Land-use and species tipping points in a coupled ecological-economic model

Abstract

Complex systems can have tipping points where the system behavior changes abruptly from one regime to another. We develop an ecological-economic model that simulates the spatio-temporal dynamics of the land-use induced by a tradable permit market and its consequences on the viability of a model species. The model analysis reveals that the land-use dynamics are subject to a tipping point with regard to changes in policy scheme design. One the level of species viability, this tipping point is amplified and a second tipping point emerges. The two tipping points interact and their location and sharpness depend on the characteristics of the species. We conclude that in the consideration of coupled ecological-economic systems tipping points can play an important role. The existence of tipping points considerably complicates the design of policy instruments for the sustainable management of ecological-economic systems because a small change in the policy design can have dramatic consequences on the system dynamics.

Highlights

- We analyze tipping points of an ecological-economic model
- The tipping points depend on the characteristics of the conserved species
- The ecological and economic tipping points amplify each other

Key words: Conservation, ecological-economic model, metapopulation, tipping point, tradable permits

1. Introduction

Systems with heterogeneous and interacting agents often show complex behavior, such as feedback loops and discontinuous or abrupt changes. Such abrupt changes are often termed tipping points and can occur in many types of systems, including physical, economic and ecological ones (Polhill et al. 2006, van Nes 2006). They all have in common that they are difficult to predict and associated with irreversibility such that once a tipping point has been crossed it is difficult or even impossible to move the system back to the original state.

Tipping points, i.e. rapid transitions between different types of structure or behaviour of a system, were first reported and analyzed in physical systems where they are termed phase-transitions (Reif 1965). Popular examples are the transitions between the solid, liquid and gaseous phases of water and other substances, or between the magnetic and non-magnetic states of iron and various other metals. In the social sciences, tipping points have, e.g., been observed with regard to opinion dynamics on networks (e.g., Holme and Newman 2006). The network structure describes which agents interact with each other. The variable of interest – the system state – is whether a certain opinion (e.g. a political preference) persists within the network. When certain model parameters describing the network topology (who interacts with whom) or the probability of an agent adopting a new opinion are varied, a discontinuous change in the system may occur. Another example is Schelling's famous model of social segregation where the spatial structure of neighborhoods abruptly changes when preferences of the residents are varied (Schelling 1978).

An ecological phenomenon related to tipping points is extinction vortices that characterize the extinction of species (Gilpin and Soulé 1986): Often, the extinction of species starts with habitat loss and fragmentation associated with land-use change, which reduces species populations to smaller numbers. These are more vulnerable to environmental influences including stochastic fluctuations. Environmental fluctuations can by chance further reduce population sizes where they become vulnerable to demographic stochasticity (caused, e.g., by adverse sex ratios and stochasticity in the sequence of birth and death events). Once a species is trapped in an extinction vortex it is difficult to save it.

To prevent species from extinction it is therefore necessary to stop threatening processes from the early beginning. This includes stopping habitat loss and fragmentation and improving the conditions of species in the remaining habitats. Habitat loss often results from the conversion of natural or extensively used land into settlements, industrial areas or intensive agriculture. The main reason for such conversions is that the new land-use types are more profitable than the original ones (MAE 2005). Market-based conservation instruments (EC 2005, OECD 2012) try to counteract this economic pressure, e.g., by financially supporting biodiversity-friendly land use through payments for environmental services (PES: Engel et al. (2008)), or by financially rewarding biodiversity-friendly land use and discouraging adverse land uses through tradable land-use permits (Panayatou 1994, Hansjürgens et al. 2011).

In a tradable permit system a conservation agency, like an environmental ministry, sets a minimum level of an environmental good that has to be produced in a region (e.g., total amount of habitat for a target species). Here the agency does not prescribe at which particular locations in the landscape conservation measures must be carried out, but each land user can decide on whether to conserve habitat and sell the associated land-use permits on the market or buy land-use permits and use the land for economic purposes (e.g., agriculture). An advantage of this approach is that land users can adapt to changing conditions (e.g. changing economic costs of conservation).

