil, but we used the latter for generation length estimate because of a more similar size	Miller et al., 2009
14	<i>Elephas maximus</i>	-	Roca et al. 2015
15	<i>Elephas maximus</i>	<i>Mammuth</i> is a genus of the extinct family Mammutidae, and belongs to the Proboscidae order. Mastodons are less closely related to the Elephantidae family than the Woolly Mammoth but the Asian elephant can be used as a proxy for generation length estimate	Shoshani & Tassy 2005
16	<i>Panthera leo</i>	Sabre-tooth cats do not have any close living relative. Here we use the African lion as a proxy to estimate generation length, as both species are the same size and Janczewski et al. (1992) showed low genetic divergence between the two of them within the Felidae family.	Janczewski et al. 1992
17	<i>Dugong dugon</i>	-	Turvey & Risley 2006
18	<i>Monachus schauinslandi</i>	-	Scheel et al. 2014
19	<i>Lipotes vexillifer</i>	The species is still listed as CR by the IUCN, and generation length estimates are available	IUCN 2015
20	<i>Glaucopsyche lygdamus palosverdesensis</i>	Both the Xerces and the Palos Verdes blue butterfly are subspecies of <i>Glaucopsyche lygdamus</i> . Palos Verdes is an univoltine species, therefore we assume a generation length of one year	Arnold 1987

**Table S2**

<b>Species</b>	<b>Common name</b>	<b>Country</b>	<b>Extinction</b>	<b>Date of first release</b>	<b>Time since local extinction</b>
<i>Austropotamobius pallipes</i>	White-clawed crayfish	France	1885	1983	98
<i>Capra ibex</i>	Alpine ibex	France	1850	1995	145
<i>Cervus elaphus elaphus</i>	Red deer	France	1650	1958	308
<i>Cervus elaphus corsicanus</i>	Corsican deer	France	1960	1984	24
<i>Lutra lutra</i>	European otter	France	1980	1998	18
<i>Lutra lutra</i>	European otter	Netherlands	1989	2002	13
<i>Lynx lynx</i>	Eurasian lynx	France	1885	1970	85
<i>Lynx lynx</i>	Eurasian lynx	France	1650	1983	333
<i>Phoca vitulina</i>	Harbor seal	France	1960	1974	14
<i>Ursus arctos</i>	Brown bear	Poland	1890	1938	48
<i>Ursus arctos</i>	Brown bear	France	1990	1996	6
<i>Aegypius monachus</i>	Cinereous vulture	France	1970	1992	22
<i>Aegypius monachus</i>	Cinereous vulture	France	1840	2004	164
<i>Aegypius monachus</i>	Cinereous vulture	France	1840	2005	165
<i>Ciconia ciconia</i>	White stork	France	1954	1956	2
<i>Ciconia ciconia</i>	White stork	France	1954	1957	3
<i>Ciconia ciconia</i>	White stork	Swiss	1950	1965	15
<i>Gypaetus barbatus</i>	Bearded vulture	France	1935	1973	38
<i>Gypaetus barbatus</i>	Bearded vulture	France	1935	1986	51
<i>Gypaetus barbatus</i>	Bearded vulture	France	1935	1993	58
<i>Gyps fulvus</i>	Griffon vulture	France	1930	1971	41
<i>Gyps fulvus</i>	Griffon vulture	France	1930	1981	51
<i>Gyps fulvus</i>	Griffon vulture	France	1930	1999	69
<i>Oxyura leucocephala</i>	White-headed duck	France	1966	2001	35
<i>Tetrao urogallus</i>	Western capercaillie	France	1990	2007	17
<i>Salmo salar</i>	Atlantic salmon	France	1965	1971	6
<i>Salmo salar</i>	Atlantic salmon	France	1940	1975	35
<i>Salmo salar</i>	Atlantic salmon	France	1850	1976	126
<i>Salmo salar</i>	Atlantic salmon	France	1927	1977	50
<i>Salmo salar</i>	Atlantic salmon	France	1950	1980	30
<i>Salmo salar</i>	Atlantic salmon	France	1930	1981	51
<i>Salmo salar</i>	Atlantic salmon	France	1940	1983	43
<i>Testudo hermanni hermanni</i>	Hermann's tortoise	France	1986	1999	13
<i>Testudo hermanni hermanni</i>	Hermann's tortoise	France	1986	2005	19
<i>Testudo hermanni hermanni</i>	Hermann's tortoise	France	1986	2005	19

