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LETTER

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Habitat percolation transition undermines sustainability in social-ecological agricultural systems

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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.

KEYWORDS
habitat fragmentation, landscape ecology, land-use management, percolation transition, social-ecological systems, spatially explicit model, sustainable agriculture

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 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 & 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 & 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 & Alexander, 2017). Low-intensity, wildlife-friendly farming (Chappell & LaValle, 2011; Perfecto & Vandermeer, 2010) 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 & 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 (Balmford et al., 2019; Phalan et al., 2011). Rather than mixing agriculture with biodiversity conservation, 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 fertilisers, 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 & 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 (Baldassini & Paruelo, 2020; Boers et al., 2017; Ordway et al., 2017; Ruiz-Vásquez et al., 2020; Staal et al., 2020; Stoy, 2018; Tölle et al., 2017).

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 & Stauffer, 1991). 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 (Gardner et al., 1989; O'Neill et al., 1988), biodiversity conservation (Boswell et al., 1998; With, 1997) and species distribution (He & 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, Suarez-Castro, et al., 2015). 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 modelling 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 (Balbi et al., 2020; Motesharrei et al., 2014). Models that account for population dynamics (Bengochea Paz et al., 2020; Cazalis et al., 2018; Henderson & Loreau, 2019, 2020; Lafuite et al., 2017, 2018) 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 was 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 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 centralised 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 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-dimensionalisation in Appendix 1.

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 neighbouring cells. Empirical evidence shows that ecosystem service supply scales nonlinearly 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, Bennett, et al., 2015) or concave-down based on the Biodiversity-Ecosystem Function literature (Hooper et al., 2005; Loreau, 2000, 2001). 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 for the choice of the exponent value). Assuming that the flow of ecosystem services is limited to the closest neighbours of a natural cell yields the following expression for the total amount of service provision ε_i in cell i

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

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 neighbourhood and constrain the non-dimensional ecosystem services provision within the interval $[0,1]$ using the $1/4$ normalisation factor (see Appendix 1 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 (Dainese et al., 2019; Gallai et al., 2009; Garibaldi et al., 2011; Power, 2010), 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