Originally designed for emissions control, Drechsler and Wätzold (2009) applied the tradable permit approach to the field of biodiversity conservation, taking into account that spatially connected habitats generally are ecologically more valuable, i.e. have a stronger influence on population viability, than isolated ones. This required introducing some kind of neighborhood bonus, as it has been suggested by Parkhurst et al. (2002). The neighborhood bonus implies that the creation of a habitat next to other habitats earns more permits than the creation of an isolated habitat, and the destruction of a connected habitat requires more permits than the destruction of an isolated habitat. Drechsler and Wätzold (2009) showed that such a market is subject to a tipping point: if the neighborhood bonus is small compared to the spatial heterogeneity of conservation costs the emerging land use will lead to spatially dispersed habitats while for large neighborhood bonuses the habitats will be clustered. Between these two "phases" there is a discontinuous transition – a tipping point.

The number, size and spatial arrangement of habitats have a decisive influence on the survival of the species in a landscape (Hanski 1999, Frank and Wissel 2002, Hanski 2015). Loss and fragmentation of habitat are major factors responsible for the decline of species worldwide (MEA 2005, Haddad et al. 2015). To counteract these processes several strategies have been discussed such as habitat restoration and the establishment of dispersal corridors and stepping stones to increase the total amount and the spatial connectivity of habitats (Fischer et al. 2006, Ayram et al. 2015).

Habitat loss and fragmentation are interrelated and difficult to separate, since the former affects the latter (Fahrig 2003, Hanski 2015). The impact of habitat loss on habitat fragmentation has recently been observed in a global study of rainforest fragmentation (Taubert et al. 2018). The authors are able to explain the observed spatial patterns of rainforest remnants by a simple spatially random process of habitat loss and predict that if this process continues, a tipping point will be reached soon at which the proportion of small forest remnants and the isolation of these remnants abruptly increase. This type of tipping point can be observed in many spatial systems and is termed a percolation threshold (Staufer and Aharony 1994).

The impact of such a habitat loss and fragmentation process on the viability of a species population has been analysed by Oborny et al. (2007) who find that by crossing the percolation threshold the viability of the population abruptly declines.

Altogether, both the tradable permit market and the species dynamics on the resulting landscape are subject to tipping points and the question arises what happens if both components are coupled and the response of the species to the permit market is analyzed. Will the tipping points amplify or attenuate each other? Our main focus in the present study will be the effect of policy parameters (the amount of permits that have to be produced in the model region and the magnitude of the neighborhood bonus) and species parameters (the species colonization and local extinction rates) on species survival and possible tipping points. A similar coupled ecological-economic model has been analyzed by Hartig and Drechsler (2009). However, it focused on the cost-effectiveness of different market designs and ignored the issue of tipping points in the system.

2. Methods

The following section describes the economic module and the integration of the ecological module into the economic module. The two modules and their interaction as well the procedures for the model analysis (see below) were implemented and coded in C++. The section concludes with a description of the way in which the combined model is analyzed.

2.1 Economic module

The economic module simulates a market for tradable land-use permits where a conservation agency imposes on each land user the obligation to conserve some of his or her land. If a land user conserves more land than demanded by the agency the excess conservation effort can be sold to other land user in the region through land-use permits. In turn, a land user who wishes to conserve less land than required can buy some of these land-use permits on the market to compensate for his or her shortfall of conservation effort. The module has been described in detail by Drechsler and Wätzold (2009). Below we provide a brief outline.

We consider a region of land parcels arranged in a square grid. Each land parcel *i* is owned by a land user and can be managed in two ways: conservation (i.e. creation of habitat for some target species) or economic use, such as (intensive) agriculture or forestry. Conserving a land parcel *i* reduces agricultural or forestry profits on the land parcel, which reflects in conservation (opportunity) costs of magnitude z_i. The z_i are assumed to be uncorrelated uniform random numbers drawn from the interval [1-σ, 1+σ], where σ denotes the cost variation. To model economic change the conservation costs z_i are randomly re-drawn in each time step (year). Economic use does not earn any land-use permits while conservation of a land parcel *i* generates land-use permits of an amount

$$v_i = 1 + wm_i$$

where m_i is the proportion of conserved land parcels in the Moore neighbourhood around land parcel *i*. The Moore neighbourhood consists of the eight land parcels adjacent to land parcel *i*. Parameter *w* is the weight attached to the presence of other habitats in the Moore neighbourhood. It is chosen by the policy maker and can take any non-negative value. If $w = 0$ conserving a land parcel adjacent to other conserved land parcels generates as many land-use permits as the conservation of an isolated land parcel. An isolated land parcel generates land-use permits of an amount $v_i = 1$. If $w > 0$ conserving a land parcel adjacent to other conserved land parcels increases the amount of generated land-use permits by wm_i. Therefore, by choosing a large (small) value of *w* the conservation agency can set a strong (weak) incentive to the land users to conserve land particularly next to other conserved land.