## References for Supporting Appendix 1

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# General Discussion

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## **Representativeness, distinctiveness and conservation prioritization**

Similarly to what has been achieved in the context of protected areas management (Thuiller et al., 2015; Veron et al., 2016), I have sought to assess the representativeness of reintroduction targets at large scale. In the first two chapters, we showed that some phylogenetic and functional diversity patterns arise when studying the implementation of past and current reintroduction projects in Europe. The breadth of evolutionary histories, calculated as the Phylogenetic Diversity, captured by reintroduced birds and mammals is relatively narrow compared to what would be expected from random null models. Reintroduced mammals are also poorly representative of the functional diversity of the European assemblage, but this pattern does not apply for reintroduced birds.

By considering both the representativeness and the distinctiveness of reintroduction targets, our results show that despite very strong taxonomic biases (see chapter 3), the debate surrounding the allocation of reintroduction efforts cannot be reduced only to a focus on large and charismatic species, and that the contribution of reintroductions to biodiversity conservation and recovery might be more complex. Beyond the context of reintroduction research, the first two chapters of this thesis also provide empirical evidence showing that a conservation strategy focusing on original species does not ensure a good representativeness of the functional or phylogenetic diversity at large scale if there is a lack of complementarity between species (Redding et al., 2008).

These findings provide a retrospective assessment of the distribution of reintroduction efforts at the European scale, which can be seen as the emergent property of the sum of local projects shaped by various motivations, constraints and contingencies. Importantly, we do not argue that a lack of phylogenetic or functional representativeness reflects some inadequacy of the selection of reintroduced species in Europe, or that large scale considerations should systematically guide local conservation efforts.

In the context of protected areas, the selection of target areas is likely to reflect top down decision-making and implementation, especially in Europe with the Natura 2000 network ([www.natura2000.fr](http://www.natura2000.fr)). Because such implementation is a spatial exercise, the expansion of protected area networks needs to ensure that costs are minimized compared to expected conservation benefits, which are usually measured as the coverage of biological diversity components per geographic unit. Optimization of large-scale efforts is thus strongly anchored in the context of protected area planning and management. In contrast, in single species conservation approaches, studying the representativeness of a set of conservation targets comes with some limitations. Unlike in gap analyses that explicitly aim to guide the expansion of current protected areas network, a large scale collective consultation aiming at maximizing PD or FD in the selection of future reintroduction targets is not necessarily compatible with local decision processes and contingencies. For example, based on our findings, we could have argued that future reintroductions of mammals in Europe should involve any members of the Eulipotyphla or Chiroptera orders in order to significantly increase the phylogenetic representativeness of reintroduced mammals in Europe, but this would completely overlook all the biological, sociological and economic aspects that influence the determination of a candidate species for reintroduction.

Distinctiveness measures are more likely to influence decision making in the context of species-centered conservation, as compared with representativeness measures. We showed that reintroduced birds in Europe and reintroduced mammals in Europe and North America tend to be more evolutionarily distinct than expected by chance. Thus, although evolutionary considerations are not likely to have driven the selection of reintroduction targets, the phylogenetic patterns uncovered suggest that reintroduction practitioners have focused on highly evolutionarily distinct species at the continental scale. This finding calls for further research on the decision processes underlying the selection of species for reintroduction programs, as well as on the complex relationships between evolutionary distinctiveness, large scale conservation status (which were not considered here) and any potential driver of reintroduction projects, including the perception or popularity of species by biologists, managers and the general public.

