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Modelling the effect of land-use management strategies on the sustainability of social-ecological systems

Diego Bengochea Paz

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THÈSE

En vue de l'obtention du

DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par : *l'Université Toulouse 3 Paul Sabatier (UT3 Paul Sabatier)*

Présentée et soutenue le *06 Décembre 2021* **par :**

Diego BENGOCHEA PAZ

Modelling the effect of land-use management strategies on the sustainability of social-ecological systems

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Abstract

Human population growth, together with increases in per capita resource consumption, are exerting enormous pressure on the biosphere. The rising demand for resources is driving unprecedented agricultural expansion and intensification in the landscapes across the world. As a consequence, habitat loss and fragmentation are attaining alarming levels in several of the most pristine and biodiversity-rich regions of the world, thereby threatening ecosystem services provision. However, agricultural production depends on the services provided by the ecosystems like pollination, pest control, or nutrient cycling. This raises concerns regarding the sustainability of the global agricultural system, such that achieving food security while conserving nature is a paramount concern for human societies worldwide.

Research on sustainable land-use management strategies has focused on designing optimal landscape configurations that jointly maximize agricultural yields and biodiversity. Two opposed management strategies emerged from this perspective: land-sparing, i.e. segregating high-intensity agriculture and natural land and land-sharing, i.e. integrating wildlife-friendly, low-intensity agriculture in the natural matrix. The land-sparing vs. land-sharing framework contributed to the advancement of land-use management research. However, it presents a number of limitations that impede development of policies for the sustainable management of agricultural landscapes. First, although the issue of spatial patterns is central to the framework, the issue of scale has been largely absent from the debate. Second, the debate ignores the socio-economical drivers of land-use change, thereby failing to capture the complexity of social-ecological agricultural landscapes.

The objective of this thesis is to integrate, bi-directional feedbacks between human demography, decision-making and land dynamics into land-use management research to develop a more comprehensive understanding of the sustainability of coupled human-land systems across multiple land-use management scenarios. This is achieved through the development of dynamical models that describe the coupled dynamics of human population size and land-use. First, I examine to what ex-

tent increases in agricultural intensification need to be accompanied by reductions of agricultural expansion to be sustainable. I demonstrate how a well-intentioned policy imposing a uninformed threshold between intensification and expansion can lead to social-ecological collapse. Second, I develop a spatially explicit model to examine the effect of agricultural intensification and aggregation on landscape fragmentation and social-ecological dynamics. Specifically, I demonstrate how an unexpected feedback between landscape fragmentation and human population dynamics causes the collapse of the social-ecological system. Third, I examine the effect of the interplay between management spatial scale and strategy on the sustainability of social-ecological agricultural landscapes. I find that mixed strategies, in which land-sparing is prescribed to large farms and land-sharing is recommended for small farms, increase sustainability odds.

Titre de la thèse en français:

Modélisation de l'effet des stratégies de gestion de l'utilisation des sols sur la durabilité des systèmes socio-écologiques

Resumé

La croissance de la population humaine, ainsi que l'augmentation de la consommation de ressources par habitant, exercent une pression énorme sur la biosphère. La demande croissante de ressources entraîne une expansion et une intensification agricoles sans précédent dans les paysages du monde entier. En conséquence, la perte et la fragmentation des habitats atteignent des niveaux alarmants dans plusieurs des régions les plus vierges et riches en biodiversité du monde, menaçant ainsi la fourniture de services écosystémiques. Cependant, la production agricole dépend des services fournis par les écosystèmes comme la pollinisation, la lutte antiparasitaire ou le cycle des nutriments. Cela soulève des inquiétudes concernant la durabilité du système agricole mondial, de sorte que atteindre la sécurité alimentaire tout en préservant la nature est une préoccupation primordiale pour les sociétés humaines du monde entier.

La recherche sur les stratégies de gestion durable de l'utilisation des sols s'est concentrée sur la conception de configurations paysagères optimales qui maximisent conjointement les rendements agricoles et la biodiversité. Deux stratégies de gestion opposées ont émergé de cette perspective : le 'land-sparing', c'est-à-dire la séparation entre l'agriculture à haute intensité et des terres naturelles et le 'land-sharing', c'est-à-dire l'intégration d'une agriculture de faible intensité, respectueuse de la biodiversité, dans la matrice naturelle. Le cadre conceptuel 'land-sparing' vs. 'land-sharing' a contribué à l'avancement de la recherche sur la gestion de l'utilisation des sols. Cependant, elle présente un certain nombre de limitations qui constituent

un obstacle au développement de politiques de gestion durable des paysages agricoles. Premièrement, bien que la question des modèles spatiaux soit au cœur du cadre conceptuel, la question des échelles spatiales auxquelles il faut appliquer les strategies n'a pas été débatue en profondeur. Deuxièmement, le débat ignore les moteurs sociaux du changement d'affectation des terres, omettant ainsi la complexité socio-écologique des paysages agricoles.

L'objectif de cette thèse est d'intégrer des rétroactions bidirectionnelles entre la démographie humaine, la prise de décision et la dynamique des terres dans la recherche sur la gestion de l'utilisation des sols. Le but étant de développer une compréhension plus complète de la durabilité des systèmes couplés homme-paysage à travers de multiples scénarios de gestions des terres. Ceci est réalisé grâce au développement de modèles dynamiques qui décrivent la dynamique couplée de la population humaine et de l'utilisation des sols. Premièrement, j'examine dans quelle mesure, les augmentations de l'intensification agricole doivent s'accompagner de réductions de l'expansion agricole pour garantir la durabilité du système. Je démontre comment une politique bien intentionnée imposant un seuil naïf entre intensification et expansion peut conduire à un effondrement socio-écologique. Deuxièmement, je développe un modèle spatialement explicite pour examiner l'effet de l'intensification et de l'agrégation agricoles sur la fragmentation du paysage et les dynamiques socio-écologiques. Plus précisément, je démontre comment une rétroaction inattendue entre la fragmentation du paysage et la dynamique des populations humaines provoque l'effondrement du système socio-écologique. Troisièmement, j'examine l'effet de l'interaction entre l'échelle spatiale et la stratégie de gestion sur la durabilité des paysages agricoles au niveau socio-écologique. Je démontre que les stratégies mixtes, dans lesquelles les grandes exploitations font du 'land-sparing' et les petites du 'land-sharing', augmentent les chances de durabilité.

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This thesis came to an end as rapidly as it started. Now that I finished writing all the science, I am taking the time to pause, look back and contemplate with broader perspective all of what happened in the past years. In the lines below I wish to thank all the people that in a way or another contributed to the realization of this thesis. Please forgive me if I forgot you.

I first want to thank my advisors, Michel and Kirsten for their trust when accepting to supervise this thesis in a field I was completely ignorant. Although I was already familiar with biology, jumping from biological physics to social-ecological systems represented quite an abrupt change. I want to thank them for their trust and support throughout all these years, during which they gave me the independence to explore and develop my own ideas, while being present and ready to help when I needed it. I would also like thanking the members of my thesis committee Jean Clobert, Cédric Gaucherel and Maxime Lenormand who offered me precious advice during our annual meetings. Finally, I thank Stefano Balbi, Jérôme Chave, Sandra Luque, Jean-Denis Mathias and Mathew Mitchell for accepting to be part of my thesis' jury.

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General Introduction

Human population growth, together with increments of per capita resource consumption, are driving agricultural expansion and intensification to satisfy the soaring resource demand. This has resulted in severe environmental degradation (Kehoe et al., 2017), habitat loss and fragmentation (Taubert et al., 2018) that put at risk the maintenance of ecosystem services provision. However, agricultural production depends on ecosystem services (Power, 2010), hence there are raising concerns on the sustainability of current agricultural practices. Understanding the coupled dynamics of human population and agricultural land-use is therefore of uttermost importance for the development of sustainable agriculture.

The principal objective of this thesis is to integrate bi-directional feedbacks between human demography, decision-making and land dynamics into land-use management research to develop a more comprehensive understanding of the sustainability of coupled human-land systems across multiple land-use management scenarios. This is achieved through the development and numerical exploration of mechanistic social-ecological models.

In this introduction, I present an overview of the interactions between human societies and nature across human history, and stress how the emergence of agriculture led human societies from the Paleolithic to the Anthropocene. Second, I discuss the threats that agricultural expansion and intensification represent to nature conservation and present a brief review of the literature on sustainable land-use management practices, in which I analyze its strengths and limitations. Third, I illustrate the complexity of social-ecological agricultural landscapes through the contemporary

real-world example of the Paraná river droughts in 2020-2021. Fourth, I present a brief review of the social-ecological modelling literature to provide better context to the modelling approaches used in the thesis. Finally, I present the structure of the thesis and discuss the motivations, objectives and main results of each chapter.

A short story of the relationship between human societies and the biosphere

The living world is structured by the complex arrangement of species in interaction between each other. The nature and strength of the interactions determine the persistence of the species which depend on each other. Humans are part of this living world, and their persistence depends on their interactions with the species they harvest as resources. The relationship between human societies and the rest of the living world has drastically changed in the last $12,000$ years with the emergence of agriculture and animal domestication. Although hunter-gatherer societies in the paleolithic had already populated the entire world, population densities remained marginal and so did human influence on ecosystems at large-scales (Louys et al., 2021). Estimates for late paleolithic human population densities in North America yield an average of 1.6 inhabitants per 100 squared kilometers (Morin, 2008), which is almost half of Greenland's population density at the present time. The emergence and spread of agriculture led to the formation of the first urban settlements and to rapid population growth across the world (Gignoux et al., 2011) that progressively increased humans' pressure on the biosphere.

The emergence of agriculture fostered human population growth and the development of complex societies (Kuijt and Goring-Morris, 2002). Although in average human societies have expanded since the emergence of agriculture, manifested by the continuous growth of population numbers as well as the geographical spread of human settlements, diverse examples of societal collapse have been documented throughout history (Cumming and Peterson, 2017). The proposed explanations are multifactorial and involve a complex entanglement of social, economical, politi-

cal and environmental mechanisms influencing one another (Tainter, 1988; Turchin, 2009; Middleton, 2012). Thus, the identification of the primary cause behind past societal collapses can be incredibly complex. However, for many of them, evidence points to problems in resource production following environmental changes that cascade into economical and social issues (Cumming and Peterson, 2017). In the case of the Mesopotamian Akkadian Empire or the Peruvian Moche, it is argued that extreme climatic events, independent from human action, caused a decrease of agricultural productivity and resource scarcity that triggered societal changes (Weiss and Bradley, 2001). In other cases, like the Mayan or the Anasazi, evidence suggests that agricultural expansion and intensification led to land degradation that increased the vulnerability of resource production to perturbations (Diamond, 2005). In the 1930s, during an episode called the Dust Bowl, agricultural intensification in the southern Great Plains of the United States increased farmland vulnerability to drought, which resulted in the major loss of soil by wind erosion and with long-lasting impacts on agricultural production (Baveye et al., 2011; Hornbeck, 2012). In all these cases, human populations and societies did not vanish, but rather adapted, usually by re-locating and re-organizing in more resilient ways (McAnany and Yoffee, 2009). As the amplitude of human perturbations grows and spreads geographically, possibilities for adaptation by re-locating reduce.

Since the emergence of agriculture, technological development has progressively led to higher agricultural yields fostering the growth of human population numbers. In turn, the growth of population numbers and per capita resource consumption led to further agricultural expansion and intensification. This bi-directional coupling between human population dynamics and agricultural expansion and intensification constitutes a positive feedback loop that fosters continuous agricultural expansion and human population growth: increases in one cause increases in the other. In the span of 12.000 years, the influence and transformative power of human societies on the biosphere has come to such an extent that led ecologist Eugene F. Stoermer and atmospheric chemist Paul J. Crutzen to baptise the current geological epoch as the Anthropocene.

Agriculture and the current biodiversity and climatic crisis

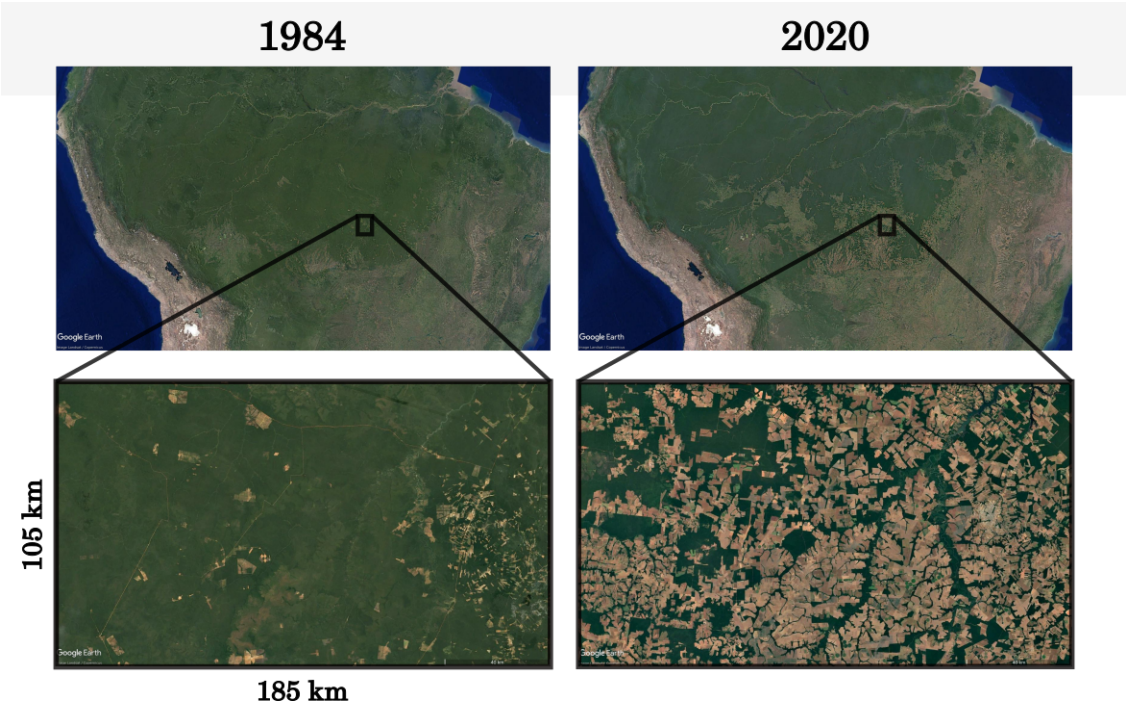

Figure 1: Satellite images showing the habitat loss and fragmentation at the expense of agriculture in the southern Brazilian Amazon in a 34 year period. The area of the zoomed portion is roughly twice the area of Corsica.

Agriculture is the human activity that constitutes the most significant threat to biodiversity conservation (Tilman, 1999; Kehoe et al., 2017). Human societies have transformed the world's landscapes to such and extent that in some continents, like Europe or Southern Asia, human-managed landscapes represent more than half of the land cover. Nowadays agricultural expansion is causing unprecedented habitat loss and fragmentation in some of the world's most pristine and biodiversity-rich regions (Figure 1). Recent analysis of satellite images show that tropical forests in South America, Africa and Asia are close to a habitat percolation transition due to agriculture-led deforestation (Taubert et al., 2018). A percolation transition is the abrupt emergence of large-scale landscape fragmentation as a consequence of progressive habitat loss when the fraction of natural habitat in the landscape crosses a well-defined percolation threshold (Figure 2). Although there are claims that habitat fragmentation does not represent a threat to biodiversity conservation

(Fahrig, 2017; Fahrig et al., 2019), recent evidence from large-scale fragmentation experiments (Haddad et al., 2015, 2017; Fletcher et al., 2018) suggests that fragmentation has negative effects on the persistence of animal populations', biodiversity and ecosystem functions and services, whose manifestation can be delayed in time and their intensity can increase over time. This raises the alarm on the worrying consequences of a large-scale fragmentation event in the tropics if agricultural expansion persists. Furthermore, large-scale deforestation is also a source of climatic alterations and increases the vulnerability of social-ecological landscapes to the effects of climate change (Rosenzweig et al., 2001; Puma et al., 2015; Ray et al., 2019).

In the last century, agricultural intensification substantially increased agricultural yields and contributed to food security, specially in the Global South during the 1960s Green Revolution (Evenson, 2003). Yield increases were achieved thanks to the mechanization of agriculture, the use of chemical fertilizers and pesticides, the use of high-yield varieties and artificial irrigation systems. Food production increases came however at the cost of a deeper environmental impact of agriculture on the cultivated land and the proximal environment through spillover effects (Matson et al., 1997; Tilman et al., 2002; Matson and Vitousek, 2006; Dudley and Alexander, 2017). The extended use of synthetic pesticides and fertilizers led to a reduction of soil biodiversity (Tsiafouli et al., 2015) and the alteration of nutrient (Quinton et al., 2010) and water cycles (Davidson et al., 2012). They also contributed to the pollution of water systems through filtration to underground and surface water systems (Matson et al., 1997). In some cases artificial irrigation systems have deviated water with effects on the downstream ecosystems, contributing to the drought of rivers and perturbation of river ecosystems and wetlands (Richter et al., 2003). The increased mechanization led to larger soil erosion (Van Oost et al., 2006) making the fertile soils more vulnerable to extreme climatic events such as winds and floods. Furthermore, agricultural intensification also generated societal changes, by changing patterns of land-ownership that favoured large farms it promoted rural-to-urban migration (Grau and Aide, 2008). By changing small-holder diverse agriculture by commodity crops, it increased small-holders access to economical gains, but also reduced diet variety and in some cases increased the vulnerability of yields to climate change

(Balbi et al., 2020). Overall, yield increases from agricultural intensification came at the cost of a more significant environmental degradation and socio-economical changes on rural livelihoods.

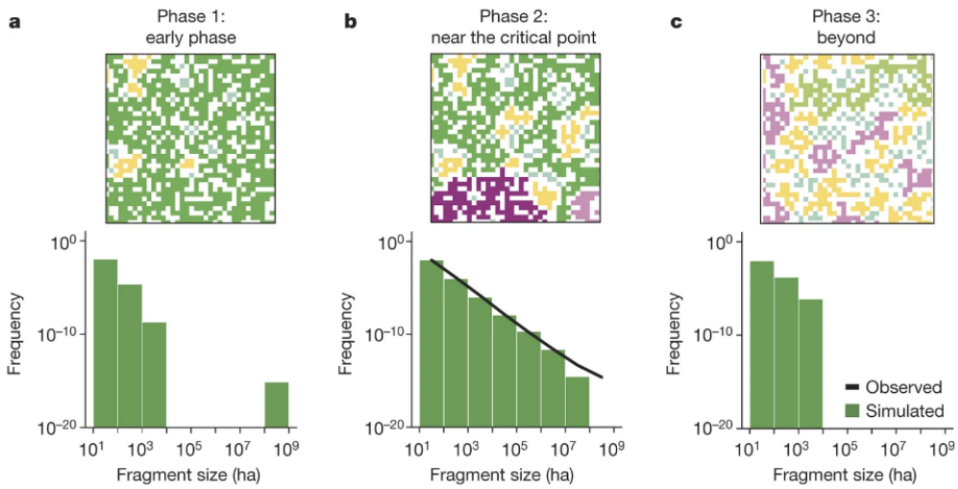

Figure 2: Diagram illustrating landscape structure before, during and after a habitat percolation transition. Figure adapted from Taubert et al. (2018). Initially the landscape is composed by very few large sized connected natural fragments, and several smaller fragments. When the landscape approaches the critical percolation threshold, the larger fragments are reduced in size and medium-sized fragments begin to appear. At the critical point the fragment size distribution is well described by a power-law function with exponent close to -2. After the transition large connected natural fragments disappear and the landscape is composed of a huge number of small disconnected fragments. Taubert et al. (2018) show that tropical forests across the world all show a fragment-size distribution consistent with the critical one, that leads to think that a large-scale fragmentation event is likely to happen.

Steady increases in human population size and per capita resource consumption are incrementing humans' demand for resources (Barrett et al., 2020). Although it has been argued that achieving food security is principally a matter of resource accessibility and distribution, rather than resource availability (Chappell and LaValle, 2011; Tscharntke et al., 2012), increases in resource demand have commonly caused increases in agricultural production mediated by further agricultural expansion and intensification. The resulting loss, fragmentation and degradation of habitats are exerting increased pressure on nature and threaten the stability and persistence of ecosystem services. However, agricultural production itself is dependent to various extents on diverse ecosystem services (Power, 2010; Balvanera et al., 2014; Dainese et al., 2019). Empirical evidence on the contribution of pollination (Garibaldi et al., 2011), pest control (Tscharntke et al., 2005), water quantity and quality (Power, 2010) to agricultural production raise concerns about the sustainability of current

agricultural systems. Agriculture depends on the environment that it vastly contributes to degrade. Although to some degree agricultural intensification can maintain high yields by decoupling production from ecosystem services, for example change the mineral composition of the soil or bring pollinators from distant places, the greater toll it has on the environment can lead landscapes to severe degradation. This poses doubts on the sustainability of intensification at huge spatial scales like it happens in South America for example (Fearnside, 2001; Grau et al., 2005b, 2013).

The sustainability quest: land-use management strategies

Concerns about the sustainability of agricultural systems have driven decades of research on the best management practices to jointly produce enough resources to match the raising demand and preserve the biosphere (Fischer et al., 2014; Arroyo-Rodríguez et al., 2020). At the beginning of the century, Green et al.'s 2005 seminal work introduced the land-sparing vs. land-sharing conceptual framework, which contributed to the advancement of research on sustainable agricultural land-use management strategies. Green et al.'s work crystallized the diverging opinions on how to simultaneously optimize resource production and biodiversity conservation in two diametrically opposed management strategies: land-sparing and land-sharing. Land-sparing consists on segregating natural land from high-intensity agricultural land, while land-sharing consists on integrating low-intensity, wildlife-friendly agriculture in the natural matrix. In a broader perspective, the framework provides a compass to characterize agricultural land-use management strategies by their degree of intensification and spatial aggregation (Figure 3). In its origins, the debate focused on the relationship between agricultural yields and in-farm biodiversity, supposing that higher-yields are a synonym of larger intensification, to determine the optimal strategy among the two (Balmford et al., 2005). However, in this thesis the framework is used as a compass to describe strategies and explore the effects of the agricultural intensification and aggregation dimensions on social-ecological

dynamics.

The rationale of land-sparing is to concentrate food production in the smallest possible areas to set aside large fragments of natural land for biodiversity conservation (Balmford et al., 2005; Phalan, 2018). Justification for land-sparing strategies is based on empirical evidence that shows that biodiversity in farmed land is substantially lesser than in natural land, leading to the conclusion that the larger environmental costs of high-intensity agriculture are compensated by the conservation of large, biodiversity-rich natural fragments (Balmford et al., 2005; Phalan et al., 2011a; Balmford et al., 2018; Phalan, 2018; Balmford et al., 2019). On the other side of the spectrum, land-sharing consists on integrating wildlife-friendly agricultural land on the natural matrix to create heterogeneous managed landscapes in which resource production and biodiversity conservation occur in the same space (Fischer et al., 2008; Perfecto and Vandermeer, 2010; Fischer et al., 2011; Fahrig, 2017). Land-sharing is based on the observation that wildlife-friendly, productive land can, sometimes, host as much biodiversity as natural land, as for example with coffee shade plantations in the tropics (Perfecto et al., 1996; Clough et al., 2011). Critics of land-sharing argue that the typically lower yields of wildlife-friendly agriculture require larger agricultural areas to achieve the same production as high intensity agriculture, and that overall the in-farm biodiversity gains are offset by the decline mediated by the loss of natural habitat (Balmford et al., 2019). However, recent work has shown that high-yields can be attained without synthetic inputs by optimally managing ecosystem services (Chappell and LaValle, 2011; Bommarco et al., 2013; Ponisio et al., 2015). Furthermore, it has been argued that the spatial segregation of natural and agricultural land can hinder ecosystem service provision in cultivated fields, reducing fertility and putting at risk their persistence in the long-term (Bommarco et al., 2013). Beyond the dichotomic land-sparing vs. land-sharing view, considerable work has argued, based on empirical evidence, that landscape sustainability requires heterogeneous, multifunctional landscapes and that although best management practices are most certainly case dependent, in general, mixed strategies are the most appropriate (Fischer et al., 2008; Rey Benayas and Bullock, 2012; Dudley and Alexander, 2017; Arroyo-Rodríguez et al., 2020; Finch et al., 2020).

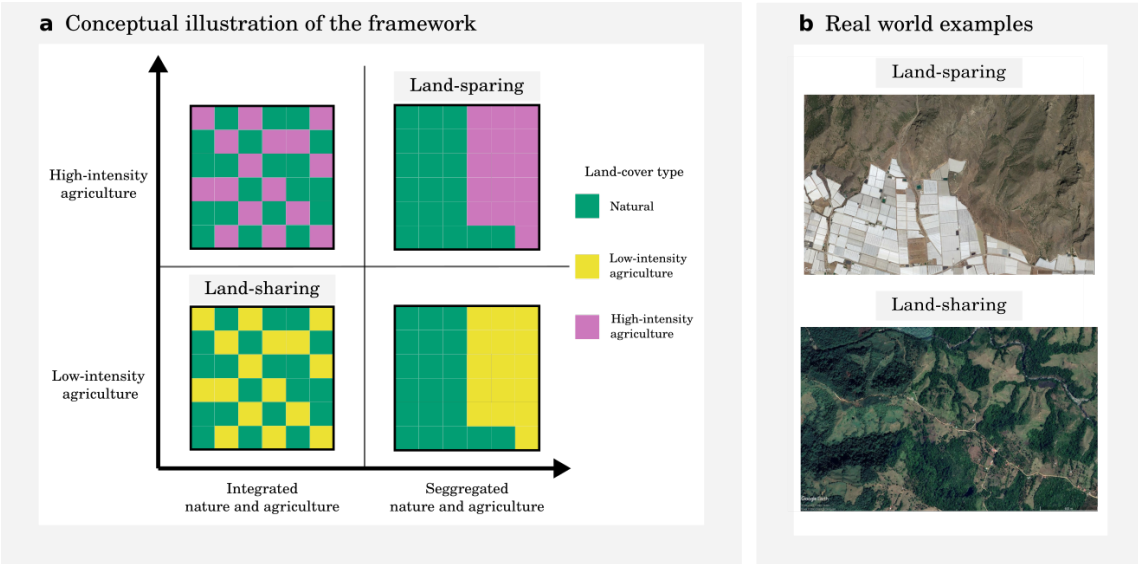

Figure 3: Illustration of the land-sparing vs. land-sharing framework in the sense it is used in this thesis. a) Conceptual diagram showing landscape structure and composition along the two dimensions of the land-sparing vs. land-sharing framework: the level of intensification and the level of clustering of agricultural land. Land-sparing and land-sharing strategies as typically debated in the literature are located in the top-right and bottom-left of the plot respectively. b) Real-world examples of agricultural landscapes which fall more or less closer to each category. The land-sparing example is a satellite image from the greenhouses of Almeria in Southern Spain. The land-sharing example is a satellite image of the Coto Brus region in Costa Rica.

The original framework and the work that has followed, present limitations that make findings hard to apply to the design of sustainable land-use management policies (Fischer et al., 2014). First, management strategies in the land-sparing vs. land-sharing framework are not related to any particular spatial scale, thus most studies are unclear about the spatial scales they address. Land-sparing is generally assumed to imply the segregation of large, contiguous natural fragments from agricultural land, while land-sharing generally implies their integration at finer scales (Fischer et al., 2014). However a number of studies consider small-scale conservation measures, such as preserving natural field margins as land-sparing (Egan and Mortensen, 2012; Gabriel et al., 2013), while for other authors small-scale conservation leads to 'land-sharing' patterns at the landscape scale (Fischer et al., 2008; Rey Benayas and Bullock, 2012). As a consequence, supporting evidence for each of the strategies should consider spatial scales explicitly, an issue that is generally not addressed (but see Ekroos et al. (2016)). This is problematic because farm size distribution is highly variable across world-regions. While in South-America and Australia, farmland is concentrated in farms larger than 200 hectares, in Sub-

Saharan Africa and South and East Asia agricultural production is dominated by farms smaller than 5 hectares, and in Europe medium-sized farms are the most common (Samberg et al., 2016; Herrero et al., 2017). Thus, for example, the application of land-sparing at the farm-level in different world regions leads to diverse spatial land patterns at the landscape level. Second, a large number of studies focus on finding optimal landscape configurations that jointly maximize resource production and species richness (Brosi et al., 2008; Hodgson et al., 2010; Butsic et al., 2012; Butsic and Kuemmerle, 2015; Legras et al., 2018; Arroyo-Rodríguez et al., 2020). However, they typically lack a dynamical perspective that considers social-ecological feedbacks and the ways through which they could affect static predictions. Decision-making on agricultural expansion and intensification is inevitably dynamic since it is primarily driven by economic reasons, that can shift over time and places due to changes in dietary preferences, trade policies or population growth, among others (Lambin and Meyfroidt, 2011; le Polain de Waroux et al., 2016). For example, while it is expected that the adoption of high-intensity agriculture promotes rural-to-urban migration fostering the recovery of abandoned farmland, in Argentina and Brazil it resulted on increased deforestation. Increments in foreign demand raised commodity prices, and investors saw an opportunity for financial profit in large-scale high-intensity monocultures (Grau and Aide, 2008; Grau et al., 2013). Ultimately, the adoption of high-intensity agriculture opened the doors to habitat loss.

A contemporary example of social-ecological complexity: droughts in the Paraná-Paraguay river system

Complexity in social-ecological systems arises from the intrinsic complexities of ecosystems and human societies and from the strong non-linear interactions between each other (Levin et al., 2013). Understanding the keys for the sustainable management of social-ecological systems requires a holistic perspective that accounts for the feedbacks between human and natural systems (Carpenter et al., 2009).

Social-ecological dynamics are characterized by non-linearities, tipping points and cascading effects that can propagate over space due to biophysical and societal connections, like river systems and international trade, respectively (Levin et al., 2013; Rocha et al., 2018). Complex feedback loops between human decision-making, governance and ecosystems can trap social-ecological systems in the path to unsustainability (Cumming et al., 2014). In this section I discuss the example of the Paraná river droughts in 2020 and 2021 (Figure 4) to illustrate the complexity of social-ecological agricultural landscapes and the importance of bi-directional feedbacks to address sustainability issues.

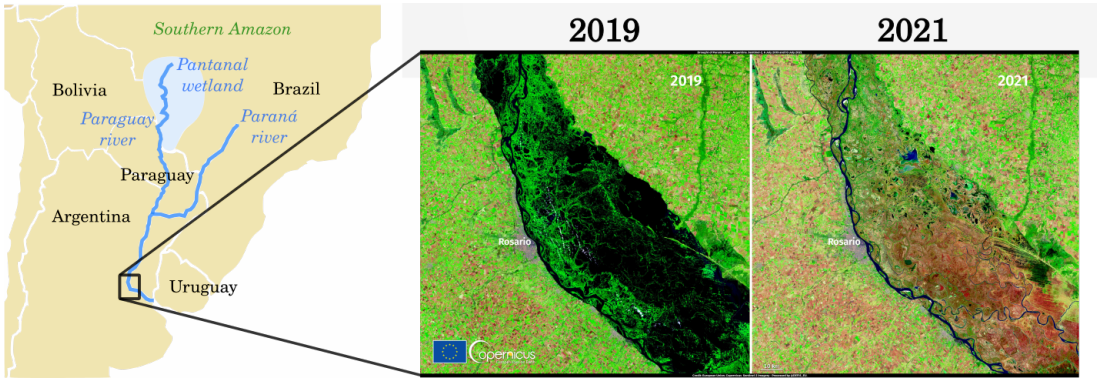

Figure 4: On the left: schematic representation of the Paraná-Paraguay river system and the Pantanal wetland. On the right: satellite images showing the difference in water levels in the lower section of the Paraná river between July 2019 and July 2021. Dark blue colours represent larger water amounts and brown/red colours represent drought areas. Credits: European Union, Copernicus Sentinel-2 Imagery.

Since the early 2000s, increases in foreign demand, mainly from China and the UE, have driven deforestation for soybean production in Argentina, Bolivia, Brazil, Paraguay and Uruguay (Fearnside, 2001; Grau et al., 2005b). In some cases, soybean production has become one of the main economic activities in terms of gross domestic product and weight on the trade balance of the countries. The Paraná-Paraguay river system is a crucial part of this social-ecological system. In the first place, it is one of the largest river basins in the world, carrying sediments from most of central-south South America, and greatly contributing to soil fertility in Argentina. Additionally, an enormous part of the production is transported downstream to be exported from the large ports in the Atlantic coast. However, since 2020, the Paraná river is suffering from severe droughts (Figure 4) with negative impacts on agricultural yields. For two consecutive years, a river whose native name translates

to "as big as the sea", has become unnavigable, thereby altering trade routes. The economical cost of this year's drought is estimated in 315 million dollars for Argentinian farmers (Treboux and Bergero, 2021). A significant fraction of the water in the Paraná river comes from rainfall in the wetlands of the Pantanal region located in Brazil next to Paraguayan and Bolivian borders (Figure 4). However, in the last years the Pantanal wetland is also experiencing severe yearly droughts and studies point the alteration of water cycles caused by deforestation in the Amazon forest as the cause for the lack of rainfall (Marengo and Espinoza, 2016; Marengo et al., 2021). Soybean production along the Paraná river in Argentina, and in the southern Amazon are oriented to the same export markets. Thus, it is possible that the production gap in Argentina will be compensated by agricultural expansion in the southern Amazon, among other places. As a result, deforestation in the southern Amazon cascades in a lack of water in Argentina that reduces agricultural production, thus potentially causing further agricultural expansion in the southern Amazon, closing an unsustainable social-ecological feedback loop.

A brief review of social-ecological modelling

Social-ecological systems are understood as complex adaptive systems (Levin et al., 2013). Their dynamics are driven by non-linear feedbacks, abrupt transitions, self-organization or learning processes that emerge from the multiple interactions between social agents, from individuals to institutions, and managed ecosystems across diverse spatial and temporal scales (Schlüter et al., 2012). As a consequence, social-ecological systems are characterized by the emergence of unexpected dynamics and patterns which can only be explained by the interactions between human and natural systems. This vast complexity represents an obstacle to the understanding of social-ecological systems and thus to the development of management guidelines and policies for their sustainability. Furthermore, dynamics in some social-ecological systems, as in agricultural landscapes, or fisheries for example, are characterized by very large temporal and spatial scales, relative to human scales, thereby increasing the difficulty of empirical approaches. In this context, modelling approaches for the

study of social-ecological systems are very promising since they provide world abstractions where hypotheses can be tested and scenarios explored. Overall, models have a great potential to contribute to the development of sustainability in social-ecological systems. In this section I provide a non-exhaustive review of the use of models in social-ecological systems research.

The use of models as a support tool for natural resource management emerged almost 50 years ago with the development of resource economics (Clark, 1974). These models applied neoclassical economic theory to find optimal exploitation strategies of natural, renewable resources, that maximized social-welfare in the long-term (see Schlüter et al. (2012) for a review). From a mathematical point of view, these models build on the theory of dynamical systems and use ordinary differential equations to represent the temporal changes in the resource stock. Although over time these bio-economic modelling approaches incorporated greater complexity in the description of ecological dynamics, they consider resource exploitation as a constant pressure that is external from the system (Clark, 1974; Carpenter et al., 1999; Anderies et al., 2002). Thus, they fail to capture the complexity that can emerge from the feedbacks between human management and decision-making and the state of the natural resource (Levin et al., 2013). Further advances in the field of social-ecological modelling came with the inclusion of social norms, for example a harvesting rate, as dynamical variables responding to ecological dynamics, thereby introducing social-ecological feedbacks (Janssen et al., 2000; Crépin, 2007; Henderson et al., 2016; Anderies et al., 2019). Apart from dynamical systems, agent-based models have been largely used to simulate social-ecological systems since they provide a convenient way to represent decision-making processes and introduce social heterogeneities (Janssen, 2002; Filatova et al., 2013; Schulze et al., 2017; Mathias et al., 2020). Thus, they are remarkably interesting tools to study the emergence of macro-scale patterns and behaviour from micro-scale rules. Agent-based models have been extensively applied to fisheries (Monk et al., 2018), tourism (Balbi et al., 2013), climatic migration (Bell et al., 2021) or land-use change (Parker et al., 2003) among other fields. Finally, in the field of spatially explicit land-use change models, landscapes are generally represented as cellular automata, in which transition rules between states obey to

ecological and social processes (Parker et al., 2003). In this thesis, these three types of modelling approaches, i.e. dynamical systems, agent-based models and cellular automata, are used in the different chapters (Figure 5).

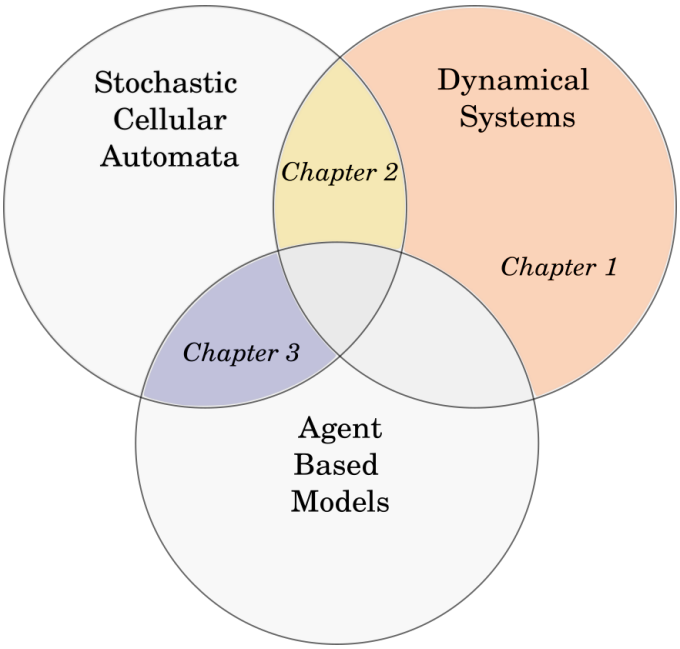

Figure 5: Conceptual diagram of the different modelling techniques used in social-ecological models of land-use dynamics. The coloured parts depict the techniques that are used in this thesis. In the first chapter I develop a model purely based on a system of coupled ordinary-differential equations, while in the second and third chapters I use hybrid approaches including cellular automata for the spatially explicit description of the landscape and agent-based modelling to represent heterogeneity in human decision-making. The agent-based approach used in the third chapter does not incorporate adaptive behaviour nor interactions between agents and thus is less complex than the standards in the field.

Although human population growth, together with consumption increases, constitute the main sources of human pressure on nature, there are few social-ecological modelling studies that have endogenously included human population dynamics. This approach has typically been reserved to studies of past societal collapse (Brander and Taylor, 1998; Roman et al., 2018) but there are few studies that address human-nature dynamics from a broader perspective with the objective of developing more general principles that could be applied to contemporary societies (Anderies, 2003; Motesharrei et al., 2014). These studies use a dynamical systems approach and model diverse drivers of human population growth, like technology or inequalities, resulting in fairly complex descriptions of human demographic processes. However, they represent nature as a single renewable resource that is exploited by humans, thereby failing to capture ecological complexity, and the diverse ways through which

nature can impact human systems.

More recently, concerns on the sustainability of current socio-agricultural systems and on the devastating effect of agricultural expansion on biodiversity, motivated a study that modelled human population dynamics as a function of changes in technology and biodiversity, and showed how time-delayed biodiversity decreases as a response to habitat loss could undermine sustainability in social-ecological agricultural systems (Lafuite and Loreau, 2017). The model built on top of Brander and Taylor's 1998 and Anderies's 2003 work, but included land conversion processes to model agricultural expansion, and thus added complexity on resource production. Land conversion was modelled from a market equilibrium perspective, meaning that agricultural land stocks were instantaneously adjusted to match resource demand. However, the model explicitly included the effects of biodiversity on ecosystem service provision and agricultural production, adding more complex bi-directional feedbacks between the human and land systems (Figure 6). Extensions of this model included the effect of dynamical changes in consumption patterns (Lafuite et al., 2017) and high-level governance through taxes (Lafuite et al., 2018) that broadened the considered social-dynamics.