The conservation agency imposes an obligation on each land user i to generate a certain amount N of land-use permits. The maximum of land-use permits a single land user can ever generate from his or her land parcel is $1+w$ which is obtained when the land parcel is conserved and completely surrounded by conserved land parcels ($m_i = 1$). Rather than demanding this maximum the agency demands from each land user to generate a certain proportion of it. The proportionality factor is denoted as $\lambda \in [0,1]$, so each land user has to generate an amount of $N = \lambda(1+w)$ land-use permits. To interpret the two extreme values of λ, a value of $\lambda = 0$ implies that no land-use permits have to be produced and there is no conservation in the model region while λ=1 implies that each land user has to generate the maximum possible amount of land-use permits and all land parcels need to conserved. For λ in between not all but some land will be conserved in the model region.

The land users are allowed to trade permits (meaningful only for $0 < \lambda < 1$). Assuming that each land user maximises his or her profit, for land parcels with low conservation costs z_i it is likely to be profitable to generate more land-use permits than required and sell the excess permits on the market. For land parcels with high conservation costs, in contrast, it is likely to be profitable to buy land-use permits on the market which allows conserving less and instead carrying out profitable agriculture or forestry. Through interaction between the land users a permit market emerges, together with an equilibrium permit price which is reached when supply and demand of land-use permits are equal. This (partial) equilibrium is assumed to be reached in each individual model time step.

Two important policy parameters are contained in the tradable-permit scheme: λ which controls the total amount of habitat in the study region, and w which (in relation to the magnitude of the cost variation σ) controls whether habitat patches are clustered or dispersed in the region. As outlined above, for large w the incentive to conserve land adjacent to other conserved land is high, so conservation activities are likely to agglomerate in space; while for small *w* the incentive to agglomerate conservation activities is low and land users will generate a more scattered pattern of conserved land parcels (Drechsler and Wätzold (2009)). In the following we denote a particular combination of the two policy parameters λ and *w* a “policy scheme”.

2.2 Ecological module

The amount and clustering of habitat and the rates of habitat destruction and creation affect the dynamics and survival of species inhabiting the region. Applying the metapopulation concept (Hanski 1999), in the present model the species is characterized by two processes (Hanski 1999, Oborny et al. 2007): extinction of local populations and colonization of empty land parcels. Each conserved land parcel may be occupied by a local population that goes extinct with probability *e* per time step. A local population colonizes neighboring land parcels with probability *c* per time step. As neighborhood we consider again the Moore neighborhood of the eight adjacent land parcels around the focal land parcel. A land parcel that turns from economic use to conservation is empty until it becomes occupied through colonization, and a conserved land parcel that is turned into economic use becomes empty immediately. Economically used land parcels cannot become occupied by the species.

To analyze the model we simulate the ecological-economic dynamics and record: (i) the number of conserved land parcels, (ii) the degree of clustering, measured by the average number of conserved neighbors around a conserved land parcel, (iii) whether at least one land parcel is occupied at the end of the simulation run (species survival), and (iv) the number of land parcels occupied by the species.

The described ecological-economic model contains several random elements: the assignment of the random conservation costs to the land parcels and the processes of local extinction and colonisation.

To encompass the stochasticity in the simulation runs we carry out 100 runs and take averages of the variables of interest. Counting the number of runs in which the species survives (item (iii)) delivers the species' survival probability.

Simulating only the economic dynamics of land use and permit market reveals that it takes up to 40 time steps to reach the steady state where the system variables like number and clustering of conserved land parcels do not change any more. We therefore simulate the economic dynamics for 40 time steps before we consider the ecological species dynamics, starting with 50% of conserved land parcels occupied. From then on we run the combined model for another 60 time steps.
We are interested in the influence of the policy parameters λ and w (as introduced above) on the viability (survival probability and number of occupied land parcels) and how this is related to the land-use dynamics outlined above. We do this separately for 100 different species formed by systematic variation of c from 0.1 to 1 and e from 0 to 0.9 in steps of 0.1.