In chapters 1 and 2, I showed some trends in the allocation of reintroduction efforts toward more evolutionarily distinct mammals and birds, and toward more functionally distinct mammals. However these studies are not sufficient to conclude as to whether there is some actual “bias”, and if reintroduction practitioners intentionally favour original species. Decision

processes in the selection of reintroduction candidates vary from one species to another, and even between programs for a given species. Further, although we acknowledge the importance of recent developments in the reintroduction science literature (and especially those regarding decision-making), our data cover a long period (1960s-2010s, Supplementary Materials Chapter 1), over which decision processes might have changed. Thus, our data do not allow us to quantify the level of importance attributed to evolutionary history or functional traits when selecting reintroduction candidates. In the first two chapters, our approach remained phenomenological and we did not explicitly incorporate the underlying decision processes involved. Hence, our null random models do not represent biologically or sociologically relevant expectations; the patterns may not indicate a clear bias in the selection of reintroduction targets. Nevertheless, our goal here was to assess whether, despite known taxonomic biases, reintroduced species could represent significant phylogenetic or functional diversity and thereby be making a greater contribution to biodiversity conservation than expected. Although very basic, we think that our null models were appropriate to evaluate the departure of the observed process from a simple reference random process (which does not constitute an expectation). In their well-cited paper, Seddon et al. (2005) used a similar approach to assess the taxonomic bias in reintroduction projects by comparing the allocation of reintroduction efforts to “the numbers of reintroduction projects per taxon that would be expected if projects were in proportion to known species”. Here the null model does not constitute an a priori expectation for the allocation of reintroduction efforts, but offers a simple reference from which we can investigate phylogenetic and functional diversity patterns.

## **Reintroductions and different facets of biodiversity**

Conservationists are increasingly aware that neither evolutionary nor functional diversity sufficiently captures all facets of biological diversity (Brum et al., 2017; Devictor et al., 2010). Some authors have argued that phylogenetic diversity provides a good proxy for the study of the differences in species ecological niches, and so that assessing both the functional and evolutionary diversity of a set of species may end up redundant (Faith, 1992; Losos, 2008). This claim is based on the assumption that, if species’ traits evolve steadily through time, then the phylogenetic differences between species in an assemblage should reflect their ecological dissimilarity and inform us on functional diversity patterns (Webb et al., 2002; Webb and

Losos, 2000). However, the assumptions underlying the use of measures of phylogenetic diversity as proxies for functional diversity have been challenged (Cadotte et al., 2017; Mouquet et al., 2012), and have received mixed empirical evidence (Mazel et al., 2018, 2017). Comparing results from Chapter 1 and 2, I found that evolutionary distinctiveness and functional distinctiveness scores of European birds and mammals are weakly correlated (Figure 1).