Further studies treated land-cover stocks as dynamical variables, and incorporated greater level of detail on the description of land-dynamics by considering more types of land-cover (Henderson and Loreau, 2018; Cazalis et al., 2018; Henderson and Loreau, 2019). Henderson and Loreau (2018) represented land dynamics by the flows between stocks of natural, agricultural and degraded land, that responded to ecological and social drivers. Following Lafuite and Loreau (2017), Henderson and Loreau (2018) explicitly model the contribution of natural land to ecosystem services provision and the feedbacks to agricultural production and human demographic rates, thereby leading to a complex interdependence between humans and the landscape. Further work broadened the spectrum of connections between human and natural systems by explicitly integrating diverse effects of multiple ecosystem services on human population dynamics (Cazalis et al., 2018). Recent extensions of these models incorporated socio-economical heterogeneities by applying the approach to two interconnected regions with social-inequalities (Henderson and Loreau,

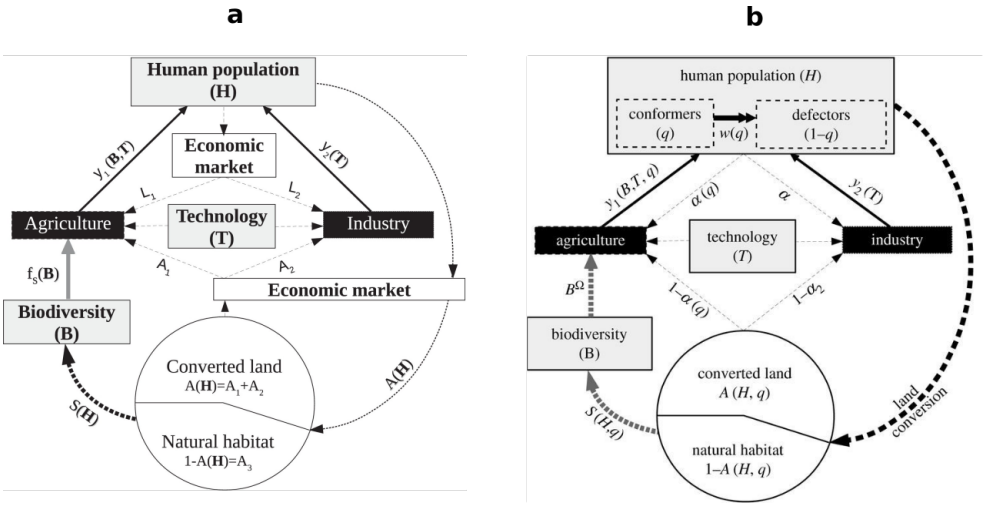

Figure 6: Conceptual diagrams describing the interactions between human and natural systems in the models presented in Lafuite and Loreau (2017) (a) and Lafuite et al. (2017) (b). Human population dynamics are driven by agricultural and industrial resources, and in turn changes in human population drive land conversion with feedbacks on biodiversity and agricultural production. The strong interconnectedness between the human and natural system leads to highly non-linear dynamics. In Lafuite et al. (2017) (b) complexity was added to the social dynamics by including dynamical changes in consumption norms through separating humans in low and high consuming categories, conformers and defectors respectively. Figure adapted from Lafuite and Loreau (2017) and Lafuite et al. (2017).

2021).

This thesis is inspired by all these studies that model human population dynamics endogenously in social-ecological systems (Figure 8) and uses the same description of land-cover types than Henderson and Loreau (2018). However, I adopt a simpler description of human population dynamics, which considers resource production as the sole driver of population changes, because this thesis' focus is on the effect of land-use management strategies on social-ecological dynamics (Figure 8). From a modelling perspective this thesis broadens the research field by adopting a spatially explicit description of the landscape, thereby allowing the emergence of feedbacks between landscape fragmentation and human population dynamics. Furthermore, it also incorporates spatial heterogeneity in management practices, providing a framework to tackle some of the limitations of the land-sparing vs. land-sharing debate from a social-ecological perspective.

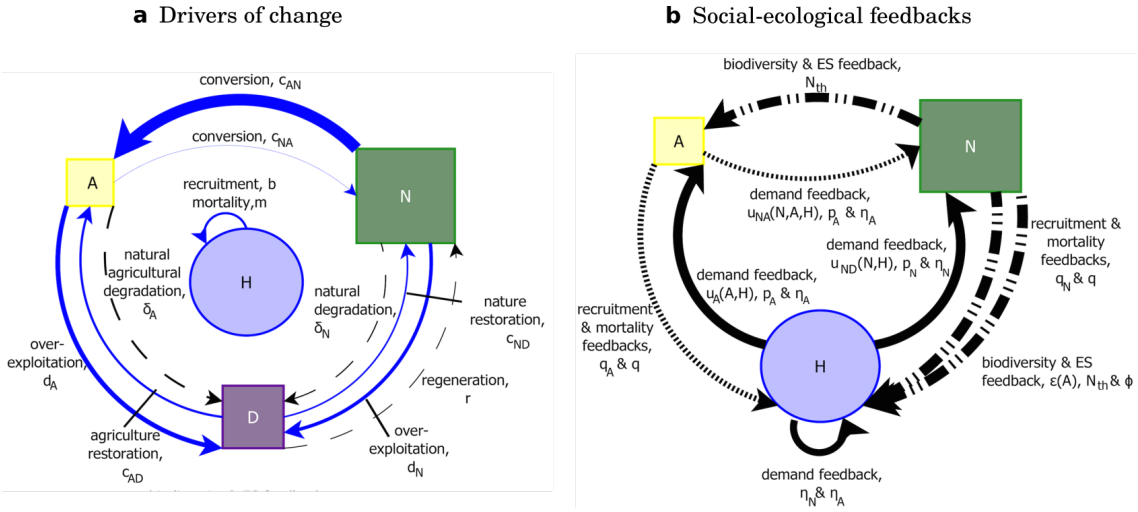

Figure 7: Conceptual diagrams describing the drivers of land-use and human population change (a) and the social-ecological feedbacks (b) included in Henderson and Loreau's 2018 human-land model. Figure adapted from Henderson and Loreau (2018). Land-use changes can be driven by ecological and human drivers, and feedbacks between ecosystem services provision (ES) and the human population can occur through multiple pathways.

Summary of the chapters

The general objective of this thesis is to integrate bi-directional feedbacks between human demography, decision-making and land dynamics into land-use management research to develop a more comprehensive understanding of the sustainability of coupled human-land systems across multiple land-use management scenarios. This is done through the development and numerical exploration of mechanistic models that describe the coupled dynamics of human population size and landscape configuration. In the models, social-ecological feedbacks are mediated by resource production, that affects human population dynamics and land-use management strategies that in turn dictate how humans transform the landscape to produce resources (Figure 8). The thesis is structured in three chapters that address increasingly complex aspects of the interplay between management strategies, landscape configuration and human population dynamics. In this section, I provide a brief description of each chapter, including the motivations, specific objectives and methodologies, and main results and conclusions for each.

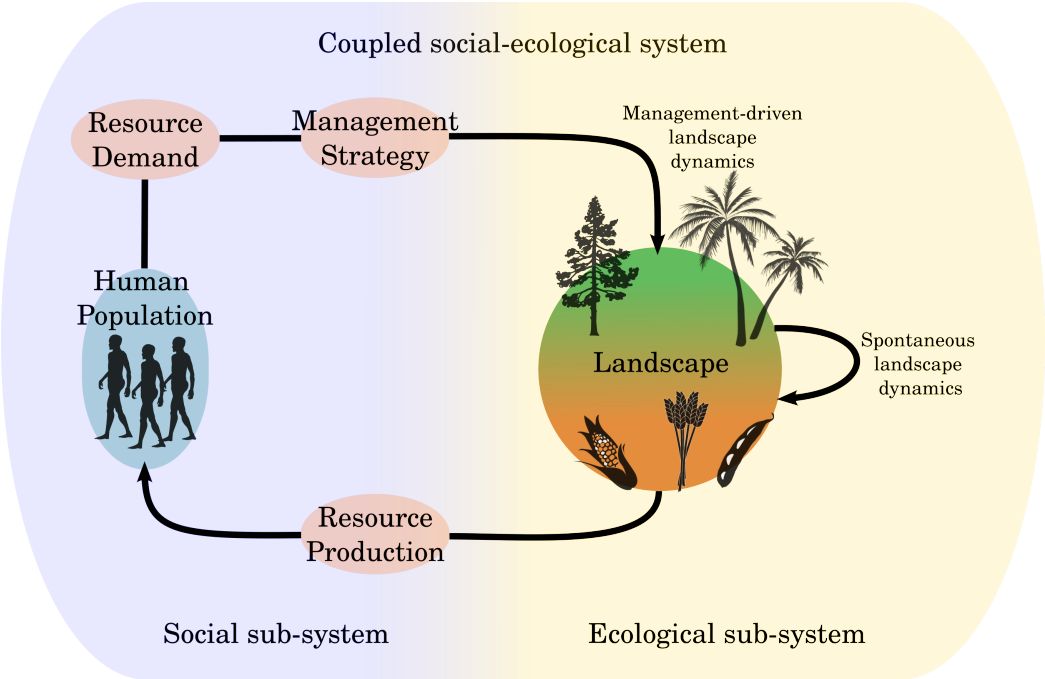

Figure 8: Conceptual diagram of the modelling framework adopted in the thesis. The land and human subsystems are parts of a higher-level, connected social-ecological system. The interactions between the human and land subsystems are mediated by resource production and demand, and land-use management strategies.

Chapter 1: The dangers of naive land-use management policies

Motivation

Empirical work has supported the hypothesis that land-sparing outperforms land-sharing in the joint maximization of resource production and species richness (Phalan et al., 2011a,b). This conclusion is in part based on the expectation that the productivity increases brought by higher intensification result in reduced agricultural expansion (Balmford et al., 2018, 2019). However, it has been shown that social and economical factors can impede this, making the success of land-sparing strategies dependent on the enforcement of policies that actively discourage agricultural expansion (Grau et al., 2013). Yet, we lack knowledge on the degree to which agricultural expansion should be contained for different degrees of intensification, which can lead to the failure of well-intentioned policies.

Objective and methods

The objective of this chapter is to **explore how a well-intentioned policy that imposes a simple, non-informed trade-off between agricultural intensification and expansion can lead to unsustainable dynamics and social-ecological collapse**. In this chapter I present a non-spatial model of coupled human-land dynamics where a linear trade-off is imposed between agricultural intensification and expansion (Figure 9). The landscape is described by three land-covers: natural, agricultural and degraded; and the degree of agricultural intensification is modelled as a continuous parameter. All agricultural land is homogeneously managed. Through multiple numerical experiments I show the conditions for sustainable social-ecological dynamics.

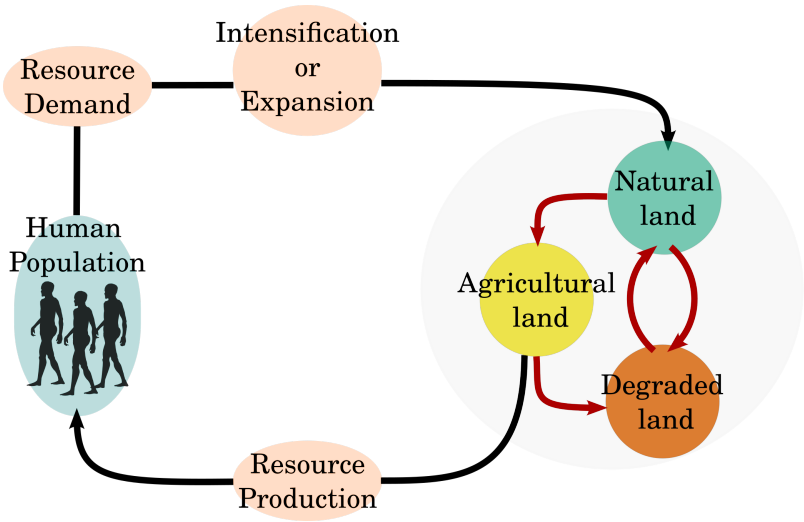

Figure 9: Conceptual diagram illustrating the model developed in the first chapter of this thesis. The management strategy is controlled by the degree of agricultural intensification and the land conversion effort, which is a parameter that controls agricultural expansion. The feedbacks between the natural and human system are represented by the black arrows and the modelled land-use transitions are represented by the red arrows.

Main results and conclusions

I show that **a linear trade-off between agricultural intensification and expansion leads to social-ecological collapse at intermediate intensification levels.** In the absence of detailed knowledge of the social-ecological system behaviour, non-linearities make the design of a suitable trade-off highly unlikely. Over-

all, the first chapter stresses the importance of informed policy development in land-use planning that accounts for the complexity in social-ecological systems.

Chapter 2: Fragmentation feedback on decision-making undermines sustainability

Motivation

Theoretical modelling studies have examined how ecosystem service provision varies with landscape structure (Mitchell et al., 2015b) and established the link with agricultural production (Montoya et al., 2020). Moreover, data-driven modelling studies have examined the trade-offs between ecosystem services and their impact on agricultural production in spatially explicit contexts (Balbi et al., 2015). However, there is a lack of studies that address the interplay between landscape spatial configuration, ecosystem services and agricultural production from a dynamical perspective that incorporates the feedbacks between resource production, human decision-making and demography.

Objective and methods

The objective of this chapter is **to examine the effects of landscape fragmentation on human decision-making and population dynamics**. In this chapter I present a spatially explicit extension of the model of the human-land model used in Chapter 1. The landscape is modelled as a cellular automaton in which the state of each cell is determined by its land-cover type. Contrary to Chapter 1, agricultural land is now differentiated in high-intensity and low-intensity, and a parameter controls the preference for high-intensive agriculture. Decision-making in the landscape is centralized in one manager and driven by the resource demand of an external population (Figure 10). Through a set of numerical experiments, I explore the effect that different management strategies, defined by the preference for high-intensity agriculture and the degree of spatial aggregation of agricultural land,

have on landscape structure and social-ecological dynamics.

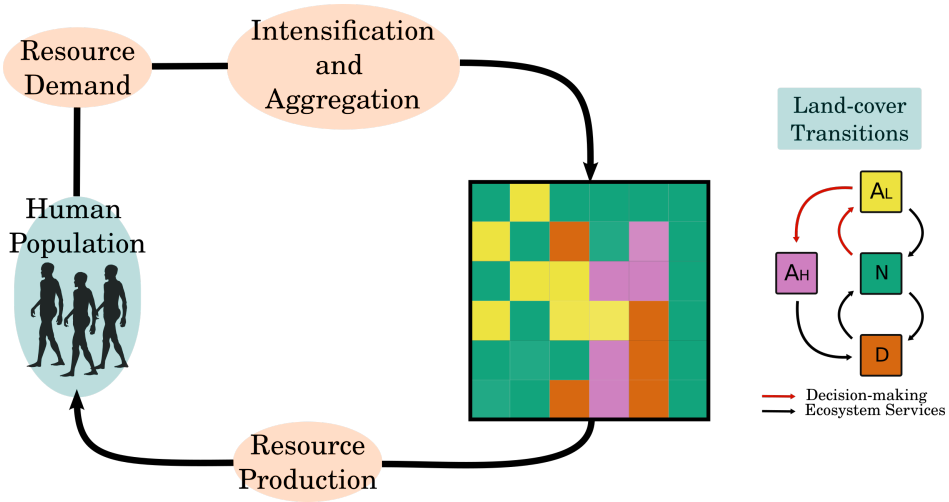

Figure 10: Conceptual diagram illustrating the model developed in the second chapter of the thesis. The landscape is modelled in a spatially explicit way using a cellular automaton approach. The state of the landscape cells represent the land-cover type: natural (N), low-intensity agriculture (A_L), low-intensity agriculture (A_H) and degraded (D). Agricultural expansion and intensification in the landscape are driven by the resource demand of an external human population. Decision-making regarding management strategies is centralized in a single manager, and strategies are represented by the preference of agricultural intensification and the degree of spatial aggregation, or clustering, of agricultural cells.

Main results and conclusions

I demonstrate that **an unexpected feedback between landscape fragmentation and human decision-making can undermine the sustainability of the social-ecological system.** We show that progressive habitat loss caused by agricultural expansion can cause abrupt large-scale fragmentation when the landscape undergoes a percolation transition. We find that ecosystem services provision and agricultural production are impaired by large-scale fragmentation, which results on increasing agricultural expansion to compensate production losses. This positive social-ecological feedback loop further habitat loss and fragmentation leading to the collapse of the system. Finally, I show that **neither pure land-sparing nor land-sharing strategies are the most resilient in landscapes with limited amounts of natural land-cover and that maintaining connectivity is key to prevent abrupt transitions** .

Chapter 3: The interplay between management strategy and scale determines sustainability

Motivation

Although the importance of spatial scales and patterns has been long recognized in ecology (Levin, 1992; Chave, 2013), the issue of scale has been largely absent in the land-sparing vs. land-sharing literature. However, spatial planning is an intrinsic part of the land-sparing vs. land-sharing framework, and the application of the same planning rules at different spatial scales can lead to dissimilar patterns at the landscape level, with consequences on ecosystem functions and services. Furthermore, farm size distribution is highly variable across the world, thus land-use management policies aimed at the farm level cannot be universal and need to account for farm size. This represents an obstacle to the application of results and insights from the land-sparing vs. land-sharing debate to policy design.

Objective and methods

The objective of this chapter is **to explore how the interplay between management strategy and scale influences social-ecological dynamics and identify which strategies are more sustainable at which spatial scales**. To achieve this, I extended the spatially explicit model that was presented in Chapter 2 to incorporate multiple decision-makers that manage different farms in the landscape, according to a land-sparing or a land-sharing strategy, implemented at the farm level. A parameter controls the fraction of land-sparing farms, and the number of farms. At equal landscape size, increasing the number of managers leads to a smaller average farm size. Through a set of numerical experiments, I explored the effect of changing the average farm size on landscape structure, ecosystem services provision and social-ecological dynamics for land-sparing, land-sharing and mixed strategies (Figure 11).

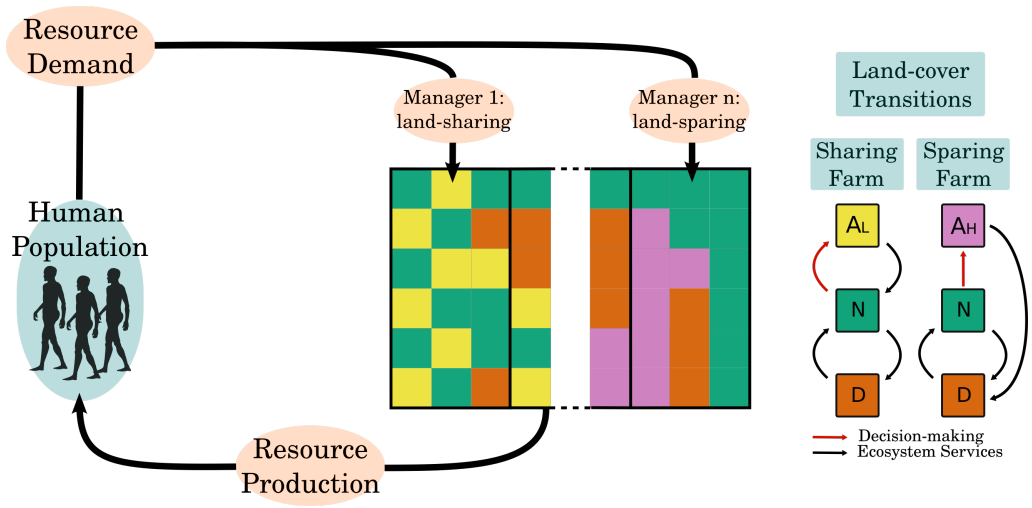

Figure 11: Conceptual diagram illustrating the model developed in the third chapter of the thesis. The landscape description is the same as in Chapter 2 and considers the same four land cover types: natural (N), low-intensity agriculture (A_L), low-intensity agriculture (A_H) and degraded (D). In this model management is not centralized anymore. The landscape is subdivided in several pieces that represent farms independently managed. At the farm level, management strategies are either land-sparing or land-sharing, and a parameter controls the fraction of land-sparing farms in the landscape. The likelihood of agricultural expansion is determined by the resource demand of an external population. Contrary to the model developed in Chapter 2, in land-sparing farms, conversion of natural land to high-intensity agriculture happens directly.

Main results and conclusions

I demonstrate that **a land-sharing strategy is unsustainable at large management scales and that a land-sparing strategy is unsustainable at small management scales**. Furthermore, I show that a mixed strategy, in which half of the landowners do land-sharing and the other half land-sparing, leads to a sustainable long-term state across all the possible management scales. This result supports the increasing evidence that heterogeneous, complex landscapes are key for sustainability. Altogether, the results suggest that in landscapes with non-homogeneous farm size distributions, enforcing **land-sharing in the smaller and land-sparing in the larger farms increases the odds of sustainability**.

Chapter 1

The dangers of naive land-use management policies

Title of the scientific article:

Agricultural land use and the sustainability of social-ecological systems[1]

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Theoretical and Experimental Ecology Station, CNRS, Moulis, France

Abstract

Agricultural land expansion and intensification, driven by human consumption of agricultural goods, are among the major threats to environmental degradation and biodiversity conservation. Land degradation can ultimately hamper agricultural production through a decrease in ecosystem services. Thus, designing viable land use policies is a key sustainability challenge. We develop a model describing the coupled dynamics of human demography and landscape composition, while imposing a trade-off between agricultural expansion and intensification. We model land use strategies spanning from low-intensity agriculture and high land conversion rates per person to high-intensity agriculture and low land conversion rates per person; and explore their consequences on the long-term dynamics of the coupled human-land system. We seek to characterise the strategies' viability in the long run; and understand the mechanisms that potentially lead to large-scale land degradation and population collapse due to resource scarcity. We show that the viability of land use strategies strongly depends on the land's intrinsic recovery rate. We also find that social-ecological collapses occur when agricultural intensification is not accompanied by a sufficient decrease in land conversion. Based on these findings we stress the dangers of uninformed land use planning and the importance of precautionary behaviour for land use management and land use policy design.

[1]Published in Ecological Modelling, Volume 437, 1 December 2020, 109312

Introduction

Food production is the most basic and tangible example of humans' dependence on nature. From Paleolithic hunter-gatherers, who relied on direct harvest from nature, to contemporary complex societies that rely on agriculture and livestock, human survival ultimately depends on what the land provides. An ever growing population and demand for food are putting unprecedented pressure on the environment (Tscharntke et al., 2012). Increased food consumption necessitates agriculture expansion; however, the last IPBES report (Bongaarts, 2019) highlights the role of agricultural land expansion as the main threat to biodiversity loss, mediated by the fragmentation and degradation of habitats (Corvalán et al., 2005; Jacobson et al., 2019; Nowosad and Stepinski, 2019). Degradation of the natural environment brings societal and economic consequences for human populations, as it can result in decreasing agricultural yields (Mitchell et al., 2014) and public health issues (Power, 2010). Conservation of biodiversity and natural spaces are often considered secondary objectives when compared to food security, but biodiversity and ecosystem services play an integral role in maintaining food supply. Agricultural productivity is strongly dependent on ecosystem services, such as pollination, nutrient cycling and pest control, that surrounding natural spaces provide (Mitchell et al., 2013). Therefore, conservation goals should not be seen as opposed to agricultural production or human well-being, as natural land is essential to provisioning services (Cazalis et al., 2018; Braat and de Groot, 2012). Allying natural and agricultural lands is the key to achieve sustainability and avoid a potential socio-ecological collapse.

The introduction of agriculture permitted the apparition of the first permanent human settlements. However, Neolithic settlements quickly became heavily reliant on the agricultural system and, as a result, when environmental disasters struck, the food supply and the population suffered (Downey et al., 2016). In some cases, as much as 60% of the population was lost due to failed crops. Over time technological developments made it possible for human societies to adopt more intense forms of agriculture, which increased resource production and food security. Agricultural production enabled the population to grow and allowed the development

of complex societies via social differentiation and territorial expansion (Kuijt and Goring-Morris, 2002). This drive to increase agricultural production, however led to deforestation (DeFries et al., 2010), excessive freshwater use (Lilienfeld and Asmild, 2007), soil biodiversity loss (Tsiafouli et al., 2015), altered nutrient (Quinton et al., 2010) and water cycles (Davidson et al., 2012), decreased pollinator abundance, and increased vulnerability to environmental change, all of which can have deleterious effects on agricultural production. Agriculture is thus dependent on the natural environment, but it also heavily transforms this environment. The aim of future societies is to have agriculture improve social welfare, but how to achieve this, while limiting environmental degradation, is a major unknown.

Agriculture has been responsible for both the rise and fall of societies. Historical examples of societal collapse are geographically diverse and have occurred over various time scales(Cumming and Peterson, 2017). Several social, political and economical mechanisms have been proposed to explain such collapses (Tainter, 1988). However, for a number of them, the roots of societal decline can be traced back to ecological problems caused by resource over-exploitation and poor agricultural land management. The Mayan and the Anasazi collapses are two classic examples. In both cases, collapse is thought to have resulted from feedbacks between population growth and agricultural expansion and intensification, which led to greater environmental degradation and made the food production system unviable (Diamond, 2005; Cumming and Peterson, 2017; Roman et al., 2018). Food scarcity sows the seeds of economic trouble, social unease and political instability, which trap societies in positive feedback loop leading to collapse.

The current environmental crisis has reignited scientific interest in societal collapse. There is a general agreement that overpopulation and overconsumption are the main threats to environmental conservation and sustainability (Barrett et al., 2020). Thus, recent studies have addressed sustainability questions by explicitly considering human demography and consumption behaviour. In particular, modelling approaches have shown great potential to shed light on sustainability challenges, as they allow the exploration of different scenarios that would be impossible to reproduce experimentally. In a recent study, Motesharrei et al. (2014) used a dy-

namical model to show how social inequalities, in terms of resource consumption and contribution to labour, can undermine sustainability and cause societal collapses. This finding can be linked to other issues such as population growth (Kentor, 2001) and over-consumption (Ceballos et al., 2017), which contribute to environmental degradation and social instability. More recently, Henderson and Loreau (2018) and Henderson and Loreau (2019) proposed a general theoretical framework to explain human demography across history in relation to resource accessibility, which can be used to explain the population explosion in the last century and potential future scenarios. Broadening the spectrum of possible connections between nature and human populations, Cazalis et al. (2018) built a model to explore socio-ecological dynamics through the dependence of humans on several ecosystem services. Through an economic-ecological model Lafuite and Loreau (2017), Lafuite et al. (2017) and Lafuite et al. (2018) investigated how time lags in the response of biodiversity to anthropic perturbations can feedback on the human population via shortages in food production and undermine the sustainability of the socio-ecological system. These studies provide the basis for our work, showing a link between humans and the environment through food consumption, which we represent by feedbacks between human population growth and agricultural land use.

Research on sustainable agricultural land use has led to the land sharing-sparing debate (Grau et al., 2013; Power, 2010). Whether it is better to protect larger areas of natural land and cultivate high-intensity fields on the remaining land; or protect smaller areas of natural land while practicing wild-life friendly, low-intensity agriculture, is a question that has not yet been fully answered. Different authors often arrive at different conclusions, some defending the sparing/intensification paradigm (Phalan et al., 2011b,a; Balmford et al., 2019) and others the sharing or agroecological one (Perfecto and Vandermeer, 2010; Power, 2010). The sparing-sharing debate has been criticized for omitting the coupling between land use and human demography (Phalan, 2018). Furthermore, the discussion generally examines discrete, opposing strategies, yet there is an entire spectrum between these two extremes. The impact of agricultural intensification on sustainability is an important issue at present, as in the developing countries foreign demand is fueling the conversion of

large areas of natural land into intensively cultivated monocultures (Fearnside, 2001; Pengue, 2005; Reboratti, 2010; Soares-Filho et al., 2006). The result is a uniform landscape that is highly vulnerable to environmental fluctuations, destruction of natural habitats, fragmentation, contamination of underground water sources and nutrient runoff. These practices are detrimental to the environment, but agriculture is necessary to feed the population. It is obvious that a balance needs to be achieved between food production and natural land conservation, as the actions taken today could jeopardize the population's viability in the long run.

Here we build a model to explore the effects of different agricultural land use strategies on long-term human-environment dynamics. Through a simple and tractable model accounting for the interaction between human demography and land dynamics, we study the viability of agricultural socio-ecological systems under different land use strategies along an intensification-expansion spectrum. We introduce a trade-off between intensification and the land conversion effort and investigate for which land use strategies the population collapses due to land degradation. Our central premise is that increasing agricultural production can promote further population growth. Thus, agricultural intensification, via increasing agricultural yields, can have a positive feedback on human demography, initiating the need for larger production and therefore causing further natural land conversion to agriculture, which eventually leads to a more degraded landscape. We test the conditions under which increasing agricultural intensification fails to spare enough natural land and promotes unsustainable population growth, pushing the environment through a tipping point and ultimately leading the social-ecological system to collapse.

Model and Methods

Bidirectional coupling between human demography and land dynamics

Our model considers the conversion of natural land to agricultural land in relation to the demand from the human population. As population dynamics are driven by the resources humans can access and consume, they ultimately depend on the landscape's composition. Resource production depends on the landscape composition but also on agricultural intensity. We conceive agricultural land use along two dimensions: the conversion effort, which controls the spatial extension of agricultural land, and agricultural intensity. In the model, humans adopt a land use strategy ranging from low intensity and high land conversion rates, to high intensity and low land conversion rates. This negative relation between agricultural intensity and the land conversion effort is grounded in the land sparing-sharing debate. Highly expansive and intense agricultural land uses have been identified as unsustainable. Hence, the debate is whether the focus to achieve sustainability should be put on increasing intensification to reduce the converted areas or extensification to have a wildlife friendly agricultural landscape. We aim to reproduce these two strategic poles by imposing a trade-off between agricultural intensity and land conversion effort, hence reducing the two strategical dimensions to a single parameter. In this study, we do not consider the evolution of the strategy over time and assume it remains constant.

Agricultural land is exhausted and degraded, at different rates depending on the surrounding landscape, and ultimately becomes unproductive (Henderson and Loreau, 2019; Cramer et al., 2008). Natural land contributes to the recovery of surrounding land, acting, for example, as a species pool necessary for recolonization by native species (Cramer et al., 2008; Baeten et al., 2010). Hence, fragmentation of natural areas and degradation of natural patches surrounding degraded land can obstruct its spontaneous recovery. On the other hand, natural land can also become degraded. Indeed, a degraded state of land can propagate into a natural one, as is

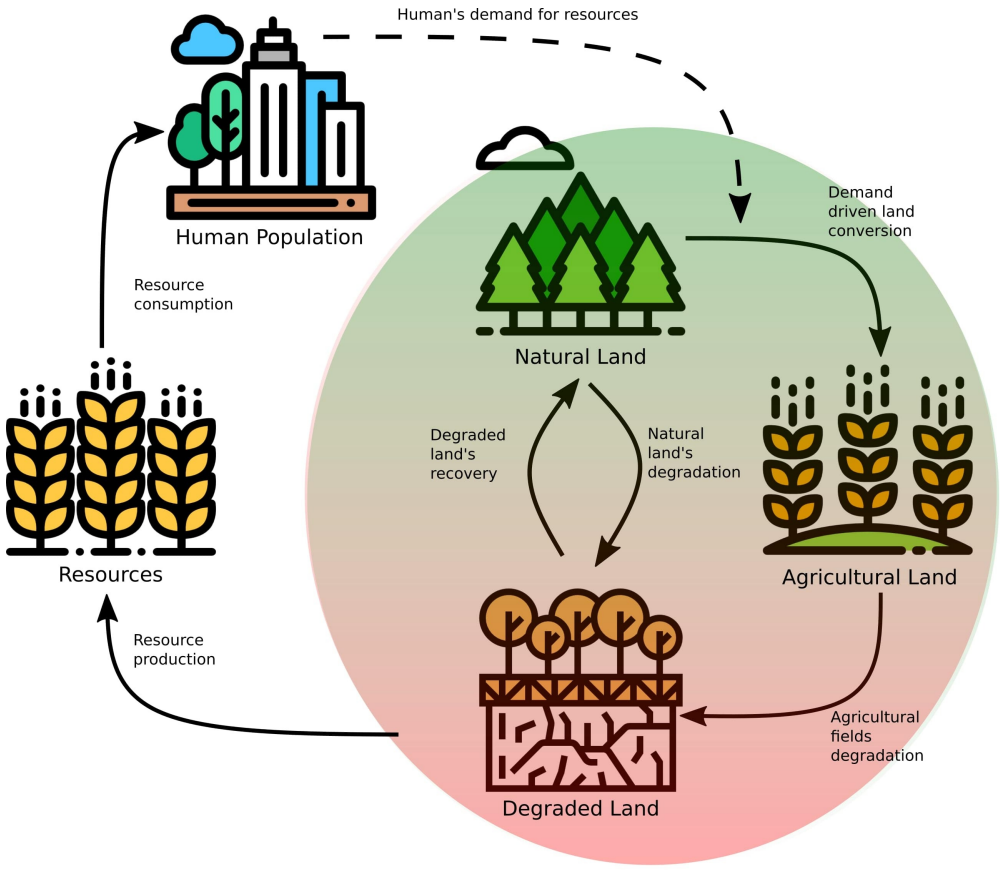

Figure 1.1: **Model's graphical representation.** The right part of the diagram represents the landscape, composed of natural land, agricultural land and degraded land. The arrows between the three land types represent the possible land transformations we consider (conversion, recovery, degradation). Both the agricultural intensity and the landscape composition determine the number of resources that are produced and consumed by the human population. Human demography is entirely determined by resource access. Changes in the human population size modify the population's demand for resources and feedback on the landscape's composition by increasing or decreasing the conversion of natural land for agricultural purposes.

the case with a desertification front that propagates on semi-arid landscapes (Zelnik et al., 2017; Zelnik and Meron, 2018). The balance between the recovery and degradation processes depends not only on the extension of both natural and degraded land, but also on the borders between the two types of lands and on the level of degradation (Cramer et al., 2008).

Human demography

A number of studies have discussed the idea of a human carrying capacity and pointed to food supply as one of the main constraints to human population growth (Cohen, 1995; Hopfenberg, 2003; Fanta et al., 2018). In this study, we follow the same reasoning and assume human population size p follows logistic growth with a carrying capacity that evolves over time subject to changes in food supply.

The use of the logistic equation to describe the dynamics of human populations has been previously criticized (Mote et al., 2020; Board on Environmental Change and Society et al., 2014) and other studies have opted to explicitly model fertility and mortality processes by various functions related to consumption levels (Motesharrei et al., 2014; Lafuite and Loreau, 2017; Henderson and Loreau, 2019). Furthermore, Cohen (1995) has stressed the difficulties of estimating a human carrying capacity given that several bio-physical and social mechanisms that might constrain human population growth are dynamically evolving and possibly unidentified. However, historical population trends have been well recovered by logistic models using food-dependent carrying capacities (Goldberg et al., 2016; Fanta et al., 2018). Additionally, the unprecedented population increase of the 1960s to 2000s was also modelled using a logistic model, where Hopfenberg (2003) quantified the human carrying capacity using food production, showing good agreement with empirical data. More recently, Suweis et al. (2013) used the link between water availability and food production to calculate a human carrying capacity based on access to water resources, using population data from 1970 to 2011.

We assume the human carrying capacity to be the ratio between total resource

production and per capita consumption $K_p = Y/C$, where Y is total resource production, depending on the landscape's composition, and C is per capita resource consumption. As such, the carrying capacity endogenously changes over time as food production changes driven by the feedbacks between humans and the landscape. For a given consumption intensity, the maximum number of humans that can be sustained is then given by the ratio of production over per capita consumption:

$$\frac{dp}{d\tau} = r_0\, p \left(1 - \frac{p}{K_p}\right) = r_0\, p \left(1 - \frac{Cp}{Y}\right), \tag{1.1}$$

where r_0 is the population's growth rate at very low densities. We assume that r_0 and C remain constant over time. This is a simplification, as it is known that technological developments and cultural evolution have driven changes in human fertility and consumption, as well as in agricultural productivity, which inevitably impact the human carrying capacity. However, in this study we do not consider the role of cultural and technological evolution, instead we focus on the land dynamics. Based on a previous model of socio-ecological interactions that included variations in food production efficiency (Cazalis et al., 2018), the inclusion of technology in the carrying capacity would likely shift the onset of collapse, vary the size of the collapse range and alter the viability range of parameters, but would not change the overall or long term trends.

Agricultural production

The number of resources produced (Y) depends on the area of agricultural land (a), but also on that of natural (n) and degraded (d) land, as well as on agricultural intensity, β. Noncultivated land, whether natural or degraded, provides ecosystem services that are crucial for agricultural production, such as pollination, nutrient cycling, pest control and water quality regulation (Mitchell et al., 2014). However, greater land degradation leads to fewer and lower-quality ecosystem services. Therefore, we do not consider natural and degraded land to contribute equally to

agricultural production. Instead, we introduce an effective land function $\varepsilon_l(n, d, \beta)$, which represents the effective area of non-cultivated land that provides ecosystem services to agricultural land:

$$\varepsilon_l = n + (1 - \beta)\, d. \tag{1.2}$$

The contribution of degraded land to effective land decreases with its level of deterioration, which in turn depends on the level of agricultural intensification (β). We assume that more intensive agriculture results in higher degrees of land degradation and as such intensive agriculture transitions to highly degraded land. For simplicity, the contribution of degraded land to effective land decreases linearly with agricultural intensity.

We model agricultural resource production Y as the sum of the contributions from the total cultivated area (area contribution) and from the border of agricultural land with non-cultivated land, both natural and degraded, represented by the effective land ε_l (border contribution). Therefore, the "area contribution" scales with agricultural land area and the "border contribution" with the square root of agricultural land area. Furthermore, we assume the relative weights of area, and border contributions in production depend on agricultural intensity (β). As agricultural intensification grows, production, Y, becomes less dependent on the ecosystem services provided by the surrounding non-agricultural land and more dependent on human inputs. Hence, increasing intensification diminishes the border contribution and increases the area contribution on production. Therefore, we assume the area contribution increases linearly with agricultural intensity, β, while the border contribution decreases linearly with β.