3. Results

We observe three categories of species. *Strong species* with comparatively high ratios of colonization and local extinction rates (c/e) survive under many combinations of policy parameters λ and w. An example is shown in Fig. 1 (blue color). *Weak species* have low ratios c/e, do not survive under any combination of λ and w and are not considered any further (Fig. 1, red color). A few parameter combinations with ratios c/e in between, characterizing *intermediate species*, lead to intermediate levels of species viability (Fig. 1, light color).

We consider three strong species, characterized by $(c,e)=(0.8,0.1),(0.2,0.1),(0.8,0.6)$. The strongest species is the first one and from that the second species is obtained by reducing c and the third by increasing e.

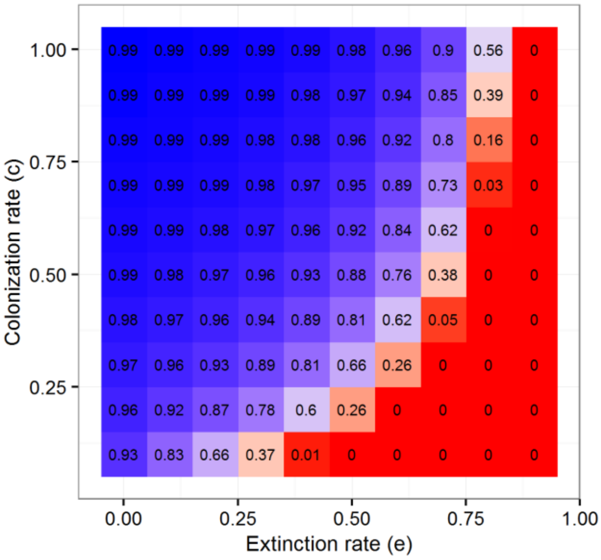

Figure 1: Proportion of occupied habitats at the end of the simulation as a function of the colonization rate c and the local extinction rate e. The policy parameters are set at medium values: λ=w=0.5.

With one exception we obtain the same results for all three species, i.e. the two policy parameters λ and w have about the same influences on the viability of the species (Fig. 2). Starting with the effect of the neighborhood bonus w, the species viability (occupancy and survival probability) increases with increasing w (unless it is already maximal) (all panels of Fig. 2) and correlates with the average number of habitat neighbors around habitats (Fig. 3a). Thus, as the average number of neighbors is subject to a tipping point as w increases, so is the species viability. However, a closer look reveals that in Fig. 2 the colors change more sharply than in Fig. 3 as w increases, indicating that the tipping point in the species viability is sharper than that in the number of habitat neighbors. One can further observe that the values of the tipping points are similar for all species (and related to the tipping point in the average number of habitat neighbors, Fig. 3) and decrease as λ increases, so that at large λ small (or even zero) values of w already lead to high species viability.