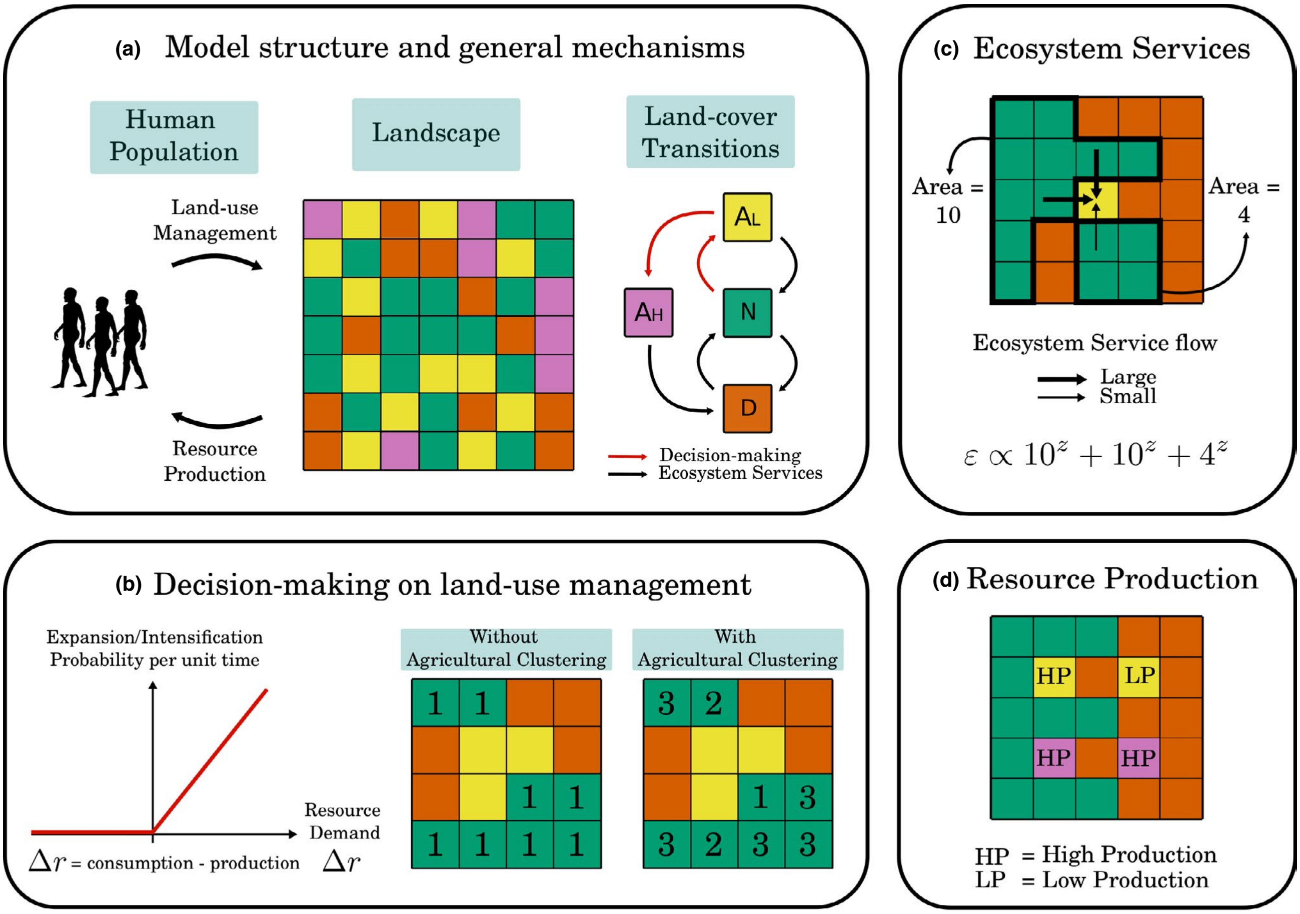

FIGURE 1 Conceptual diagram of the social-ecological model. (a) The relation between the human sub-system and the landscape is done via resource production. The abundance or lack of resources drives human population dynamics and land-use management decision making. The landscape is modelled as a square lattice where each cell is characterised 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 with 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

$$Y = \sum_{i \in \mathcal{A}_L} \left(y_0 + \varepsilon_i\right) + y_1 \sum_{i \in \mathcal{A}_H} 1, \tag{2}$$

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 1 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:

$$\frac{dP}{dt} = P\left(1 - \frac{P}{Y(t)}\right). \tag{3}$$

Note that the per capita consumption per unit time does not appear explicitly in the carrying capacity as it is encapsulated in the non-dimensionalisation of the population density (see Appendix 1 for details). Both P and Y are non-dimensional in Equation 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 as follows:

$$\pi_E(i) = \begin{cases} \frac{1}{M|\mathcal{N}|}\,\sigma\,\Delta r\,(1-\alpha), & \text{if}\,\Delta\text{r} > 0 \\ 0, & \text{otherwise.} \end{cases} \tag{4}$$

$$\pi_I(i) = \begin{cases} \frac{1}{M|\mathcal{A}_L|}\,\sigma\,\Delta r\,\alpha, & \text{if}\,\Delta\text{r} > 0 \\ 0, & \text{otherwise.} \end{cases} \tag{5}$$

$|\mathcal{N}|$ 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 normalisation 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 neighbourhood of low-intensity agricultural cells and intensify low-intensity cells in the neighbourhood of high-intensity ones. The larger the number of neighbours, the most probable the transition (see Appendix 1 for details on the formalisation). 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 the following equation:

$$\pi_L(i) = \rho_L\left(1 - \varepsilon_i\right), \tag{6}$$

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 a 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 recolonisation of a degraded cell by species present in neighbouring 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 as follows:

$$\pi_R(i) = \rho_R \varepsilon_i, \tag{7}$$

$$\pi_D(i) = \rho_D \left(1 - \varepsilon_i\right), \tag{8}$$

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)'s Stochastic Simulation Algorithm coupled with a Runge-Kutta 4 solver for the population density differential equation (see Appendix 3 for details and pseudo-code). By individually simulating every land-cover transition, Gillespie's algorithm generates exact realisations 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 40 × 40 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 characterise 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 four 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 clustering 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 initialising the landscape in a lowly managed state, that is 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 5, where we make it explicit). The initial human population size was initialised at equilibrium with production. For the bifurcation diagrams in Figure 2b, d and the heatmap of 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, and a sensitivity analysis of the model in Appendix 4.

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 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 stabilising effect on the system dynamics and leads to a sustainable state in the long-term (Figure 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 2a, b purple lines).

Introducing agricultural intensification results in the disappearance of reversible collapses (Figure 2d). A small area of intense agriculture is sufficient to prevent landscape recovery following a collapse, making the degradation irreversible (Figure 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 2d). In this case, intensification limits agricultural expansion and decouples resource production from ecosystem services provision which contributes to stabilising 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 2a, c).