The amplitude of the area and border contributions is modulated by the functions $Y_A(\beta)$ and $Y_B(\beta)$. These two functions can be interpreted as the characteristic productivity of the area and border contributions, respectively. For a given agricultural intensity (β), $Y_A(\beta)$ is the production per unit area of agricultural land and $Y_B(\beta)$ is the production per unit area of effective land per unit length of the

agricultural land's border.

$$Y = \underbrace{Y_A(\beta)\,\beta\,a}_{\substack{\text{Area}\\ \text{contribution}}} + \overbrace{Y_B(\beta)\,(1-\beta)\,\varepsilon_l\sqrt{a}}^{\substack{\text{Border}\\ \text{contribution}}} = y_A\beta\left(\beta a + Q\,\varepsilon_l\,(1-\beta)\sqrt{a}\right) \tag{1.3}$$

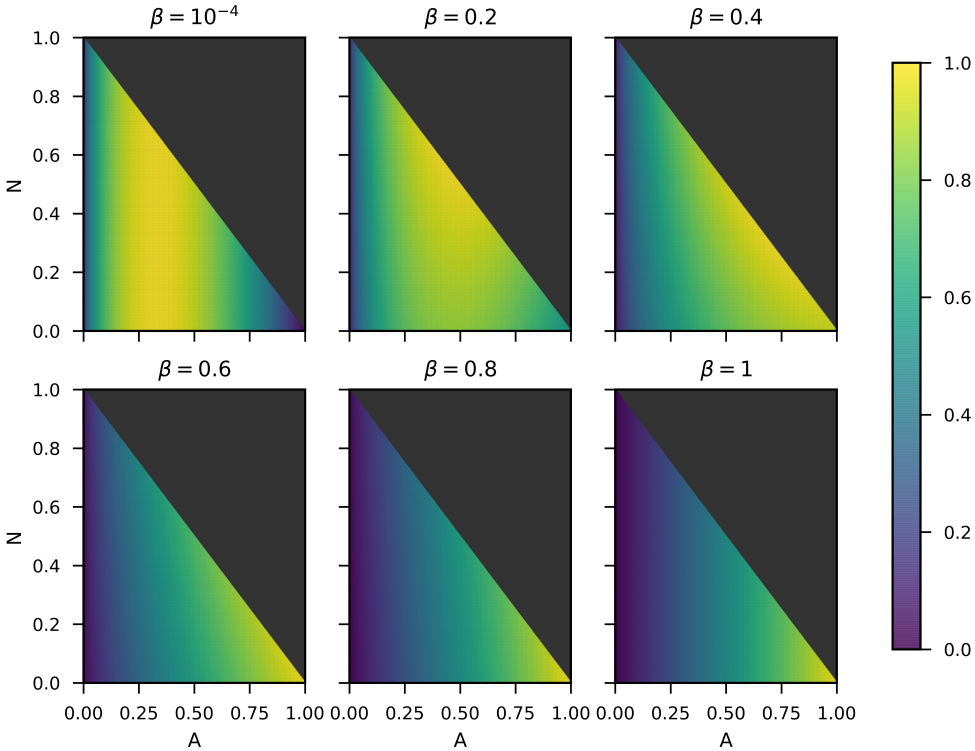

Figure 1.2: **Agricultural production as a function of landscape composition for different agricultural intensities.** The x and y axis correspond to the fraction of agricultural and natural land respectively. Each subplot corresponds to a different agricultural intensity (β). The production is normalised for each case, hence comparison of agricultural production's magnitude between strategies is not possible. Instead, the figure shows the different effect that landscape composition has on each case. When agricultural intensity is very low ($\beta = 10^{-2}$) , production strongly depends on the services provided by the non-agricultural landscape, hence it decreases when the fraction of agricultural becomes bigger than a certain threshold ($A \simeq 0.4$ in the plot). As intensification grows, natural land's importance for production diminishes ($\beta = 0.2, 0.4, 0.6, 0.8$). On the high intensification extreme ($\beta = 0.99$), the production becomes exclusively dependent on human inputs, hence it grows monotonically with agricultural area.

Agricultural intensity (β) ranges from 0 to 1, 0 being extreme low-intensity agriculture and 1 extreme high intensity. As intensification increases agricultural yields, we model the characteristic productivity of the area (Y_A) and border (Y_B) contributions

as increasing functions of agricultural intensification. For simplicity, we assume a linear dependency, i.e., $Y_A(\beta) = y_A\,\beta$ and $Y_B(\beta) = y_B\,\beta$. The parameters y_A and y_B are then the productivities per unit of intensification. We introduce the parameter $Q = y_B/y_A$, which represents the relative importance of the border and area contribution to resource production.

Figure 1.2 shows the magnitude of agricultural resource production as a function of landscape composition. When β is close to 0, maximum production is obtained in a landscape where about a third of the land is agricultural. The food production is exclusively dependent on the services provided by the non-anthropogenic landscape. As we assume the services that non-cultivated land provides to agricultural land depend both on the area and quality of non-cultivated land and on the length of the border between them, at this extreme of the spectrum production scales with the square root of agricultural area. At the extreme, the fraction of natural land is not important because the degradation caused by the agricultural activity is extremely low, such that natural and degraded land contribute equally to effective land. As β grows, the fraction of natural land starts to have an impact, as degraded and natural land are not interchangeable anymore. When β approaches 1, production becomes exclusively dependent on agricultural land area. This is a scenario of extremely high agricultural intensity, where agricultural yields become independent of the services provided by the non-agricultural landscape, and rely exclusively on human inputs, such as fertilizers or pesticides. In the high intensity case, production is proportional to the area of agricultural land. Figure 1.2 also shows that yields increase with intensification, as maximum attainable production (yellow areas in the figure) grows with β.

Land dynamics: agricultural land equation

Land conversion is driven by the human population's demand for agricultural goods, which results on the conversion of natural land to agriculture. We assume that demand is equal to the total desired food consumption (Cp). Since we aim to investigate the impact of different land use strategies along the intensification-

extensification spectrum on human-land dynamics, we impose a trade-off between agricultural intensity and land conversion rate. We model land conversion rate as a decreasing affine function of agricultural intensity (β). Nutrient runoff and soil erosion cause agricultural land degradation, which increases with intensity. Therefore, we model the degradation rate of agricultural land as a linear function of β, capturing the fact that high-intensity agriculture degrades the land faster than does low intensity agriculture. The dynamical equation for the agricultural land area is given by

$$\frac{da}{d\tau} = \underbrace{\left[K_0 + (K - K_0)\,(1-\beta)\right]\, Cp\, n}_{\text{Conversion}} - \overbrace{E\beta\, a}^{\text{Degradation}} \quad . \tag{1.4}$$

Parameters K_0 and K are the minimum and maximum conversion rates per unit of demanded resources Cp, respectively. As the demand for resources is proportional to population density, K_0 and K are also per capita rates of conversion. Therefore, in the following we will call them per capita conversion rates. In the extreme high intensity scenario ($\beta = 1$), the conversion rate per person is at its minimum K_0. In the extreme low intensity scenario ($\beta = 0$), the conversion rate per person is at its maximum K.

Land dynamics: natural land equation

Apart from being converted to agriculture, natural land area can either increase through the spontaneous recovery of degraded land or decrease by the propagation of the degraded state of land. The natural land at the edges of degraded land fosters its spontaneous recovery through both biotic and abiotic processes. It acts as a species pool, promoting native species recolonization, or as a source of good quality water or chemical compounds to restore soil chemistry (Cramer et al., 2008; Baeten et al., 2010). The size of the natural patches is also important as larger patches foster more species and are more resilient to abiotic fluctuations (Mitchell et al., 2013, 2015b). Hence, the recovery process depends both on the area of

natural patches and on the size of their border with degraded land. We propose a spontaneous recovery term that scales both with natural land area n and with degraded land's border $\propto \sqrt{d}$ (Mitchell et al., 2015b). The propagation of degraded land's occurs through a symmetric mechanism, where the potential for degradation grows with degraded land area and with the natural land's border. Therefore, the equation for the change in natural land is

$$\frac{dn}{d\tau} = \underbrace{R\, n\sqrt{d}}_{\text{Recovery}} - \overbrace{D\beta\, d\sqrt{n}}^{\text{Degradation}} - \underbrace{[K_0 + (K - K_0)\,(1-\beta)]\; Cp\, n}_{\text{Conversion}}. \tag{1.5}$$

The parameters R and $D\beta$ are the recovery and degradation rates, respectively. The degradation rate scales linearly with the agricultural intensification, such that more intensive agricultural land is more heavily degraded. Furthermore, heavily degraded land contributes to a greater extent to the degradation of natural land.

Nondimensionalization

We rescale the dynamical system by introducing the non-dimensional variables P, N, A and t, for population, natural land area, agricultural land area and time respectively:

$$t = \frac{\tau}{T_0} = r_0\,\tau, \quad N = \frac{n}{A_0}, \quad A = \frac{a}{A_0}, \quad P = \frac{p}{P_0} = p\,\frac{C}{y_A\,A_0}.$$

Time is rescaled to the characteristic timescale of human demography $T_0 = 1/r_0$. Parameter A_0 is the total amount of land, hence variables N and A represent the fraction of natural and agricultural land in the landscape, respectively. We normalize the population by $P_0 = y_A A_0/C$. P_0 represents the population size that could be sustained if the whole landscape was cultivated with the highest intensity agriculture $\beta = 1$, given per capita consumption C. Indeed, when $\beta = 1$, if the whole landscape is cultivated, production is $Y = \beta^2\, y_A\, A_0 = y_A\, A_0$. The following dimensionless parameters emerge from the non-dimensionalisation: k_0 – minimum land conversion

rate, k – maximum land conversion rate, e – agricultural land degradation rate, r – spontaneous recovery rate of degraded land, d – degradation rate of natural land, and q – the relative importance of the border contribution to agricultural production:

$$k_0 = \frac{K_0\, y_A\, A_0}{r_0}, \quad k = \frac{K\, y_A\, A_0}{r_0}, \quad e = \frac{E}{r_0},$$
$$q = Q\sqrt{A_0} \quad r = \frac{R\,\sqrt{A_0}}{r_0}, \quad d = \frac{D\,\sqrt{A_0}}{r_0}$$

The dynamical equations describing the non-dimensional system behaviour are

$$\begin{cases} \frac{dP}{dt} & = P\left(1 - \frac{P}{\mathcal{Y}}\right) \\ \frac{dA}{dt} & = [\,k_0 + (k - k_0)(1-\beta)]\; P\,N - e\,\beta\,A \\ \frac{dN}{dt} & = \begin{array}{r} r\,N\,\sqrt{1-A-N} - d\,\beta\;(1-A-N)\;\sqrt{N} - \\ [\,k_0 + (k-k_0)(1-\beta)]\;P\,N \end{array} \\ \mathcal{Y} & = \beta\left(\beta A + q(1-\beta)(N + (1-\beta)(1-A-N))\sqrt{A}\right) \end{cases} \tag{1.6}$$

Parameter	Interpretation	Dimension	Non-dimensional	Value
r_0	Population growth rate at low densities	time^{-1}		
y_A	Maximum production per cultivated area	mass/area		
C	Resources consumption per person	mass/person		
K_0	Minimum land conversion rate per resources demand	$\text{mass}^{-1}\ \text{time}^{-1}$	k_0	0.5
K	Maximum land conversion rate per resources demand	$\text{mass}^{-1}\ \text{time}^{-1}$	k	4.5
E	Maximum agricultural fields degradation rate	time^{-1}	e	1.0
Q	Ratio between area and border contribution	length^{-1}	q	1.0
R	Recovery rate of degraded land per length of frontier with natural land	length^{-1} time^{-1}	r	$[0.1-3.5]$
D	Maximum degradation rate of natural land per length of frontier with degraded land	length^{-1} time^{-1}	d	$[0.1-3.5]$
β	Land use strategy parameter		β	$[0-1]$

Table 1.1: Description of the model's parameters and values used in the simulations.

A list of the parameters, their interpretation, their non-dimensional equivalent and the values used in the simulations can be found in Table 1.1.

Results

Exploitation of a pristine landscape: sustainable vs. unsustainable land use strategies

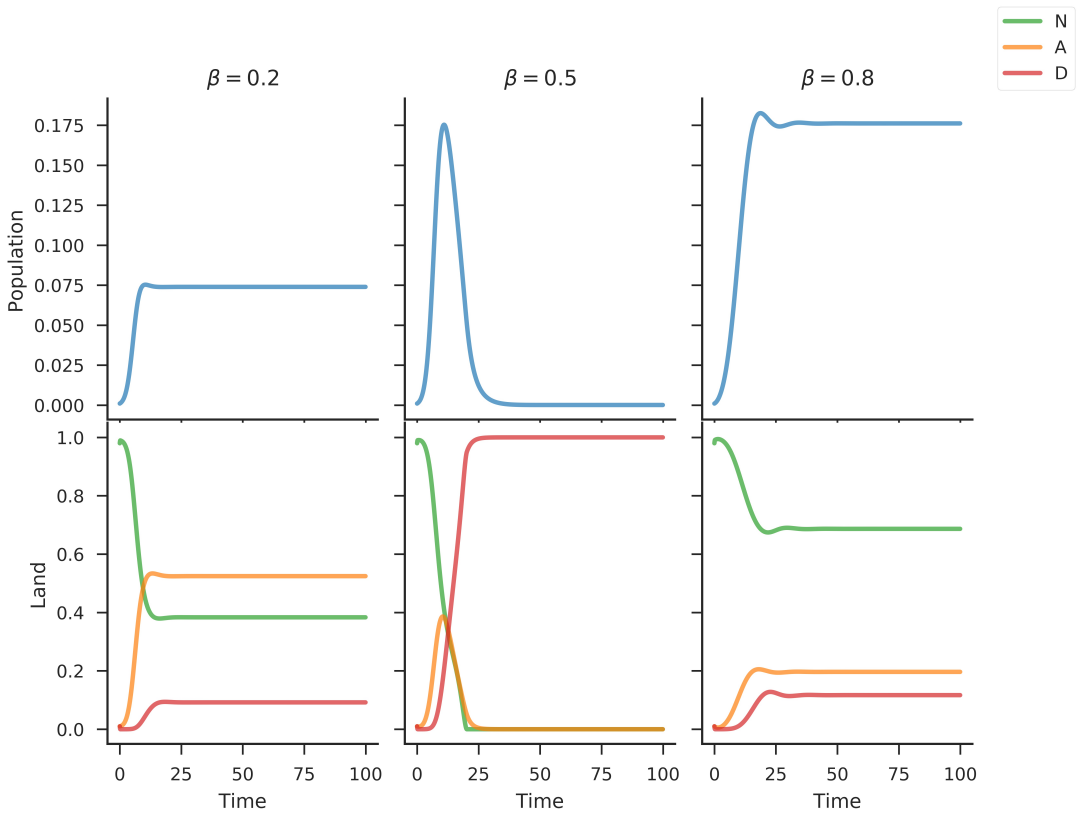

Figure 1.3: **Temporal dynamics of the socio-ecological system for different agricultural land use strategies.** *On the left:* dynamics emerging from low intensity agriculture and a high land conversion effort. The socio-ecological system reaches a viable equilibrium. *Center:* dynamics emerging from intermediate agricultural intensity and conversion effort. The socio-ecological system collapses. *On the right*: dynamics emerging from high intensity agriculture and low land conversion effort. A viable equilibrium is reached again. *Parameter values:* $r = 1.0$, $d = 1.0$, $k = 4.5$, $e = 1.0$, $k_0 = 0.5$, $q = 1.0$.

We first look at the dynamics that follow the introduction of a small population in a pristine landscape. The time series are depicted in Figure 1.3. No matter the land use strategy, the early transient dynamics are identical. The human pop-

ulation converts the natural land into agricultural fields, thus increasing resource production, which positively feeds back on the human population. The increased population, in turn, accelerates land conversion. This positive feedback loop causes a population explosion accompanied by a transformation of the landscape. Agricultural land expansion fuels an increase in degraded land. Both land conversion and increasing amounts of degraded land contribute to the decline of natural land. The decrease in natural land area ultimately causes a deceleration of agricultural expansion until no more land is converted. The human population peaks with the agricultural area.

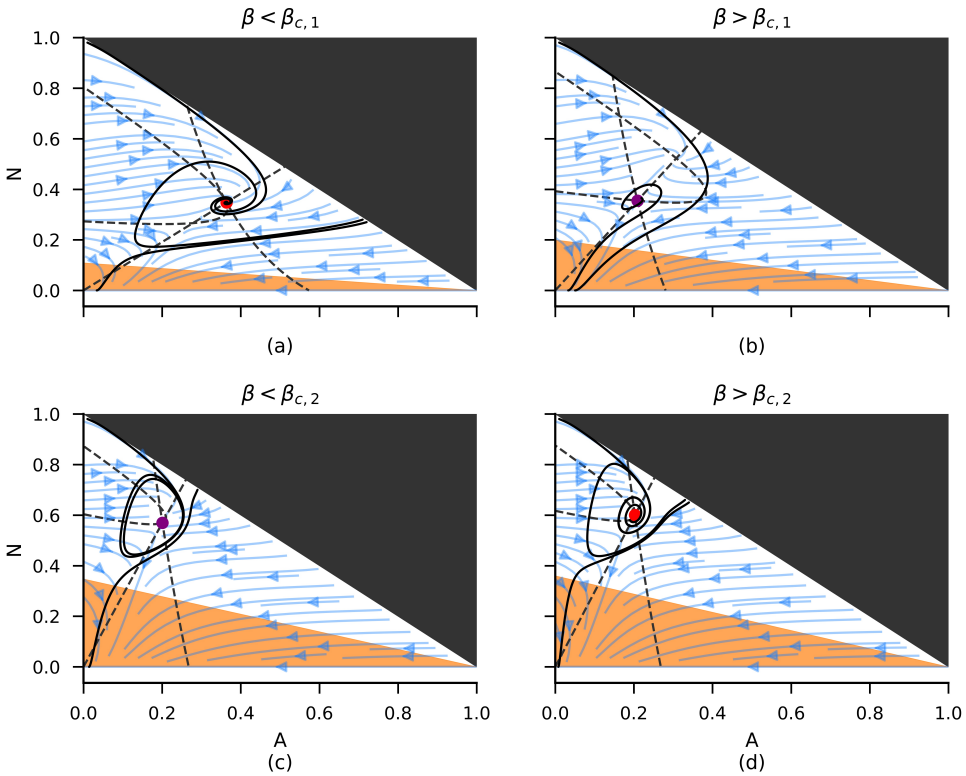

Figure 1.4: **Phase representations of the socio-ecological system for strategies in the viable and collapse regions of the strategy spectrum.** The plots correspond to particular landscape planes of the three-dimensional phase space. The chosen planes are the ones containing the system's viable equilibrium, hence determined by setting the population at its viable equilibrium value. The dotted grey lines are projections of the null planes for the population, the natural land and the agricultural land on the chosen landscape plane. The black solid lines are projections of simulated trajectories. The vector field depicted with blue arrows indicates the landscape's direction of change for each landscape composition given a population at equilibrium. *On the top:* before (a) and after (b) the first transition to collapse. A subcritical Hopf bifurcation causes the stability loss of the viable equilibrium explaining the transition to collapse. *On the bottom:* emergence of a stable limit cycle (c) from a stable focus node (d) after a supercritical Hopf bifurcation. *Parameter values:* $r = 1.0$, $d = 1.0$, $k = 4.5$, $e = 1.0$, $k_0 = 0.5$, $q = 1.0$.

Degraded land cannot be converted back to agricultural land. This introduces a time delayed feedback as the stock of natural land is not instantaneously regenerated. The time delayed feedback causes the population to overshoot its carrying capacity. After the overshoot, the socio-ecological system can reach two different equilibria depending on the land use strategy β. We call *viable equilibrium* the one where the human population exists in the long term, and *collapse equilibrium* the one where the population goes extinct. In the viable equilibrium, the human population exists within a complex landscape, composed of a natural, agricultural and degraded land mosaic. In contrast, the landscape in the collapse equilibrium is fully degraded. Without agriculture, there is no resource production and the human population cannot be maintained.

The land use strategy spectrum can be divided into three regions according to the system's asymptotic behaviour, as a function of the strategy β. The first region corresponds to values of β between 0 and the transition to the collapse equilibrium at the critical point $\beta = \beta_{c,1}$. We call this region the *sharing* side of the spectrum, as land use strategies in that range mimic land-sharing kinds of strategy (e.g. low intensity agriculture over large areas). The *collapse range* (referred to as $\Delta\beta$ later in the text) refers to the region of the spectrum where strategies lead to the collapse equilibrium. When land use strategies are inside the collapse range, the degraded land propagates into the whole landscape, leading to a population collapse. The region between the collapse range and the viable equilibrium is designated the sparing side of the spectrum, as the strategies in this region mimic land-sparing kind of strategies (e.g. high intensity agriculture over small areas).

On the path to socio-ecological collapse

The existence of the collapse range is due to changes in the stability of the viable equilibrium as a function of the agricultural land use strategy β. On the sharing side of the spectrum, the viable equilibrium is a stable focus-node. Hence, in the phase space, trajectories follow spirals before reaching the fixed point (Figure 1.4 (a)), which translate into damped oscillations over time (column (a) of Figure 1.5).

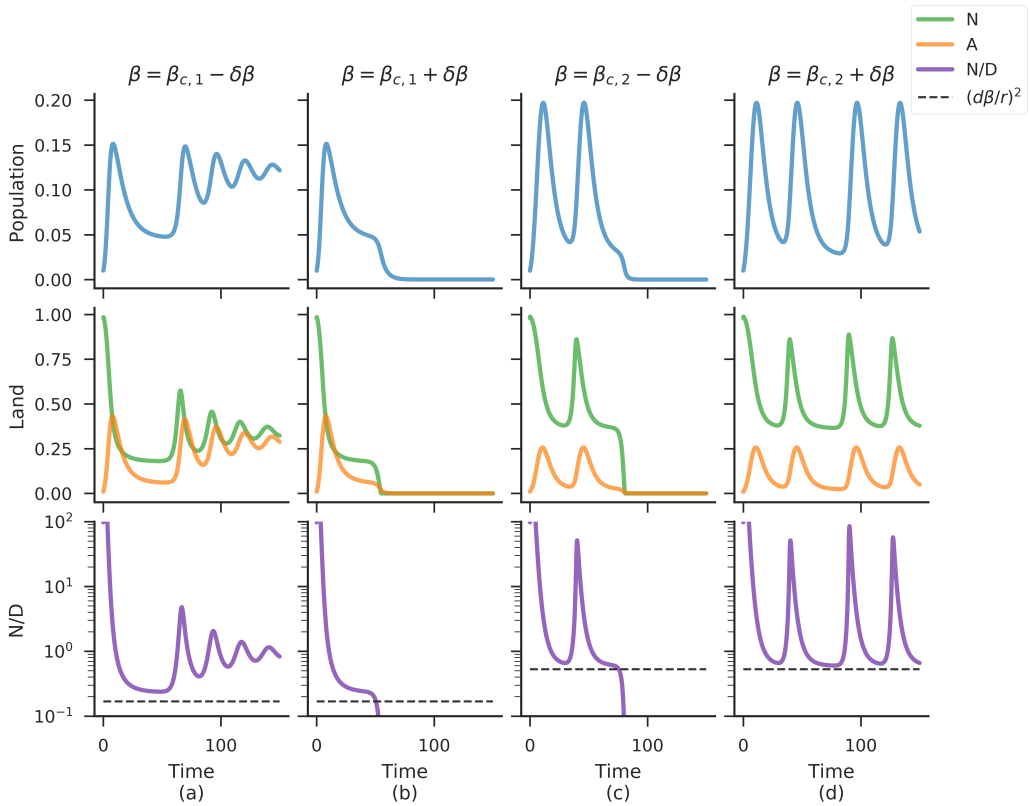

Figure 1.5: **Temporal dynamics of the socio-ecological system at the edges of the collapse range.** *Column (a):* dynamics before the first transition to collapse. The equilibrium is reached after large amplitude damped oscillations. *Column (b):* dynamics after the first transition to collapse. *Column (c):* dynamics after the second transition to collapse. The growth of the oscillations' amplitude pushes the system through a threshold and causes the collapse (bottom plot) . *Column (d):* dynamics before the second transition to collapse. The collapse is avoided as the system oscillates around the equilibrium without reaching it. *Parameter values:* $\beta_{c,1} = 0.4106108$, $\beta_{c,2} = 0.7272030$, $\delta\beta = 10^{-7}$, $r = 1.0$, $d = 1.0$, $k = 4.5$, $e = 1.0$, $k_0 = 0.5$, $q = 1.0$.

As land use strategies come closer to the collapse range (β increases), the amplitude of the oscillations grow, which delays the system's convergence to the viable equilibrium. When the land use strategy enters the collapse range, the viable equilibrium becomes a saddle-focus and loses stability (Figure 1.4 (b)). The stability loss is caused by a subcritical Hopf bifurcation which leaves the collapse equilibrium as the sole stable attractor for the socio-ecological system.

On the sparing side of the spectrum, the transition to collapse has a different origin. As for the sharing side of the spectrum, the system converges to a viable equilibrium via damped oscillations (Figure 1.4 (a)) which grow in amplitude as the collapse range is approached. However, in this case the system undergoes a supercritical Hopf transition when the critical point is reached. Hence, the stability

loss of the viable equilibrium is accompanied by the birth of a stable limit cycle, which allows the socio-ecological system to potentially escape the collapse equilibrium (Figure 1.4 (c)) and oscillate around the viable equilibrium. However, the amplitude of the oscillations grows as the land use strategy moves in the sharing direction (β decreases). Eventually, the oscillations become large enough to push the system through a tipping point provoking a socio-ecological collapse (bottom of column (c) in Figure 1.5).

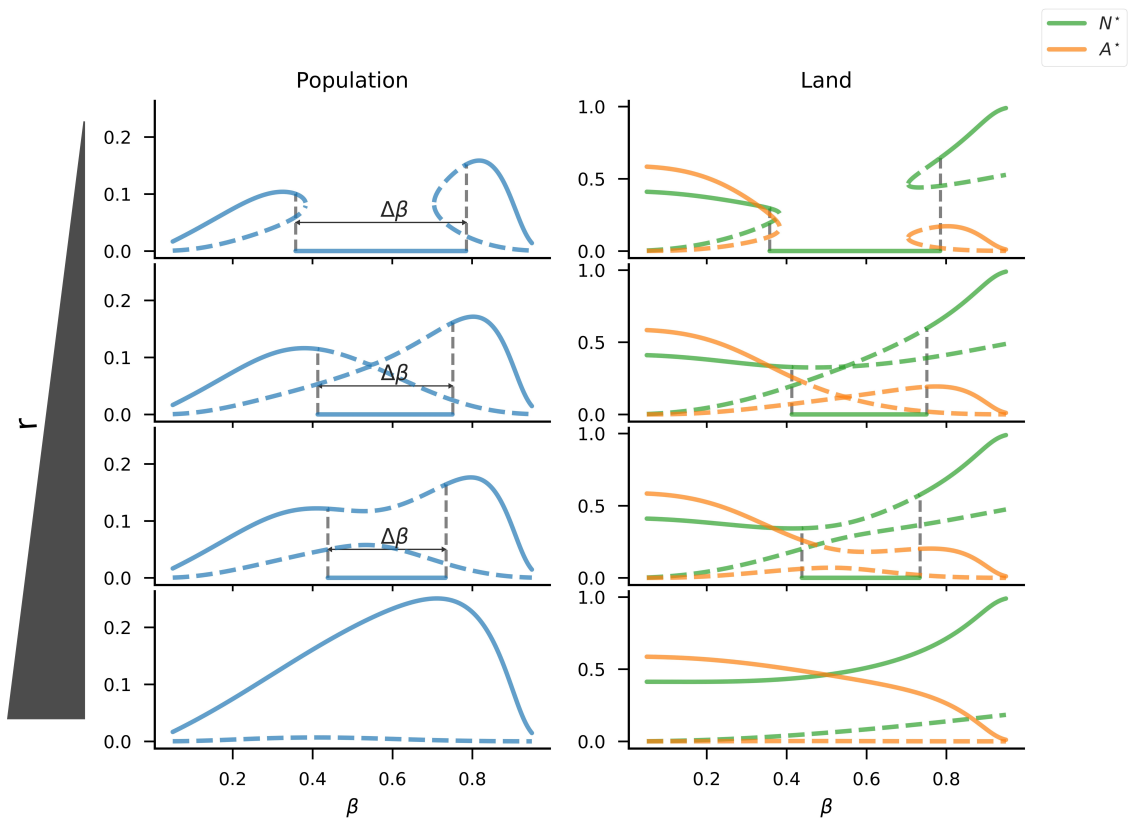

Figure 1.6: **Bifurcation diagrams for the land use strategy parameter β and for different values of natural land's recovery capacity.** Socio-ecological steady states are plotted as a function of the land use strategy. The dotted lines correspond to the unstable equilibria and the solid ones to the stable ones. The size of the collapse region is $\Delta\beta$. From the top to the bottom, the natural land's recovery capacity increases. The values of the recovery capacity increase from top to bottom and were chosen to give a full picture of the steady state branches' behaviour. $\Delta\beta$ decreases until disappearance as the recovery rate r increases. Parameter values for these simulation are $r = 0.9$, 0.97139, 1, 2, $d = 1.0$, $k = 4.5$, $e = 1.0$, $k_0 = 0.5$ and $q = 1.0$.

Analytically, we can determine a threshold landscape composition after which socio-ecological collapse is unavoidable. Analysis of the natural land's dynamical

equation gives the following condition

$$\frac{N}{D} \leq \left(\frac{d\,\beta}{r}\right)^2, \tag{1.7}$$

where $D = 1 - A - N$ is the fraction of degraded land. The threshold depends on the land recovery potential r, as well as on the degradation potential $d\,\beta$. The threshold represents the point at which the landscape is so deteriorated that the remaining fraction of natural land is not sufficient to recover the degraded land nor to maintain its natural state. Hence, degraded land starts propagating into the natural land, resulting in the complete degradation of the landscape and population extinction. Close to the second transition to collapse, oscillations approach the previous threshold (column (d) of Figure 1.5). A small change in the land use strategy increases the oscillations' amplitude and pushes the system through the tipping point, driving it to collapse (column (c) of Figure 1.5).

Role of land recovery potential on the size of the collapse range

The size of the collapse range $\Delta\beta = \beta_{c,2} - \beta_{c,1}$ is highly dependent on the degraded land's recovery potential (r), as Figures 1.6 and 1.7 show. As the land recovery potential increases, the size of the collapse range decreases until it disappears. It is interesting to note that on the sharing side of the spectrum, when $\beta < \beta_{c,1}$, an increase in β leads to higher agricultural yields and larger populations. However, the decrease in the land conversion effort is not high enough to prevent the fraction of natural land to decrease. Indeed, agricultural intensification increases the natural land's degradation rate βd, increasing the potential of degraded land to propagate into the rest of the landscape. When agricultural intensification is not accompanied by a sufficiently large reduction in the conversion effort, the system enters the path to collapse. At the critical point, the levels of degradation are sufficiently high to cause a socio-ecological collapse.

On the sparing side of the spectrum, when $\beta > \beta_{c,2}$, the decrease in the land

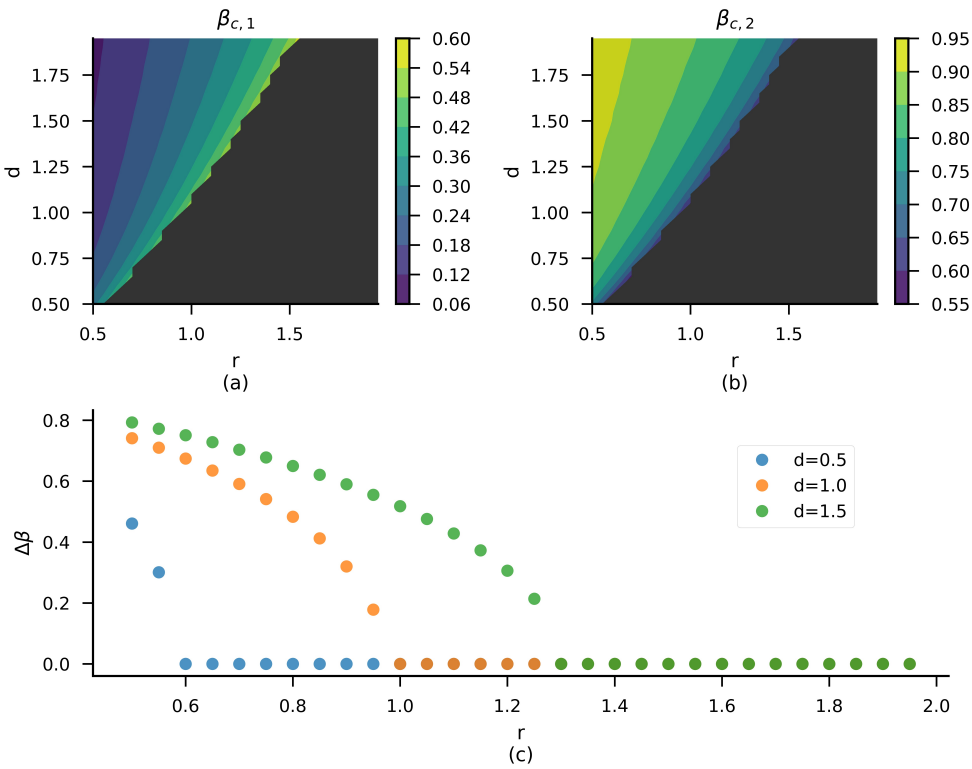

Figure 1.7: **Collapse range size $\Delta\beta$ in function of landscape's intrinsic characteristics.** *On the top:* critical values $\beta_{c,1}$ (a) and $\beta_{c,2}$ (b) in function of the land's recovery r and degradation d rates. The black colour depicts the region of the parameter space (r, d) where the human population is viable no matter the land use strategy. *On the bottom:* Size of the collapse range $\Delta\beta = \beta_{c,1} - \beta_{c,2}$ in function of the land's recovery rate for different degradation rates. The amplitude of the collapse region sharply increases when r decreases. The parameter values are $k = 4.5$, $e = 1.0$, $k_0 = 0.5$ and $q = 1.0$.

conversion effort that accompanies the increase of intensification succeeds in sparing natural land and allows larger populations to exist in a landscape with a higher fraction of natural area. At the extreme of the sparing strategy spectrum, populations decrease when β rises. This is due to the decrease in the land conversion effort. Only a small fraction of land is converted to agriculture and as such a much lower population can be sustained with the same consumption level.

We investigated in more detail the relationship between the size of the critical region $\Delta\beta$ and the landscape intrinsic parameters r and d (Figure 1.7). The controur plots of Figure 1.7 show the variation of the critical values $\beta_{c,1}$ and $\beta_{c,2}$ as a function of r and d. For a given natural land degradation rate (d), increasing the recovery rate of degraded land (r) rises $\beta_{c,1}$ and diminishes $\beta_{c,2}$. When the difference between the two critical values reaches 0, the collapse range ceases to exist (black region in

contour plots of Figure 1.7). The non-linearity of the edge between the coloured ($\Delta\beta > 0$) and black regions ($\Delta\beta = 0$) of the contour plots shows that the collapse frontier is more sensitive to r than d, such that when an increase in degradation requires a smaller increase in r to off-set the increase in degradation.

The dangers of naive agricultural land use planning

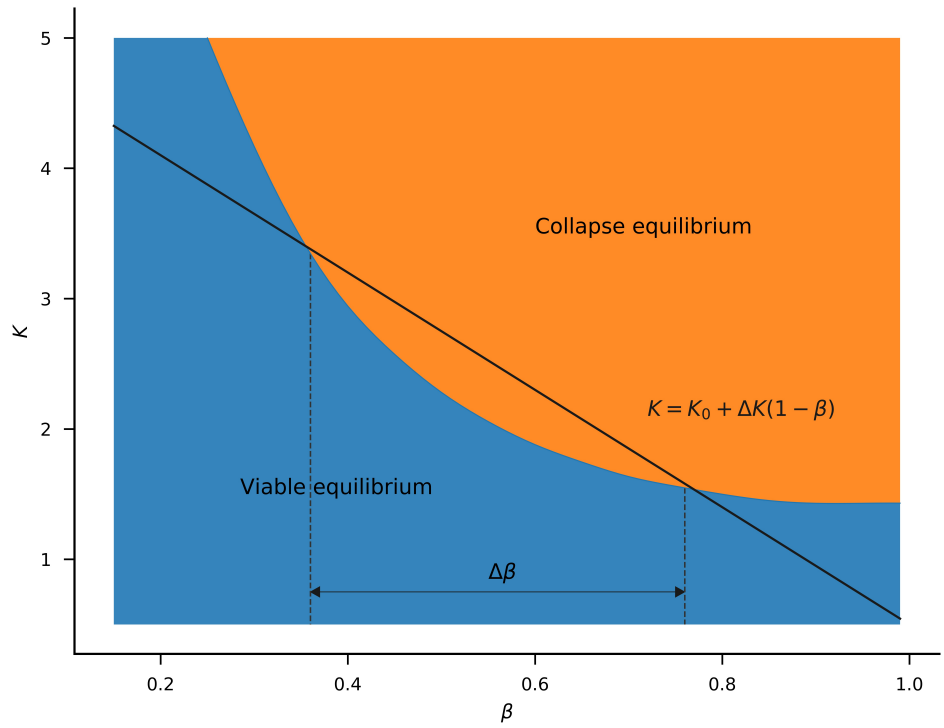

Figure 1.8: **Long-term system's behaviour in the two-dimensional land use strategy space**. Land use strategy is defined by the couple intensification β and conversion effort K. The blue region corresponds to the set of strategies leading to a viable socio-ecological equilibrium, and the orange region corresponds with the ones leading to socio-ecological collapse. The solid black line depicts the linear trade-off between intensification and conversion effort that we were previously assuming. The border between the two regions is non-linear, which explains the existence of the collapse range $\Delta\beta$.

As it is formulated, our model does not allow us to know how much the land conversion effort should diminish for a given increase in agricultural intensification, in order to avoid socio-ecological collapse. This is because we fixed a linear trade-off between the conversion effort and the intensity. In reality, the relationship between them can be highly nonlinear. In order to address the question, we release the

linear trade-off assumption and let the land conversion effort to be independent of agricultural intensity. We then explore land use strategies along the two dimensions of intensification and extensification. In practice, this means we now have two parameters K (land conversion effort) and β (agricultural intensity) to describe a land use strategy instead of a single one. Hence, the equations for land become:

$$\begin{cases} \frac{dA}{dt} & = K\,P\,N - e\,\beta\,A \\ \frac{dN}{dt} & = r\,N\,\sqrt{1-A-N} - d\,\beta\,(1-A-N)\,\sqrt{N} - K\,P\,N \end{cases} \tag{1.8}$$

In Figure 1.8 we plot the regions of the land use strategy space, defined by the land conversion effort K and the agricultural intensity β where either the collapse equilibrium or the viable equilibrium are attained. The border between the two regions is concave rather than linear, which explains the existence of the collapse range $\Delta\beta$ we previously described. A linear decrease in the conversion effort in relation to agricultural intensity (solid black line in the graph) makes it unavoidable to cross the border between the viable and collapse equilibria. This result shows the non-triviality of designing sustainable land use strategies.

Discussion

We investigated the impact of different land use strategies on the long-term sustainability of an agriculturally based human society. We considered agricultural land use planning along two strategical dimensions: expansion and intensification. Inspired by the land sparing-sharing debate we introduced in our model a land use strategy parameter (β) that controls the trade-off between agricultural intensity and land conversion effort, thus reducing the two dimensions of the strategy to a single parameter. We then studied the behaviour of the coupled socio-ecological system across a continuum of strategies ranging from low agricultural intensity and high conversion effort ($\beta = 0$) to high agricultural intensity and low conversion effort ($\beta = 1$). We find that agricultural intensification leads to irreversible land degra-

dation and population collapse when not accompanied by a strong reduction of the land conversion effort. Furthermore, the relationship between agricultural intensification and conversion effort is not straightforward. Uninformed land use planning can drive the socio-ecological system to a critical transition that undermines sustainability and leads to irreversible collapse.

Our model predicts that the most suitable strategy to ally a large population and nature conservation is to practice extremely intense agriculture and minimise the conversion of natural land to agriculture. Alternatively, low agricultural intensification and high conversion efforts (i.e., extensive agriculture) lead to preserved landscapes, but with significantly lower population sizes. Therefore, for our current population the model seems to support the advocates of the sparing hypothesis. However, the existence of a collapse region in the middle of the strategy spectrum suggests that it is not simply a question of sparing.

Gradual increases in intensification eventually cause the adoption of land use strategies within the collapse region of our model. Therefore, if technological development in the agriculture sector stagnates, there is a greater risk of getting trapped in the collapse region. Furthermore, technology is not a panacea for all socio-ecological issues, as technology can lead to greater environmental degradation through what is known as 'the Jevons paradox' (Alcott et al., 2012). With reference to this paradox, increasing agricultural production efficiency has the potential to increase demand which ultimately degrades more land and drives the system towards collapse. Socio-ecological collapse can be avoided in the model by changing land use strategies quickly. Whether the levels of intensification required to overcome the collapse region are attainable or how to accurately measure intensity to know where we are on the spectrum are unclear.