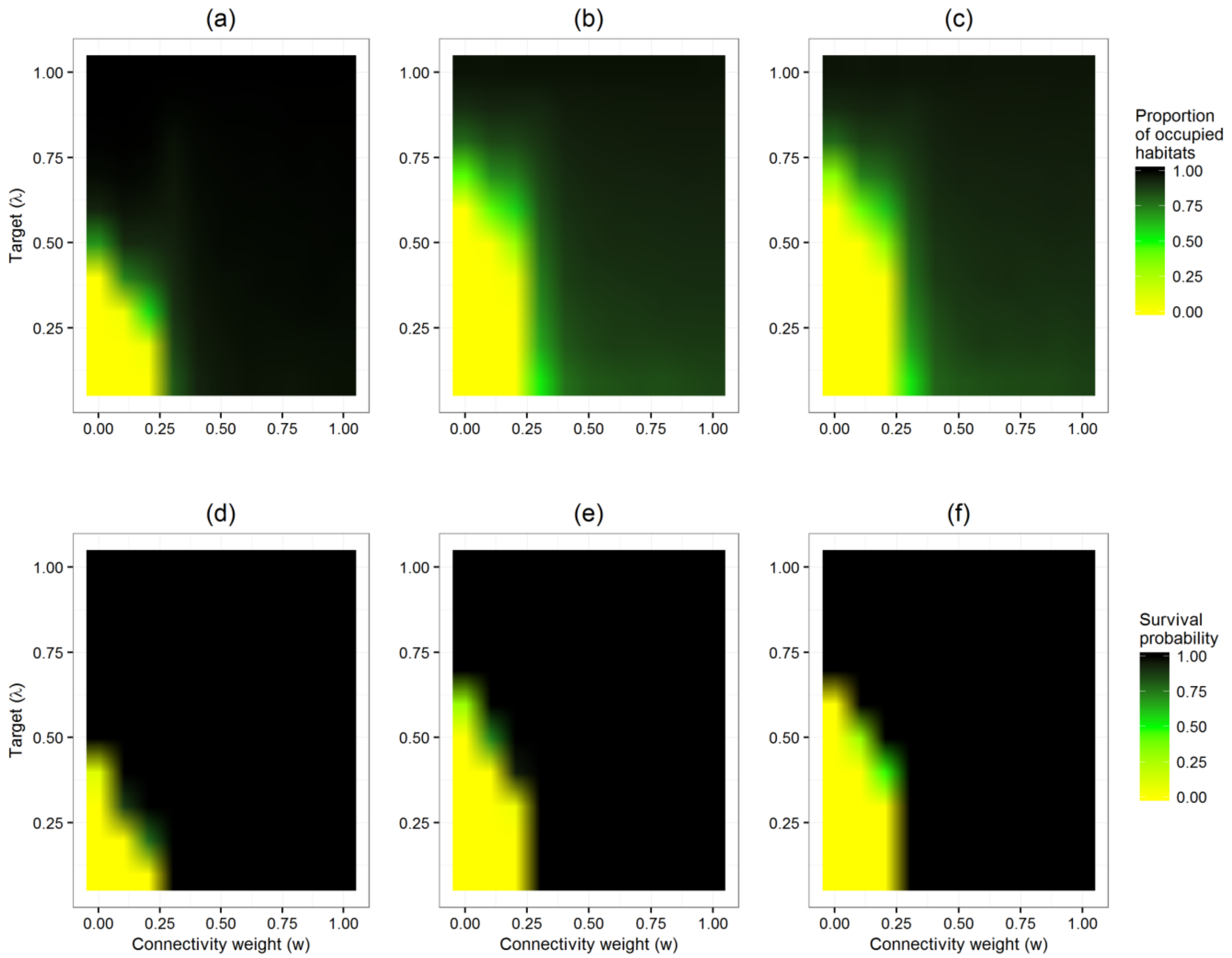

Figure 2: Proportion of occupied habitats (upper row of panels) and survival probability (lower row of panels) by color as functions of the policy parameters λ and w for three strong species (panels a,d: c=0.8, e=0.1; panels b,e: c=0.2, e=0.1; panels c,f: c=0.8, e=0.6).