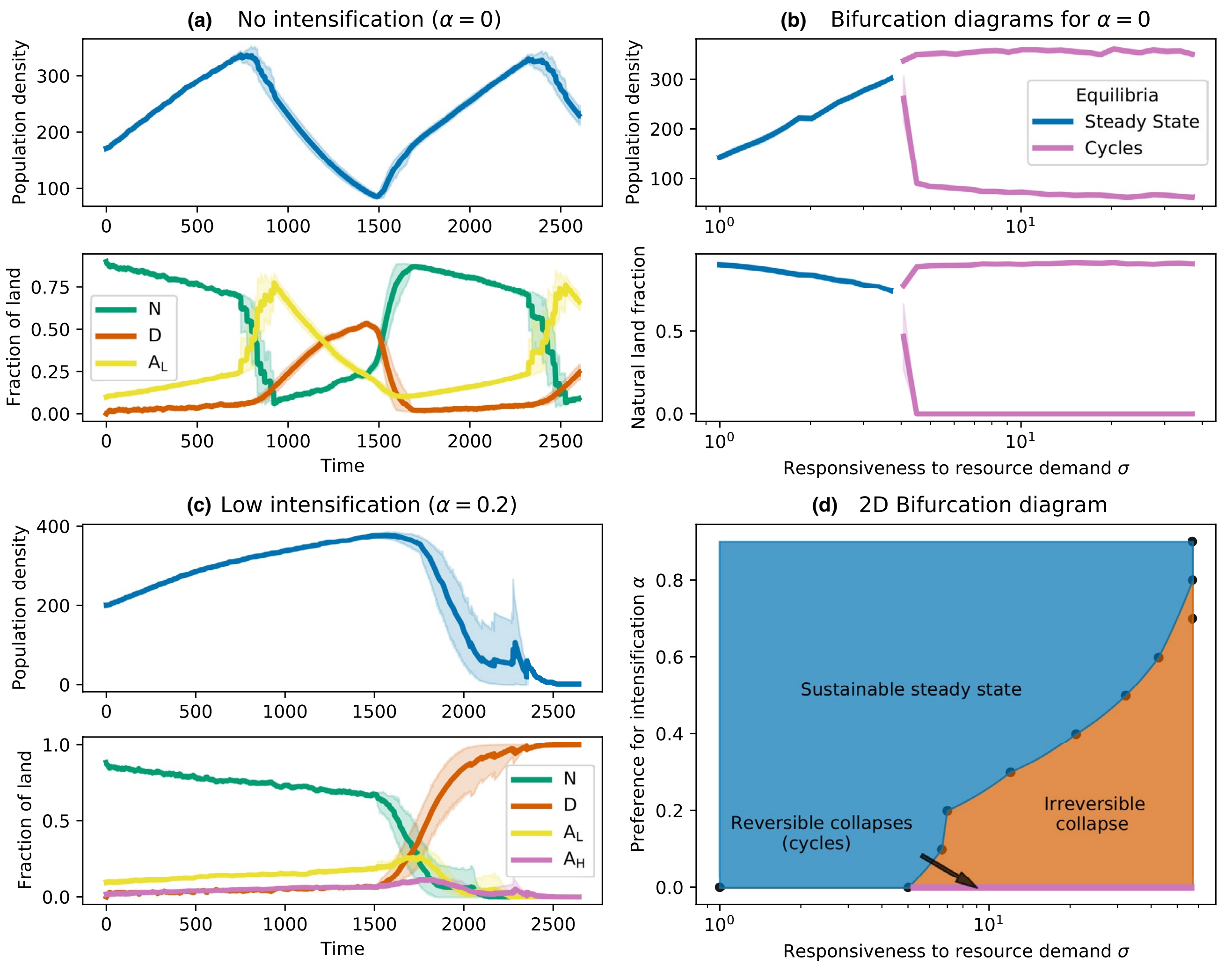

FIGURE 2 Effect of agricultural intensification on the temporal dynamics and the long-term states of the system. (a) Collapse-recovery cycles in the absence of agricultural intensification ($\alpha = 0$) and clustering ($\omega = 0$) when the responsiveness to resource demand is high ($\sigma = 10$). 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 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 $\sigma \in [1-40]$ into 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 5. (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 a 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

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 in 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 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 3a). The disappearance of large natural fragments results in a diminution of ecosystem services provision (Figure 3b) which translates into a marked reduction in resource production (Figure 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.

Preventing landscape fragmentation by clustering agricultural land

Agricultural clustering decouples habitat loss from habitat fragmentation, thereby diminishing the effects of a percolation transition (Figure 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 4a), in agreement with percolation theory. In Figure 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 stabilise social-ecological dynamics and lead to sustainable steady-states in the long term (Figure 2d & Figure 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 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 5).