It is evident that simultaneous increases in both agricultural expansion and intensification cannot be viable in the long term. However, current practices favour both intensification and expansion. The last century's Green Revolution is a recent and striking example of how agricultural intensification can increase yields and food security. However, this was also the period of fastest population growth in

history, which further increased demand and motivated agricultural intensification and expansion. The societal and economic benefits of agricultural intensification that ensure food security are undeniable. However, agricultural intensification and expansion have caused several environmental problems such as soil erosion, nutrient runoff, water pollution or habitat destruction and fragmentation. It has also caused profound societal transformations, in particular the disappearance of small agricultural producers, that fuel urbanisation and change consumption patterns.

Agricultural intensification is considered a plausible explanation of past societal collapses, such as in the Roman or Mayan examples (Diamond, 2005). Population collapse emerges from our model as a consequence of large-scale land degradation, which impairs agricultural production in two ways: first, the deterioration of the landscape critically depletes the stock of natural land, which is the primary source for conversion to agriculture; second, natural land depletion reduces the provision of ecosystem services to existing agricultural areas. Since land degradation can critically decrease agricultural production, it seems ironic that agricultural land use is nowadays considered to be among the major causes of land degradation. This dangerous feedback loop poses a serious threat to sustainability as agricultural expansion and/or intensification to cope with reduced production can further reduce production in the long term by accentuating land degradation. Thus, we stress the major importance that agricultural land use planning has on the sustainability of socio-ecological systems.

Furthermore, our results also highlight the importance of socio-ecologically informed agricultural land use policies to achieve sustainability. By removing the trade-off between land conversion and agricultural intensity in our model, we showed that sustainable land use strategies can be obtained for the entire spectrum of intensification we consider. However, the frontier between unsustainable and sustainable land use is far from trivial. The existence of unsustainable land use strategies comes from a bad evaluation of the needed reduction of land conversion for a given increase on intensification. As our model is a simplification of real population dynamics and land use planning, we do not claim that the frontier between sustainable and collapse paths is as we describe. However, we show that it is very likely for this frontier

to be far from trivial, hence making it easy for uninformed land use planning to fail. Much the same way that science-based policies are considered crucial for climate change mitigation or human population sustainability (Motesharrei et al., 2016), our work stresses the need to incorporate informed agricultural land use planning into the policy agenda to achieve sustainability.

Globally, at an aggregated scale, it could be argued that we have not yet reached a critical point or planetary boundary (Steffen et al., 2015), however at a local scale this might not be true. Agricultural land use is not spatially homogeneous and agricultural production is often strongly localised: the Pampas in South America and the Great Plains in the United States are two examples. Moreover, these major agricultural regions are mostly expansive and intensive monocultures. Hence, at a regional scale there is neither sparing nor sharing, rather extensive exploitation, which makes the landscape highly susceptible to irreversible ecological degradation. In South American grasslands and forests, these practices have already caused major environmental degradation (Guerschman and Paruelo, 2005; Fearnside, 2001; Pengue, 2005), in addition to societal problems (Pengue, 2005). Agricultural expansion has already destroyed most of Brazil's Atlantic Forest (Centre for Applied Biodiversity Science, 2003; Ribeiro et al., 2011), and now it is advancing over the Amazon Forest, one of the world's biodiversity hotspots (Soares-Filho et al., 2006; Davidson et al., 2012; Lovejoy and Nobre, 2018; Nepstad et al., 2008). The variations in land management practices highlight the interest of considering a continuous range of both agricultural expansion and intensification rather than discrete levels of intensity (Roman et al., 2018) in modelling studies. The possibility of local collapses poses a threat to global sustainability, as it is unclear how these local collapses can propagate over the world, via environmental degradation but also via changes in trade or migration networks.

Our model is a simplified representation of agricultural practices, human demography and social structure, which allows us to explore a range of scenarios and understand the behaviours within the model, but it also omits details of our complex society. For example, it does not account for social and economic inequalities, which have been recognized as important drivers of socio-ecological dynamics (Motesharrei

et al., 2016). Social and economic inequalities push the system away from a sustainable human-nature equilibrium (Cumming and von Cramon-Taubadel, 2018), thus would likely have a amplifying effect on the results. Additionally, the logistic model we use to describe human population dynamics is heuristic and does not reflect the actual mechanisms responsible for variations in human fertility and mortality (Mote et al., 2020). Lastly, we have assumed that humans cannot adapt to environmental degradation by changing land use strategies or fertility and consumption behaviours over time. This is a major limitation, as adaptive strategies could potentially prevent the predicted population collapse. However, these simplifications do not reduce the pertinence of our results, as the current trends have the potential to cause a collapse, if habits go unchanged. Moreover, if humans succeed, through changes in cultural patterns, to avoid a drastic population reduction, it is very likely that the changes will be dramatic and involve, for example, a complete socio-economical restructuring (Cumming and Peterson, 2017). Hence, our results highlight that our current socio-ecological system might be heading towards dramatic changes, even though it is hard to predict the form they will take.

Conclusions

By exploring a continuum of land use strategies, our work differentiates from previous models of coupled human-land dynamics and shows the importance of quantifying agricultural expansion and intensification levels to assess sustainable land use strategies. We modelled agricultural land use planning along two dimensions: expansion, given by the population's conversion effort, and intensification. Expansion and intensification can act in synergy to increase landscape degradation, but there are also trade-offs between them. Agricultural expansion increases the stock of potential degraded land, while agricultural intensification can both speed and deepen agricultural land's degradation.

Our results show how increasing agricultural intensification leads to socio-ecological collapse when there is an insufficient reduction of the land conversion effort. Agri-

cultural intensification increases agricultural production, hence human population size, if consumption levels are kept equal. Population growth feeds back on the landscape's composition by further accelerating land conversion. Eventually, land degradation reduces resource production and causes the population to overshoot its carrying capacity and ultimately decline.

It could be argued that technological development has the potential to stave off collapse, however the impact of new technologies on the environment is ambiguous. Technology has the potential to increase production efficiency, but could also further decouple food production from nature by replacing ecosystem services with synthetic inputs. The cure-all technology argument neglects feedbacks between technology and human behaviour, as well as its underlying dependence on the environment. Future work will put a greater focus on the links between changes in technology and behaviour and its impact on socio-ecological dynamics.

Our model illustrates a potential mechanism that may explain the decline of past societies but also a possible future collapse. As the global human population is projected to keep growing in the coming decades adapted agriculture management will become more important and reduce the potential risks of future socio-ecological collapse. Our model points to agriculture intensification as a possible solution, however it is imperative that this is not in combination with expansion. However, we also stress that determining the limits to agricultural expansion that are necessary to achieve sustainability is not a trivial task. Hence precautionary land use planning should be accompanied by changes in social norms, such as a reduction of consumption to increase the likelihood of a sustainable future.

By modelling the bi-directional feedbacks between human demography and land use, we have shown how misguided or uninformed agricultural land use planning can lead a socio-ecological system to collapse. This stresses the importance of informed land use planning to achieve sustainability. Through evidence based policy design, humans have the tools to modify precarious land use patterns and reduce the impact of agriculture on the environment, setting our socio-ecological system on a more sustainable path.

Acknowledgements

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Code accesibility

All the open-source software to reproduce our analysis and the associated plots is available at https://doi.org/10.5281/zenodo.3988256.

Chapter 2

Fragmentation feedback on decision-making undermines sustainability

Title of the scientific article:

Habitat percolation transition undermines sustainability in social-ecological agricultural landscapes [1]

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Abstract

Steady increases in human population size and resource consumption are driving rampant agricultural expansion and intensification. Habitat loss caused by agriculture puts the integrity of ecosystems at risk and threatens the persistence of human societies that rely on ecosystem services. We develop a spatially explicit model describing the coupled dynamics of an agricultural landscape and human population size to assess the effect of different land-use management strategies, defined by agricultural clustering and intensification, on the sustainability of the social-ecological system. We show how agricultural expansion can cause natural habitats to undergo a percolation transition leading to abrupt habitat fragmentation that feedbacks on human's decision making, aggravating landscape degradation. We found that agricultural intensification to spare land from conversion is a successful strategy only in highly natural landscapes, and that clustering agricultural land is the most effective measure to preserve large connected natural fragments, prevent severe fragmentation, and thus, enhance sustainability.

Introduction

In recent decades, the global human population has continued growing and so has the mean per capita food consumption (Barrett et al., 2020). The increased demand

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for resources has led to worsening environmental degradation, such that food security and nature preservation are paramount concerns for human societies worldwide. Both zero hunger and environmental conservation are among the United Nations' Sustainable Development Goals (UN, 2015). Furthermore, food security and nature are interdependent, as nature provides essential ecosystem services to agricultural systems (Power, 2010). Even though it has been signalled that ending hunger is a matter of resource accessibility more than resource availability (Chappell and LaValle, 2011; Tscharntke et al., 2012), it is widely assumed that increasing agricultural production is the key to achieving food security in the future (Chappell and LaValle, 2011). However, agriculture remains a leading driver of environmental degradation, therefore increasing agricultural production will undoubtedly come with an environmental cost (Kehoe et al., 2017). This raises questions about the trade-offs between the zero hunger and environmental conservation goals, as they may counteract each other. Achieving global food security while preserving the environment is thus one of this century's key sustainability challenges.

Increases in food production will require either agricultural expansion or intensification. Agricultural expansion relies on the cultivation of vaster areas of land to achieve greater food production, while agricultural intensification principally relies on greater synthetic inputs to increase production per unit area. Agricultural expansion constitutes today's primary threat to biodiversity conservation as it directly causes habitat loss and fragmentation (Tilman, 1999), but agricultural systems can also contribute to the conservation of biodiversity (Dudley and Alexander, 2017). Low-intensity, wildlife-friendly farming (Perfecto and Vandermeer, 2010; Chappell and LaValle, 2011) is one such method for combining food production and conservation. However, low-intensity agriculture requires vaster land surfaces to achieve the same production. The expansion of agricultural land could encroach on ecosystems that serve as habitats for wild species (Bengtsson et al., 2005; Perfecto and Vandermeer, 2010). Furthermore, it has been shown that the biodiversity in wildlife-friendly agricultural land is lower than in natural land, making it unclear whether low-intensity practices can compensate for changes in land use (Phalan et al., 2011b; Balmford et al., 2019). Rather than mixing agriculture with biodiversity conserva-

tion, agricultural intensification has been suggested as a sustainable solution to increase food production while sparing natural land from conversion. However, conventional intensification relies on substantial use of fertilizers, pesticides, artificial irrigation and machinery, all of which foster the degradation of the cultivated land as well as nearby habitats and freshwater systems by spillover (Tscharntke et al., 2012).

Without integral land use management policies at national and international scales or a clear consensus on the land sparing-sharing debate, the choice of expansion or intensification is based on food production and economic gains (Lambin and Meyfroidt, 2011; le Polain de Waroux et al., 2016). At present, the majority of land suitable for agricultural expansion is located in tropical regions (Byerlee et al., 2014). Thus tropical forests and grasslands in Africa, Asia and Latin America currently face rampant deforestation, putting at risk the integrity of some of the world's species-richest ecosystems. On all three continents, agricultural expansion and intensification are occurring simultaneously in response to the soaring global food demand and fluctuations in international markets. The devastating environmental consequences of such radical changes in land use are already present and are expected to worsen if nothing changes (Tölle et al., 2017; Ordway et al., 2017; Boers et al., 2017; Stoy, 2018; Staal et al., 2020; Ruiz-Vásquez et al., 2020; Baldassini and Paruelo, 2020).

Taubert et al. (2018) assessed the current state of forest cover across the Asian, African and Latin American tropics through an analysis of satellite images, and concluded that tropical forests may be close to a percolation transition (Aharony and Stauffer, 2003). A percolation transition occurs when progressive habitat loss causes an abrupt increase in landscape fragmentation if habitat amount drops below a certain threshold. In practice, this causes the disappearance of large-sized connected habitat fragments, which are replaced by many smaller ones. Percolation theory has been used in landscape ecology since the seminal work of Gardner et al. (1987) as a theoretical tool to predict critical thresholds and scales at which changes in landscape composition and structure affect ecosystem processes. The theory's best known result is the existence of a percolation threshold when a landscape's habitat

fraction is at 0.59, below which the landscape suddenly becomes highly fragmented if habitat is randomly removed. Further contributions developed novel landscape connectivity metrics (Keitt et al., 1997) and applied results from percolation theory to the study of animal dispersion (O'Neill et al., 1988; Gardner et al., 1989), biodiversity conservation (With, 1997; Boswell et al., 1998) and species distribution (He and Hubbell, 2003) in fragmented landscapes.

Habitat fragmentation may initially increase the flow of ecosystem services to human-transformed systems by expanding their edges with natural land fragments (Mitchell et al., 2015b). However, as habitat patches become smaller, more isolated and with a larger edge-to-area ratio, the deleterious effects of habitat fragmentation on ecosystem functioning grow, to the point where fragments become too small to provide ecosystem services to the surrounding area (Haddad et al., 2015, 2017). Long-term experiments have shown that fragmentation leads to the degradation of crucial ecosystem services for agricultural production such as nutrient retention and pollination, increases the vulnerability of natural systems and threatens their persistence (Haddad et al., 2015, 2017). When faced with a decline in agricultural production associated with a decrease in regulating and supporting services, land managers are likely to turn to cropland expansion to compensate their losses, causing further habitat loss. Alternatively they may attempt to increase yields via intensification, furthering the degradation of habitat quality. Current agricultural practices raise many sustainability concerns, especially considering that habitat loss can cause disproportionally large habitat fragmentation with deleterious consequences for ecosystem service provision, as the landscape undergoes a percolation transition.

Achieving food security while preserving the environment requires informed and careful land use policies and management. The large spatial and time scales at which landscape and social processes occur make it difficult to identify paths towards sustainability using empirical studies alone. Theoretical and modeling approaches provide valuable perspectives that shed light on the possible outcomes of alternative future scenarios for land use management and policy. Coupled human-nature dynamical models are of particular interest to address these questions as they explicitly take into account the bi-directional feedbacks between the environment and

human societies (Motesharrei et al., 2014; Balbi et al., 2020). Models that account for population dynamics (Lafuite et al., 2017, 2018; Cazalis et al., 2018; Henderson and Loreau, 2019, 2020; Bengochea Paz et al., 2020) are particularly suitable to study long-term dynamics, as changes in population size greatly affect societal pressures on the environment. However, within the current body of literature, there are no models accounting for human population dynamics and land dynamics that explicitly account for spatial structure.

The aim of the present work is to understand the implications of uninformed land-use management on the sustainability of social-ecological agricultural systems. We build a model coupling human population dynamics with spatially explicit land-cover dynamics to investigate the influence of different management practices in landscape structure and resource production. We use percolation theory to interpret the consequences of habitat loss on habitat fragmentation and more specifically on ecosystem service provision and agricultural production. Additionally, we illustrate how bidirectional feedbacks between natural and human systems can trigger naive decision-making in the wake of a habitat percolation transition that traps the system in a path of social-ecological collapse. Finally, we focus on agricultural intensification and spatial planning as potential measures to enhance the sustainability of agricultural landscapes. Furthermore, we study the likelihood of their success depending on the initial landscape composition. Our work sheds light on how to better design agricultural land-use management policies for conservation and sustainability purposes, as consumption demands and the human population continue to grow.

Model and Methods

Model overview

We formulate a spatially explicit stochastic model of land cover change coupled with human population dynamics. We model the landscape as a square periodic

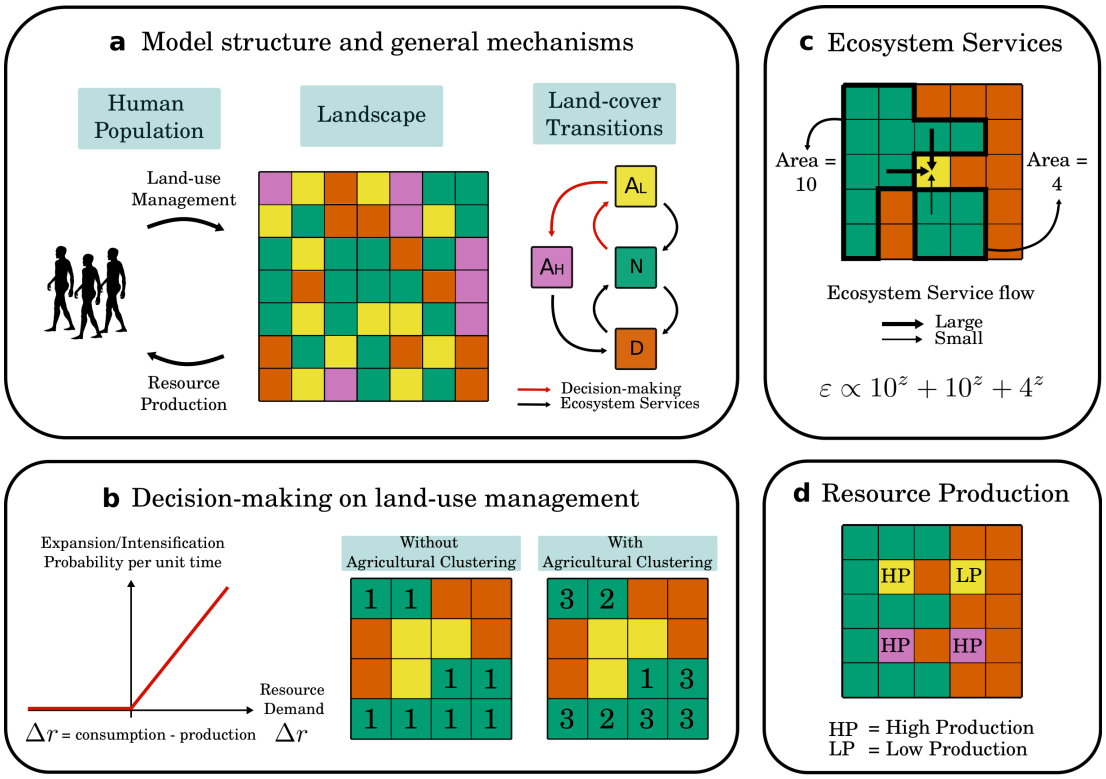

Figure 2.1: Conceptual diagram of the social-ecological model. a) The relation between the human sub-system and the landscape is done via resource production. The abundance or lack of resources drives human population dynamics and land-use management decision-making. The landscape is modelled as a square lattice where each cell is characterized by its land-cover type. We model four different land-cover types: natural ($\mathcal{N}$), degraded ($\mathcal{D}$), low-intensity agriculture ($\mathcal{A}_L$) and high-intensity agriculture ($\mathcal{A}_H$). The transitions between land-cover types are specified in the right panel where the colour of the arrows represents whether the transition is spontaneous and driven by Ecosystem Service provision, or whether the transition is a direct consequence of human action. There are three kinds of spontaneous transitions: land recovery (degraded to natural), land degradation (natural to degraded) and fertility loss (agriculture to natural or degraded). There are two kinds of human-driven land-cover transitions: agricultural expansion (natural to low-intensity agriculture) and agricultural intensification (low-intensity agriculture to natural). b) When resource consumption is larger than resource production, the propensities of expansion or intensification transitions are linear functions of the population's demand for resources Δr. When resource production is larger than resource consumption expansion or intensification propensities are zero. In the central and right panels, we depict the role of agricultural clustering regarding where human-driven agricultural transitions occur. In this example, we consider an expansion transition and the numbers represent the order of preference of each cell. In the absence of clustering (central panel) every natural cell has the same probability of being converted to agriculture. In the presence of agricultural clustering (right panel) a cell a higher number of agricultural neighbours has a greater probability of being converted, leading agricultural land to be clustered in space. c) We depict the provision of ecosystem services from two natural fragments to an agricultural cell. Ecosystem services flow from the natural fragments to the agricultural cell via their shared borders. We count a contribution from each border of the agricultural cell in contact with a natural fragment. The magnitude of the flow is larger if it comes from larger natural fragments. d) Resource production is different between low-intensity and high-intensity cells. In low-intensity cells production is enhanced by Ecosystem Service provision whereas in high-intensity cells production is the same regardless of Ecosystem service provision. In the scenarios we explored, high-intensity cells invariably have a high production that can be matched by low-intensity cells when Ecosystem Service provision is high.

lattice where the state of each cell corresponds to its land-cover type: natural, degraded, low-intensity and high-intensity agriculture. Changes in land-cover can be either spontaneous, driven by ecosystem services, like the passive recovery of degraded areas; or caused by direct human management, like natural land conversion to agriculture. Human population is external to the landscape, and land-use decision-making is centralized in a single agent that manages the whole landscape in response to the population's demand for resources. Changes in human population density are driven by resource production in the landscape's agricultural areas. We provide a conceptual diagram of the model in Figure 2.1. Our work aims to identify sustainable land-use management practices through the study of the impact of agricultural intensification and the spatial configuration of agricultural land on coupled human-land dynamics.

In what follows, all the equations and mathematical expressions for the transition propensities are presented in their non-dimensional form. We provide the details of the full derivation of the equations and the non-dimensionalization in Appendix 2.A.

Measure of ecosystem services provision

Ecosystem services are described by how their supply scales with the area of natural fragments and how they flow to neighboring cells. Empirical evidence shows that ecosystem service supply scales non-linearly with natural area (Barbier et al., 2008) and although the shape of the relationship depends on the service considered (Dobson et al., 2006), the function is frequently described as saturating (Mitchell et al., 2015a) or concave-down based on the Biodiversity-Ecosystem Function litterature (Loreau, 2000, 2001; Hooper et al., 2005). In this study we assume that the magnitude of ecosystem services provided by a natural land fragment is a sub-linear power-law function of the fragment's area (see Appendix 2.B for the choice of the exponent value). Assuming that the flow of ecosystem services is limited to the closest neighbors of a natural cell yields the following expression for the total amount

of service provision ε_i in cell i

$$\varepsilon_i = \frac{1}{4} \sum_{j \in \mathcal{N}_i} a_j^z \tag{2.1}$$

where the sum is carried over all the natural cells $\mathcal{N}_i$ in the neighbourhood of cell i, and a_j represents the relative area of the natural fragment to which cell j belongs. $z < 1$ is the saturation exponent. We use a Von Neumann neighborhood and constrain the non-dimensional ecosystem services provision within the interval $[0, 1]$ using the $1/4$ normalization factor (see Appendix 2.A for details). Given the previous definition, $\varepsilon_i = 0$ when there are no natural cells in the neighbourhood of cell i, and $\varepsilon_i = 1$ when all the landscape is in a natural state.

Resource production

The total amount of resource perceived by the human population is the sum of the production per unit time of all agricultural cells in the landscape. To account for the contribution of ecosystem services to agriculture (Gallai et al., 2009; Power, 2010; Garibaldi et al., 2011; Dainese et al., 2019), we assume the productivity of low-intensity agricultural cells is a linear function of the ecosystem services they receive. On the contrary, we assume the productivity of high-intensity agricultural cells is constant and independent of ecosystem services provision. The equation for total resource production per unit time Y is

$$Y = \sum_{i \in \mathcal{A}_L} (y_0 + \varepsilon_i) + y_1 \sum_{i \in \mathcal{A}_H} 1, \tag{2.2}$$

where the sums are over the sets of low-intensity $\mathcal{A}_L$ and high-intensity $\mathcal{A}_H$ agricultural cells and y_0 and y_1 are non-dimensional parameters representing the baseline productivity of low-intensity agriculture and high-intensity agriculture respectively (see Appendix 2.A for details).

Human population dynamics

We assume that human population density P follows deterministic logistic dynamics with a carrying capacity that evolves over time subject to changes in resource production (Bengochea Paz et al., 2020). We define the human carrying capacity as the maximum population density that can be supported for a given resource production Y and per capita consumption per unit time. Assuming a constant per capita consumption per unit time yields the following non-dimensional equation for the population density:

$$\frac{dP}{dt} = P\left(1 - \frac{P}{Y(t)}\right). \tag{2.3}$$

Note that the per capita consumption per unit time does not appear explicitly in the carrying capacity as it is encapsulated in the non-dimensionalization of the population density (see Appendix 2.A for details). Both P and Y are non-dimensional in equation 2.3, hence using Y alone as a carrying capacity is justified.

Agricultural land use management

We consider two land use transitions related to agriculture: expansion and intensification. Expansion is defined as the transition from a natural state to low-intensity agriculture and intensification is the transition from low-intensity to high-intensity agriculture. We assume that the expansion $\pi_E(i)$ and intensification $\pi_I(i)$ propensities at cell i grow linearly with the human population's demand for resources $\Delta r = P - Y$, equal to the difference between total resource consumption (P in its non-dimensional form) and production (Y in its non-dimensional form). The equations for expansion and intensification propensities, assuming that both occur with uniform probability in space, are:

$$\pi_E(i) = \begin{cases} \frac{1}{M|\mathcal{N}|}\,\sigma\,\Delta r\,(1-\alpha)\,, & \text{if } \Delta r > 0 \\ 0, & \text{otherwise.} \end{cases} \tag{2.4}$$

$$\pi_I(i) = \begin{cases} \frac{1}{M|\mathcal{A}_L|}\,\sigma\,\Delta r\,\alpha, & \text{if } \Delta r > 0 \\ 0, & \text{otherwise.} \end{cases} \tag{2.5}$$

$|\mathcal{N}|$ and $|\mathcal{A}_L|$ represent the total number of natural and low-intensity agricultural cells in the landscape respectively. Parameter $\alpha \in [0 : 1]$ controls the preference for agricultural intensification and σ represents the manager's responsiveness to the population's demand for resources. Larger σ values mean that given an equal resource demand, expansion or intensification occurs more rapidly on average. M is a normalization factor to ensure that the sum of the expansion and intensification propensities is always equal to $\sigma\Delta r$.

To examine the role of the spatial configuration of agricultural land, we introduced a clustering parameter ω that controls the likelihood of aggregating agricultural cells of identical type together. Larger ω values increase the probability of converting natural cells in the neighborhood of low-intensity agricultural cells and to intensify low-intensity cells in the neighborhood of high-intensity ones. The larger the number of neighbours, the most probable the transition (see Appendix 2.A for details on the formalization). This results in landscapes where agricultural land is aggregated when $\omega > 0$ and in a uniform spatial distribution of agricultural land when $\omega = 0$.

Loss of agricultural land

We consider fertility loss due to soil erosion as the leading driving factor of agricultural land degradation (Pimentel, 2006). Urban expansion over fertile agricultural land remains also a significant cause of current cropland loss, however we do not account for this mechanism since we do not model human settlements in a spatially

explicit way. We assume the average time to fertility loss is a function of the amount of ecosystem services an agricultural cell receives. A large amount of ecosystem services contributes to maintain fertility over longer periods of time. The propensity $\pi_L(i)$ of a fertility loss transition in agricultural cell i is given by:

$$\pi_L(i) = \rho_L \ (1 - \varepsilon_i) \tag{2.6}$$

where ρ_L is the sensitivity of fertility loss to ecosystem services provision and represents the decrease in the rate per unit of ecosystem service of the fertility loss propensity. The time required for old agricultural land to undergo natural succession and return to pre-agricultural conditions depends on the magnitude of land degradation and recovery times, which can vary from a decade to a century in the absence of active restoration (Cramer et al., 2008; Yang et al., 2020). To account for this difference, in a simple way, and given that intensification has greater impact on the soil, we assume that as a result of the fertility loss transition, low-intensity agricultural cells transition back to a natural state, whereas high-intensity cells transition to a degraded state.

Passive land recovery and degradation

We call land recovery (degradation) the transition from a degraded (natural) to a natural (degraded) state without human intervention. Land recovery represents the recolonization of a degraded cell by species present in neighboring natural cells that ultimately restore ecosystem functioning in the degraded cell. Land degradation represents the loss of species and ecosystem functioning in a natural cell due to increasing isolation from other natural cells. We assume that the propensity of a recovery (degradation) transition grows (diminishes) with ecosystem services provision (Cramer et al., 2008). The land recovery $\pi_R(i)$ and degradation $\pi_D(i)$ propensities in cell i are:

$$\pi_R(i) = \rho_R \, \varepsilon_i \tag{2.7}$$

$$\pi_D(i) = \rho_D \, (1 - \varepsilon_i) \tag{2.8}$$

where ρ_R and ρ_D are land recovery and land degradation sensitivities to ecosystem services provision, respectively. Passive recovery and degradation transitions allow for the propagation or the containment of human induced perturbations on the landscape.

Computational implementation and numerical experiments

We simulate the social-ecological dynamics in continuous time using Gillespie's (1977) Stochastic Simulation Algorithm coupled with a Runge-Kutta 4 solver for the population density differential equation (see Appendix 2.C for details and pseudo-code). By individually simulating every land-cover transition, Gillespie's algorithm generates exact realizations of our stochastic model that are solutions of the model's Master Equation. This approach presents the advantage of improving in accuracy since no approximation is made during the simulation of landscape dynamics. The size of the landscape lattice is 40x40 cells (1600 pixels) and border conditions are periodic to avoid border effects. Model runs were replicated to account for model stochasticity. All the code is open access and released in the repository https://doi.org/10.5281/zenodo.4905944.

Through a set of numerical experiments, we aim to characterize and understand how different land-use management strategies affect the long-term sustainability of the social-ecological system. To that aim we structured the Results section in 4 subsections. First, we focus on the effects of agricultural intensification and responsiveness to resource demand on the sustainability of the social-ecological system. Second, we provide an explanation of social-ecological collapses based on feedbacks between landscape fragmentation and decision-making. Third, we show that clus-

tering agricultural land to preserve landscape connectivity can prevent collapses. Fourth, we demonstrate how the success of land-use management strategies is subject to the initial landscape configuration.

We obtained the results presented hereafter by initializing the landscape in a lowly managed state, i.e. by assuming 90% of natural land cover and 10% of agricultural land-cover distributed between low-intensity and high-intensity according to preference for intensification α and arranged in space according to the clustering parameter ω (with the exception of the results presented in Figure 2.5, where we make it explicit). The initial human population size was initialized at equilibrium with production. For the bifurcation diagrams in Figure 2.2 b & d and the heatmap of 2.5, simulation times where large enough to ensure our data points correspond to the system's long-term equilibrium (5000 non-dimensional time units). Insight on the effect of parameters that we do not explore in the main text can be found in Appendix 2.B, and a sensitivity analysis of the model in Appendix 2.D.

Parameter	Interpretation of the non-dimensional parameters	Values
z	Scaling exponent of ecosystem services provision with the area of a natural fragment	0.25
y_1	Yield of intense agriculture relative to the yield contribution of ecosystem services to low-intensity agriculture	1.2
y_0	Baseline yield of low-intensity wildlife friendly farming relative to the yield contribution of ecosystem services to low-intensity agriculture	0.2
α	Preference for agricultural intensification over agricultural expansion	$[0.0 - 1.0]$
ω	Clustering of agricultural land	$[0.0 - 10.0]$
σ	Responsiveness to resource demand: increase rate of the expansion and intensification propensities per unit of resource demand	$[1 - 100]$
ρ_L	Fertility loss's sensitivity to ecosystem services provision: decrease rate of the fertility loss propensity per unit of ecosystem services	0.02
ρ_R	Land recovery sensitivity to ecosystem services provision: increase rate of the land recovery propensity per unit of ecosystem services	0.2
ρ_D	Land degradation sensitivity to ecosystem services provision: decrease rate of the land degradation propensity per unit of ecosystem services	0.02

Table 2.1: Description of the model's non-dimensional parameters and numerical values used for the simulations presented on this article. Details regarding the parameter values can be found in Appendix 2.B. Details on the impact of the parameters with fixed values on the social-ecological dynamics can be found in Appendix 2.B.

Results

Agricultural intensification: a double-edged sword

Starting from a lowly managed landscape, passive land cover fluctuations drive social-ecological dynamics as they constantly force the population density away from an equilibrium with resource production. For example, passive land degradation can diminish ecosystem services provision and resource production leading to either adjustment in population density or resource production via agricultural expansion. In the absence of agricultural intensification, the system results in collapse-recovery cycles or a sustainable steady state depending on the manager's responsiveness to population's demand for resources (Figure 2.2a & b).

A crucial factor determining whether the social-ecological system collapses is the speed of human-driven land use changes relative to the speed of demographic changes, controlled by σ, the responsiveness to resource demand. If the responsiveness to resource demand is low, human population density adjusts to a lower resource level faster, on average, than agriculture expands to increase resource production. Constraining the growth of population density has a stabilizing effect on the system dynamics and leads to a sustainable state in the long-term (Figure 2.2b blue line). When the responsiveness to resource demand is high, resource scarcity is compensated by agricultural expansion, leading to sustained growth of both agricultural land and population density that precludes stability within the system. As a consequence, the social-ecological dynamics enter cycles of reversible collapses (Figure 2.2a & Figure 2.2b purple lines).

Introducing agricultural intensification results in the disappearance of reversible collapses (Figure 2.2d). A small area of intense agriculture is sufficient to prevent landscape recovery following a collapse, making the degradation irreversible (Figure 2.2c). In contrast, a bias (i.e., high preference) for intense agriculture results in greater resilience against increases in the responsiveness to resource demand (Figure 2.2d). In this case, intensification limits agricultural expansion and decouples re-

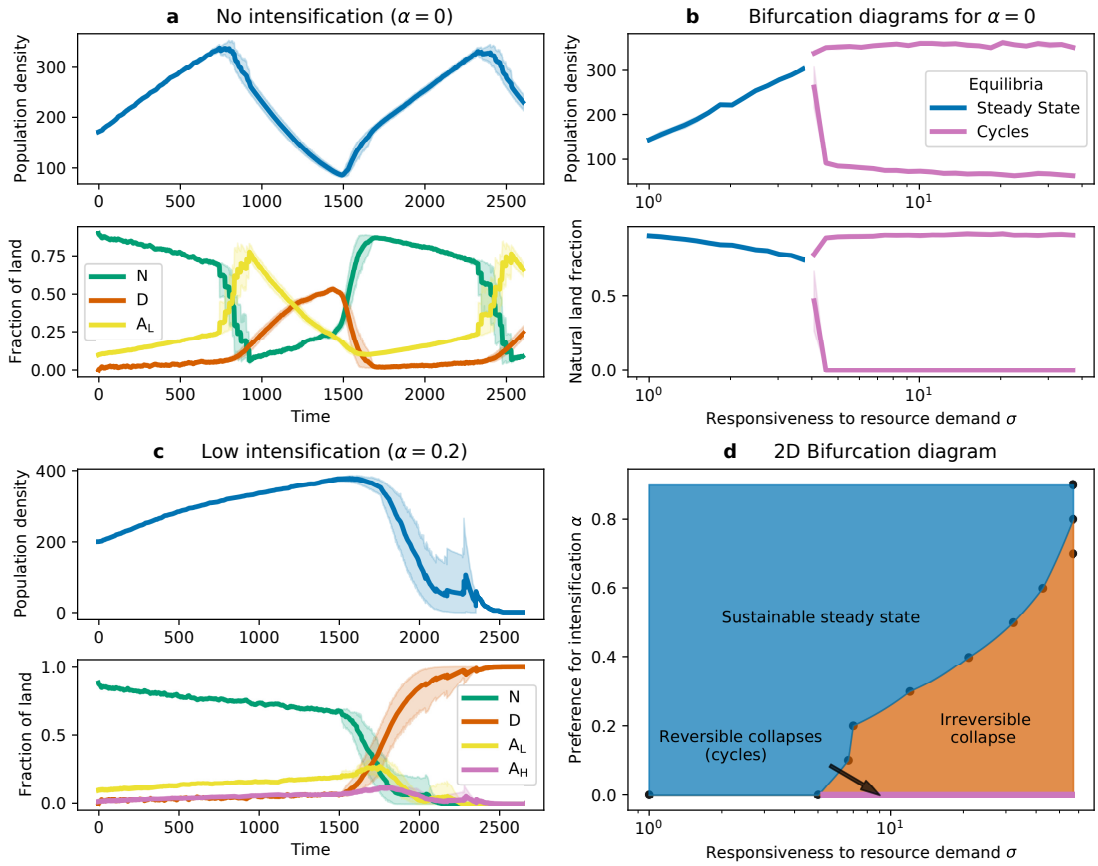

Figure 2.2: Effect of agricultural intensification on the temporal dynamics and the long-term states of the system. a) Collapse-recovery cycles in the absence of agricultural intensification ($\alpha = 0$) and clustering ($\omega = 0$) when the responsiveness to resource demand is high ($\sigma = 10$). Solid lines are the average of 40 replications and the shading is the 95% confidence interval. Values for the rest of the parameters are specified in Table 2.1. b) Bifurcation diagram for the responsiveness to resource demand σ in the absence of agricultural intensification ($\alpha = 0$) and clustering ($\omega = 0$). When the responsiveness to resource demand is low the long-term state of the system is a sustainable steady state. When it is high, the social-ecological system goes into collapse-recovery cycles. The purple lines depict the maximum and minimum values of the population density and the fraction of natural land during the oscillations. The σ line is initially explored by subdividing the range $\sigma \in [1 - 40]$ in 40 steps of equal size in logarithmic scale. To achieve better resolution close to the bifurcation point we added 10 points by re-sampling the range $\sigma \in]3.6 - 4.2]$ in steps of 0.06. Solid lines are the average of 10 replications at each of the 50 sampled σ values and the shading is the 95% confidence interval. A complement for this sub-figure where the bifurcation diagrams are plotted for several α values can be found in Appendix 2.E. c) Irreversible collapse dynamics of the social-ecological system in a scenario of low preference for intensification ($\alpha = 0.2$) and no clustering ($\omega = 0$). The responsiveness to resource demand is the same as in subfigure a). Solid lines are the average of 40 replications and the shades are the 95% confidence interval. d) Two-dimensional bifurcation diagram presenting the various types of social-ecological equilibria as a function of the preference for intensification and the responsiveness to resource demand. The cycles of collapse and recovery (purple line) only exist in the absence of intensification. Given our chosen initial conditions ($N = 0.9, A_L = 0.1$), a greater preference for intensification increases the system's resilience to increments in the responsiveness to resource demand. The α line was sampled by steps of 0.1 in the range $\alpha \in [0.0, 1.0]$. The frontier between the different equilibria was estimated using an interval halving method with 10 steps as stopping criterion for each α value (black dots in the figure). At each step of the method, the equilibria were estimated by averaging over 10 replications.

source production from ecosystem services provision which contributes to stabilizing the system in a sustainable state.

Collapse dynamics: percolation transition and habitat fragmentation

The abruptness of collapse is in striking contrast to the initial phase of gradual land conversion (Figure 2.2a & Figure 2.2c). This sudden shift in the social-ecological dynamics is explained by the natural habitat undergoing a percolation transition, wherein the loss of a few natural patches results in an abrupt increase of habitat fragmentation. In agreement with classic results from percolation theory, we observe that in the absence of agricultural clustering, the percolation transition occurs when the fraction of natural land is close to the threshold of 0.59 (Figure 2.3a).

The destruction of a small amount of habitat close to the percolation threshold ($N \simeq 0.59$) causes abrupt landscape fragmentation manifested in the sudden disappearance of a large natural fragment together with an increase in the number of disconnected natural patches (Figure 2.3a). The disappearance of large natural fragments results in a diminution of ecosystem services provision (Figure 2.3b) which translates into a marked reduction in resource production (Figure 2.3c). As a consequence, we observe a steep increase in the agricultural expansion propensity that leads to further habitat loss and fragmentation and worsens ecosystem services provision and therefore agricultural productivity. The social-ecological system is trapped in a positive feedback loop, where natural land is depleted to compensate for production losses, without success, more land is converted and the cycle continues.