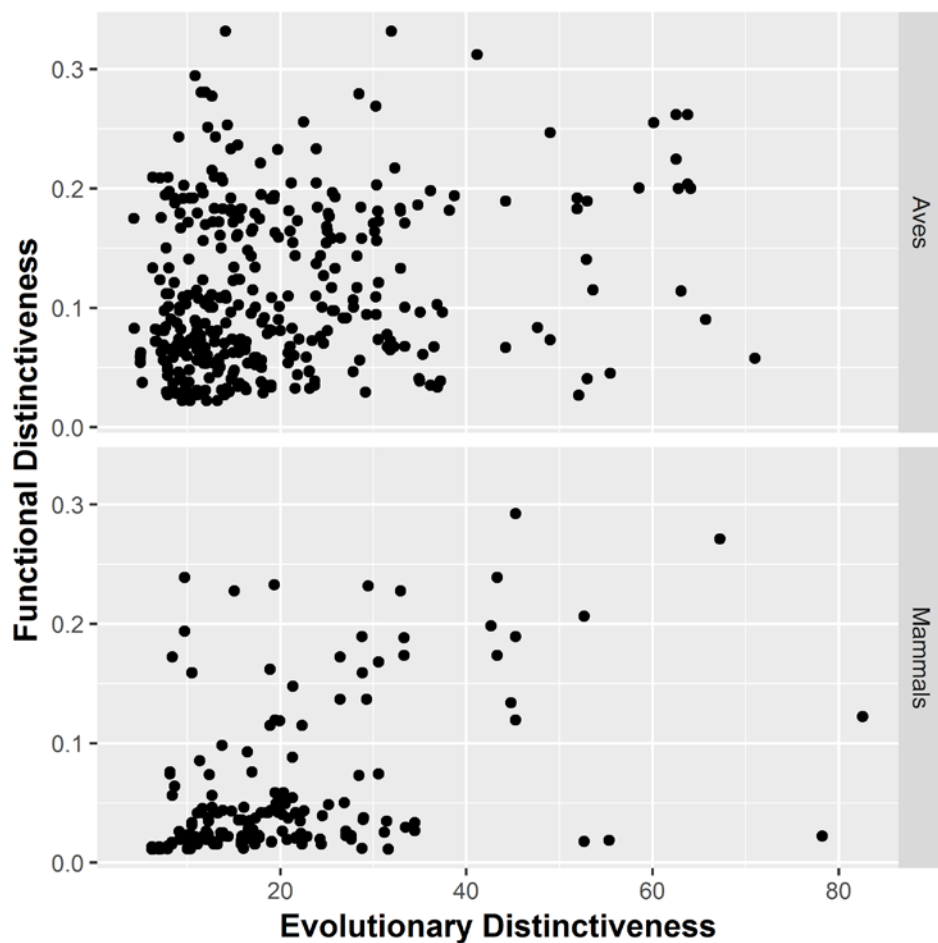


Figure 1: Relationships between the Evolutionary Distinctiveness (ED) and Functional Distinctiveness (FDist) of European terrestrial birds (top panel,  $n = 378$ ) and mammals (bottom panel,  $n = 202$ ). In both cases ED and FDist scores are positively correlated (birds:  $F\text{-stat}_{1,376} = 19.79$ ,  $p\text{-value} < 0.001$ ; mammals:  $F\text{-stat}_{1,200} = 50.97$ ,  $p\text{-value} < 0.0001$ ), but the relationship is weak (birds:  $R^2 = 0.05$ ; mammals:  $R^2 = 0.2$ ).

Highly evolutionary distinct reintroduced mammals are not necessarily functionally distinct, and *vice versa*. For example the European beaver (*Castor fiber*) ranks among the most evolutionary distinct terrestrial mammals in Europe ( $\text{rank}_{\text{ED}} = 2/202$ ), but does not support

highly distinct combination of functional traits ( $\text{rank}_{\text{FDist}} = 126/202$ ). On the contrary, the pine marten (*Martes martes*) is highly functionally distinct in the European mammal assemblage ( $\text{rank}_{\text{FDist}} = 4/202$ ) but is not evolutionary distinct ( $\text{rank}_{\text{ED}} = 174/202$ ). The difference in phylogenetic and functional patterns is more noteworthy for reintroduced birds which showed relatively lower PD and higher ED than expected considering the European bird assemblage, whereas FD value and FDist scores did not depart from our null models. Our results show that both the evolutionary and functional facets of biodiversity provided complementary insights when evaluating how reintroductions in Europe can assist the conservation of diversity in birds and mammals. However, it is important to underline that the strength (or lack of strength) of the relationship between phylogenetic and functional diversity is influenced by the type and number of traits considered, and on the level of phylogenetic conservatism (Tucker et al. 2018). Functional trait data are increasingly made available (Faurby et al., 2018), and further studies could incorporate more traits in order to describe functional dissimilarities between species in continental assemblages.