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

TABLE 1 Description of the model's non-dimensional parameters and numerical values used for the simulations presented in this article. Details regarding the parameter values can be found in Appendix 2. Details on the impact of the parameters with fixed values on the social-ecological dynamics can be found in Appendix 2

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

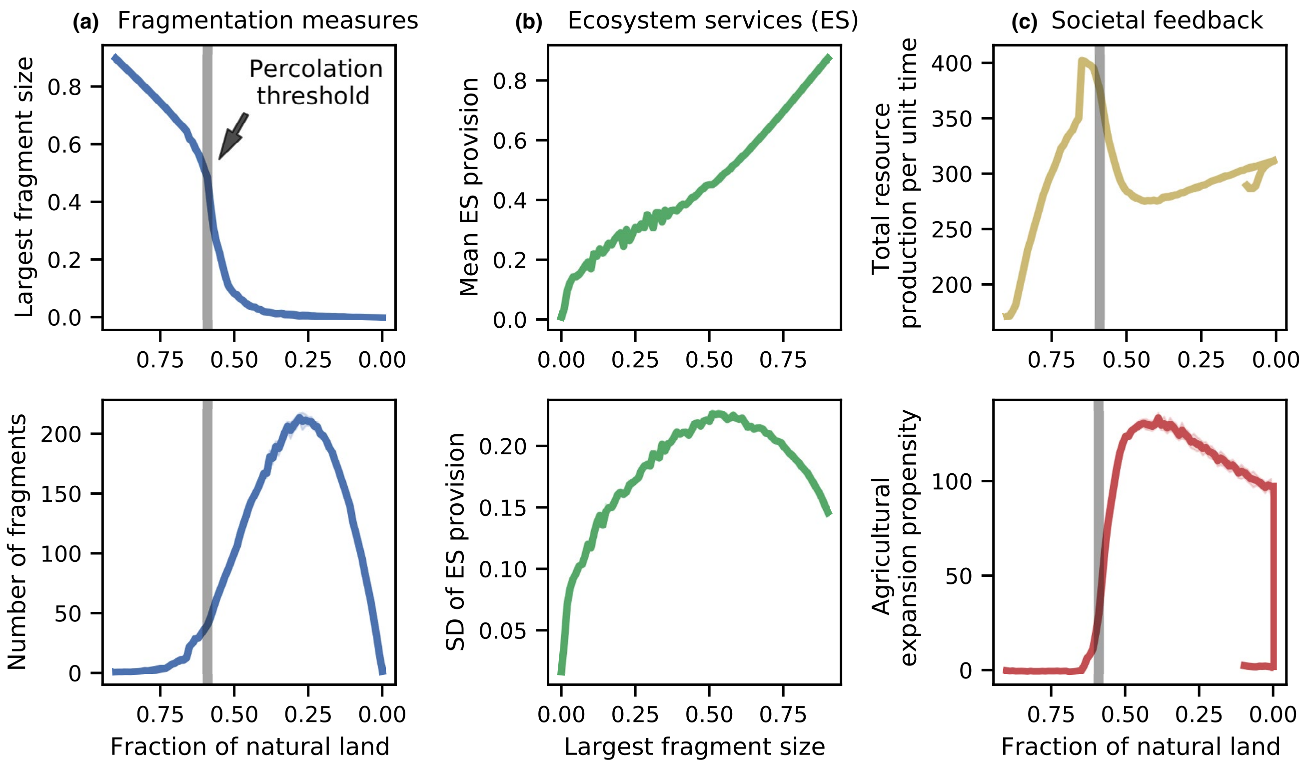

FIGURE 3 Signatures of a habitat percolation transition and the effects of habitat fragmentation on ecosystem services and land-use changes. (a) Measures of habitat fragmentation. Both the size of the largest natural fragment in the landscape and the number of fragments present a highly nonlinear relationship 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 ($N \simeq 0.59$, grey 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 the 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 no 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 realised 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 1

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 in 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 the 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, modelling 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