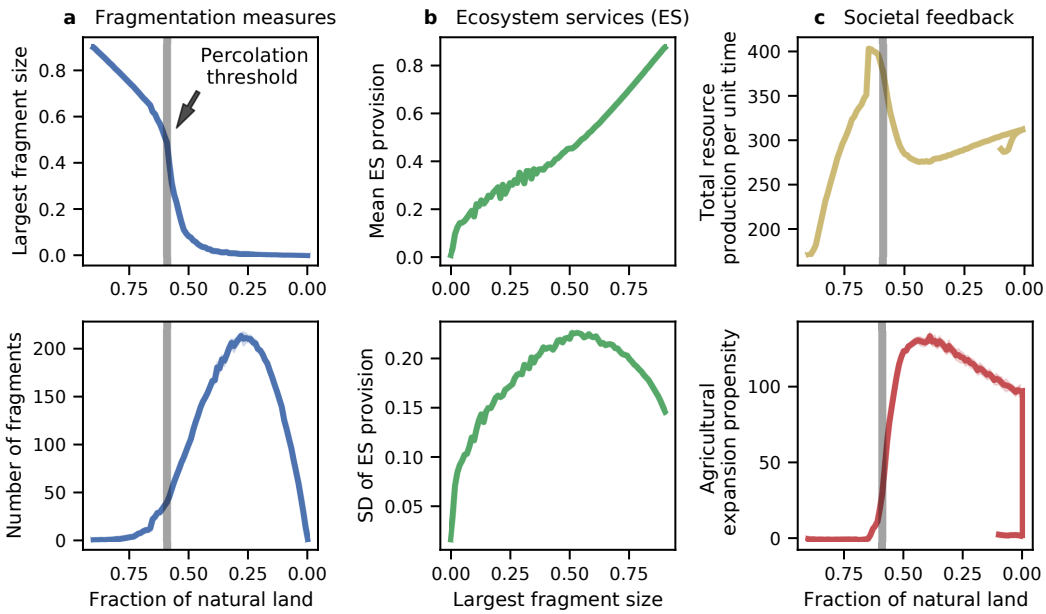

Figure 2.3: Signatures of a habitat percolation transition and the effects of habitat fragmentation on ecosystem services and land-use changes. a) Measures of habitat fragmentation. Both the size of the largest natural fragment in the landscape and the number of fragments present a highly non-linear relationship with the fraction of natural land. The abrupt decrease in the size of the largest natural fragments coincides with the abrupt increase in the number of fragments when the fraction of natural land reaches the percolation threshold ($N \simeq 0.59$, gray line in the plot). This is a signature of severe landscape fragmentation as a large number of small disconnected natural fragments emerge from the disappearance of a single large area of natural land. b) The average ecosystem services provision shows an almost linear dependence with the size of the largest natural fragment in the landscape. The spatial variance in ecosystem services provision increases as the size of the largest natural fragment decreases. The variance peaks when the size of the largest natural fragment is around half of the landscape size which coincides with the percolation transition (see panel a)). c) Agricultural production peaks just before the percolation transition and drops abruptly afterwards. This causes an explosive increase in the agricultural expansion propensity which results in rapid conversion of natural land to agriculture. Natural land conversion persists as long as agricultural production is below the desired level. The amount of cultivated area needed to satisfy resource demand increases with land conversion since habitat loss and fragmentation cause a systematic decrease in ecosystem services provision, thereby in agricultural productivity. When the fraction of natural land is below 0.5 agricultural expansion starts compensating the loss of ecosystem services and resource production gradually increases. This is however not enough to meet the population's demand, hence expansion continues. When the fraction of natural land reaches 0, there is not room for expansion anymore and population density starts decreasing gradually towards an equilibrium with resource production, hence the expansion propensity tends to 0. The data for each curve comes from the realized dynamics over 4000 non-dimensional time units of 40 model replications and the shades depict the 95% confidence interval. Parameter values are: $\alpha = 0$, $\omega = 0$, $\sigma = 10$. Values for the rest of the parameters are specified in Table 2.1.

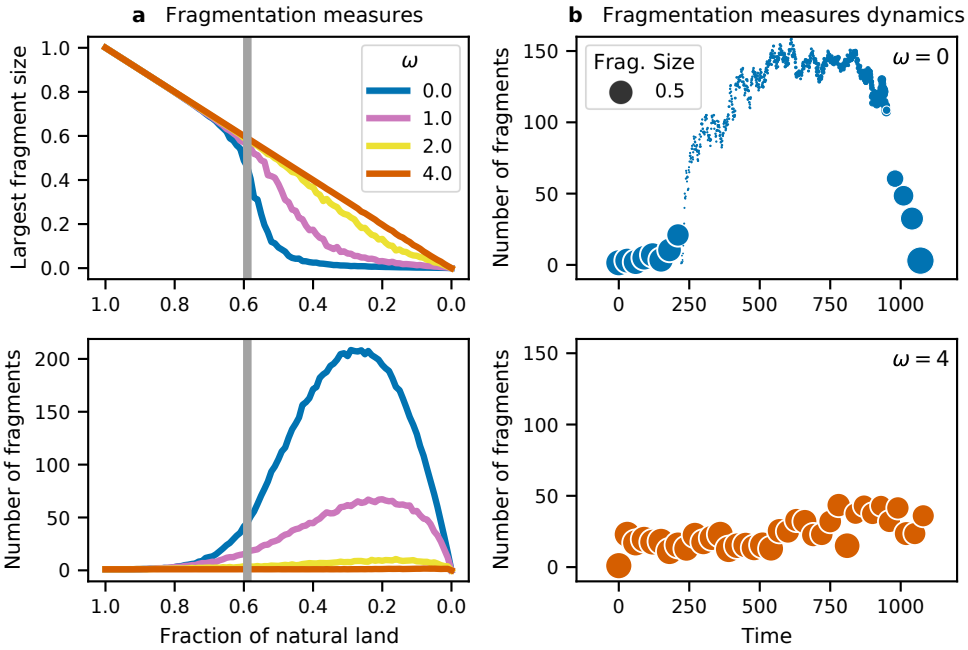

Figure 2.4: The effect of agricultural clustering on preserving landscape connectivity and the avoidance of a percolation transition. a) Fragmentation metrics as a function of the fraction of natural land for different values of agricultural clustering. Increasing agricultural clustering results in a linearization of the relationship between the size of the largest natural fragment and the fraction of natural land. This means that there is a decoupling between habitat loss and habitat fragmentation which results in the maintenance of natural land connectivity and the avoidance of a percolation transition. There are fewer disconnected natural patches as agricultural clustering increases, thus maintaining natural land connectivity. Contrary to Figure 2.3 a, the curves are not obtained by realized model dynamics but by calculating the fragmentation measures just after initializing the landscape at different levels of natural land fraction from 0.0 to 1.0 by steps of 0.01. There is, therefore, no information about model dynamics in these curves but exclusively about the relation between natural land area and fragmentation at different levels of clustering. Each curve is the average of 40 replications. b) Temporal changes in fragmentation metrics over time for no-clustering (top) and high-clustering (bottom). In the absence of agricultural clustering the changes in the size of the largest fragment and the number of fragments are surprisingly abrupt. The time required for landscape connectivity recovery is considerably greater than the time to widespread fragmentation. When agricultural clustering is high, the habitat percolation transition is avoided and both the size of the natural fragments and the number of fragments are preserved over time. Each data point is the average of 40 replications. Parameter values are: $\alpha = 0$, $\sigma = 10$. Values for the rest of the parameters are specified in Table 2.1.

Preventing landscape fragmentation by clustering agricultural land

Agricultural clustering decouples habitat loss from habitat fragmentation, thereby diminishing the effects of a percolation transition (Figure 2.4a). With adequate clustering the risk of a percolation transition can disappear altogether. When agricultural clustering is large, the linear relationship between the size of the largest natural fragment and the fraction of natural land reveals natural habitat connectivity is preserved upon habitat loss (Figure 2.4a), in agreement with percolation theory. In Figure 2.4b we depict the temporal changes of the fragmentation metrics to show the percolation transition is avoided if agricultural clustering is high.

Sustainable land-use management as a function of the landscape state

In lowly managed landscapes, both agricultural intensification and clustering stabilize social-ecological dynamics and lead to sustainable steady-states in the long term (Figure 2.2d & Figure 2.4a). The analysis of the effect of the landscape's initial configuration on management strategies shows that their success is highly dependent on the initial fraction of natural land (Figure 2.5). Greater preference for intense agriculture increases the need for natural land in the landscape to prevent collapses. Additionally, we observe that neither land-sharing (low intensification, low clustering) nor land-sparing types of strategy (high intensification, high clustering) are the most sustainable in highly managed landscapes, instead a combination of high clustering and low intensification is the best strategy (Figure 2.5).

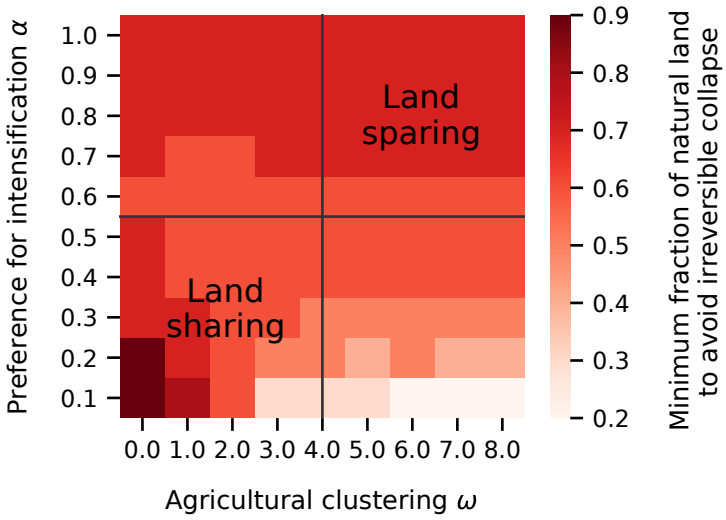

Figure 2.5: Suitability of different land-use management strategies as a function of the landscape's initial conditions. The colors show the minimum fraction of natural land needed to be certain that a given land-use management strategy will not lead to an irreversible collapse. This puts into perspective some of the aforementioned results, as it shows that the success of intensification strategies are highly dependent on the amount of natural land in the landscape. The figure shows that agricultural clustering is effective in increasing social-ecological resilience in highly managed landscapes but that intensification counteracts it (Land sparing square). More interestingly this suggests that neither pure land sharing nor land sparing are the most suitable strategies towards sustainability in highly managed landscapes. We sampled the preference for intensification line by steps of 0.1 and the agricultural clustering line by steps of 1.0. For each point in the management strategy plane (α, ω) we performed a set of simulations varying the initial fraction of natural land from 0.1 to 0.9 by steps of 0.1 and selected the lowest value at which out of 20 replications an irreversible collapse was not observed. The rest of the landscape was initialized in an agricultural state where the fraction of intense agriculture responds to the value of α. Parameter values: $\sigma = 10$ and values for the rest of the parameters are specified in Table 2.1.

Discussion

Study overview

Agricultural management lies at the heart of the sustainability debate (UN, 2015). Agricultural expansion and intensification have greatly increased food availability, keeping pace with growing resource demands in recent decades (Barrett et al., 2020). But these practices also deeply transform landscapes across the world and, by doing so, drive the loss and degradation of natural habitats (Kehoe et al., 2017). This has prompted society to question whether it is possible to promote food security and environmental conservation. We demonstrated how gradual agricultural expansion can push the landscape through a percolation transition which causes abrupt

landscape fragmentation and results in a diminution of ecosystem service provision followed by a substantial reduction of agricultural production. Most importantly, we showed how naive and uninformed management responses to the production drop (i.e., continuous conversion to agriculture without gains in yields) deepen landscape degradation and fail to compensate production losses. Our work stresses the importance of understanding social-ecological feedbacks to design better practices for managed ecosystems.

Fast agricultural responses to resource demand threaten sustainability

We approached land use management from a social-ecological perspective, modeling the likelihood of agricultural expansion and intensification as a function of a population's demand for resources. From this perspective, we showed that the prime factor determining whether the social-ecological system collapses is the speed of human-driven land use changes relative to the speed of demographic changes. When the management response to resource demand is slow compared to demographic timescales, population numbers adjust to resource availability before agriculture is expanded or intensified to increase production. The social response to an insufficient level of resources is, in this case, a reduction of the population's pressure on the environment. On the contrary, when there is an urgent response to resource demand compared to demographic timescales, small production drops are systematically replenished by further agricultural expansion and intensification. In this scenario, the population's response is to increase pressure on the environment which can result in a social-ecological collapse.

Reducing per capita consumption in response to a lack of resources is an alternative to reducing population numbers and is equally effective in terms of decreasing the human pressure on the environment. Due to its simplified nature, our model does not account for changes in consumption levels as a reaction to changes in resource availability. Modifying the model to account for these changes, however, would not

affect our principal findings since the effects of per capita consumption levels and population size on the environment are the same, and one variable can be substituted for the other. Our results stress that the path to sustainability relies on the society's ability to determine when an increasing societal pressure on the environment can lead to severe, and potentially irreversible, environmental degradation.

Social-ecological feedbacks make habitat fragmentation fuel habitat loss

Long-term experiments provide increasing evidence on the deleterious effects of fragmentation on biodiversity and ecosystem functioning (Haddad et al., 2015, 2017; Fletcher et al., 2018). Yet Fahrig (2017); Fahrig et al. (2019) claimed that such negative effects are not a direct result of fragmentation but instead confounded with those of habitat loss and that the effects of fragmentation on biodiversity are generally positive. Our modelling work reveals unexpected interactions between habitat loss and fragmentation. While fragmentation is inevitably caused by habitat loss, we show the opposite can also be true when societal responses to fragmentation fuel habitat conversion to agriculture. Concretely, in our model the reduction in fragments' area entailed by fragmentation after the percolation transition impairs ecosystem service provision (Bregman et al., 2014; Haddad et al., 2015) and thus agricultural production, resulting in vaster agricultural expansion to compensate for the productivity loss.

The magnitude of agricultural expansion in the aftermath of the percolation transition depends on the amplitude of the production drop. This drop depends on two factors: the scaling between ecosystem service supply and the area of natural fragments (Mitchell et al., 2014, 2015a), and the sensitivity of crop yields to ecosystem service provision. For the former, we show that the larger the scaling exponent (i.e. the closer z is to 1) the larger the production drop, and hence the strongest the drive to agricultural expansion (see Appendix 2.B). For the latter, we show that the stronger the dependence of yields on ecosystem services, the larger the produc-

tion drop (see Appendix 2.B). Although a thorough quantitative estimation of the contribution of different ecosystem services to agricultural production is currently lacking, substantial progress has been made on the quantification of some essential services, such as pest control (Dainese et al., 2019) and pollination (Garibaldi et al., 2011). The impact of these services on production varies with the type of crop, geographical regions and the type of agriculture (Gallai et al., 2009). For example, even though approximately 40% of total food crop production comes from animal pollinated crops globally (Power, 2010), cereal production is completely independent of animal pollination. These levels of variability and uncertainty stress the fact that the strength of potentially harmful social-ecological feedbacks is hard to predict and needs to be addressed in a case-specific way.

Insights on the sparing vs. sharing debate

Green et al.'s (2005) seminal work on land sparing and land sharing provided a framework for research about the best land-use management strategies that jointly achieve sufficient resource production and conservation of the environment. Studies typically relied on empirical characterizations of the relation between agricultural yields and species abundance (or other environmental metrics: see Balmford et al. (2018)) to determine whether it is worthier to integrate low-intensity agriculture in the natural matrix, i.e. land-sharing (Perfecto and Vandermeer, 2010; Fahrig, 2017), or to separate the natural from high-intensity agricultural areas, i.e. land-sparing (Balmford et al., 2005; Phalan et al., 2011b; Balmford et al., 2019), or a mix between both (Arroyo-Rodríguez et al., 2020; Finch et al., 2020). With respect to landscape planning, agricultural clustering and intensification are, the core components that differentiate land-sharing from land-sparing strategies. Although we do not explicitly model the relationship between yield and species abundance, we borrow the land sparing-sharing framework to examine which combinations of agricultural clustering and intensification are more promising for the sustainability of a coupled human-land system.

In our model, preserving landscape connectivity to prevent a percolation transi-

tion offers a solution to avert the collapse. Our model suggests that keeping agricultural land aggregated to preserve landscape connectivity at lower fractions of natural land is efficient in preserving ecosystem service provision (Finch et al., 2021; Camba Sans et al., 2021) and stabilizing human-land dynamics to reach sustainability in the long term. Our model describes connectivity as touching neighboring cells, but in reality maintaining ecosystem functioning and services may not require direct contact between natural patches. We did not broaden our analysis to include ecosystem service flows beyond the closest neighbours nor to let connectivity be maintained beyond the closest neighbours. Flow and connectivity distances are dependent on both the ecosystem and the services considered, and varying them would provoke changes in the landscape percolation threshold. We expect ecosystem service provision to become more resilient to habitat loss and fragmentation when the spatial span of ecosystem functions and services increase.

Land sparing relies on the potential for intensive agriculture to diminish agricultural expansion, preventing habitat loss and thus fragmentation (Phalan et al., 2011b; Balmford et al., 2019). Our work shows that in lowly managed landscapes, a large prevalence of intensive agriculture contains agricultural expansion and prevents a landscape percolation transition, consequently leading the social-ecological system to a sustainable long-term state. The simplified nature of our decision-making modelling, which does not account for more complex economic or social motivations, means the results should be interpreted with caution. For instance, an empirical correlation between intensification and agricultural contraction has not been found (Tscharntke et al., 2012; Kremen, 2015), probably for social-economic reasons. In South America for example, the gains in efficiency that were brought by intensification increased economic profit and accelerated the expansion of intense soy-bean cropland (Gusso et al., 2017).

We show that the long-term success of land-sparing strategies is subject to the initial configuration of the landscape. Although in lowly managed landscapes land-sparing strategies are highly successful, we find they lead to social-ecological collapse in moderately to highly managed landscapes where more than 30% of the land is used for agriculture. This is due to the emergence of enormous degraded clus-

ters where there formerly was intensive agriculture, that cannot recover passively, which is in agreement with previously reported detrimental effects of intensive agriculture on ecosystems (Tilman, 1999; Dale and Polasky, 2007; Montgomery, 2007; Galloway et al., 2008; Chappell and LaValle, 2011; Tscharntke et al., 2012; Tsiafouli et al., 2015). Agro-ecological intensification that promotes crop productivity through ecosystem service management, however, has the potential to maintain spared natural landscapes by reducing environmental degradation from synthetic inputs (Bommarco et al., 2013; Garnett et al., 2013). Although our quantitative predictions are approximative, our model highlights the dangers of large-scale intensive agriculture and the importance of spatial scales in the sparing-sharing debate.

Conclusion and perspectives

Globalization is displacing croplands to the most pristine regions of the world, decoupling production sites, primarily in the Global South, from consumption ones, primarily in the Global North. This decoupling can delay or mask human-nature feedbacks, with the effect of prolonging over time unsustainable resource consumption at the expense of the world's wilderness. By showing how uninformed management decisions in response to habitat fragmentation can sharply accelerate habitat loss, our work stresses the importance of understanding the dynamical feedbacks between human societies and their natural environment to preserve the increasingly anthropised ecosystems of our world. The development of global land-use change models that account for migration and trade would constitute a significant step to respond to the challenges that globalization presents. We encourage further studies focusing on the interactions between ecological processes, management practices, cultural traits and economics to identify pathways to a sustainable future.

Acknowledgements

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Authorship

All authors contributed to the design of the study. DBP elaborated the model, performed and analyzed the simulations, and wrote the first draft of the manuscript. All authors contributed substantially to revision.

Data accessibility statement

Data available from the repository https://doi.org/10.5281/zenodo.4905944.

Appendix

2.A Derivation and non-dimensionalisation of model's equations

Here we follow the structure of the Model and Methods section of the main text and introduce greater details into the derivation of the equations and its non-dimensionalisation.

Ecosystem services provision

As explained in the main text, we formalize ecosystem services as a quantity generated by natural fragments and flowing to the rest of the landscape. We assume that the magnitude of ecosystem services generated by a fragment saturates with its area and choose to use a power-law function with exponent smaller than 1 to model the saturation. We further assume that the services flow from a natural patches to their closest neighbours defined in this model as the Von-Neumman neighbourhood in the lattice, i.e. the northern, eastern, southern and western cells. The amount of ecosystem services E_i that nature provides to landscape cell i is:

$$E_i = \sum_{j \in \mathcal{N}_i} E_0 \, A_j^z, \tag{2.9}$$

where $\mathcal{N}_i$ is the set of natural neighbours of cell i, E_0 is the prefactor of the saturation

function, A_j is the area of natural neighbour j of cell i and z is the saturation exponent. Given a landscape size, a cell receives the maximum possible amount of ecosystem services when the whole landscape is in a natural state. The maximum possible amount of ecosystem services provided to a cell E_{max} can then be written:

$$E_{max} = 4\, E_0\, A_T^z, \tag{2.10}$$

where A_T is the total area of the landscape and prefactor 4 comes from the sum of the contribution over the 4 neighbours. We non-dimensionalize the measure of ecosystem service provision by expressing as a fraction of the possible maximum. The non-dimensional ecosystem service provision ε for cell i is written:

$$\varepsilon_i = \frac{E_i}{E_{max}} = \frac{1}{4} \sum_{j \in \mathcal{N}_i} \left(\frac{A_j}{A_T} \right)^z = \frac{1}{4} \sum_{j \in \mathcal{N}_i} a_j^z, \tag{2.11}$$

where $a_j = A_j / A_T$ is the fraction of the landscape occupied by natural fragment j.

Production of agricultural resources

Total agricultural production per unit time in the landscape is obtained by summing over the production per unit time of every low-intense and high-intense agricultural cells. We assume that the low-intense agricultural production is positively affected by the amount of ecosystem services the agricultural cell receives, hence we write it as the sum of a baseline production and a contribution related to ecosystem service provision. On the contrary, we assume that resource production in high-intensity cells is fixed and completely independent of ecosystem service provision. We write total resource production $\mathcal{Y}$ as follows:

$$\mathcal{Y} = \sum_{i \in \mathcal{A}_L} (\mathcal{Y}_0 + Y_E E_i) + \sum_{i \in \mathcal{A}_H} \mathcal{Y}_1, \tag{2.12}$$

where $\mathcal{A}_L$ and $\mathcal{A}_H$ are the sets of low-intense and high-intense agricultural cells respectively, $\mathcal{Y}_0$ is the baseline production per unit time of low-intense agricultural cells, Y_E is the production per unit time per unit of received ecosystem service of low-intense agricultural cells and $\mathcal{Y}_1$ is the production per unit time of high-intensity agricultural cells. We non-dimensionalize total resource production by expressing it relative to the maximum possible contribution of ecosystem services to resource production: $Y_E E_{max}$. This yields the following expression for non-dimensional total resource production per unit time Y:

$$Y = \frac{\mathcal{Y}}{Y_E E_{max}} = \sum_{i \in \mathcal{A}_L} \left(\frac{\mathcal{Y}_0}{Y_E E_{max}} + \varepsilon_i \right) + \sum_{i \in \mathcal{A}_H} \frac{\mathcal{Y}_1}{Y_E E_{max}} = \sum_{i \in \mathcal{A}_L} (y_0 + \varepsilon_i) + \sum_{i \in \mathcal{A}_H} y_1, \tag{2.13}$$

where y_0 and y_1 are non-dimensional parameters that represent the baseline productions per unit time of low-intense and high-intense agriculture relative to the ecosystem services contribution respectively.

Differential equation for human population dynamics

We assume that Human population dynamics follows logistic growth with a time-evolving carrying capacity determined by the maximum population density that can be sustained given an amount of resource production $\mathcal{Y}$ and a per capita consumption c per unit time. The equation for Human population density P is then as follows:

$$\frac{dP}{dT} = rP \left(1 - \frac{cP}{\mathcal{Y}} \right), \tag{2.14}$$

where r is the growth rate of the population density when density is very low compared to the carrying capacity $\mathcal{Y}/c$. We choose to non-dimensionalize the population density by expressing it relative to the population density that can be sustained via the maximum possible contribution of ecosystem services in one low-intensity agricultural cell $Y_E E_{max}$. This means that the non-dimensional population density

p can be written $p = c\,P/(Y_E E_{max})$ and By replacing in equation 2.14 and non-dimensionalizing the time by expressing it relative to the inverse of the population growth rate r, we obtain the following non-dimensional equation for the human population dynamics:

$$\frac{dp}{dt} = p\left(1 - \frac{p}{Y}\right). \tag{2.15}$$

Propensities of land use/cover transitions

We derive the propensities of land use/cover transitions by defining the average time that it takes a given transition to occur given the system's state. Assuming that land use/cover transitions are a memory-less stochastic process, the propensity, here defined as the probability per unit time, of a transition can be written as the inverse of the expected time that one should wait to observe the transition given the state of the system. Hereafter we detail the reasoning behind the equations for the average expected waiting times before the transitions and show how we obtain the propensities' expressions.

Agricultural expansion and intensification

The expected time T_A before expansion or intensification of agriculture depends on the resource demand $\Delta R = cP - \mathcal{Y}$ experienced by the human population. The greater the resource demand, the faster Humans respond by enlarging agricultural activities via agricultural expansion or intensification. We further assume that this time tends to the infinity as the resource demand tends to zero, and that it tends to zero as the resource demand tends to the infinity. If the resource demand is negative, meaning that resource production exceeds the demand neither expansion nor intensification can occur, hence $T_A \to \inf$ when $\Delta R < 0$. Hereafter we will only write the equations in the case that $\Delta R > 0$. A parsimonious choice for a function

satisfying such demands is an inverse function of the resource demand:

$$T_A = \tau_A \frac{1}{\Delta R} = \tau_A \frac{1}{cP - \mathcal{Y}}, \tag{2.16}$$

where τ_A is rate of decrease of the average time before the transition per unit of resource demand. Re-scaling the time by $1/r$ and replacing population density and total resource production by their expression in function of their non-dimensional equivalents we obtain the following non-dimensional equation for the average waiting time before agricultural expansion or intensification:

$$rT_A = r\tau_A \frac{1}{\Delta R} = \frac{r\tau_A}{Y_E E_{max}} \frac{1}{p - Y}, \tag{2.17}$$

The non-dimensional propensity π_A of agricultural expansion or intensification occurring somewhere in the landscape is then obtained by taking the inverse of equation 2.17:

$$\pi_A = \frac{Y_E E_{max}}{r\tau_A} (p - Y) = \sigma \Delta r, \tag{2.18}$$

where σ (non-dimensional) is the responsiveness to the population's demand for resources and represents the increase rate of expansion or intensification propensity per unit of resource demand, and Δr is the non-dimensional resource demand.

We assume that whether expansion or intensification is chosen depends on the value of parameter α which represents the preference for agricultural intensification and is the probability of choosing intensification over expansion if an agricultural land use transition is to occur. The expansion $\pi_E(i)$ and intensification $\pi_I(i)$ propensities in cell i assuming that both processes occur with uniform probability in space are then :

$$\pi_E(i) = \begin{cases} \frac{1}{M|\mathcal{N}|}\,\sigma\,\Delta r\,(1-\alpha), & \text{if } \Delta r > 0 \\ 0, & \text{otherwise.} \end{cases} \tag{2.19}$$

$$\pi_I(i) = \begin{cases} \frac{1}{M|\mathcal{A}_L|}\,\sigma\,\Delta r\,\alpha, & \text{if } \Delta r > 0 \\ 0, & \text{otherwise.} \end{cases} \tag{2.20}$$

Where $|\mathcal{N}|$ denotes the cardinal i.e. the number of elements in the set of natural cells, and accordingly $|\mathcal{A}_L|$ the number of low-intensity agricultural cells. M is a normalization factor that guarantees that the sum of the expansion and intensification propensities, i.e. the propensity of either expanding or intensifying is always equal to $\sigma\Delta r$:

$$\pi_A = \sum_{i\in N} \pi_E(i) + \sum_{i\in\mathcal{A}_L} \pi_I(i) = \sigma\,\Delta r, \tag{2.21}$$

To study the influence of non-uniform spatial configurations of agriculture in the landscape on the social-ecological dynamics we introduce an agricultural clustering parameter ω which controls the likelihood of converting cells that are neighbours of other cells with the same type of land cover after the transition. For example, if $\omega > 0$ it is more likely to convert to agriculture a natural cell that is in the neighbourhood of a low-intensity agricultural cell than a natural cell surrounded by other natural cells, or high-intensity cells. The same applies to intensification: low-intensity agricultural cells close to high-intensity ones would be preferred. As ω increases the probability of converting cells close to already converted ones increases and the distribution of agricultural land becomes increasingly clustered by land use type. The dependence of the expansion or intensification propensities with respect to the clustering parameter ω is:

$$\pi_E(i) = \begin{cases} \frac{1}{M|\mathcal{N}|}\,\sigma\,\Delta r\,(1-\alpha)\,\left[\max(0.1, |\mathcal{A}_L(i)|)\right]^{\omega}, & \text{if } \Delta r > 0 \\ 0, & \text{otherwise.} \end{cases} \tag{2.22}$$

$$\pi_I(i) = \begin{cases} \frac{1}{M|\mathcal{A}_L|}\,\sigma\,\Delta r\,\alpha\,\left[\max(0.1, |\mathcal{A}_H(i)|)\right]^{\omega}, & \text{if } \Delta r > 0 \\ 0, & \text{otherwise.} \end{cases} \tag{2.23}$$

$$\tag{2.24}$$

where $|\mathcal{A}_L(i)|$ and $|\mathcal{A}_H(i)|$ are the number of low-intensity and high-intensity agricultural neighbours of cell i respectively. This formulation means that the likelihood of choosing a cell in the neighborhood of other cells of the same desired kind is $(10\#|\text{Neighbours}|)^{\omega}$ larger compared to a cell without any neighbour of the desired kind.

Fertility loss of agricultural land

We model the lost of agricultural cells are lost as a consequence of fertility loss (Pimentel, 2006) and assume that the time until fertility loss $T_L(i)$ of an agricultural cell i depends on the amount of ecosystem services that it perceives. We further assume that $T_L(i)$ tends to the infinity as E_i tends to E_{max} and that $T_L(i)$ is finite and positive when $E_i = 0$. A parsimonious choice for a function satisfying the previous demands is:

$$T_L(i) = \tau_L \frac{1}{E_{max} - E_i}, \tag{2.25}$$

where τ_L is the rate of increase of the average fertility loss time per unit of ecosystem service provision. As previously, we re-scale the times by $1/r$, and introduce the non-dimensional ecosystem services provision ε_i in the previous equation to obtain the

following non-dimensional equation:

$$rT_L(i) = \frac{r\tau_L}{E_{max}} \frac{1}{1-\varepsilon_i}, \tag{2.26}$$

Taking the inverse of the previous equation yields the following expression for the non-dimensional fertility loss propensity $\pi_L(i)$ in cell i:

$$\pi_L(i) = \frac{E_{max}}{r\tau_L}\left(1-\varepsilon_i\right) = \rho_L\left(1-\varepsilon_i\right), \tag{2.27}$$

where ρ_L (non-dimensional) is fertility loss's sensitivity to ecosystem service provision and represents the decrease rate of fertility loss propensity per unit of ecosystem service. The fertility loss process is identical for low-intensity and high-intensity agricultural cells, with the exception that low-intensity agricultural cells transition to a natural state and high-intensity ones transition to a degraded state when they lose fertility. The assumption behind this modelling choice, is that the time-scales at which an old low-intensity agricultural field goes back to a natural state is fast relative to other land cover transitions, hence we make the approximation of assuming that it happens instantaneously in the model.

Spontaneous land recovery and degradation

We also model the average time until land recovery T_R or degradation T_D in cell i as a function of the ecosystem services E_i that the cell receives. We assume that the dependence of land degradation average time on ecosystem service provision is identical as the one of fertility loss. Following the same steps as before we arrive to the following non-dimensional expression for the land degradation propensity $\pi_D(i)$ in cell i:

$$\pi_D(i) = \rho_D\left(1-\varepsilon_i\right), \tag{2.28}$$

where ρ_D (non-dimensional) is land degradation's sensitivity to ecosystem service provision and represents decrease rate of land degradation propensity per unit of ecosystem service.

For land recovery, we assume that $T_R(i)$ tends to the infinity when E_i tends to 0 and that it has a finite and positive value when $E_i = E_{max}$. A parsimonious choice for a function satisfying the previous demand is:

$$T_R(i) = \tau_R \frac{1}{E_i}, \tag{2.29}$$

where τ_R is the rate of decrease of the average land recovery time per unit of ecosystem service. By introducing the non-dimensional from of E_i and re-scaling the time by $1/r$ we obtain the following non-dimensional equation:

$$rT_R(i) = \frac{r\tau_R}{E_{max}} \frac{1}{\varepsilon_i}, \tag{2.30}$$

and taking the inverse we obtain the expression of the non-dimensional land recovery propensity $\pi_R(i)$ in cell i :

$$\pi_R(i) = \rho_R \varepsilon_i, \tag{2.31}$$

where ρ_R is land recovery's sensitivity to ecosystem service provision and it represents the increase rate of land recovery propensity per unit of ecosystem service.

2.B Estimation of parameter values

We searched the literature for orders of magnitude characterising the different processes we incorporated in the model to estimate the parameters' values. This approach yields parameter values that are not precise enough to provide highly confident quantitative predictions of future land-use and population changes. It does

however set reasonable scales for their value that allow us to explore different possible scenarios for the future and provide plausible qualitative predictions as well as mechanistic explanations of the processes leading to habitat loss and fragmentation that emerge from the bi-directional feedbacks between Humans and Nature. This approach is justified by the extreme difficulty of making precise estimations of this kind of parameters from empirical data. For example, data on the timescales of the recovery of degraded land is highly dependent on geographical locations and considered ecosystems and quantification of the relationship between the level of ecosystem service provision and the speed of recovery do not exist to our knowledge. What we can do to surpass this issue is to use parameter values that are in the order of magnitude of such processes. Below we detail the reasoning and provide the references that we used to estimate parameter values. We do not discuss neither the estimation of the per capita resource consumption or of agricultural yields as they only intervene in the non-dimensionalization of Human population density and do not have a qualitative influence in the dynamics of the non-dimensional model. The only information that can be gathered by their estimation is a quantitative prediction of changes in Human population density but that is not the goal of our study.

Estimation of the saturation exponent of ecosystem service provision with area z

The saturation exponent of ecosystem services provision with the area of natural fragments was set to $z = 1/4$ so that a ten-fold decrease in a fragment's area causes around of a two-fold decrease of ecosystem service provision. Decreasing the saturation exponent (i.e. increasing saturation) has the effect of containing the propagation of degraded land but enlarges variability in the dynamics (Figure 2.B-1). It also contains the negative effects of fragmentation in the wake of the percolation transition (Figure 2.B-2c) since large ecosystem service provision is maintained for relatively small sized natural fragments (Figure 2.B-2b). On the contrary, increasing the saturation exponent makes the system more vulnerable to habitat loss

and fragmentation, as ecosystem service provision decreases too fast with fragment area reaching almost a linear relationship between mean ecosystem service provision and the area of the largest natural fragment (Figure 2.B-2b). This has the effect of diminishing the likelihood of recoveries after social-ecological collapses (Figure 2.B-1).

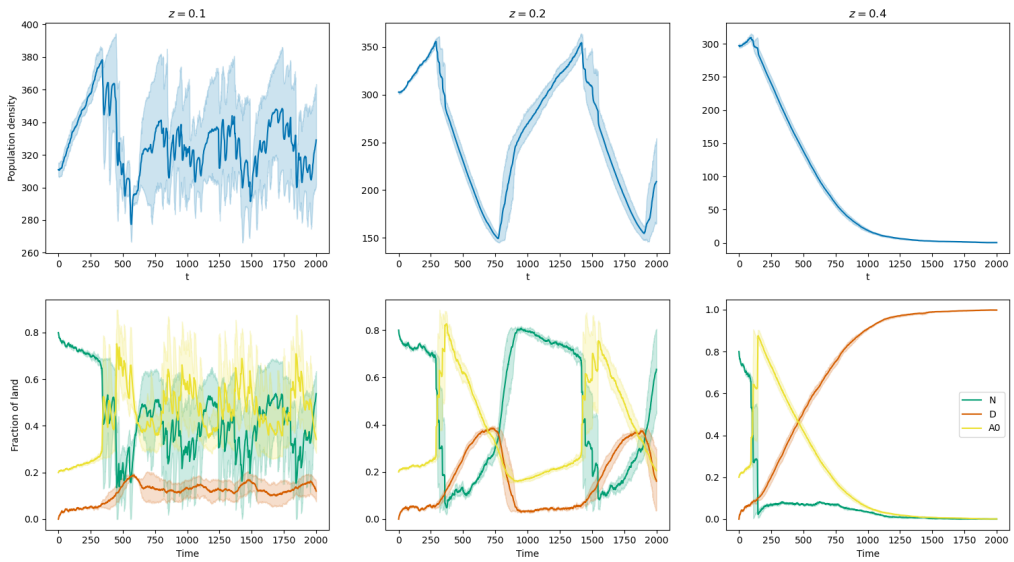

Figure 2.B-1: Social-ecological dynamics for different values of the ecosystem service saturation exponent. Solid lines are the mean of 5 replications and the shades represent the 95% confidence interval. Low values of the exponent (i.e. high saturation) help the containment of land degradation but dynamics become increasingly variable. As z increases in value the amplitude of the collapses increases. High values of the exponent (i.e. low saturation) render collapses irreversible. In these simulations: $a = 0$, $w = 0$, $\sigma = 10$, $a_0 = 0.2$ and the rest of the parameters are set to the value presented on the main text table.

Estimation of the low-intensity and high intensity baseline yields y_0 and y_1 (non-dimensional)

The baseline yield of low-intensity agriculture was estimated based on evidence from the literature on the contribution of natural pollination and pest control on agricultural yields (Bommarco et al., 2013; Bengtsson, 2015). Extrapolating to account for the contribution of other non-accounted ecosystem services we defined that 4/5 of the production in low-intensity agricultural patches depends on ecosystem service provision. Decreasing the dependence on ecosystem service provision (i.e. increasing

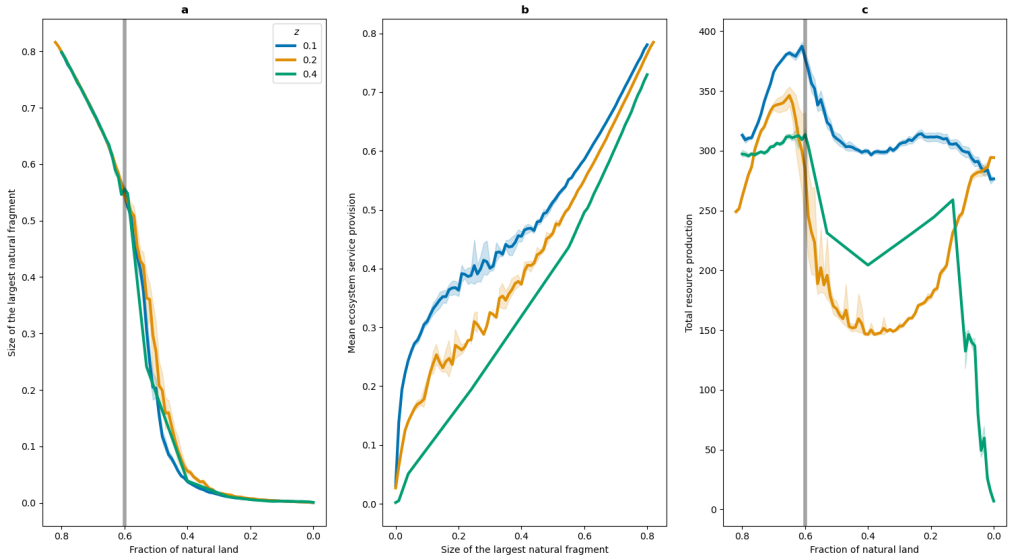

Figure 2.B-2: Landscape structure and consequences on ecosystem service provision and agricultural production for different values of the ecosystem service saturation exponent. Solid lines are the mean of 5 replications and the shades represent the 95% confidence interval. a) Size of the largest natural fragment as a function of the fraction of natural land. The large decrease on the size of the largest fragment at the percolation transition is the same no matter the value of z. b) Lower values of the saturation exponent (i.e. high saturation) helps preserving ecosystem service provision when giant natural fragments disappear. c) The amplitude of the production drop increases when the saturation exponent increases (i.e. lower saturation). In these simulations: $a = 0$, $w = 0$, $\sigma = 10$, $a_0 = 0.2$ and the rest of the parameters are set to the value presented on the main text table.

baseline production) contains agricultural expansion in the wake of the percolation transition (Figure 2.B-3), as less land is required for the same production in the absence of ecosystem services (Figure 2.B-4). However, the effects of the percolation transition are not attenuated as increasing the decoupling between agricultural yields and ecosystem service does not help in containing land degradation. Precise assessments of the contribution of ecosystem services on agricultural are needed to make confident assessments of the sustainability of agricultural landscapes in the presence of habitat loss and fragmentation. The yield of high-intensity agricultural patches was then chosen so that it equals the yield of low-intensity patches when ecosystem service provision is at its possible maximum (Chappell and LaValle, 2011).