Trait-based approaches were originally developed to find generalities and represent the different roles of species in a community. The assumption that higher levels of functional trait diversity are linked to ecosystem functioning came from the study of plant ecology, but may not apply to animal food webs because it ignores the complexity arising with animals involved in more diverse trophic networks (Gravel et al., 2016). Here, the study of the diversity of functional traits encapsulated by reintroduction target allowed us to discuss a complementary aspect of biodiversity representativeness at the continental scale, however it provides little information regarding the contribution of reintroductions to the restoration and maintenance of ecological processes. Functionally distinct species are those that support a combination of functional traits that is not supported by other species, however how this measure of originality relates to the actual impact of a species on its environment is unclear. Functional distinctiveness is not similar to the concept of a keystone species, a species that affects many other organisms in an ecosystem and is expected to have a strong impact on its environment (Mills et al., 1993; Paine, 1969).



## **Quantifying the actual contribution to biodiversity restoration at large scale**

With this thesis, I questioned the relevance of reintroductions through the analysis of the allocation of reintroduction efforts. These studies surely provide some insights, but the main priority for reintroduction research remain the improvement of reintroduction practice in order to ensure our ability to re-establish viable populations. The assessment of the level of success of reintroduction projects remains to be determined, and must first involve the definition of generic success criteria that we discussed in chapter 5. We hope that our demographic conceptual framework will contribute to a more unified approach to the assessment of the level of success of a project, independently of the taxon, by accounting for differences in establishment, growth and regulation processes. Instead of considering success based on the number of achieved goals, which can vary in number and scale, we propose that different level of success may be assessed by differentiating outputs from outcomes, and by differentiating milestone achievements from efficiency. This will require the development of analytic tools to help determine in which phase the population is (establishment, growth or regulation).

While my work has focused on reintroductions, most of the methods and analysis applied here could be used to assess the relevance of other conservation translocations. With the comprehensive searches of the reintroduction-related literature (chapter 1 and 3), this thesis contributed to the development and implementation of a database aimed at inventorying conservation translocation programs of flora and fauna in the Western Palearctic region. Up to March 2018, we have identified more than 860 translocations of plant populations and 530 reintroduction programs of animals implemented in Europe and near the Mediterranean Sea. These programs mostly involve angiosperms, mammals and birds, but also gymnosperms, mosses, ferns, reptiles, amphibians, fishes and insects. The TRANSLOC webdatabase (<http://translocations.in2p3.fr>) is still under development but should soon provide a free access to the list of past and ongoing programs per taxon and location (Figure 2). The main objectives of this collective webdatabase are (i) to support meta-analyses on translocations management and success, and (ii) to improve networking activities among a large diversity of translocation scientists, practitioners and stakeholders, and inform future managers on past implemented translocations. For each program, an index will provide an overview of knowledge gaps so that reintroduction practitioners can check the validity of the data, and hopefully add complementary information. The database will provide standardized data on release strategies

and locations, biological material, and post-translocation monitoring when available. Hopefully this collective database will gather and standardize substantial information on many characteristics of conservation translocation projects that will allow us to explore other aspects of the relevance of translocation efforts at large scale, such as the economic costs of programs, the investment in post-release monitoring, or how reintroduction projects contribute to the improvement of a species' conservation status at different scales.

In this thesis I focused on birds and mammals mainly because of the availability of data, hence I contributed to the publication bias toward these groups (a classic case of “do as I say, but not as I do”). However, by bridging a gap among disciplines (i.e., phylogenetics, functional trait-based ecology and conservation translocations), I hope that this thesis will contribute to the understanding of the large scale effect of conservation practices, and hopefully further studies will investigate the contribution of reintroductions to the conservation of different biological diversity facets in other taxonomic groups.