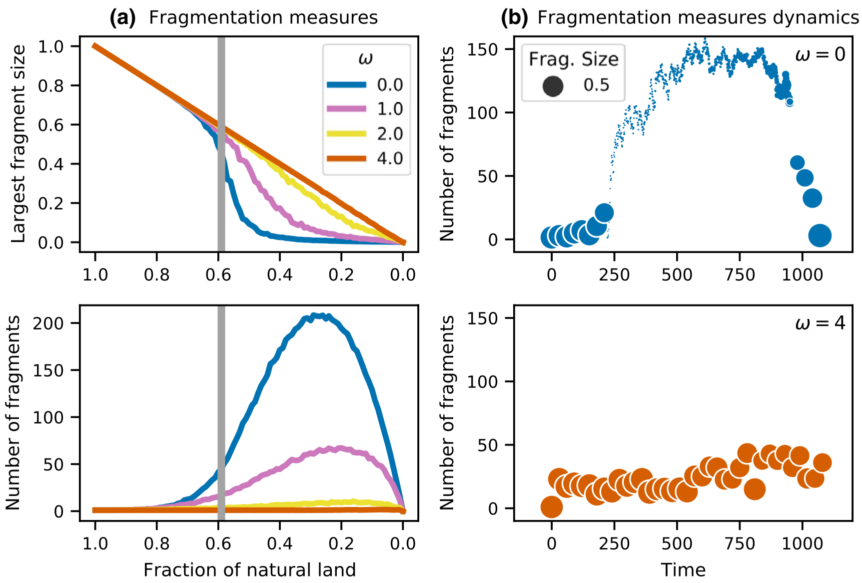

FIGURE 4 The effect of agricultural clustering on preserving landscape connectivity and the avoidance of a percolation transition. (a) Fragmentation metrics as a function of the fraction of natural land for different values of agricultural clustering. Increasing agricultural clustering results in a linearisation 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 3 a, the curves are not obtained by realised model dynamics but by calculating the fragmentation measures just after initialising 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 an 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 an average of 40 replications. Parameter values are as follows: $\alpha = 0$, $\sigma = 10$. Values for the rest of the parameters are specified in Table 1

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 in 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 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 (Fletcher et al., 2018; Haddad et al., 2015, 2017). 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

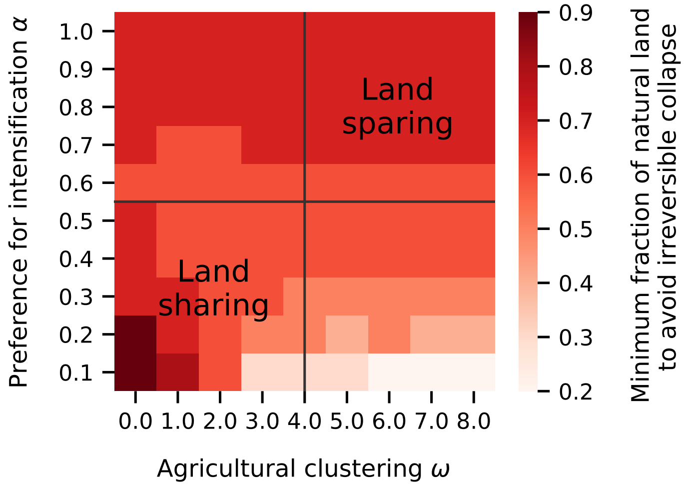

FIGURE 5 Suitability of different land-use management strategies as a function of the landscape's initial conditions. The colours show the minimum fraction of natural land needed to be certain that a given land-use management strategy will not lead to an irreversible collapse. This puts into perspective some of the aforementioned results, as it shows that the success of intensification strategies is 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 initialised 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 1

ecosystem service provision (Bregman et al., 2014; Haddad et al., 2015) and thus agricultural production, resulting in a 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 Bennett, & Gonzalez, 2014; Mitchell, Bennett, et al., 2015), 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). For the latter, we show that the stronger the dependence of yields on ecosystem services, the larger the production drop (see Appendix 2). 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 land sparing vs. land 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 characterisations 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, that is land-sharing (Fahrig, 2017; Perfecto & Vandermeer, 2010), or to separate the natural from high-intensity agricultural areas, that is land-sparing (Balmford et al., 2005, 2019; Phalan et al., 2011), 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 transition 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 (Camba Sans et al., 2021; Finch et al., 2021) and stabilising human-land dynamics to reach sustainability in the long term. Our model describes connectivity as touching neighbouring 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 (Balmford et al., 2019; Phalan et al., 2011). 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 (Kremen, 2015; Tscharntke et al., 2012), 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 clusters where there formerly was intensive agriculture, that cannot recover passively, which is in agreement with previously reported detrimental effects of intensive agriculture on ecosystems (Chappell & LaValle, 2011; Dale & Polasky, 2007; Galloway et al., 2008; Montgomery, 2007; Tilman, 1999; 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

Globalisation 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 globalisation 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.

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AUTHORSHIP

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

PEER REVIEW

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OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at: https://doi.org/10.5281/zenodo.4905944

DATA AVAILABILITY STATEMENT

All the code and information needed to reproduce our simulations and analyse the data to obtain the results can be found in https://doi.org/10.5281/zenodo.4905944.

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