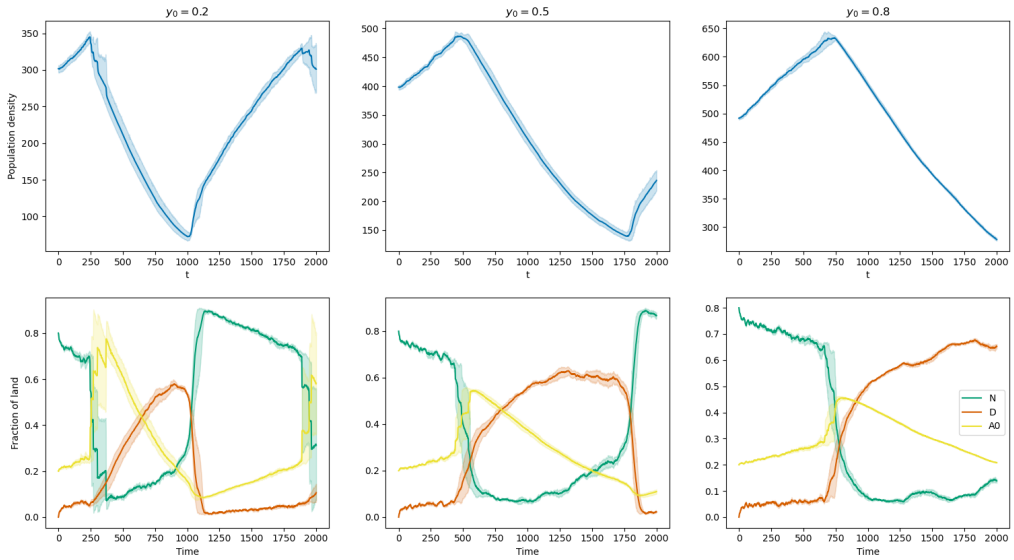

Figure 2.B-3: Social-ecological dynamics for different values of the baseline yield of low-intensity agriculture. Solid lines are the mean of 5 replications and the shades represent the 95% confidence interval. Increasing the baseline production decreases the dependency of agricultural production one ecosystem services and thus makes Humans response to the percolation transition less intense. Although agricultural expansion is accelerated, it doesn't need to explode as much to compensate production losses due to habitat fragmentation. This does not contain land degradation resulting in reversible collapses. The frequency of the collapse-recovery cycles decreases as the baseline production y_0 increases. In these simulations: $a = 0$, $w = 0$, $\sigma = 10$, $a_0 = 0.2$ and the rest of the parameters are set to the value presented on the main text table.

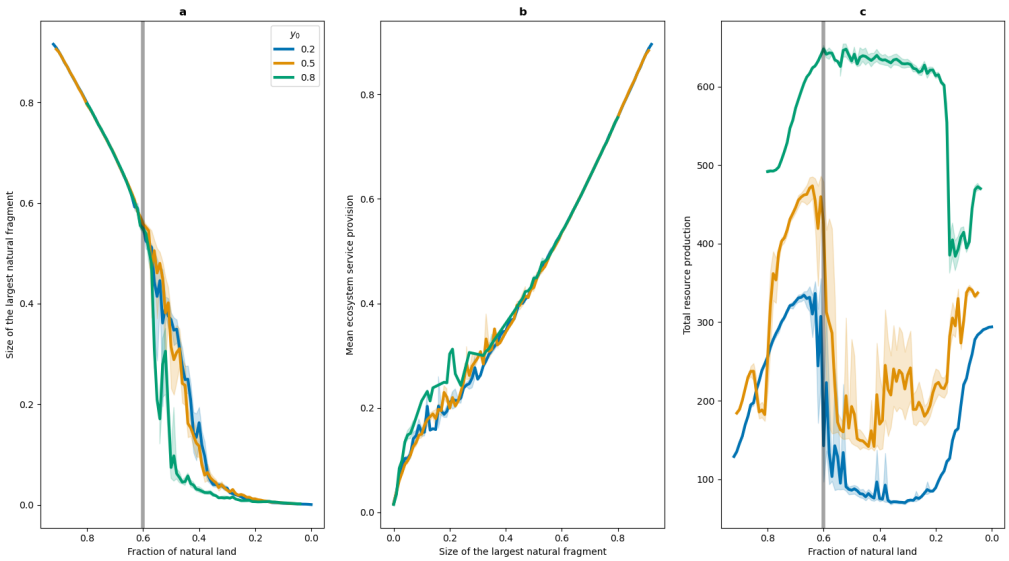

Figure 2.B-4: Landscape structure and consequences on ecosystem services provision and agricultural production for different values of the ecosystem service saturation exponent. Solid lines are the mean of 5 replications and the shades represent the 95% confidence interval. a) Size of the largest natural fragment as a function of the fraction of natural land. The large decrease on the size of the largest fragment at the percolation transition is the same no matter the value of z. b) Baseline production does not have an effect on the relationship between mean ecosystem service and the size of the largest natural fragment. c) Increasing baseline production of low-intensity agricultural land reduces its dependence on ecosystem service provision and thus increases the resilience of agricultural yields against the fragmentation occurring after the percolation transition. In these simulations: $a = 0$, $w = 0$, $\sigma = 10$, $a_0 = 0.2$ and the rest of the parameters are set to the value presented on the main text table.

Estimation of the population growth rate r (dimensional)

Parameter r is Human density growth rate when the density is very low compared to the carrying capacity. A precise estimation of r with empirical data would require data on the difference between per capita food supply and per capita resource consumption across time, as their ratio would be the Human carrying capacity (which changes over time). Knowledge of the Human carrying capacity across time would allow to fit a logistic function to population trends and obtain an estimation of parameter r. In standard datasets (FAOSTAT for example) per capita consumption data is actually data on food supply making the distinction between both impossible. To overcome this limitation we estimate that population density in the presence of an almost infinite amount of resources (i.e. population density very low compared to the carrying capacity) can double in a time ranging from 1 year (human pregnancy timescale) to 1 decade. The doubling time at very low population densities compared to the carrying capacity is $\ln(2)\,1/r \simeq 1/r$. In our simulations we assumed $1/r = 2$ which gives a doubling time around of 2 years.

Estimation of land use transitions sensitivity to ecosystem service provision ρ_R, ρ_D, ρ_L (non-dimensional)

We searched the literature for references in the characteristic timescales of degraded land's recovery. Based on Heydari et al. (2020); Meli et al. (2017), we made the estimation that degraded lands surrounded by good quality habitat can be recolonized in times of the order of the decade. Hence we assume land recovery's sensitivity to ecosystem services (non-dimensional) is $\rho_R \simeq 0.2$. This means that the average land recovery time is of 10 years when the ecosystem service provision is at the maximum possible level.

We placed ourselves in the optimistic scenario where in the absence of Humans a landscape composed by 10% of natural land and 90% of degraded land is able to fully recover in the long-term with probability equal to 1 (see Fig 2.B-5). A reasonable assumption for land degradation's sensitivity to ecosystem service provision $\rho_D \simeq$

0.02 meaning that the average degradation time at null ecosystem service provision is of 100 years.

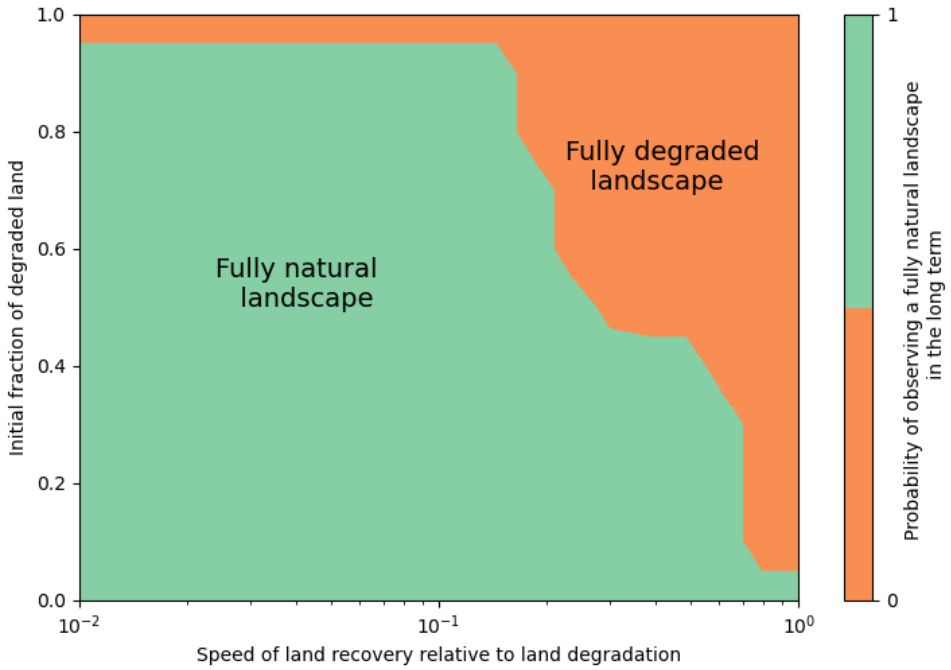

Figure 2.B-5: Final landscape state in the absence of Humans as a function of the initial fraction of degraded land and the relative speed of land recovery compared to land degradation respective to ecosystem service provision. Choosing the recovery time at maximum ecosystem service provision to be 10 times smaller than degradation time at null ecosystem service provision place the landscape in a scenario where even at a 90% of degradation is fully recovered in the long-term.

Finally, we assumed that fertility loss happens at the same timescales than degradation and chose to have an identical value for both parameters $\rho_D = \rho_L$. Large sensitivity of fertility loss with respect to ecosystem service provision shortens the average life time of agricultural cells and eventually agricultural patches do not persist enough time for them to provide resources to Humans thus causing population decrease or complete stagnation of population density growth (Figure 2.B-6). In the limit we placed ourselves, the average fertility loss is not a limitation to population growth in landscapes where natural land is very abundant.

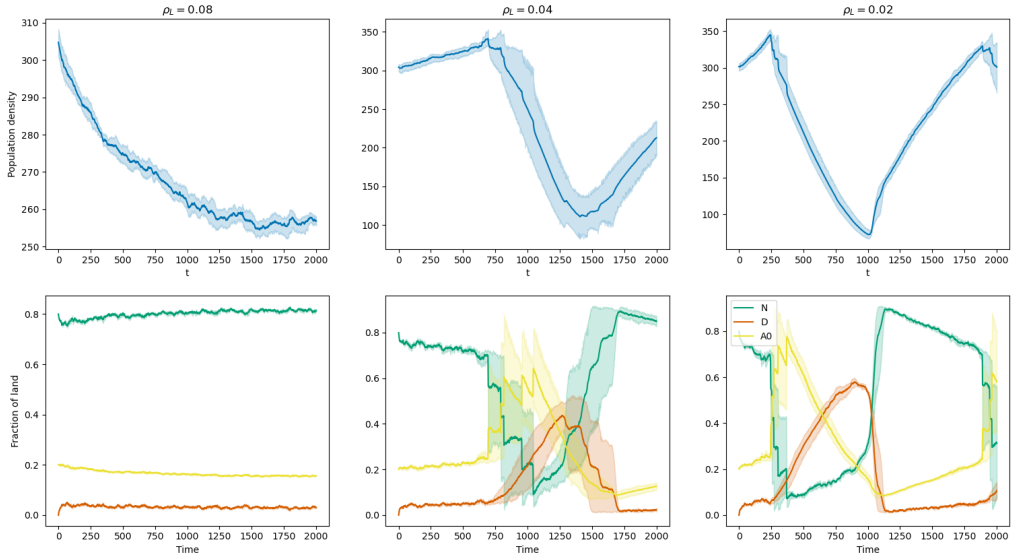

Figure 2.B-6: Social-ecological dynamics for different values of the sensitivity of fertility loss propensity per unit of ecosystem service. Solid lines are the mean of 5 replications and the shades represent the 95% confidence interval. Large sensitivity causes population decrease in a landscape with abundant natural land as the lifespan of agricultural cells is to short with respect to demographic processes making population density growth impossible. As the sensitivity increases, the percolation transition occurs before in time and with higher amplitude. The frequency of the collapse-recovery cycles decreases as the baseline production y_0 increases. In these simulations: $a = 0$, $w = 0$, $\sigma = 10$, $a_0 = 0.2$ and the rest of the parameters are set to the value presented on the main text table.

2.C Simulation algorithm

Our model has an hybrid structure where the deterministic dynamics of Human population density are coupled to the stochastic dynamics of a landscape modelled as a cellular automaton (i.e. with discrete spatialisation). Formulating landscape dynamics via the transition propensities between different types of land cover allow us to use the Stochastic Simulation Algorithm developed by (Gillespie, 1977) that yields exact realizations of the Stochastic Process (i.e. non-approximated solutions of the stochastic process master equation) in continuous time. In a nutshell, Gillespie's algorithm exploits the knowledge of the distribution probabilities of each transition to choose via drawing a random number the next time at which a transition occurs and the type of transition that occurs. This results in the simulation of every transition occurring as time in the simulation is always advanced to the time at which a transition occurs. This simulation scheme is in conflict with the numerical solving in discrete time of the population dynamics ODE. We developed an hybrid Stochastic Simulation Algorithm to deal with this conflict. In the hybrid version, the population dynamics ODE is solved at fixed time-steps, but all the transitions occurring between these time-steps are simulated. This is done by comparing each time the Gillespie time-step (which is the time until the next transition) and the demography time-step to assess what occurs first. When the Gillespie time-step is larger, population density is adjusted and in the opposite case the transition is simulated. Pseudo-code for the hybrid simulation algorithm is provided below in Algorithm 1.

2.D Sensitivity Analysis

We performed the model's exploration with OpenMole platform [2]. We carried on a Morris Sensitivity Analysis to determine the relative importance of different parameters on the model's outputs as well as the model robustness to changes in some parameters. The sensitivity analysis showed that the parameters that have

[2] https://openmole.org/

Algorithm 1 Hybrid Gillespie algorithm

```
Initialize population size, landscape and parameters;
Initialize simulation time T and time-step for population ODE dtp;
dt ← dtp
while t < T do
    Calculate the probability per unit time of each transition to occur on each patch;
    Generate a random number to calculate the time until next transition dτ;
    if dτ < dt then
        Generate a random number to choose which transition will occur;
        Change the landscape according to the chosen transition;
        t ← t + dτ;
        dt ← dt − dτ;
    if dτ ≥ dt then
        Solve the population size ODE
        t ← t + dt
        dt ← dt_p
```

the greatest influence on the model's outputs are the degree of agricultural clustering ω, the baseline yield of low-intensity agriculture y_0 and the fertility loss ρ_L and land recovery ρ_R sensitivities to ecosystem service provision. The importance of the influence of ρ_R and ρ_L was however trivial. On the one hand allowing very fast (very slow) land recovery drastically diminishes (increases) the likelihood of observing collapses. On the other hand and as discussed in Appendix 2.B, very fast fertility loss can prevent extremely unsustainable land-use management strategies from causing a collapses since the rapid loss of agricultural land prevents population growth. On the contrary, if fertility loss is very slow, agricultural land will accumulate and population grow enormously dramatically increasing the likelihood of a social-ecological collapse. The large importance of y_0 on the model outputs' was also expected since increasing y_0 has the role of both increasing low-intense agricultural production but also decoupling it from ecosystem service provision making it immune to habitat loss and fragmentation. The sensitivity analysis shows that increasing y_0 has positive effects both on human population size and the amount of natural land, as well as on containing degraded land. In terms of real-world interpretation this highlights the enormous importance that sustainable intensification, i.e. achieving high-yields with wildlife-friendly low-impact agriculture, will have on future sustainability (Bommarco et al., 2013). The importance of agricultural clus-

tering in the model's outputs was less trivial but is completely understood following the model exploration. Our work highlights the importance of maintaining large connected natural fragments in agricultural landscapes to ensure ecosystem service provisioning by avoiding an habitat percolation transition and following massive fragmentation. Increasing ω has the effect of concentrating habitat loss in smaller regions of the space allowing for the persistence of very large natural fragments in the landscape and contributing to sustainability.

The difference of the impact between these parameters and the rest is not however huge, and no single parameter completely dominates model behaviour (see Figure 2.D-1). As we showed in the main-text, the responsiveness to resource demand σ and the preference for agricultural intensification α can explain the appearance or disappearance of reversible collapses and sustainable steady-states. When we exclude ρ_R and ρ_L from the analysis (as their influence is trivial), the importance of σ and α becomes more apparent.

2.E Complement to Figure 2.2 of the main text

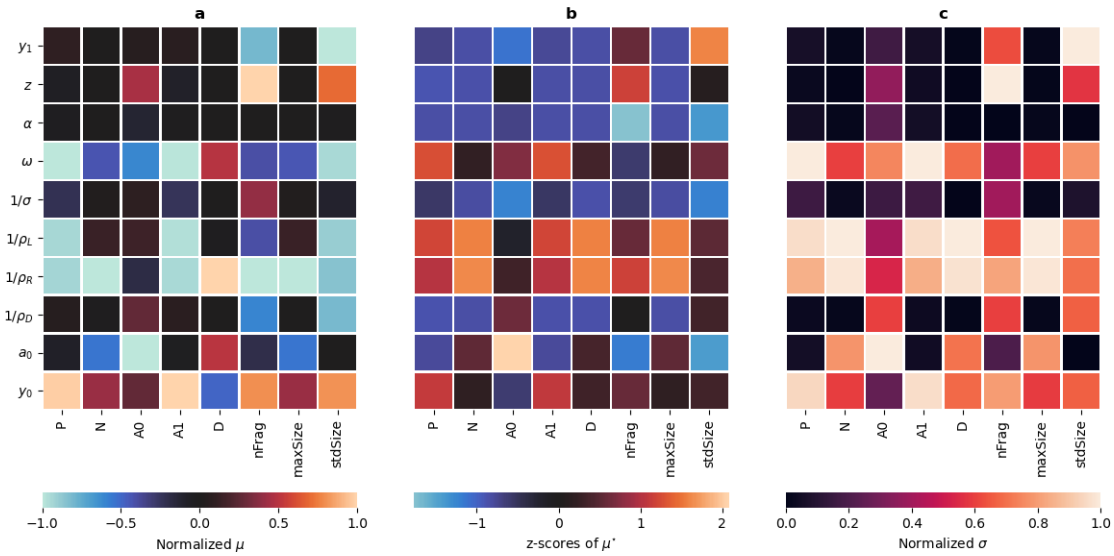

Figure 2.D-1: Sensitivity measures from the Morris sensitivity analysis. Each row corresponds to a non-dimensional model parameter and each column to a measured output: nFrag is the number of natural fragments, maxSize the size of the largest fragment and stdSize the standard deviation of the fragment sizes. a) Normalized average of the elementary effects of each parameter on each output. A positive value means that changes in the parameter value cause changes in the same direction for the outputs. A negative value means that the changes occur on the opposite direction. By construction this measure can have a value of zero if large effects on both directions are compensated. b) Z-score of the average of the absolute values of the elementary effects of changes of parameters on the model's outputs. This measure reflects the overall intensity of the effect of each parameter on the outputs of the model. Positive (negative) values mean that the parameter has an effect larger (smaller) than the mean of the effects. c) Normalized standard deviation of the elementary effects of changes in a model parameter on the outputs. This measure captures the level of non-linearity of each parameter on the outputs. A value of zero means that changes in a parameter have a linear effect on the output. The larger the value the more non-linear are the effects.

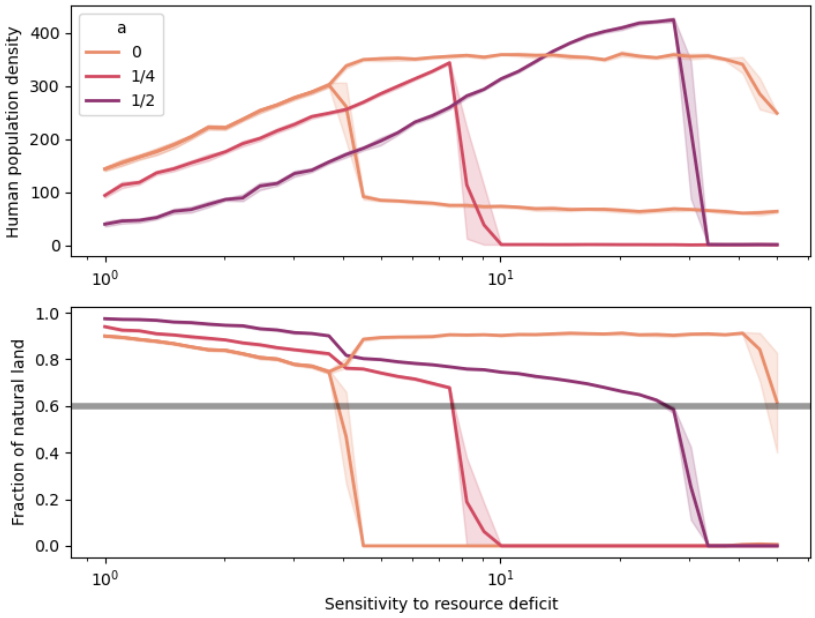

Figure 2.E-1: Bifurcation diagram for the human population density and the fraction of natural land as a function of control parameter σ the responsiveness to resource demand and for different values of the preference for agricultural intensification a. Solid lines are the mean of 5 replications and the shades represent the 95% confidence interval. The grey line in the bottom plot represents the percolation threshold for the natural fraction of land. Increasing the preference for intensification increases the resilience of the system with respect to the responsiveness to resource demand, but however makes the collapses irreversible. For $a = 0$ the high and low lines after the bifurcation ($\sigma \simeq 4$ represent the cycles highest and lowest values respectively. In these simulations: $a = 0$, $w = 0$, $a_0 = 0.1$ and the rest of the parameters are set to the value presented on the main text table.

Chapter 3

The interplay between management strategy and scale determines sustainability

Title of the scientific article:

The interplay between management scale and strategy determines sustainability in social-ecological agricultural systems [1]

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Abstract

The challenge of preserving nature while ensuring food security for a growing population has been addressed through a conceptual framework that proposes the segregation of high-intensity agriculture from natural land, i.e. land-sparing, and the integration of wildlife-friendly agriculture in the natural matrix, i.e. land-sharing, as two rival strategies that can succeed in preserving nature while satisfying growing resource demands. Although the advantages and disadvantages of each strategy have been widely debated, little attention has been given to the issue of spatial scales. We develop a model of human population dynamics and agricultural land-use management, in which a spatially explicit landscape is subdivided in multiple farms. Each farm is managed by independent agents that implement either a land-sparing or a land-sharing strategy at the farm-level. We explore the effect of reducing management scale on social-ecological dynamics, for multiple land-use management scenarios. We show that identical farm-level management strategies can lead to collapse or sustainability depending on management scale. Finally, we find that heterogeneity in the farms' land-use strategies leads to sustainable social-ecological landscapes across the entire range of management scales.

[1] In preparation

Introduction

Reconciling food production and nature preservation is one of the key sustainability challenges of the 21st century (UN, 2015). The continuous growth of human population numbers and resource consumption keeps increasing human demand for resources worldwide (Barrett et al., 2020). As a consequence, agricultural expansion and intensification are driving unprecedented habitat loss and fragmentation in some of the world's most pristine and biodiversity-rich regions (Taubert et al., 2018). Empirical evidence of and time-delayed negative consequences of habitat loss and fragmentation on ecosystem service provision (Haddad et al., 2015) raises questions about the sustainability of current agricultural practices, since agriculture itself relies on ecosystem services to be productive (Power, 2010). This is specially valid for smallholder agriculture, whose contribution elevates to more than 50% of global calories production (Samberg et al., 2016; Herrero et al., 2017; Ricciardi et al., 2021). Designing land-use management strategies that preserve the ecosystems and the services they provide is therefore of uttermost importance and urgency. Although recent empirical and theoretical work (Phalan, 2018; Perfecto and Vandermeer, 2010; Bengochea Paz et al., 2020) has advanced our understanding of the best management practices to achieve sustainable agricultural landscapes, little work has devoted explicit attention to management scales in assessing the suitability of management strategies.

The issue of spatial patterns and scales is central in ecology but transcends discplinary boundaries (Levin, 1992; Cumming et al., 2006; Chave, 2013). In managed landscapes, for example, social-ecological dynamics arising from the interplay between decision-making and ecological scales can determine landscape sustainability (Cumming et al., 2006, 2013; Cumming and Epstein, 2020). Agriculture transforms the structure of landscapes and leads to the emergence of diverse spatial patterns, which vary depending on management practices and scales. The effects of landscape patterns on ecological processes depend on the relation between their respective spatial scales (Cattarino et al., 2014). For example, identical fragmentation patterns will have different effects on the dispersal of species with different movement ranges

(Cattarino et al., 2016). Scaling up from species to ecosystem functions and services, identical fragmentation patterns could disrupt pollination services while preserving nutrient cycling. The sustainability of agricultural landscapes depends on societies' capacity of transforming land-cover without altering important landscape-level patterns that sustain ecosystem services provision. However, the application of identical spatial planning rules at the farm level leads to widely different patterns at the landscape level, if the landscape is managed by two large, or a thousand small farms. Thus spatial scales should be central in the design of land-use planning policies.

Ultimately, the spatial scale at which landscapes are managed depends on how the land is distributed among land-owners. This varies substantially across the world's regions, leading to remarkably diverse farm size distributions. For example, in Australia, New Zealand and South America, agricultural production is highly concentrated in farms larger than 200 hectares, while in Sub-Saharan Africa, South and East Asia it is concentrated in farms smaller than 20 hectares (Samberg et al., 2016; Herrero et al., 2017; Meyfroidt, 2017). Although sustainable landscape configurations might be identified, achieving them in practice is another issue. The design of land-use planning policies needs to consider the distribution of land-ownership, since identical directives at the farm scale can lead to vastly different outcomes at the landscape scale, depending on the farms size. Although cooperation between different land-owners sometimes occurs, making large-scale policies possible, it is not the most common practice. Furthermore, the existence of diverse farm-size distributions across the world makes it hard to propose universal land-use management directives. Thus management policies should be adapted to the scale at which decision-making is done in different places.

The land-sparing vs. land-sharing debate (Green et al., 2005; Balmford et al., 2005) provides a useful conceptual framework to examine the effects of management scales at the landscape level on management strategies. Land-sparing and land-sharing represent the two poles of a continuous strategy gradient spanning from the spatial segregation of high-intensity agriculture from natural land, i.e. sparing, to the spatial integration of low-intensity, wildlife-friendly agriculture on the natural matrix, i.e. sharing (Phalan, 2018). Landscape structure is at the core of the de-

bate, since different strategies along this gradient lead to different spatial patterns. More remarkably, applying these strategies at different scales can lead to completely different landscape configurations at the landscape scale. Land sparing at the whole landscape level would result in the separation of the land in two regions, one with high-intensity agriculture and the other with natural land. However, applying a land-sparing strategy at the farm level in the absence of coordination between different land-owners results in a more fragmented pattern at the scale of the landscape. For the land sparing strategy the area of agricultural clusters and spared natural fragments is highly dependent on farm-size distribution in the landscape. Diminishing farm size, thus management scale, eventually results on the sparing of fragments too small to ensure the viability of ecological populations, and thus the preservation of ecosystem services. Most studies deal with the scale issue in an implicit way, we know of no studies that apply the land-sharing/sparing to landscapes with different farm size distributions. The design of management practices to foster sustainable landscapes requires policies to account for the spatial scales at which they will be applied.

The aim of the present work is to explore the effects of management scale on land-use management strategies. We develop a spatially-explicit model of land-use management, in which the landscape is subdivided in different farms with independent managers. Farm managers respond to the resource demand of an external population and make decisions following either a land-sparing or land-sharing strategy. Through numerical experiments we examine how changes in the management and ecological scales affect the landscape-level patterns that emerge from identical farm-level management strategies. We show how the changes in landscape-level patterns affect ecosystem services provision and thus social-ecological dynamics. Thus, our results stress that the success of different management strategies on achieving sustainability in the long-term depends on management scales. Finally, we show that in landscapes where there is heterogeneity in farm-level strategies, the social-ecological system reaches a sustainable state for all the management scales. Our work highlights the relevance of spatial scales in designing better land-use management policies, and stresses the importance of landscape heterogeneity for sustain-

ability.

Model and Methods

Model Overview

We developed a spatially explicit model of land-use change in agricultural landscapes coupled with human population dynamics, to study the effect of the spatial scales of land-use decision-making on sustainability. We build on the modeling framework we presented in Chapter 2 to allow several landowners, with alternative management practices, to coexist in the same landscape. Landowners uniquely manage their own parcels, hereafter called farms, and do so according to one of two strategies: land-sharing, i.e. integrating low-intensity agriculture with natural land in the farm, or land-sparing, i.e. segregating high-intensity agriculture and natural land in the farm. The resources produced in the landscape are consumed by an external human population, whose size changes in response to changes in resource production. In turn, agricultural expansion in the landscape emerges as a response from landowners to the human population's demand for resources. Please find a graphical, conceptual description of the model in Figure 3.1. The focus of our work is to examine the effect of the interplay between mean farm size, landscape connectivity distances and land-use management strategies on the sustainability of the coupled human-land system. Hereafter, all the model equations, variables and parameters are presented in their non-dimensional form. For details on the non-dimensionalization please refer to Appendix 2.A and 3.A.

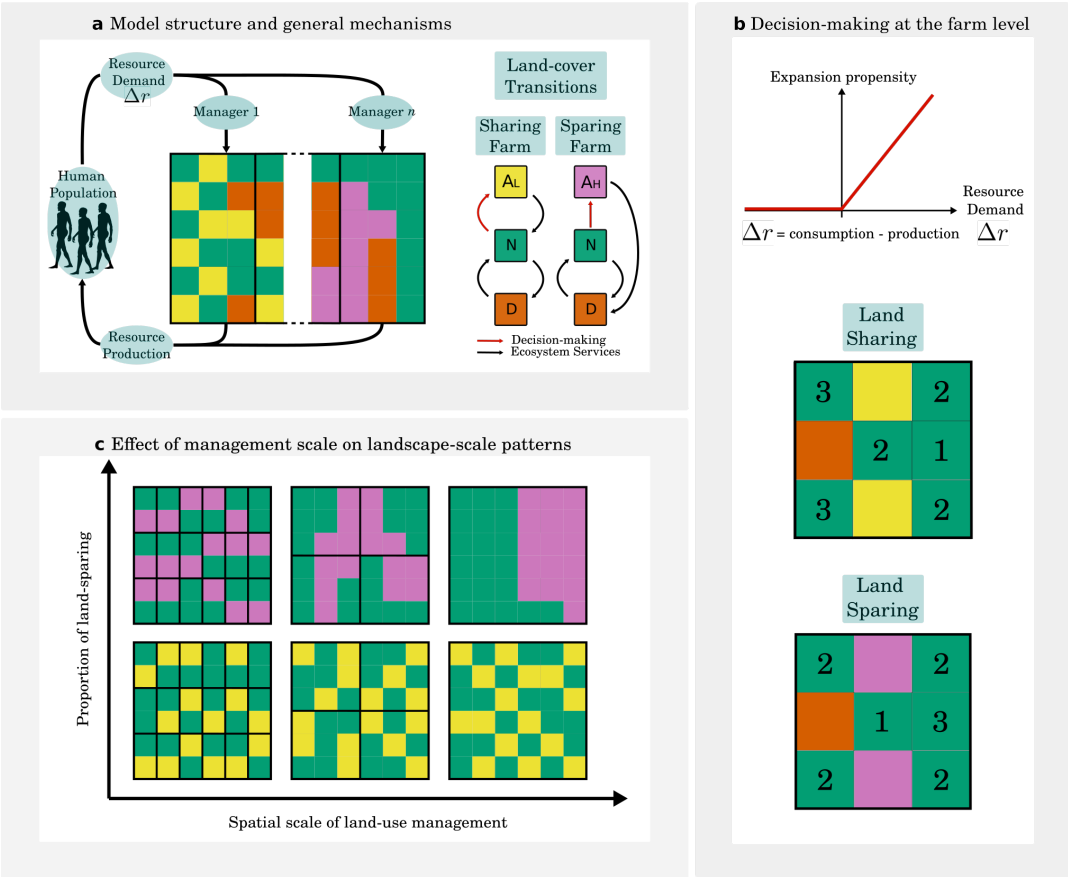

Figure 3.1: **Conceptual representation of the social-ecological model.** a) The landscape is subdivided in an arbitrary number of farms managed by independent agents. In each farm, the managers are associated with a land-sharing strategy or a land-sparing strategy. The management strategy remains fixed over time. Land-cover transitions are different in each type of farm. Specifically, in land-sharing farms, low-intensity agricultural patches transition to a natural state, while in land-sparing farms, high-intensity agricultural patches transition to a degraded state when they loose fertility. Land conversion to agriculture is the sole transition driven by human decision-making. The remaining land-cover transitions are spontaneous and depend on ecosystem services provision, thus ultimately on landscape structure. Agricultural expansion in the farms responds to the resource demand of an external population. In turn, the agricultural resources produced in the farms are consumed by this population. b) The propensity of converting natural land to agriculture grows linearly with the human population's demand for resources. If the demand for resources is negative, i.e. more is produced than it is consumed, agricultural expansion propensity is null. In the central and right panel we depict the spatial rules for land conversion in land-sharing and land-sparing farms. The numbers represent the order of preference in the location of future agricultural patches. While in the land-sharing farm the preferred location for a new agricultural patch is the where contact with natural land is maximized, in the land-sparing case the preferred location is next to other agricultural patches. c) Illustration of the effect of management scale on landscape-level patterns for land-sparing and land-sharing strategies applied at the farm level. The number of agricultural patches is kept constant. Given a constant landscape size, management scale is reduced by increasing the number of farms. Diminishing the management scale leads to more similar landscape-level patterns independently of the strategy. In the land-sparing case, diminishing the management scale clearly leads to more fragmented landscapes. Although we did not represent it, in this study we also consider mixed strategies, in which some farms do land-sparing and others land-sharing.

Landscape description

Overview

We model the landscape as a square 40x40 lattice with periodic border conditions. Each cell represents a land patch of 4 hectares, which corresponds to what is denominated a small farm in the literature. Refer to Appendix 3.B for more details on the choice of landscape cells' size. A cell's state is determined by its land-cover type: natural, degraded, low-intensity or high-intensity agriculture. Natural cells are responsible for the supply of ecosystem services in the landscape and agricultural cells produce the resources that are consumed by the human population. The landscape is subdivided into various farms with either a land-sharing or a land-sparing strategy.

Management and ecological spatial scales

We define the management scales via the mean farm area. To generate the farms in the landscape, we specify a number of farms and produce a Voronoi tessellation of the landscapes with that number of farms. We do this by distributing a number of seeds equal to the number of farms with uniform probability across the landscape and simulate a radial growth departing from the seeds. The result is a Voronoi tessellation of the landscape, where each Voronoi cell is a different farm. Note that this procedure cannot guarantee that all the farms are of exact same size, since the seeds are not distributed evenly across the landscape.

We introduce ecological spatial scales by letting cell neighbourhoods vary in size. We use extended Von Neumann neighbourhoods of range d_N, where d_N is the manhattan distance below which two cells are considered neighbours. In the model, the distance at which ecosystem services flow and the distance at which two natural cells are connected are equal to the connectivity distance d_N.

Measure of ecosystem services provision

We describe ecosystem services by how their supply scales with the area of natural fragments and how they flow to neighboring cells. We use the same formulation as in Chapter 2, and let the supply of ecosystem services be a sub-linear power-law function of a natural fragment's area and the flow to be constrained to the extended Von Neumman neighbourhood of the natural cells. The total amount of ecosystem service provision ε_i in cell i is

$$\varepsilon_i = \frac{1}{V} \sum_{j \in \mathcal{N}_i} a_j^z \tag{3.1}$$

where the sum is carried over all the natural cells $\mathcal{N}_i$ in the neighbourhood of cell i, $z < 1$ determines the shape of the relationship between area and ecosystem service supply and a_j represents the relative area of the natural fragment to which cell j belongs. We constrain the non-dimensional ecosystem service provision within the interval $[0, 1]$ using the $1/V$ normalization factor where V is the number of neighbours of cell i. The number of neighbours of the cell depends on the connectivity distance d_N. This formulation of ecosystem services provision implies that the flow the more neighbours there are the less each individual neighbour contributes to ecosystem services provision. This increases the stability of ecosystem services provision against the loss of an equal number of natural neighbours. However, losing an equal fraction of natural neighbours has the same negative effect on ecosystem services provision independently from the connectivity distance. Given the previous definition, $\varepsilon_i = 0$ when there are no natural cells in the neighbourhood of cell i, and $\varepsilon_i = 1$ when all the landscape is in a natural state.

Metric of landscape structure

We use Moran's I to characterize the landscape's spatial structure. Moran's I is a measure of spatial autocorrelation with values ranging from -1 to 1. A value of 1 means that different types of land-cover are completely segregated in space, while a

value of -1 means that they are completely integrated (checkerboard pattern). A value of 0 means that the spatial distribution of different land-cover types is perfectly random. We calculate the Moran's I based on whether a cell's land-cover is natural or not:

$$I = \frac{1}{V} \frac{\sum_{i,j \in \mathcal{L}} v_{ij} \, (l_{iN} - \bar{l})(l_{jN} - \bar{l})}{\sum_{i \in \mathcal{L}} (l_{iN} - \bar{l}^2)} \tag{3.2}$$

where V is the number of neighbours of the landscape's cells, L is the set of cells in the landscape, $v_i j$ equals one if cell i and j are neighbours and 0 otherwise, $l_i N$ equals 1 if cell i is natural and 0 otherwise, and $\bar{l}$ is the average value of the indicator $l_i N$. Although this metric provides some degree of information on the spatial distribution of agricultural land, the Moran's I we calculate is principally a measure of the spatial distribution of the landscape's natural land.

We also use the ratio between the largest connected natural fragment and the total amount of natural land in the landscape as an indicator of fragmentation 3.3. When the ratio is close to 1, this means that almost all the natural land in the landscape is concentrated in a single patch. When the ratio is close to 0, the natural land in the landscape is distributed among several isolated fragments, thus the landscape is more fragmented. The relationship between the ratio and the fraction of natural land in the landscape is highly non-linear. Specifically, there is a critical value of natural land fraction, called the percolation threshold, around which the size of the largest natural fragment relative to the total amount of natural land drops abruptly from 1 to 0. This is the manifestation of a habitat percolation transition. A natural habitat percolation transition is the abrupt emergence of large-scale landscape fragmentation following small losses of habitat when the natural land fraction is close to the percolation threshold. Refer to Chapter 2 of this thesis for a more thorough discussion of percolation transitions.