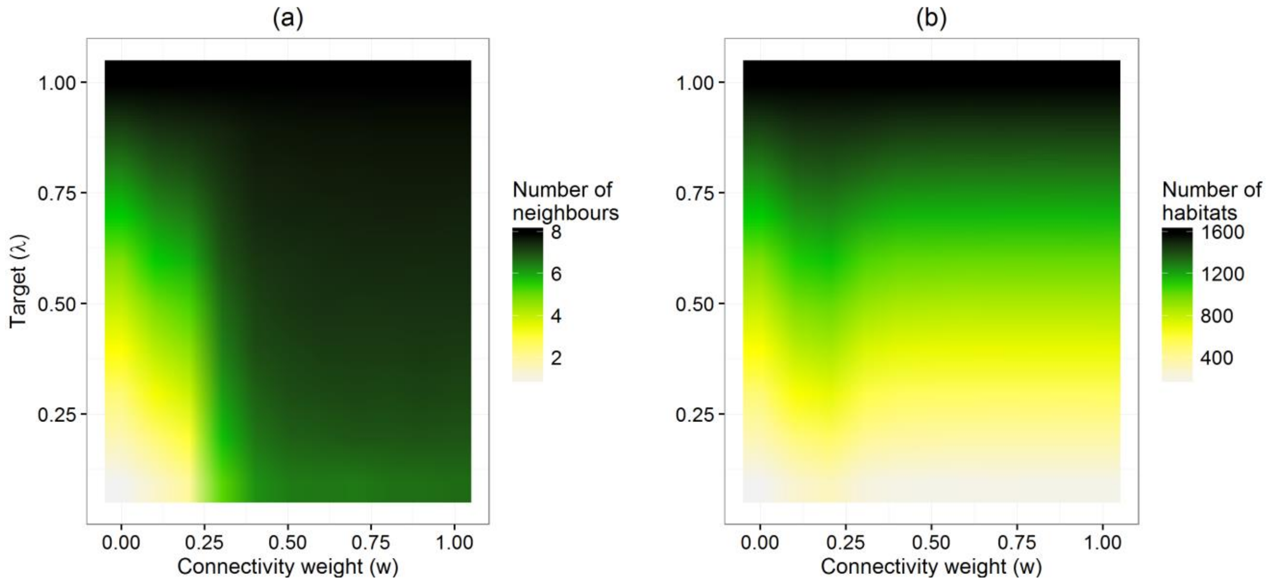

Figure 3: Average number of habitat neighbors around habitats (panel a) and number of conserved land parcels (habitats) (panel b) as functions of the two policy parameters λ and w.

The viability of all three species increases with increasing λ. For the occupancy (upper panels in Fig. 2) we observe a gradual increase (note the green transition area between yellow and black) which correlates with the average number of habitat neighbors (Fig. 3a). In contrast, for the survival probability (lower panels in Fig. 2) we observe a tipping point as λ increases. As announced above this behavior is observed for all three species; the exception is that for the slightly weaker species (lower c or higher e) the value of the tipping point is larger, i.e. larger λ are required to obtain high species survival.

Now we turn to the intermediate species (Fig. 4). Like in the strong species, the species viability increases with increasing w (except for high λ), but in contrast to the strong species, w has little or no effect on the species viability when λ is small. In this region, the species viability correlates with the number of habitats in the region (Fig. 3b).

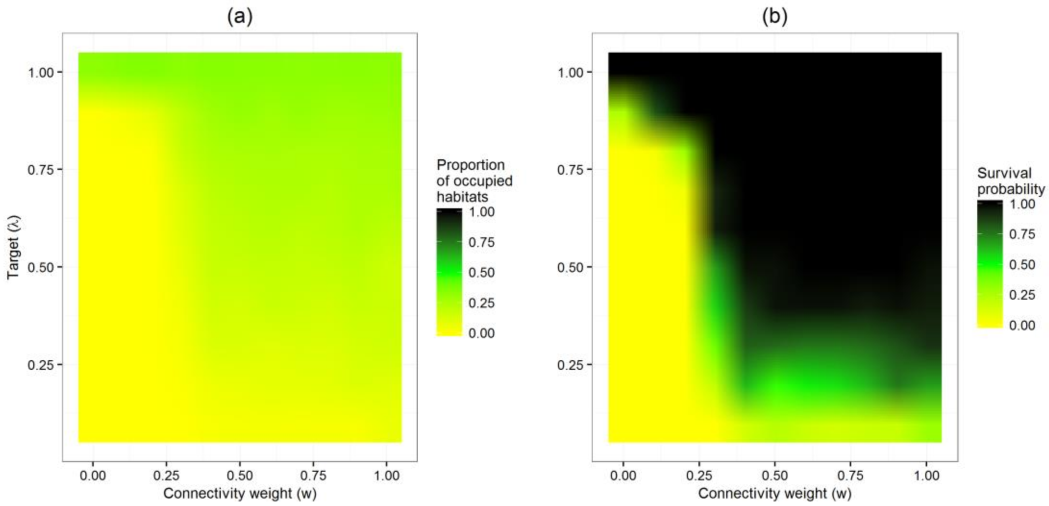

Figure 4: Proportion of occupied habitats (panel a) and survival probability (panel b) (by color) as functions of the two policy parameters λ and w. The panels show results for an intermediate species (c=e=0.8).

4. Discussion

We developed an ecological-economic model of a tradable-permit market and a species population affected by the induced land-use pattern. We were interested in discontinuous changes (tipping points) when the design of the permit scheme is varied. As policy parameters we considered the amount of permits that have to be produced in the region (λ) and the neighborhood bonus (w) that rewards creating habitat in the neighborhood of other habitats. The systematic analysis of the model lead to results that can be summarized as follows:

1. Increasing λ and w increase the degree of spatial clustering of habitats, measured by the average number of habitat neighbors around a habitat. Increasing λ further increases the total number of habitats in the region while increasing w temporarily increases and then decreases the number of habitats.