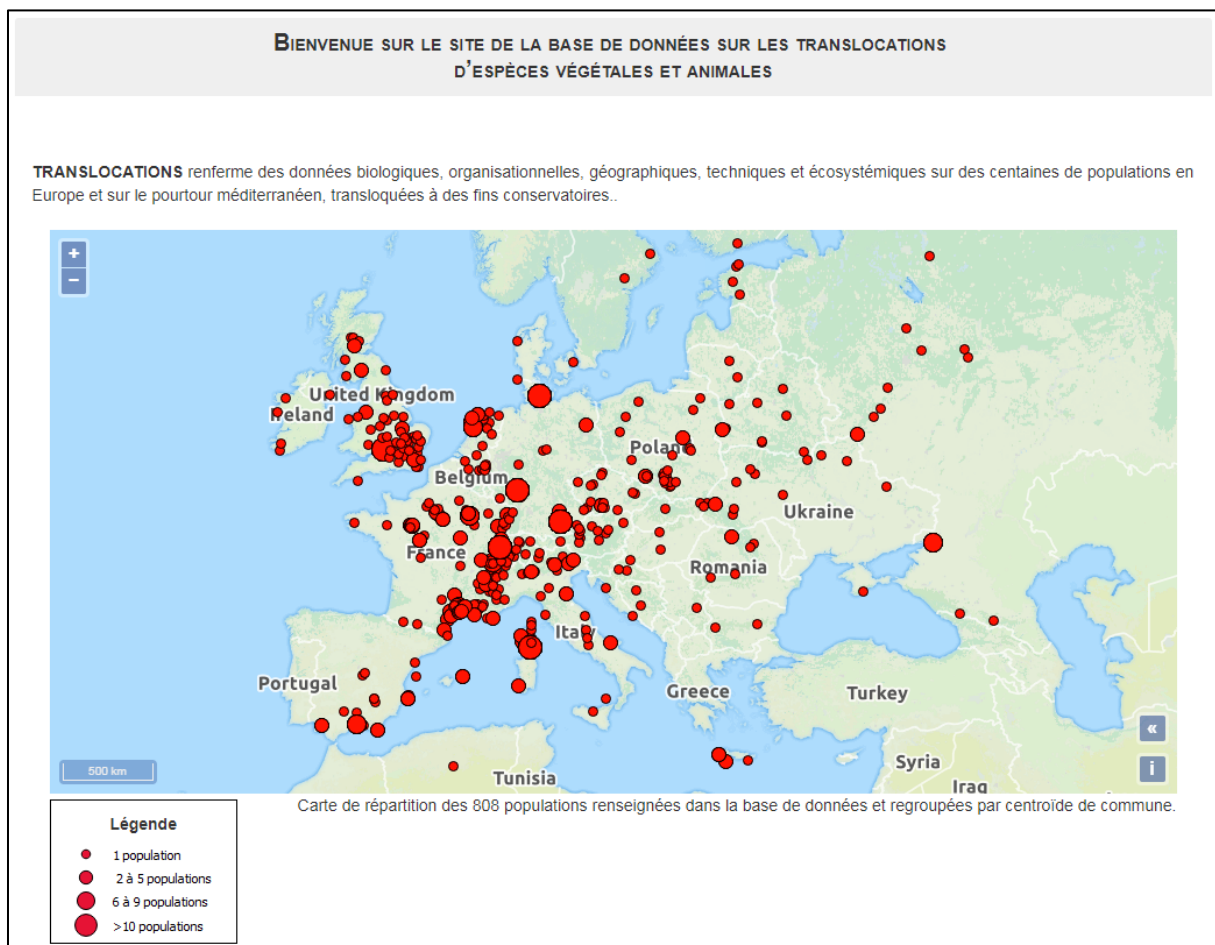


Figure 2: Homepage of the webdatabase TRANSLOC (<http://translocations.in2p3.fr>) which will soon be available for researchers and reintroduction practitioners.



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