Resource production

The total amount of resource perceived by the human population is the sum of the production per unit time of all agricultural cells in the landscape. We use the same formulation as in Chapter 2 and assume that the productivity of low-intensity cells is a linear function of the ecosystem services they receive, while that of high-intensity agricultural cells is constant and independent of ecosystem service provision. This results in the following equation for total resource production per unit time

$$Y = \sum_{i \in \mathcal{A}_L} (1 - \beta + \beta \varepsilon_i) + \sum_{i \in \mathcal{A}_H} 1, \tag{3.3}$$

where the sums are over the sets of low-intensity $\mathcal{A}_L$ and high-intensity $\mathcal{A}_H$ agricultural cells and β is the share of low-intensity productivity that depends on ecosystem services provision. When $\beta = 0$, the productivity of low-intensity agricultural cells is independent from ecosystem services provision. When $\beta = 0.5$, half of the productivity comes from ecosystem services provision. This formulation assumes that when ecosystem service provision is at its maximum, agricultural productivity in low-intensity and high-intensity agricultural cells is identical. Refer to Appendix 3.A for details on the derivation and non-dimensionalization of the resource production equation.

Human population dynamics

We describe human population size by the number of households P and model human population dynamics as a stochastic process consisting in the joint realization of birth and death events. Building on Chapter 1 and Chapter 2 of this thesis, we model human population dynamics as a logistic growth process with carrying capacity equal to the ratio between total resource production and per capita resource consumption per unit time. The derivation of households' birth and deaths propensities following logistic growth yields the following expressions:

$$\text{Birth event}: \quad P \xrightarrow{1} 2P, \tag{3.4}$$

$$\text{Death event}: \quad P \xrightarrow{P/(K_0 Y)} \emptyset, \tag{3.5}$$

where K_0 is a non-dimensional parameter that encapsulates the per capita resource consumption and represents the number of households that can be sustained by a single high-intensity agricultural cell (see Appendix 3.A and 3.B for details on K_0). In this formulation, births occur with a constant propensity (1 in the present non-dimensionalization), and deaths occur with a propensity that depends on the ratio between human population size and human carrying capacity ($K_0 Y$ in the present non-dimensionalization). Therefore, when resource production exceeds resource consumption, deaths are less probable than births and the human population grows. On the contrary, when resource production falls short, deaths become more probable than births and human population declines. Refer to Appendix 3.A for the full derivation and non-dimensionalization of the human birth and death propensities.

Land-cover dynamics

Agricultural management

We associate either a land-sharing or a land-sparing type of strategy to each farm. In land-sharing farms, natural patches are converted to low-intensity agriculture in a manner that maximizes the contact of new agricultural cells with natural ones. This results in farms where low-intensity agricultural cells are perfectly integrated in the natural land. On the contrary, in land-sparing farms, natural patches are converted to high-intensity agriculture in a manner that aggregates agricultural land together. This results in farms where natural land is completely separated from agricultural land. Farm strategies are randomly distributed according to a parameter α that determines the fraction of farms that practice land sparing. Therefore, when $\alpha = 0$ all the farms practice land sharing, and when $\alpha = 1$ all farms practice land sparing.

We model the propensity of agricultural expansion π_E^i in farm i as a linear function of the population's demand for resources $\Delta r = P/K_0 - Y$

$$\pi_E^i = \frac{\sigma}{|\mathcal{F}|}\,\Delta r, \tag{3.6}$$

where σ represents farms' responsiveness to the population's demand for resources and $|\mathcal{F}|$ is the number of farms. Notice that since the responsiveness to resource demand is constant over farms, the expansion propensity is identical for every farm.

Once a farm is selected to host agricultural expansion, the exact natural cell to be converted is chosen accordingly to the farm's management strategy. In a land-sparing farm the conversion will occur with higher probability next to already cultivated land, while in a land-sharing farm conversion will occur with higher probability in cells with highly natural neighbourhoods. We model this process by introducing an affinity parameter ω that increases the probability of converting a cell with neighbours of the desired type. The conversion propensity $\pi_E^i(j)$ of cell j in farm i is:

$$\pi_E^i(j) = \frac{[\,\max(\,0.1, |\mathcal{L}(j)|\,)\,]^{\omega}}{\sum_{k\in\mathcal{N}_f(i)}[\,\max(\,0.1, |\mathcal{L}(k)|\,)\,]^{\omega}} \tag{3.7}$$

where $\mathcal{N}_f(i)$ is the set of natural cells in farm i and $|L(j)|$ represents the number of agricultural neighbours of cell j in the land-sparing scenario and the number of natural neighbours in the land-sharing scenario. When $\omega = 0$, land conversion is occurs with uniform probability in space. Larger values imply that the agricultural clustering, in the land-sparing case, or the affinity with natural land, in the land-sharing case, are more exacerbated.

Loss of agricultural land

We assume that the loss of agricultural land is driven by fertility loss (Pimentel, 2006). The fertility loss propensity depends on the amount of ecosystem services

flowing to an agricultural cell: the smallest the flow, the higher the fertility loss propensity. This mechanism represents the contributions of ecosystem services to maintaining suitable conditions for agriculture. We further assume that the relationship between ecosystem service provision and fertility loss propensity is linear, yielding the following expression for fertility loss propensity $\pi_L(i)$ in agricultural cell i:

$$\pi_L(i) = \rho_L(1 - \varepsilon(i)), \tag{3.8}$$

where ρ_L represents the rate of increase of the fertility loss propensity with respect to losses in ecosystem service provision. Although the fertility loss propensity is the same for low-intensity and high-intensity agricultural land, low-intensity cells transition to a natural state whereas high-intensity ones to a degraded state. This mechanism accounts for the larger toll that high-intensity agriculture takes on the environment.

Passive land recovery and degradation

Apart from agricultural related land-use transitions we model spontaneous passive transitions from natural to degraded states, and vice-versa. We further assume that land recovery and degradation propensities are dependent on the ecosystem services that natural or degraded cells receive. The propensity of a degraded cell increases with the flow of ecosystem services it perceives. On the contrary, the propensity of a natural cell to passively transition to a degraded state grows as the ecosystem services flowing to the natural cell diminish. This mechanism represents land degradation by isolation from other natural cells. We further assume that the propensity of both mechanisms depends linearly on ecosystem service provision. Hence the probability of passive recovery $\pi_R(i)$ and passive degradation $\pi_D(i)$ in cell i are, respectively

$$\pi_R(i) = \rho_R\, \varepsilon(i), \tag{3.9}$$

$$\pi_D(i) = \rho_D\, (1 - \varepsilon(i)), \tag{3.10}$$

where ρ_R (ρ_D) represents the rate at which the recovery (degradation) propensity grows as ecosystem service provision in cell i increases (decreases).

Computational implementation and numerical experiments

We use a Gillespie's Stochastic Simulation Algorithm to simulate social-ecological dynamics in continuous time. Although time-consuming, this approach presents the advantage of simulating every stochastic event and thus generate exact realizations of our model, without any approximation. The parameter values used for the simulations are specified in Table 3.1. Details on the estimation of parameter values can be found in Appendix 2.B and 3.B.

We focus our study on the interplay between land-use management strategies and management and ecological spatial scales. Through a set of numerical experiments, we examine the effects of the mean farm area and the connectivity distance on social-ecological dynamics for three scenarios of land-use management: all farms land-sharing ($\alpha = 0$), all farms land-sparing ($\alpha = 1.0$), and a mixed scenario with half of the farms land-sharing and the other half sparing ($\alpha = 0.5$). First, we show how changing the management scale through varying the mean farm area can affect the sustainability of identical farm-level strategies, leading to collapses in some cases. Second, we explain this change in the social-ecological dynamics by the way management scales affect spatial patterns of management strategies at the landscape level, thereby changing ecosystem service provisioning. Third, we demonstrate the effect of the connectivity distance on shifting the landscape percolation threshold. Finally, we show how the connectivity distance and the mean farm area influence the long-term state of the system.

Parameter	Interpretation of the non-dimensional parameters	Values
z	Scaling exponent of ecosystem services provision with the area of a natural fragment	0.25
β	Share of the baseline productivity of low-intensity agriculture due to ecosystem services	0.5
K_0	Number of households that can be sustained by a single high-intensity agricultural cell	15
$\lvert\mathcal{F}\rvert$	Number of farms in the landscape: given a constant landscape size this controls the average farm-size	$[1-1024]$
d_N	Connectivity distance: all the cells with a manhattan distance smaller than d_N are neighbours	$[1-16]$
α	Fraction of land-sparing farms in the landscape	$0, 0.5, 1$
ω	Affinity parameter controlling the clustering of high-intensity agriculture and integration of low-intensity agriculture with natural land	5
σ	Responsiveness to resource demand: increase rate of the expansion and intensification propensities per unit of resource demand	1.2
ρ_L	Fertility loss's sensitivity to ecosystem services provision: decrease rate of the fertility loss propensity per unit of ecosystem services	0.01
ρ_R	Land recovery sensitivity to ecosystem services provision: increase rate of the land recovery propensity per unit of ecosystem services	0.1
ρ_D	Land degradation sensitivity to ecosystem services provision: decrease rate of the land degradation propensity per unit of ecosystem services	0.01

Table 3.1: Description of the model's non-dimensional parameters and numerical values used for the simulations presented on this article. Details regarding the value of K_0 can be found in Appendix 3.B. For the parameters already present in the model developed in Chapter 2, we refer the reader to the Appendix 2.B.

Results

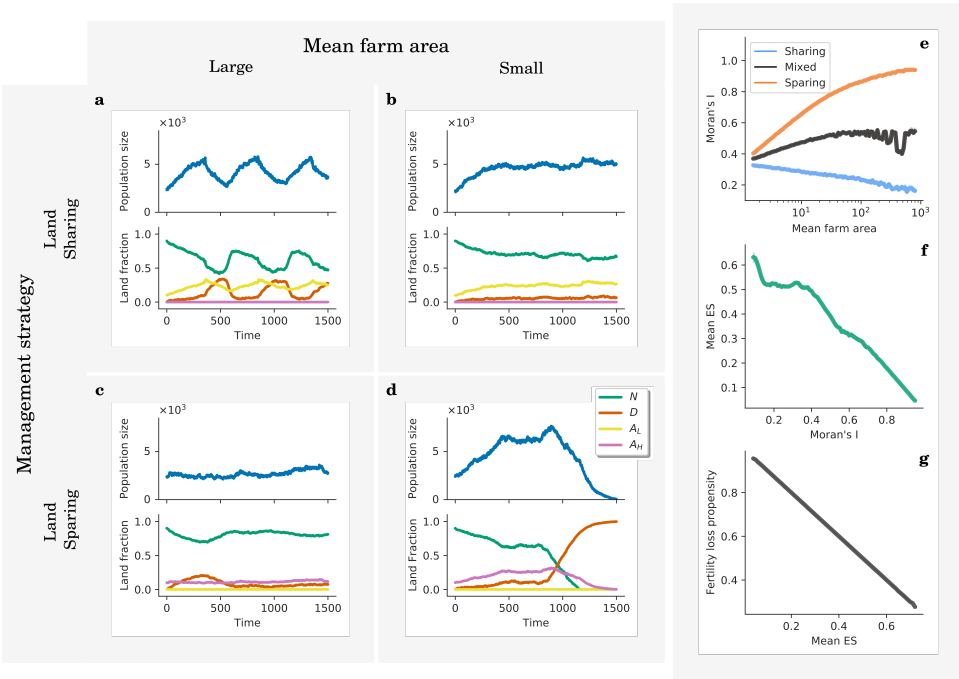

Figure 3.2: **Social-ecological dynamics for different combinations of management scale and management strategy.** In a landscape where management is centralized in a single agent at the landscape scale, a land-sharing strategy leads to cycles of collapse and recoveries of the social-ecological system (a). On the contrary, a land sparing strategy leads to a stable population and landscape configuration (b). When management scale is considerably smaller than landscape scale, i.e. average farm area $\simeq 10^{-3}$ of the landscape area, land-sharing in every farm leads to a stable population and landscape configuration (c) while land-sparing in every farm leads to a population collapse following the full degradation of the landscape (d). e) Decreasing the management scale leads to an homogeneization of landscape configuration across different strategies. f) The mean amount of ecosystem services received by agricultural cells decreases as Moran's I increases. g) The agricultural loss propensity increases with a decrease in the mean provision of ecosystem services. As a consequence, in landscapes where agricultural land is not clustered, and thus more agricultural cells are exposed to ecosystem services, fertility loss process is slower and the average life-time of an agricultural cell is longer. The curves shown in a), b), c) and d) correspond to a single model replication. The curves shown in e), f) and g) represent averages over 100 replications.

Effects of management scale and strategy on social-ecological dynamics

Social-ecological dynamics emerging from a land-use management strategy are greatly affected by the scale at which the strategy is applied. While land-sharing applied at large scales gives periodic dynamics with cycles of partial collapses and recoveries (Figure 3.2 a), reducing management scale leads to a long-term stable and sustainable state for the social-ecological landscape (Figure 3.2 b). On the contrary,

land-sparing applied at large scales yields a sustainable long-term state (Figure 3.2 c), while applied at a finer scale leads to social-ecological collapse (Figure 3.2 d). The stability of population size and landscape composition is not only dependent on the chosen land-use management strategy but also on the scale of application of the strategy.

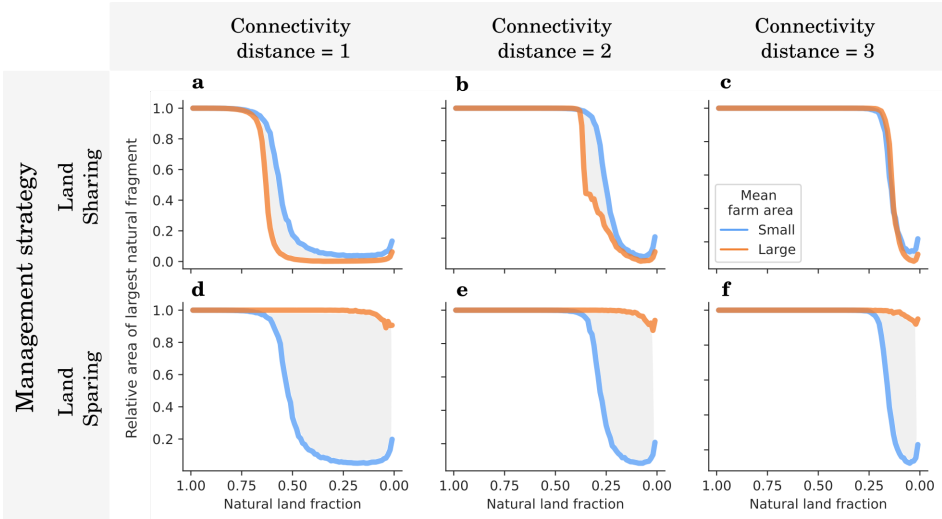

Figure 3.3: **Area of the largest natural fragment relative to the total natural area as a function of the fraction of natural land.** This is a measure of fragmentation. When the relative area of the largest fragment is close to 1, natural land is concentrated in one giant fragment. When it is close to 0, natural land is distributed among several small fragments. The abrupt shift in the relative area of the largest fragment indicates a percolation transition. The fraction of natural land at which the transition occurs is called the percolation threshold. In the land-sharing scenario, the percolation threshold is larger when management scale is larger. In the land-sparing scenario the percolation threshold increases as management scale diminishes. In both cases, increasing the connectivity distance decreases the percolation threshold and the difference between different management scales. The small mean farm area corresponds 1.5 cells, and the large mean farm area corresponds 1600 cells, i.e. the whole landscape. The curves are averages over 100 replications.

Management scale, landscape configuration and ecosystem services

The changes in social-ecological dynamics that result from changes in management scale are mediated by changes in landscape structure. When the management scale is very large, thus management is centralized in few farms, land sparing and land-sharing strategies yield opposed landscape configurations: sparing leads to a highly aggregated agricultural land and sharing to more homogeneous patterns when the fraction of natural land is high, and checkerboard-like patterns as natural land de-

creases. Landscape configuration tends to homogenize as management scale diminishes, until sharing and sparing show no difference at the landscape scale (Figure 3.2 e). Moran's I is negatively correlated with the mean amount of ecosystem services provided to agricultural land: when agricultural land is aggregated, agricultural cells receive a lower amount of ecosystem services on average (Figure 3.2 e), thereby increasing the propensity of the loss of agricultural cells. When sparing is applied in a landscape consisting of many small farms this causes an increase in population size at each fluctuation, since farms live for longer times allowing for the accumulation of the population. Eventually, land-cover fluctuations cause abrupt landscape fragmentation, disrupting ecosystem service provision and leading to the collapse of the population. In the land-sharing case, the disappearance of cycles is explained by a decrease in the percolation threshold, thereby preserving ecosystem service provision at lower levels of natural land.

Effects of connectivity distance on fragmentation

We explored the effect of shifting ecological scales by changing the connectivity distance at which two natural cells are considered connected. In agreement with percolation theory, increasing the connectivity distance leads to the persistence of a giant functionally connected natural fragment at lower fractions of natural land. This effect is important for land sharing strategies and leads to the disappearance of the difference in the percolation thresholds of different management scales (3.3 a, b & c). In the land sparing case, differences among scales are drastically reduced. This preserves ecosystem service provision at lower fractions of natural land.

Long-term states: mixed strategies increase sustainability odds

Land-sharing and land-sparing strategies both lead to sustainable steady states, except in the extremes of management scale (Figure 3.4 a). The effect of management scale on the long-term state is more important in the land-sparing scenario. In

this case, diminishing the management scale leads to larger population sizes which eventually cannot be sustained by a landscape with a natural land fraction above the percolation threshold, thereby causing a social-ecological collapse (Figure 3.4 b & c). Increasing connectivity distances has the unexpected effect of impairing the sustainability of the system, enlarging the range of management scales across which land-sharing and land-sparing strategies lead to unsustainable states. When connectivity distances are very large, the system reaches a stable state with high population sizes and very low fractions of natural land.

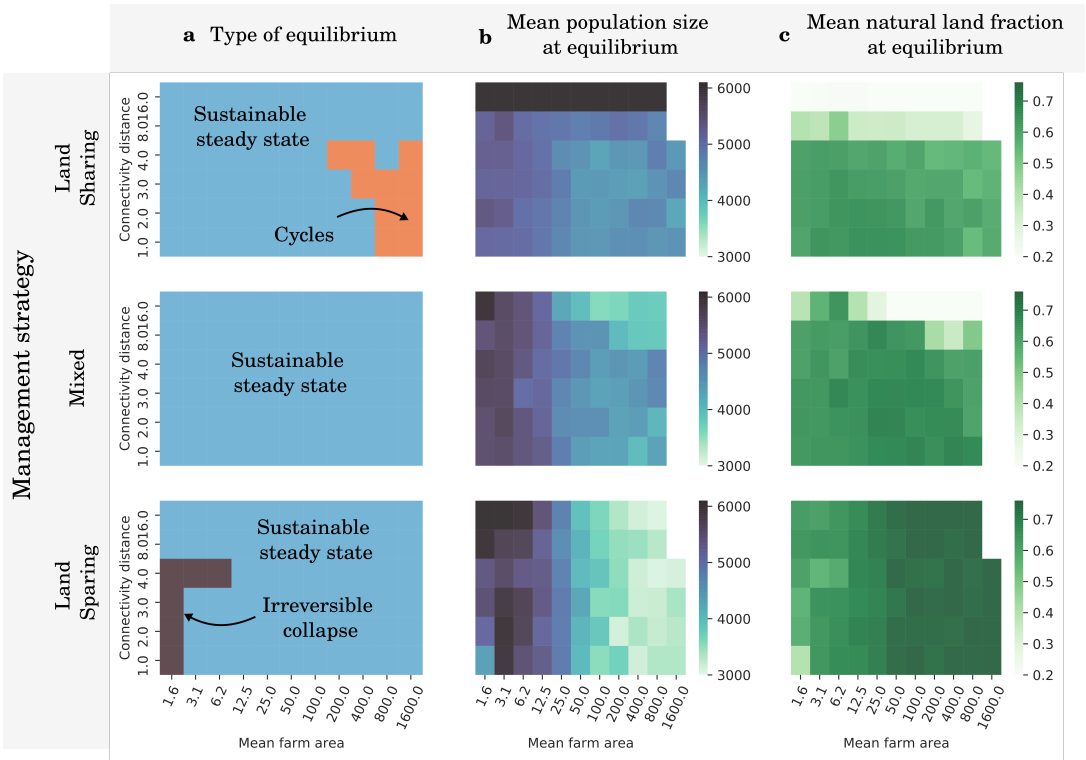

Figure 3.4: **Long-term behaviour of the social-ecological system.** a) In the land-sharing scenario there are only two possible long-term states: a sustainable steady-state or a cycles of collapse and recovery. In the land-sparing scenario, cycles are not possible but when the management scales are very small the system goes to irreversible collapses. Increasing the connectivity distance increases the range of management strategies across sharing strategies lead to cycles. A mixed strategy combining land-sparing and land-sharing yields the best results in terms of sustainability. b) & c) Changing management scales has greater effect on the long-term state of the land sparing landscapes. Where increases in population size are negatively correlated with the natural land fraction. Eventually when the populations' are too large the system heads to irreversible collapse. In the land-sharing and mixed scenarios, large connectivity distances lead to very large population sizes with very low fractions of natural land. The values are obtained by averaging over 10 replications.

Discussion

Overview

The issue of spatial scales is crucial to the management of agricultural landscapes. Although decades of research have contributed to the development of principles to guide sustainable land-use management, the interplay between management strategies and the spatial scale at which they are applied has received little attention (Fischer et al. (2014), but also see (Ekroos et al., 2016)). Moreover, research on optimal landscape design (Butsic and Kuemmerle, 2015; Arroyo-Rodríguez et al., 2020) ignores that decision-making regarding management practices is generally done at the farm level, rather than at the landscape level (but see Brosi et al. (2008)). Designing land-use policies to obtain sustainable landscape configurations emerging from the uncoordinated action of different land-owners at small spatial scales represents a hard task. Furthermore, the same guiding principles applied at different spatial scales can lead to radically different outcomes at the landscape level, with repercussions on sustainability (Fischer et al., 2014). In the present work, we examined the effect of the interplay between land-use management strategies and scales on human-land dynamics to demonstrate the importance of considering land-ownership patterns in designing land-use planning policies. We used the paradigmatic land-sparing vs. land-sharing framework to show, via a spatially explicit model of land-use dynamics, how the success of sharing or sparing strategies depends on the spatial scale at which the strategies are applied. We showed how management scale affects the expected outcome of each strategy at the landscape scale, and thus landscape-level patterns and ecosystem service provision. Finally, we explored the effect of management and connectivity scales on the long-term social-ecological state and showed that landscapes in which there is heterogeneity between farms' strategies are the most sustainable across all the range of management and connectivity scales.

Management scales, strategies and landscape structure

We showed that identical land-use management strategies can lead to very different landscape configurations depending on the spatial scale at which they are applied (Figure 3.2 e). Land-sparing in very large farms leads to the complete spatial segregation of agricultural and natural land and thus results in the preservation of large connected natural fragments. However, when management scale decreases, land-sparing at the farm level leads to less segregated patterns at the landscape level until reaching completely random patterns when management scale is very small. As a consequence, the application of land-sparing strategies at small management scales leads to more fragmented landscapes, in which percolation transitions occur at higher fractions of natural land. A percolation transition occurs when progressive agricultural expansion leads to abrupt landscape-scale fragmentation, and causes a disruption of ecosystem services provision that increases the likelihood of social-ecological collapse as shown in Chapter 2 of this thesis. Thus, land-sparing leads to landscape structures increasingly vulnerable to habitat loss as management scale diminishes. The opposite is true in a land-sharing scenario since reducing management scale shifts down the percolation threshold, increasing the robustness of the landscape to habitat loss. Overall, the substantial difference in the spatial patterns that emerge from land-sparing and land-sharing strategies when implemented at large management scales vanish as management scale decreases. At extremely small management scales, both strategies lead to the same random spatial distribution of agricultural land, and the sole difference becomes the intensity of agriculture.

Social-ecological dynamics: the interplay between management scales and strategies

The modifications of landscape structure brought by varying management scales can provoke deep changes in social-ecological dynamics, with disparate effects in different land-use management scenarios (Figure 3.2). While diminishing management scale is beneficial for sustainability in a land-sharing scenario, it leads to

social-ecological collapses in a land-sparing scenario. At large management scales, land-sharing leads to cycles of collapses and recoveries (Figure 3.2 a). The collapses are caused by agricultural expansion pushing the landscape through the percolation threshold, fostering abrupt fragmentation, impairing ecosystem service provision and thus agricultural production, as shown in Chapter 2 of this thesis. However, as management scale diminishes, the percolation threshold is shifted to lower fractions of natural land. As a consequence, the landscape resists higher levels of agricultural expansion and population sizes that were unsustainable at large management scales become sustainable at small management scales. While in the land-sharing scenario collapses are contained and the social-ecological system recovers, in the land-sparing scenario, the larger land degradation caused by high-intensity agriculture makes the collapses irreversible.

In the land-sparing scenario, diminishing management scales leads to increasing agricultural expansion and population growth, which can become unsustainable, causing an irreversible social-ecological collapse (Figure 3.2 c & d). The aggregation of agricultural land when land-sparing is applied at large management scales reduces the average flow of ecosystem services from natural to agricultural land: the patches inside the agricultural clusters do not perceive ecosystem services (Moreno et al., 2007; Brosi et al., 2008; Bommarco et al., 2013; Mitchell et al., 2014). While this does not affect the productivity of high-intensity agricultural cells, it does cause large fertility loss. As a consequence, positive fluctuations of human population size that lead to agricultural expansion are contained by the relatively quick loss of agricultural patches, resulting in stable, sustainable dynamics. As management scale diminishes, large agricultural clusters start vanishing, to the benefit of a greater integration of agricultural land into the natural landscape. Above the percolation threshold, this leads to a high average ecosystem service provision to agricultural patches and thus to a decrease in the mean fertility loss propensity. As a consequence, the longer-lasting agricultural cells sustain a higher human population growth, since positive fluctuations of population size are no longer contained. This leads to larger population sizes and smaller fractions of natural land as the mean farm area diminishes (Figure 3.4 b & c). When the resulting fraction of natural

land is too close to the percolation threshold, fluctuations of human population size or landscape composition will inevitably push the landscape through a percolation transition driving the human-land system to irreversible collapse (Figure 3.2 d & 3.4 a).

Social-ecological dynamics: unexpected effects of the connectivity distance

In the present work we introduced variation in ecological spatial scales by varying the distance over which ecological connectivity is maintained and ecosystem services flow. Connectivity distance is also an important parameter regarding the maintenance of ecosystem services provision at different levels of natural habitat loss (Mitchell et al., 2015a; Montoya et al., 2020). In agreement with percolation theory (Aharony and Stauffer, 2003), we show that increasing connectivity distance decreases the fraction of natural land at which the percolation transition occurs (Figure 3.3). Thus, ecosystem services provision in identical landscape configurations can be different depending on the connectivity distance (Mitchell et al., 2013). At low connectivity distances, large-scale fragmentation, from a functional point of view, can happen at relatively large fractions of natural land. However, if the connectivity distance is large, functional connectivity is maintained in the landscape at lower levels of natural land, thereby increasing the tolerance of ecosystem services provision to habitat loss. The effects of landscape fragmentation on biodiversity, ecosystem functions and services are dependent on functional connectivity distances (Villard and Metzger, 2014). A number of studies have empirically quantified functional connectivity distances in bird and insect species (Uezu et al., 2005; Awade and Metzger, 2008; Keller et al., 2013; Rösch et al., 2013). This work increases our understanding of fragmentation effects on the services provided by these species like pollination or pest control. However, broader knowledge and quantification of functional connectivity distances is lacking, and empirical data is scarce, thereby stimulating theoretical and modelling work that addresses these questions (Pe'er et al., 2011). Overall, our results show that increasing the connectivity distance

leads to a more linear relationship between average ecosystem service provision and the fraction of natural land. If the distance is large enough, the abrupt effects of a percolation transition on ecosystem services and social-ecological dynamics vanish.

The effect of changing connectivity distance on human-land dynamics was against our prior expectations. Although we initially expected larger connectivity distances to lead to more sustainable dynamics, we observed the opposite effect. At small connectivity distances (1 to 4), increasing them leads to unsustainable dynamics for a growing number of management scales both in the land-sharing and land-sparing scenarios (Figure 3.4 a). At large connectivity distances (8 and 16), although collapses are avoided both in the land-sharing and in the mixed scenarios, large connectivity distances lead the system to stabilize in a state with very low fractions of natural land and very large population numbers. At both small and large connectivity distances, this can be explained by the same mechanism that explains why land-sparing leads to collapse at small management scales. The robustness against habitat loss that increasing connectivity distances brings to ecosystem service provision causes large fluctuations in human population size, thereby increasing the chances of a collapse, or allowing the stabilization of the system in a highly degraded landscape.

Implications for land-use planning policies

Our findings are relevant the situation of agriculture in Sub-Saharan Africa, the world's region with the largest farmland concentrated in small farms (Samberg et al., 2016; Herrero et al., 2017). Shifting to conventional intensification and production of cash crops in Sub-Saharan African small holder agriculture is a common way to increase agricultural productivity and improve economic profits that come from better market integration (Balbi et al., 2020). Our results point out that this could lead to an unsustainable future. We demonstrated that when management scale is small, high-intensity agriculture at the farm level amplifies the system's response to fluctuations in human population size that increase the demand for resources, furthering agricultural expansion and population growth. Overall, our results suggest that in landscapes dominated by small-holder agriculture, land-sparing should be avoided

in favour of land-sharing or mixed strategies. In the mixed-strategy scenario, where one half of the farms do land-sharing and the other half land-sparing, we found that social-ecological dynamics reached sustainable equilibria across all the range of management scales and connectivity distances, supporting increasing evidence for the importance of heterogeneous landscapes for sustainability (Arroyo-Rodríguez et al., 2020; Finch et al., 2020). In more complex real-world landscape, where farm size distribution is not homogeneous and very large farms can coexist with small ones in the same landscape, our modelling work suggests that implementing land-sparing in the large farms and land-sharing in the smaller ones could be beneficial for sustainability.

Challenges and perspectives

We modelled landowners that apply the same land-use strategy over time, no matter the changes in the landscape or the human population size. However, management strategies in the real world are in constant change, driven by learning processes, adaptation to new conditions or the influence of social peers (Rathwell and Peterson, 2012; Albizua et al., 2020; Balbi et al., 2020; Albizua et al., 2021). Understanding the processes causing the changes in decision-making is key to understanding how sustainable practices can propagate among landowners and managers. Furthermore, we considered the managers as independent from one another and the conclusions of our study are influenced by this assumption. For example, in the scenario where land-sparing is applied at a small management scale, if managers would be capable to cooperate between farms to devise a land-use management strategy applied consistently at larger scales, social-ecological collapse could be avoided. Specifically, in this scenario, it would require some managers accepting to not cultivate their land. Putting this into practice needs economical cooperation between farmers, possibly in a cooperative format, in which land is shared by all the managers.

Conclusions

In the present work we developed a spatially explicit model of land-use changes coupled to human population dynamics to examine the effects of management and ecological spatial scales on the sustainability of different land-use management strategies along a land sparing-sharing axis. We demonstrated that identical farm-level management strategies applied at different management scales can lead to completely different social-ecological dynamics. We showed that social-ecological feedbacks cause unexpected effects of connectivity distance on social-ecological dynamics. Our results suggest that mixed management strategies, where land-sharing is enforced in a landscape's small-scale farms and land-sparing in the large ones, increase the odds of sustainability. Thus heterogeneous landscapes may be key to sustainability.

Acknowledgements

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Authorship

All authors contributed to the design of the study. DBP elaborated the model, performed and analyzed the simulations, and wrote the first draft of the mansucript. All authors contributed substantially to revision.

Data accessibility statement

Data available from the repository https://doi.org/10.5281/zenodo.5544008.

Appendix

3.A Derivation and non-dimensionalization of the equations

In this appendix, we uniquely address the formulations that differ from those of Chapter 2. For the thorough development of the rest of the equations please refer to Appendix 2.A.

Production of agricultural resources

Total agricultural production per unit time in the landscape is obtained by summing over the production per unit time of every low-intense and high-intense agricultural cells. We assume that the low-intense agricultural production is positively affected by the amount of ecosystem services the agricultural cell receives, hence we write it as the sum of a baseline production and a contribution related to ecosystem service provision. On the contrary, we assume that resource production in high-intensity cells is fixed and completely independent of ecosystem service provision. We write total resource production per unit time $\mathcal{Y}$ as follows:

$$\mathcal{Y} = \sum_{i \in \mathcal{A}_L} (\mathcal{Y}_0 + Y_E E_i) + \sum_{i \in \mathcal{A}_H} \mathcal{Y}_1, \tag{3.11}$$

where $\mathcal{A}_L$ and $\mathcal{A}_H$ are the sets of low-intense and high-intense agricultural cells

respectively, $\mathcal{Y}_0$ is the baseline production per unit time of low-intense agricultural cells, Y_E is the production per unit time per unit of received ecosystem service of low-intense agricultural cells and $\mathcal{Y}_1$ is the production per unit time of high-intensity agricultural cells. We non-dimensionalize total resource production per unit time by expressing it relative to the production per unit time in high-intensity agricultural cells $\mathcal{Y}_1$. This yields the following expression for the non-dimensional total resource production per unit time Y:

$$Y = \frac{\mathcal{Y}}{\mathcal{Y}_1} = \sum_{i \in \mathcal{A}_L} \left(\frac{\mathcal{Y}_0}{\mathcal{Y}_1} + \frac{Y_E E_{max}}{\mathcal{Y}_1} \varepsilon_i \right) + \sum_{i \in \mathcal{A}_H} 1. \tag{3.12}$$

Assuming that low and high-intensity productions per unit time are equal when ecosystem services provision is at its maximum, i.e. $\varepsilon = 1$, yields the following relationship:

$$\mathcal{Y}_0 + Y_E E_{max} = \mathcal{Y}_1 \implies Y_E E_{max} = \mathcal{Y}_1 - \mathcal{Y}_0, \tag{3.13}$$

and injecting in equation 3.12 this results in:

$$Y = \sum_{i \in \mathcal{A}_L} \left(1 - \frac{\mathcal{Y}_1}{\mathcal{Y}_1} + \frac{\mathcal{Y}_0}{\mathcal{Y}_1} + \frac{\mathcal{Y}_1 - \mathcal{Y}_0}{\mathcal{Y}_1} \varepsilon_i \right) + \sum_{i \in \mathcal{A}_H} 1 = \sum_{i \in \mathcal{A}_L} (1 - \beta + \beta \varepsilon_i) + \sum_{i \in \mathcal{A}_H} 1 \tag{3.14}$$

where β is a non-dimensional parameter that represents the share of low-intensity non-dimensional production per unit time dependent on ecosystem services provision.

Human population dynamics

We model human population dynamics as a stochastic process composed of household's births and deaths. We derive the propensities of births and deaths from

a logistic growth process with carrying capacity equal to the ratio between total resource production and per capita consumption per unit time. When describing the human population by a density variable p, the differential equation describing human population dynamics is

$$\frac{dp}{dt} = rp\left(1 - \frac{c\,p}{\mathcal{Y}}\right) = \underbrace{r\,p}_{\text{Births}} - \underbrace{r\,\frac{c\,p}{\mathcal{Y}}p}_{\text{Deaths}}, \tag{3.15}$$

where r represents the population growth rate at low densities compared to the carrying capacity, c is the per capita resource consumption per unit time, and $\mathcal{Y}$ is the total resource production per unit time. Decomposing the equation in a birth term and a death term yields the following interpretation: r represents the human birth rate and $\frac{rcp}{\mathcal{Y}}$ represents the human death rate. In the stochastic, individual based description we adopt to model human population dynamics, we will use the same rates as birth and death probabilities per unit time. Therefore, we write the birth and death processes for the human population as

$$\text{Birth event}: \quad \mathcal{P} \xrightarrow{r} 2\mathcal{P}, \tag{3.16}$$

$$\text{Death event}: \quad \mathcal{P} \xrightarrow{rcP/\mathcal{Y}} \emptyset, \tag{3.17}$$

where $\mathcal{P}$ and P represent a human household and the number of households respectively. Note that this representation is equivalent to the formalization of chemical reactions. A human household can yield another human household with probability per unit time equal to r, and a human household can die with probability per unit time equal to $\frac{rcP}{\mathcal{Y}}$. This implies that births occur constantly with the same probability per unit time, while deaths depend on the availability of resources. When total resource consumption is larger than resource production, the death propensity is larger than the birth propensity, thus the human population size will most likely diminish, and vice-versa. While this description is perfectly adapted for cellular reproduction it is obviously an approximation for human population. First, most

commonly sexual reproduction does not imply the duplication of the household size, since the most common is for a couple to have a child at a time. Second, we assume that new-born households can immediately procreate.

We now begin by non-dimensionalizing the time by re-scaling it with respect to $1/r$. As a consequence, the time is expressed relative to the expected time before a household duplicates in size. Also note that this non-dimensionalization is performed for the rest of the equations that are not explicitly treated in this appendix. The detail for the remaining equation can be found in Appendix 2.A. Secondly, we inject the non-dimensional expression of the agricultural production per unit time $Y = \mathcal{Y}/\mathcal{Y}_1$ in the death propensity. As a result birth and death propensities become:

$$\text{Birth propensity}: \quad 1, \tag{3.18}$$

$$\text{Death propensity}: \quad \frac{cP}{\mathcal{Y}_1 Y} = \frac{P}{K_0 Y}, \tag{3.19}$$

where $K_0 = \mathcal{Y}_1/c$ is the number of households that can be sustained by the production of a single high-intensity agricultural cell, given the constant per capita resource consumption c.

Humans demand for resources

Humans demand for resources is equal to the difference between total resource consumption and total resource production per unit time. Thus, in its dimensional form it writes:

$$\Delta R = cP - \mathcal{Y}. \tag{3.20}$$

Injecting the non-dimensional resource production $Y = \mathcal{Y}/\mathcal{Y}_1$ we obtain the follow-

ing non-dimensional expression:

$$\Delta r = \frac{\Delta R}{\mathcal{Y}_1} = \frac{cP}{\mathcal{Y}_1} - Y = \frac{P}{K_0} - Y. \tag{3.21}$$

3.B Estimation of the cell-size and parameter K_0

The estimation of the parameter values was done in the same way as in Chapter 2. Thus, in this section we only discuss the value of parameter K_0 that represents the carrying capacity of a single high-intensity agricultural patch. The reader can find all the information regarding the estimation of the remaining parameters in Appendix 2.B.

The value of K_0 indirectly determines the size of landscape cells, and thus of the landscape size. Since we want one landscape cell to represent a small farm few hectares, we assume that each cell corresponds to around 4 hectares, thus a square with a side length of 200 meters. As a consequence, we model a square landscape with a side length of 8 kilometers. Using data on caloric production and number of people fed per cultivated hectare (Cassidy et al., 2013), we roughly approximate that 10 to 20 households can be sustained by a high-intensity landscape cell, assuming that a household is composed of 4 individuals. We take the average between the two values and thus estimate that $K_0 = 15$. Although this is a rough estimation, we believe it accurately captures the correct order of magnitude.

General Discussion and Conclusion

Social-ecological models constitute a precious tool to tackle contemporary sustainability challenges related to nature preservation and food security for a growing and more consuming human population. However, studies have often treated human population dynamics as independent from managed ecosystems. Specifically, although the effects of human population growth on ecosystems are widely recognized, few studies have addressed how changes in the ecosystems can feedback to human demography. In the field of land-use management, ignoring the feedbacks from the landscapes to human demography can lead to incomplete representations of the human-land system and thus to poorly informed policy-making with potential counterproductive effects. This thesis aims to incorporate the bi-directional feedbacks between human population dynamics, decision-making and landscapes to address the issue of sustainable agricultural land-use management in social-ecological systems from a more holistic perspective. In this general discussion and conclusion, I begin by summarizing the main contributions of each of the thesis' chapters and then proceed to discuss their limitations and the emerging perspectives to further advance research in social-ecological modelling in general and human-land dynamics in particular.

Main contributions and summary of the results

Chapter 1: How to determine a sustainable trade-off between agricultural intensification and expansion?