2. The influence of *w* on the number and clustering of habitats is discontinuous, i.e., has a tipping point while the influence of λ is smooth.
3. Species viability (measured by the number of occupied habitats and the species survival probability) increases with increasing λ and *w*.
4. The influence of *w* on species viability has a tipping point that is sharper than that in the influence of *w* on the land-use pattern (number and clustering of habitats). The reason is that species viability over-linearly depends on the number and clustering of habitats which amplifies the sharpness of the tipping point.
5. The influence of λ on species viability has a tipping point despite its smooth influence on the land-use pattern. The reason is the percolation threshold discussed by Oborny et al. (2007) that leads to an abrupt increase in habitat connectivity even when the number of habitats is increased only gradually.
6. There is an interaction between the two policy parameters λ and *w* such that the increase of one of these parameters leads to a decrease in the location of the tipping point in the other parameter. The reason is a complex interaction between the influence of the policy parameters on the land-use pattern and the process of percolation.
7. The viability of *strong species* with high ratios between colonization and local extinction rates *c*/*e* only correlates with the average number of habitat neighbors of habitats. In contrast, for species with medium *c*/e (termed *intermediate species*) the species variability at larger *w* is correlated with the number of habitats in the region. Species with lower *c* and or larger *e* (*weak species*) are not viable at any value of λ and *w*.

Beyond these case-specific results we can draw some general conclusion relevant for the design of conservation policies.

1. The relevance of the policy parameters (here: number of permits that have to be produced and magnitude of the neighborhood bonus) on species viability depends on the characteristics (here: colonization and local extinction rates) of the species.
2. Because of the possible existence of tipping points, policy design has to be done with care because a small variation in policy parameters may have drastic effects on species viability.
3. The location and sharpness of tipping points depend on the species characteristics.
4. Tipping points may interact with each other and in particular amplify each other.

Our model results are based on a number of assumptions. In the economic module we assumed that the land users are myopic and have no memory, i.e. they consider only the current land-use pattern in the decision whether to conserve their land or not, and they consider only the profit for the next time step. Furthermore, the conservation costs were assumed to be spatially and temporally uncorrelated. Relaxing any of these assumptions may attenuate the sharpness of the tipping points, i.e., lead to a smoother influence of the policy parameters on the land-use pattern and the viability of the species.

The economic module is based on on the policy instrument of tradable permits. However, the deduced land-use patterns (including Fig. 3) can also be produced through payment schemes (Engel et al. 2008) where land users are offered a payment when they carry out conservation measures and the land users can voluntarily decide whether to accept the offer or reject and carry out economic land use. In particular, the concept of the neighborhood bonus has actually been adopted from a payment scheme proposed by Parkhurst et al. (2002). The only differences are that Parkhurst et al. (2002) considered only four neighbors rather than eight, and their scheme was static, i.e. the conservation costs were fixed in time. By adopting our definition of neighborhood and introducing dynamic conservation costs and dynamic payment levels the agglomeration bonus scheme proposed by Parkhurst et al. (2002) would produce the same land-use dynamics as our model.

In the ecological module we assumed that a land parcel that switches from economic use to conservation immediately and at zero economic cost turns into habitat and can be colonised by the species. This assumption is invalid in many ecosystems that recover only slowly like forests. Conversely, we assumed that a land parcel that switches from conservation to economic use immediately becomes inhabitable by the species so a local population on the land parcel goes extinct immediately. Both assumptions lead to more drastic changes in land use and living conditions for the species between time steps, and relaxing them may lead to a smoother influence of the policy parameters on the land-use pattern and the viability of the species.

In the ecological module we further assumed that individuals of the species can disperse only to adjacent habitats so only habitats in the Moore neighborhood can be colonized. This may be valid for species with a small dispersal range. For many other species, however, dispersal is more appropriately modeled to decline gradually with increasing distance, as it was done, e.g. by Hartig and Drechsler (2009). Relaxing the assumption of short-range dispersal will reduce the reliance of the species on the spatial clustering of habitats and the sharpness of the tipping points. As a consequence, long-range dispersal may reduce the sharpness of the tipping points in the influence of the policy parameters on species survival.