Empirical studies comparing species-richness between farmland and natural land in temperate areas, have supported the hypothesis that land-sparing, i.e. intensifying agriculture and segregating it from nature, is the best land-use management strategy to jointly maximize agricultural production and biodiversity conservation in managed landscapes (Phalan et al., 2011a; Balmford et al., 2005, 2019). Wildlife-friendly is typically less productive than conventional high-intensity farming, and thereby requires larger amounts of land to achieve the same production (but see Chappell and LaValle (2011)). As a consequence, although wildlife-friendly farmland supports higher levels of biodiversity, these studies conclude that these gains are offsetted by the larger natural areas that need to be converted to agriculture. However, this approach is based uniquely on ecological measurements and thus fails to capture the complexity of social-ecological landscapes. Specifically, it does not consider the human drivers behind changes in land-use (Meyfroidt et al., 2018). Although the argument is correct, its direct application to the development of land-use management policies is risky. Specifically, a hidden assumption behind the support for land-sparing policies is that increasing intensification will effectively spare natural land. Matson and Vitousek (2006) proposed two ways through which this strategy can fail. First, high-intensity agriculture has off-site consequences, such as downstream river pollution. Second, in some cases economical feedbacks can foster agricultural expansion following the adoption of high-intensity agriculture, thereby offsetting the sparing effect of intensification (Lambin and Meyfroidt, 2011; Meyfroidt et al., 2018).

The adoption of high-intensity agriculture needs to be accompanied by institutional support and policy development that aims to actively protect the land that can be spared following increasing agricultural yields (Garrett et al., 2018). However, it is unclear to what extent increases in intensification should be compensated

by decreases in expansion. In Chapter 1, I addressed this issue and showed that the non-linearities in the social-ecological system lead well-intentioned but uninformed policy making to failure. Building on Henderson and Loreau (2018) work, I developed a model of coupled human-land dynamics, where the land-use management strategy is determined by the degree of agricultural intensification and the magnitude of the land conversion effort, which controls agricultural expansion. I initially imposed a linear trade-off between agricultural intensification and expansion and explored social-ecological dynamics across intensification levels. When intensification is low, the system reaches a sustainable steady state with low population size and a large fraction of wildlife-friendly agricultural land. At high intensification levels, the system also reaches a sustainable steady-state but with large population sizes and very low fractions of agricultural land. However, for intermediate values, social-ecological dynamics led to collapse in the long-term. This is due by an insufficient reduction of agricultural expansion, which contributed to fuel human population growth that coupled with the effects of increasing intensification results in large-scale landscape degradation followed by the collapse of agricultural production.

To explain why the linear trade-off between expansion and intensification fails at intermediate levels of intensification, we relaxed this assumption and explored social-ecological equilibria over the whole range of intensification and land conversion effort. This allowed us to characterize which regions of the strategy space led to sustainability and which to collapse. We found that the border between the sustainability and collapse regions is highly non-linear. Specifically, the function describing the required reductions in expansion as a response to increases in intensification has a concave-up shape. This means that t very low levels of intensification the system tolerates large values of conversion effort, since agricultural land is managed in an almost natural way. However, as intensification increases, the reduction in the conversion effort needs to be more than linear to accommodate the changes. Our simple approach provides a proof-of-concept of the importance of precise knowledge on system dynamics and the social drivers of land-use change to design land-use management policies. We exemplified it by showing how a well-intentioned but uninformed trade-off between intensification and expansion can lead to social-ecological

collapse.

Chapter 2: What are the effects of habitat fragmentation on social-ecological dynamics?

There is alarming empirical evidence on forest structure across the tropics showing that forest habitat is close to a percolation transition (Taubert et al., 2018). A percolation transition results in large-scale landscape fragmentation following small losses of habitat. Although the effects of fragmentation on biodiversity and ecosystem services remain under debate (Fletcher et al., 2018; Fahrig et al., 2019), significant amounts of evidence from large-scale, long-term fragmentation experiments support the hypothesis that ecosystem functions and services will be deteriorated (Haddad et al., 2015, 2017). This increases the concerns on the sustainability of current food systems, since agricultural production depends on ecosystem services provision (Power, 2010; Balvanera et al., 2014; Dainese et al., 2019). In the recent years theoretical and experimental work has advanced our knowledge of the effects of fragmentation on ecosystem services provision (Mitchell et al., 2015b,a; Montoya et al., 2021). However, coupled models of human population and land dynamics have used non-spatial approaches that cannot account for fragmentation effects.

In Chapter 2, I developed a spatially explicit extension of Chapter 1 model to explore the effects of landscape spatial structure on social-ecological dynamics. In this model the landscape is described as a cellular automaton in which the cell's states represent the land-cover type. Land-use management strategies are specified via two parameters that control the preference for high-intensity agriculture and the degree of spatial clustering of agricultural land. The two strategical dimensions mimic the land-sparing vs. land-sharing debate. In this model, decision-making is centralized in a single manager that expands or intensifies agriculture depending on the resource demand of an external human population. I explored the effect of varying strategies along the clustering and intensification dimensions on landscape structure, ecosystem services provision and the resulting social-ecological dynamics.

Model simulations showed unexpected social-ecological dynamics that were punctuated by sharp bursts of agricultural expansion that in some cases led to irreversible landscape degradation and social-ecological collapses. Further analysis demonstrated that expansion bursts responded to an abrupt decrease in resource production that drove further agricultural expansion to compensate production losses. Specifically, progressive natural land conversion to agriculture led to smooth dynamics and growing population until the natural land crossed the percolation threshold leading to large-scale fragmentation and a decrease in ecosystem services provision that diminished agricultural production. To compensate production losses larger areas are cultivated thus deepening habitat loss and fragmentation and trapping the system in an unsustainable feedback loop. We showed that in the low intensity scenario, the landscape is able to recover from the shocks, but that introducing even small areas of high-intensity agriculture can lead to irreversible collapse following the percolation transition.

I further showed, in agreement with percolation theory, that increasing agricultural clustering leads to the maintenance of landscape connectivity at more significant proportions of habitat loss, thereby shifting the percolation threshold. Overall, increases in agricultural clustering resulted in stable and sustainable dynamics. Finally, I explored the role of initial landscape composition on the long-term state of the system to show that although agricultural clustering does prevent large-scale fragmentation, when it is coupled with high-intensity agriculture it can lead to social-ecological collapses in landscapes with small fractions of natural land. This result further supports the hypothesis that it is crucial to implement active conservation policies to make land-sparing effective. Overall, low-intensity agriculture in spatially clustered configurations was the most resilient strategy to habitat loss, however it results in small agricultural production and thus in small population numbers.

Chapter 3: Are there management strategies more adapted to different spatial-scales or are they universal?

Among the limitations of the land-sparing vs. land-sharing framework to design land-use management policies is the absence of explicit consideration of spatial scales in the debate (Fischer et al., 2014). Whereas in general land-sparing is considered as a large-scale strategy and land-sharing is associated with integration over a finer spatial grain (Fischer et al., 2014), some authors consider the preservation of natural field-margins as land-sparing, while others consider it a land-sharing practice, when looking at the landscape level. As a consequence, the conclusions of the studies are not tied to any particular spatial scale, thereby impeding the application of the results to policy design. Explicit consideration of spatial scales is furthermore crucial because farm-size distribution is highly variable across world-regions. As a consequence, universal recommendations concerning the spatial distribution of land-use at the farm-level can lead to diverse outcomes at the landscape-level, with possible unintended consequences.

In the third chapter of the thesis, I addressed this issue by exploring the effect of management scale on social-ecological dynamics, across multiple land-use strategies. I extended the model developed in the second chapter to include several independent agents that manage different sections of the landscapes, that represent farms. The more farms there are in the landscape, the smaller is the average farm size, and thus the management scale. I showed that while land-sharing leads to a sustainable steady-state at small management scales, as the management scale increases this strategy leads to cycles of collapse and recovery. On the contrary, land-sparing leads to a sustainable steady-state when management scales are large, but as the management scale diminish, it eventually leads to irreversible social-ecological collapse.

I demonstrated that the difference in social-ecological dynamics of applying the same type of strategy at the farm level, is caused by the alteration of spatial patterns at the landscape-level. Reducing the management scale tends to make land-sparing

and land-sharing identical from a spatial perspective, with the sole difference that in the former agricultural patches are intensively cultivated. I demonstrate that reducing the management scale leads to a shift in the landscape percolation threshold for the land-sharing case making it more resilient to habitat loss. However, in the land-sparing case, it causes an increase on the percolation threshold, diminishing the tolerance of the landscape to habitat losses. The changes on spatial patterns that come from changing management scales lead to variations in average ecosystem services provision. In the case of a land-sparing strategy, reducing the management scale leads to a dis-aggregation of agricultural land and thus to an increased flow of ecosystem services to agricultural land. As a consequence, fertility is maintained over longer times allowing for the accumulation of human population that eventually leads to a collapse. Finally, I show that a mixed management strategy leads to sustainable social-ecological dynamics across the entire range of management scales, supporting the hypothesis that heterogeneous landscapes are more resilient. Overall, results suggest that in complex real-world landscapes, the optimal management strategy is to implement land-sparing in large farms and land-sharing in the smaller ones.

Limitations and Perspectives

The limitations and perspectives discussed hereafter are mostly related to social processes related to demography, management practices, urbanization and globalization. This is because ecological processes have been more deeply discussed in the discussion of each chapter. However, in one section of this discussion I treat in greater details some issues regarding the modelling of ecosystem services.

On modelling human decision-making

In this section I initially discuss the multiple drivers of change in human decision-making with respect to land-use management strategies, human fertility and re-

source consumption. Finally, I discuss on how future modelling studies of coupled human population and land dynamics could achieve more accurate and pertinent representations of human-decision making by adopting agent-based approaches.

Management strategies: changes and adaptation

Decision-making regarding land-use management practices is a dynamical process that can be influenced by economic, social, political or ecological reasons (Matthews et al., 2007). In the models I developed in this thesis, management decision-making is solely driven by resource demand, i.e. an economic driver, and management strategies are fixed over time. However, changes in decision-making can be and important driver of social-ecological dynamics. Shifting management practices represent a way for human societies to adapt to changing conditions (Mortimore and Adams, 2001), or incorporate learning from observations (Allen and Garmestani, 2015). Some of the results presented in this thesis might be influenced the lack of dynamical management strategies. Specifically, oscillatory social-ecological dynamics, with cycles of partial collapses and recoveries, are a consequence of the lack of adaptation in management strategies, since humans incur in the same error *ad eternam*. Cyclic behaviour is not an exclusive feature of this thesis' models, but other social-ecological models describing the coupled dynamics of a human population and natural resources exhibit the same oscillatory behaviour (Roman et al., 2017; Nitzbon et al., 2017; Roman, 2018). Although cycles can also occur in models that include adaptive management (Peterson et al., 2003), in many cases the oscillations are damped (e.g. Lafuite et al. (2018)) . Below, I briefly describe the multiple potential drivers of changes in decision-making with respect to management practices.

According to theories of land-use change, the preference for agricultural expansion or intensification is mostly driven by economic reasons (Meyfroidt et al., 2018). In landscapes where land is abundant and capital is low, it is expected that increasing resource demand will translate in agricultural expansion. This is explained by the low prices of acquiring land compared to the costs of adopting high-intensity agriculture. On the contrary, in landscapes were land is scarce, it is expected for

further production increases to be achieved by increasing intensification in already cultivated land. Overall, in pristine landscapes it is expected to initially observe rapid agricultural expansion, and then a shift to intensification as land becomes an increasingly scarce good (Lambin et al., 2001; Lambin and Meyfroidt, 2011; Meyfroidt et al., 2018). Additionally, international commodity markets have also considerable influence in management practices, specifically in the type of crops. In Argentina, Brazil and Uruguay, for example, increases in commodity prices drove soybean from being a non-existent crop to become one of the principal exportation products in less than a decade (Grau et al., 2005a). Finally, high-level governance can also impact on land-use decision making by the application of taxes to limit certain management practices, or monetary incentives, such as payments for ecosystem services, to foster ecosystem recovery in managed landscapes (Farley and Costanza, 2010; Corbera and Schroeder, 2011; Pascual et al., 2014; Gianfrate and Peri, 2019).

Social norms have also been stressed as important factors in explaining management practices (Meyfroidt, 2013). Strong social norms can be of great influence on farmers' decision-making, sometimes impeding the adoption of environmentally friendly practices (Minato et al., 2010). The fear of ostracism by their peers can discourage farmers to adopt differentiated practices. However, social ties can also help propagate new management strategies. Recent work has highlighted how the structure of farmers' social network has favoured the propagation of high-intensity irrigation practices in northern Spain (Albizua et al., 2020). Specifically, social networks determine how different farmers access the knowledge and information on which they base their management strategies. Albizua et al. (2021) showed that in northern Spain, farmers using large-scale irrigation are at the core of the farmers' social network and thus have a large influence on the information that is accessed by traditional farmers. The authors argue that while traditional farmers are aware of the environmental impacts of these modern practices, the biased information they obtain from their peers has fostered the adoption of large-scale irrigation.

Finally, changes in land-use management can also be driven by environmental change. The increasing frequency and magnitude of extreme weather events associated with climate change have driven smallholders to diversify economical activities,

leading to shifts from farming to fisheries, or direct wildlife exploitation (Mortimore and Adams, 2001; Cottrell et al., 2019). Alternatively, changes in management practices can come from managers' perception of environmental degradation. While rapid degradation has been linked with the adoption of pro-environmental behaviour, slow, gradual degradation processes often go unnoticed and societies tend to minimize or accept them, e.g. pollution in cities (Meyfroidt, 2013). Incorporating these mechanisms in models of human population and land dynamics is straightforward and requires the inclusion of feedbacks from the ecological/landscape state to management strategies, e.g. stopping agricultural expansion if natural areas drop below a threshold.

Human fertility and consumption: determinants of population changes

The human-land models developed across this thesis are characterized by a reductionist description of human demographic processes. Specifically, it is assumed that the sole driver of human population dynamics is the availability of agricultural resources, thereby ignoring cultural drivers. Moreover, the relationship between both is modelled in a highly simplified way, in which resource production determines a carrying capacity to which human population numbers adapt to satisfy a fixed average per capita consumption. In this description, increased resource accessibility necessarily results in higher fertility and population growth. While this statement holds for pre-industrial societies, during the last two demographic transitions, in the European continent resource accessibility kept growing while fertility diminished (Figure 3.1 b). The explanation of fertility decreases during the demographic transitions is multifactorial and involves technological progress, e.g. large-scale access to contraception, a shift from rural to increasingly industrialised and urban societies in which the economical costs of having children outweigh the benefits, as well as shifts in cultural norms where individual life aspirations oppose to traditional family compositions (Bongaarts and Potter, 2013). Fertility changes are driven by changes in households' decision-making process as a response to changing socio-economical conditions.

Social-ecological models that use a dynamical systems approach have coped with the demographic transition in different ways. Anderies (2003) proposed a description of human population dynamics where fertility is linked to the type of goods consumed by the human population. Specifically, fertility diminishes as consumption shifts from agricultural to industrialized goods. More recently, Henderson and Loreau (2019) introduced a more complex, empirically grounded relationship between human fertility and resource accessibility (Figure 3.1 a). While at low levels, increases in resource accessibility foster fertility growth. However, if resource accessibility is high, further increases diminish fertility. This result in a U-inverted shape for the relationship between fertility and resource accessibility, with a peak at intermediate resource levels. Overall, these models manage to reproduce the demographic transitions by proposing phenomenological descriptions of the relationship between human fertility and resource consumption.

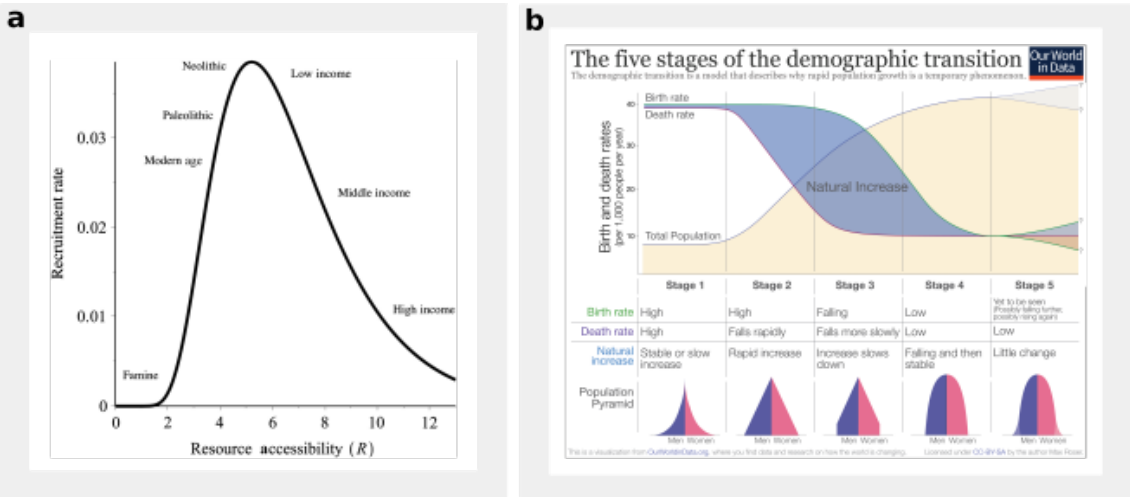

Figure 3.1: a) Example of a curve linking human recruitment rate and resource accessibility. Reproduced from Henderson and Loreau (2019). b) Illustration of the last demographic transition. Departing from a stable, low human population, technological improvements drive the reduction of mortality rates causing an increase in population size. Eventually, social and cultural changes drive the reduction in fertility until it reaches a new equilibrium with mortality. The human population now stabilizes in a high size.

The demographic transitions can be also interpreted through the lens of the child quantity-quality trade-off (Fernihough, 2017). This framework describes the different allocation strategies of resources between children. While prior to the transition fertility was high and families numerous, after the transition fertility decreases resulting in a greater number of resources allocated between fewer children.

Essentially this result in increases in per capita resource consumption rather than in population numbers as a response to increments in resource availability. Another possible expansion to the models developed in this thesis, and also to the models that impose a relationship between resource accessibility and fertility, could be to consider per capita resource consumption as a dynamical variable per se. Rising per capita consumption is highly correlated with income increases, which can be linked to increasing resource production. As a result, increasing resource availability, has the potential to drive either population or consumption growth. Resources surplus can be allocated in increasing the population size or consumption. From this perspective, population and consumption growth are two competing processes, and the speed at which they react to changes in resource availability determines which one dominates. To my knowledge, there is no model of human population dynamics using this kind of approach to account for changes in fertility.

Theories of human decision-making call for Agent-Based Models

Theories of human decision-making are formulated at the level of the individual. While several theories are based on economics, and utility maximization, such as the well-known rational choice theory (Elster, 1986), more recent developments build on knowledge from psychology and incorporate the effect of social norms and interactions on decision-making (Ajzen, 2011). Below, I illustrate this point by presenting an example of a household-level decision-making theory of human fertility, and then discuss on how to better incorporate theoretical developments in the field of decision-making in modelling studies with the use of Agent-Based Models.

In the field of demography, the Economic Theory of Fertility has been used to explain the demographic transitions from a utility maximization process at the household level (Robinson, 1997). In Europe, during the XXth century, industrialization and economic and technological development, were accompanied by progressive decreases in fertility, as societies became increasingly urban (Caldwell, 2006). While in rural societies children constitute work-force that contributes to the household's economy from very early, in highly industrialized and urban societies, children

represent a financial burden for their parents. This is because the need for qualified labour increases the schooling years, postponing children's entry on the labour market. Additionally, the development of contraceptive methods allowed for the households to better control the number of children and thus gave them means to maximize their utility. However, the hypothesis that changes in fertility are only a matter of economic development and resource accessibility, is not that well supported by the demographic transitions in Latin America. In this case, technological developments like contraceptive methods, and social norms favouring decreases in fertility were directly imported from Europe without structural changes occurring in the local economies (de Cosio, 1992; Chackiel, 2004; de Cosio, 2014). As a consequence the demographic transitions occurred extremely fast. This example highlights, the complexity and multi-factorial drivers behind changes in decision-making.

Agent-based approaches are very well adapted to model decision-making processes, as they provide a natural way to implement the postulates of behavioural theories in simulation studies. Thus, they provide a way to describe decision-making processes like shifts in management practices, or in reproductive preferences, in a more empirically grounded way. Overall, agent-based models allow the emergence of system-level patterns for individual-level rules, enriching our understanding of system dynamics. Agent-based approaches can also be used to model high-level governance, through the description of institutions as agents (Geier et al., 2019; Bourceret et al., 2021). In the field of social-ecological modelling in general, and resource and land-use management in particular, agent-based models have been widely used since the early 2000s to describe adaptation in management strategies (Janssen, 2002; Parker et al., 2003). Being individual-based, these approaches are particularly useful to the development of policies aimed at the individual or household levels. However, a recent review argues that most agent-based models in the land-use change literature lack solid theoretical foundations that support the modelling choices regarding decision-making with respect to management practices (Groeneveld et al., 2017). In the field of the social sciences, agent-based approaches have been widely used to model migration processes (Klabunde and Willekens, 2016), but studies that model changes in human fertility are marginal. In particular, social-

ecological agent-based models that describe human population dynamics are scarce and focus on societies from the past (Kohler et al., 2012). Overall, the models developed during this thesis could be expanded by including an agent-based description of demography that could represent with greater accuracy real-world scenarios. With respect to land-use management, the model in Chapter 3 could be expanded by including changes in the farmers management practices influenced by their social interactions. Agent-based approaches are widely present in the social sciences, thus I believe adopting agent-based descriptions in human-land models will contribute to greater interactions between ecologists and social scientists by eliminating methodological barriers.

On modelling ecosystem services provision

The models developed throughout this thesis adopt a simplifying description of ecosystem services, in which ecosystem services provision is collapsed in a single indicator. However, there is important variability on the behaviour of ecosystem services. For example, while the provision of ecosystem services associated with species richness like pollination, will most likely saturate with the area of pollinator habitat, carbon sequestration is likely to exhibit a linear relationship with forest cover. Moreover, the distance at which ecosystem services can flow is also service-dependent. In services provided by animal populations, the flow distance will be related to their dispersion range (Montoya et al., 2021). Finally, the contribution of ecosystem services to agricultural production varies as a function of the services and the type of crop. For example, contrary to fruits and vegetables, cereal production does not depend on animal pollination (Power, 2010).

The design of case-specific sustainable land-use management strategies requires more accurate descriptions of ecosystem services provision, including trade-offs and bundles between services (Bennett et al., 2009). In agricultural landscapes, management strategies often require to compromise the provisioning of some services to accommodate production constraints. Recent modelling work that accounts for the interplay between multiple ecosystem services and agricultural production has been

able to identify trade-offs between ecosystem services in a real-world agricultural landscape to inform best management practices (Balbi et al., 2015). However, there is little integration of these detailed models with complex social-processes that rule changes in decision-making. This would constitute an interesting step-forward for the design of sustainable management practices to be applied in specific landscapes.

There are multiple ways to achieve greater accuracy on the representation of ecosystem services in the type of models developed in this thesis. Possible model extensions could incorporate a more accurate representation of the relationship between habitat area and magnitude of ecosystem services provision, a more empirically grounded modelling of the flow distance for ecosystem services and the consideration of the time delayed effects of land-cover change on biodiversity and thereby on ecosystem services provision. Hereafter, I will expand on these three points.

In all the models developed in this thesis, I based the relationship between ecosystem service provision and natural area on the Biodiveristy-Ecosystem Function literature (Loreau, 2000, 2001) and the well-known concave-down Species-Area Relationship. The assumption I made for all the model is that Biodiversity-Ecosystem Function relationships are also concave down (Loreau, 2001). Assuming that ecosystem services are underpinned by ecosystem functions, this logically results in a concave-down ecosystem services-area relationship, that I modelled through a sub-linear power-law function. However, there is evidence that the spatial configuration of a connected natural fragment can affect species-richness. This implies that two natural fragments with equal area but different shape, e.g. different edge-to-area ratio, do not necessarily harbour the same species richness, thus ecosystem services provision can differ. An alternative to address this issue is to incorporate in the model the Species-Fragmented Area Relationships developed by Hanski et al. (2013). This modified Species-Area Relationships account for patch configuration and have shown better aagreement with empirical measures of biodiversity (Hanski et al., 2013). This approach is used by Montoya et al. (2021) to model pollination services in agricultural landscapes.

I also greatly simplified ecosystem services flows in this thesis. In Chapter 2, I

only included the flow of ecosystem services to the closest neighbours of a landscape cell. In Chapter 3, I relaxed this constraint but adopted a simple description in which a threshold distance is specified. In this formulation, ecosystem services flow without a distance decay. However, empirical evidence shows that in real landscapes there is a progressive decay in ecosystem services provision rather than an abrupt shift (Mitchell et al., 2014). Other theoretical modelling studies have used logistic and exponential decay functions (Mitchell et al., 2015a; Montoya et al., 2021), and data-driven modelling studies have used a multiplicity of decay functions adapted to each of the ecosystem services they model (Bagstad et al., 2013). While this might change quantitatively the results presented in Chapter 3, I do not believe there would be any qualitative difference with respect to the type of equilibria or the mechanisms driven the social-ecological system to sustainability or collapse.

Finally, land-use cover changes in the models presented in this thesis have immediate effects on ecosystem services provision. Although this is accurate, experimental studies have shown that the negative effects of habitat loss and fragmentation on biodiversity and ecosystem functioning can magnify over time, due to time-lagged population extinctions (Haddad et al., 2015). Accounting for time-lagged ecosystem services loss in the models presented in this thesis, will most certainly reduce the parameter ranges over which social-ecological dynamics are sustainable. Time-lag effects biodiversity loss effects were incorporated in recent human-land models and had a significant importance on driving social-ecological systems to collapse (Lafuite and Loreau, 2017; Lafuite et al., 2017, 2018). Specifically, accounting for time-lagged effects would be of great interest when considering adaptive management in social-ecological systems. While management practices could successfully adapt to present conditions, time-lagged effects can undermine the adaptation efforts.

Overall, a more accurate representation of ecosystem services provision can be achieved with a bottom-up modelling approach, from the species to the services. Recent work has modelled the robustness of ecosystem services as a function of species loss (Ross et al., 2021). The authors built on the networks that connect species and their functional traits, to the functions and services they provide at the ecosystem level. Their work provides estimations for how species loss can affect the

robustness of ecosystem services provision depending on the shape of the species-services networks. This same approach could be used in the models developed in Chapter 2 and Chapter 3, by introducing populations of various species and modelling how the changes in land-cover affect their persistence or dispersal capacities. This bottom-up approach would enrich the models developed in this thesis, as they allow the emergence of variation in ecosystem services provision as a response to changes in the species-ecosystem services networks. This could be a suitable way to model different type of ecosystems.

On the effect of urbanization on land-use changes and sustainability

Since the beginning of the XXth century, humanity progressively shifted from rural to urban living. Today, urban dwellers represent around 60% of the total human population against 10% in the 1900s. This trend will continue in the following years, as it is expected that 95% of future population growth will be located in urban areas of the Global South (Grimm et al., 2008a). Although historically cities were compact and densely populated, in the last decades this trend has reversed, and cities are expanding at faster rates than their population (Seto et al., 2011). This represents an important threat to nature conservation, as urban areas are hot-spots of environmental change, with effects that can propagate at regional and global scales (Grimm et al., 2008a; Seto et al., 2012b). The dynamics of urban land-cover were not considered in this thesis and in all the models I developed, human population was considered as non-localized and external from the landscapes. In this section, I discuss the effects of urban growth on the biosphere at local scales, and the feedbacks it can have on agricultural landscapes at regional and global scales. Finally, I discuss the potential ways of introducing urbanization processes in models of human population and land dynamics.

Urban expansion represents the most extreme type of land transformation, and its effect on local land-cover is almost irreversible, if not entirely (Seto et al., 2011).

The effects of urban expansion in local ecosystems range from habitat loss and fragmentation, increasing air and water pollution, alteration of biogeochemical cycles to changes in city climate (Grimm et al., 2008b). Additionally, urban areas sometimes grow over fertile agricultural land, displacing agriculture to marginal, less fertile land (Fazal, 2000; Jiang et al., 2013). As a consequence, the expansion of urban areas has a huge impact on local ecosystem services provision. River and coastline ecosystems are the most affected and threatened by urban expansion because human settlements were more likely located near to water courses(Grimm et al., 2008b). In China for example, a 1800 km long urban continuum is projected to occur along the East coastline (Seto et al., 2012a). Furthermore, in the near future, some of the places with higher forecasted rates of urban growth are located in biodiveristy-hotspots like the rainforests of West Africa or Sri Lanka (Seto et al., 2012a).

Although the growth of cities is a threat to the biosphere, studies have argued that the key to future sustainability is on increasing urbanization (Bettencourt et al., 2007, 2010; Lobo et al., 2013). Bettencourt and West (2010) argue that increasing interactions between humans fostered by high-population densities are the drivers of innovation. These studies bet on further technological development as the way to achieve sustainability. While this is on the realm of the possible, it represents a risky bet. Recently, Soga and Gaston (2016) have shown that increasing urbanization has led to a disconnection between humans and nature, a process called "extinction of experience" that represents an obstacle to the adoption of pro-environmental behaviour.

Although in average urban land-cover is ten times smaller than agricultural areas, the effects of urbanization on global land-use change are important. The shift from rural to urban living has been generally accompanied by industrialization, economic growth and significant societal changes. Specifically, urbanization has been linked with increments of quantity and diversity of food intake. The access to markets and higher incomes explain the dietary shifts, among other reasons (Pandey et al., 2020). As a consequence, the shift to urban living contributes to further increasing global demand for resources, fostering agricultural expansion and intensification in

far away locations. As follows, urbanization, through the changes in consumption patterns it induces, is also a significant driver of land-use change in rural landscapes (Seto et al., 2012b).

In the near future, cities will continue growing, and the fraction of the human population in urban areas will keep increasing. Thus, incorporating urbanization processes in models of human population and land dynamics would be a considerable step-forward to increase the pertinence of the models towards real-world sustainability problems. The effects of urban expansion on the landscapes can occur at local scales through the direct changes in land-cover and alteration of the local ecosystems, but also at regional and global scales through changes in consumption patterns. Tackling the latter will require implementing spatially explicit description of urban expansion, placing the modelled populations in the landscape. Regarding the former, approaches that introduce social heterogeneity through multiple social groups with different consumption levels can be a way to represent urbanization processes without modelling explicitly urban areas (e.g. Henderson and Loreau (2021)). In these approaches, the human flows between different socio-economical groups with distinct consumption, can represent in a spatially implicit way rural-to-urban migration, thereby accounting for the indirect effects of urban growth on rural land-use.

On the effect of globalization on land-use change and food security

Globalization has increased the complexity of land-use changes processes by incrementing long-range interconnections between human societies and landscapes across the world (Meyfroidt et al., 2018). In some cases this has led to the acceleration of agricultural expansion and intensification in landscapes far from the consumption places (Lambin and Meyfroidt, 2011). Additionally, food supply chains have also become highly complex, and depending on international resource exchanges, e.g. soybean production in South America destined to cattle feeding in Europe for local

consumption (Lambin and Meyfroidt, 2011). As a consequence, social-ecological dynamics in one place are highly influenced by distant places, thereby making global sustainability a complex issue that depends on the numerous social, economical and ecological interactions between world-regions. Furthermore, the decoupling between production and consumption sites has also diminished the perception that consumers have of their environmental footprint, delaying possible shifts to more environmentally friendly consumption patterns (Meyfroidt, 2013). In this thesis I examined the effect of land-use management strategies in the coupled dynamics of a single homogeneous population that transformed a single, isolated landscape. In this section, I discuss the mechanisms through which globalization affects land-use dynamics, and the importance of international food trade on global food security. Finally, I summarize on the interest of considering globalization in models of human population and land dynamics and suggest ways to move forward.

The impacts of globalization on distal land-use changes occur through displacement, rebound, and remittances effects (Lambin and Meyfroidt, 2011). Displacement occurs when agricultural activities in one place migrate to another location. Displacement has often been linked to the enforcement of nature conservation policies. By locally discouraging or prohibiting agricultural activities, the pressure for land-conversion is displaced to other regions with less policy constraints or better economic opportunities (Lambin and Meyfroidt, 2011). This generally drives agricultural expansion and intensification in countries of the Global South, where the lack of strong institutions impedes the enforcement of nature conservation. While it has been suggested that above a certain level of per capita income, economical growth fosters environmental quality, a phenomenon known as environmental Kuznets curve, this effect is many times due to the displacement of environmental degradation to other regions (Roca, 2003). In the last decades, many countries experienced and expansion of forest cover in detriment of agriculture, however this was accompanied by increasing imports of agricultural goods (Erb et al., 2009; Jadin et al., 2016). Nowadays, displacement also takes the form of "land-grabbing", i.e. capital-rich but land-poor countries buy large land areas in capital-poor and land-rich regions to cultivate export crops. Specifically, land-cover changes in Africa over

the last decade constitute a paradigmatic example (Lambin and Meyfroidt, 2011).

Rebound effects are associated with agricultural intensification failing to spare land and fostering, through economical feedbacks, further agricultural expansion. Specifically, the adoption of technological improvements that increase agricultural production efficiency many times results in increased profitability of agricultural activities (Lambin and Meyfroidt, 2011). When markets in the importing countries have a large potential for expansion, this stimulates further agricultural expansion in producing countries like it happens with soybean and oil palm production in South America and Indonesia respectively (Fearnside, 2001; Grau et al., 2005a; Curran et al., 2004). Finally, remittances effects are caused by the out-migration from poor rural areas, that increases the inflow of remittances from the migrants to their families (Adger et al., 2002). Although documentation of the remittances effect is scarce (Lambin and Meyfroidt, 2011), it has been shown that it promotes the recovery of natural habitat by fostering the abandonment of agriculture (Hecht and Saatchi, 2007) and the diversification of economic activities, sometimes linked with ecotourism (Zimmerer, 2007).

Globalization has fostered increasing complexity of international food-trade networks and food-supply chains. Today, around one-quarter of the agricultural resources consumed in the world are accessed via international trade, and several countries depend on imports to satisfy internal food demand (Marchand et al., 2016). It has been shown that the frequency and amplitude of production shocks in the commodity trade network have increased in the last decades, mostly due to extreme weather events like droughts or floods, and geopolitical crisis (Cottrell et al., 2019). This is a source of concern, because the effect of sudden production losses, i.e. shocks, can cascade through the trade network, therefore affecting multiple regions. A recent study showed that the indirect effects, caused by the propagation of a production shock through the trade network, are significantly higher than the effects suffered at the shock location (Inoue and Todo, 2019). Furthermore, societal adaptations to production shocks can involve expanding and intensifying agriculture, or shifting food production to fisheries and wildlife, thereby incrementing environmental degradation (Cottrell et al., 2019). As it is expected that the effects of global

climate change will continue to foster sudden production losses, recent studies have analyzed the resilience of current food trade-network. These studies have examined through a mix of modelling and empirical approaches, the effect of different network topologies, on the resilience to production shocks to comprehend how changes in the evolving food-trade network can affect sustainability (Kharrazi et al., 2017; Inoue and Todo, 2019; Tu et al., 2019). Specifically, they have found that the effects of changing network properties like connectivity and modularity, are highly dependent on the type of network (Tu et al., 2019), and that in scale-free networks like the food-trade one, cascading effects of shocks are more prominent and persistent (Inoue and Todo, 2019).

Overall, globalization has amplified the number of processes that can influence land dynamics. Furthermore, it has brought inter-dependencies, between remote places that make sustainability a global concern rather than a local one. Recent modelling studies that address the effect of globalization on sustainability have focused on the resilience of trade networks (Tu et al., 2019), without considering the effect of resource exchanges on the ecosystems nor the populations. Incorporating resource and human flows in models of human population and land dynamics would improve our understanding of the effects of globalization in human-land systems. Although recent work has made progress in this direction by considering trade and migratory flows between two regions in a human-land model (Henderson and Loreau, 2019), further efforts should focus on incorporating multiple regions with connections that replicate real trade and migration networks.

Concluding thoughts

In this thesis I contributed to advance our knowledge of the effect of agricultural land-use management strategies on the sustainability of social-ecological systems. I adopted a modelling approach and developed models describing the coupled dynamics of human population numbers and agricultural landscapes. Overall, this thesis highlights the crucial importance of considering social-ecological feedbacks

for the development of sustainable management strategies. Future models of human population and land dynamics should focus on integrating urbanization processes and long-range connections between land and human systems through migrations and trade. Further advances will need a greater integration between the social and ecological sciences. Specifically, more modelling studies should incorporate human population dynamics, since although a taboo, the growth of human population numbers represents a threat to nature conservation. I believe that progress would be made by adopting agent-based approaches that consider the drivers of fertility changes. Since this approach is increasingly common in social-sciences it will favour the interactions between disciplines by erasing methodological boundaries.

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TITRE:
MODÉLISATION DE L'EFFET DES STRATÉGIES DE GESTION DE L'UTILISATION DES SOLS SUR LA DURABILITÉ DES SYSTÈMES SOCIO-ÉCOLOGIQUES

DIRECTEURS DE THÈSE:
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DATE ET LIEU DE SOUTENANCE:
Lundi 6 Décembre 2021, à la Station d'Écologie Théorique et Expérimentale,
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RESUMÉ:

La croissance de la population humaine et la consommation de ressources par habitant exercent une pression sans précédent sur la biosphère. Pour accroître la production de ressources, les sociétés humaines du monde entier transforment de vastes étendues de terres naturelles en terres agricoles, avec des conséquences négatives pour la biodiversité et les écosystèmes. Or, la production agricole dépend largement des services fournis par les écosystèmes. Cela soulève des inquiétudes justifiées quant à la durabilité des systèmes agricoles actuels, puisque la poursuite de la dégradation des habitats naturels peut compromettre la production de ressources à l'avenir. Cette thèse aborde cette question du point de vue de la modélisation socio-écologique. Des modèles mathématiques et computationnels de la dynamique couplée de la population humaine et de la couverture des sols sont développés pour explorer l'effet de multiples rétroactions bidirectionnelles entre les systèmes humains et naturels sur la durabilité. Ce travail donne un aperçu des risques d'une politique naïve d'utilisation des terres et de l'effet des rétroactions entre la fragmentation de l'habitat et la prise de décision humaine, ainsi que de l'interaction entre l'échelle spatiale et la stratégie de gestion de l'utilisation des terres, sur la durabilité.

MOTS-CLÉS:

Systèmes socio-écologiques, Modélisation mathématique, Modélisation computationnelle, Gestion de l'utilisation des sols, Écologie théorique, Durabilité des systèmes agricoles, Dynamiques homme-nature.

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UNITÉ DE RECHERCHE:
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TITLE:
MODELLING THE EFFECT OF LAND-USE MANAGEMENT STRATEGIES ON THE SUSTAINABILITY OF SOCIAL-ECOLOGICAL SYSTEMS

THESIS ADVISORS:
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SUMMARY:

The growth of human population numbers together with per capita resource consumption is exerting unprecedented pressure on the biosphere. To enlarge resource production, human societies worldwide are transforming vast extents of natural land to agriculture with negative consequences for biodiversity and the ecosystems. However, agricultural production significantly depends on the services provided by the ecosystems. This raises justified concerns on the sustainability of the current agricultural systems, since further degradation of natural habitats can jeopardize resource production in the future. This thesis addresses this issue from a social-ecological modelling perspective. Mathematical and computational models of the coupled dynamics of human population and land-cover are developed to explore the effect of multiple bi-directional feedbacks between human and natural systems on sustainability. This work provides insight on the risks of naive land-use policy-making and the effect of feedbacks between habitat fragmentation and human-decision making, and the interplay between land-use management scale and strategy, on sustainability.

KEYWORDS:

Social-ecological systems, Mathematical modelling, Computational modelling, Land-use management, Theoretical ecology, Sustainability of agricultural systems, Human-land dynamics.

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