Despite the simplicity of then model, our results indicate that of conservation policies that affect both the number and spatial arrangement of habitats must be designed carefully to avoid the crossing of tipping points that lead to high habitat fragmentation and a corresponding fast decline of species populations. Future research may address our present assumptions and their relevance for the existence of tipping points. In addition, one may investigate whether there are also tipping points with regard to the cost-effectiveness (where species survival is achieved at minimum total conservation costs) of the policy (cf. Hartig and Drechsler 2009). The model can be further extended to consider multiple non-interacting (Hartig and Drechsler 2009) or interacting species. Altogether the novel question whether conservation policies are subject to tipping points is highly relevant and should be further addressed in future studies.

5. References

Ayram, C.A.C, Mendoza, M.E., Etter, A., 2015. Habitat connectivity in biodiversity conservation. A review of recent studies and applications. Progress in Physical Geography: Earth and Environment 40, 7-37.

Drechsler, M., Wätzold, F., 2009. Applying tradable permits to biodiversity conservation: effects of space-dependent ecological benefits and cost heterogeneity on habitat allocation. Ecological Economics 68, 1083-1092.

EC (2005) Agri-environment Measures Overview on General Principles, Types of Measures, and Application. European Commission, Directorate General for Agriculture and Rural Development. http://ec.europa.eu/agriculture/publi/reports/agrienv/rep_en.pdf).

Engel, S., Pagiola, S., Wunder, S., 2008. Designing payments for environmental services in theory and practice: an overview of the issues. Ecological Economics 65, 663–674.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34, 487-515.

Fischer, J, Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4, 80.86.

Frank, K., Wissel, C., 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. American Naturalist 159, 530-552.

Gilpin, M.E., Soulé, M.E., 1986. Minimum viable populations: processes of species extinction, in: Soulé, M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer, Sunderland, pp. 19–34.

Haddad, N.M., Brudvig, L.A., Clobert, J. et al., 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science 1; e1500052.

Hansjürgens, B., Antes, R., Strunz, M. (Eds.) (2011) Permit Trading in Theory and Practice. Routledge.

Hanski, I., 1999. Metapopulation Ecology. Oxford University Press.

Hanski, I., 2015. Habitat fragmentation and species richness. Journal of Biogeography 42, 989-994.

Hartig, F., Drechsler, M., 2009. Smart spatial incentives for market-based conservation. Biological Conservation, 142, 779-788.

Holme, P., Newman, M.E.J., 2006. Nonequilibrium phase transition in the coevolution of networks and opinions. Physical Review E 74, 056108.

MEA, 2005. Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Oborny, B., Szabó, G., Meszéna, G., 2007. Survival of species in patchy landscapes: percolation in space and time, in: Storch, D., Marquet, P.A., Brown, J.H. (Eds.), Scaling Biodiversity. Cambridge University Press.

OECD (2012) Evaluation of Agri-environmental Policies: Selected Methodological Issues and Case Studies. OECD Publishing. http://dx.doi.org/10.1787/9789264179332-en.

Polhill, J.G., Filatova, T., Schlüter, M., Voinov, A., 2016. Modelling systemic change in coupled socio-environmental systems. Environmental Modelling and Software 75, 318-332.

Reif, F., 1965. Fundamentals of Statistical and Thermal Physics. McGraw-Hill.

Panayatou, T., 1994. Conservation of biodiversity and economic development: the concept of transferable development rights, in: Perrings, C.A., Mäler, K.-G., Folke, C., Holling, C.S., Jansson, B.-O. (Eds.), Biodiversity Conservation. Kluwer.

Parkhurst, G.M., Shogren, J.F., Bastian, P., Kivi, J., Donner, J., Smith, R.B.W., 2002. Agglomeration bonus: an incentive mechanism to reunite fragmented habitat for biodiversity conservation. Ecological Economics 41, 305–328.

Schelling, T.C., 1978. Micromotives and Macrobehavior. Norton and Co., pp. 147-155.

Stauffer, D., Aharony, A., 1994. Percolation Theory. CRC Press.

Taubert, F., Fischer, R., Groeneveld, J. et al. 2018. Global patterns of tropical forest fragmentation. Nature 554, 519-522.

Van Nes, E.H., Arani, B.M.S., Staal, A. et al., 2016. What do you mean, ‚tipping point‘? Trends in Ecology and Evolution 31, 902-904.