This is the final draft of the contribution published as:

Surun, C., **Drechsler, M.** (2018):
Effectiveness of tradable permits for the conservation of metacommunities with two competing species
Ecol. Econ. **147** , 189 - 196

The publisher's version is available at:

http://dx.doi.org/10.1016/j.ecolecon.2018.01.016

Effectiveness of tradable permits for the conservation of metacommunities with two competing species

Abstract

Market-based instruments are gaining relevance for biodiversity conservation, since they promise higher cost-effectiveness than other instruments like planning. Previous studies have analysed the effectiveness of market-based instruments on single or multiple but independent species. On the example of tradable land-use permits we address an important issue for the first time: the conservation of interacting species (metacommunities). We consider two competing species where the superior competitor locally replaces the inferior competitor. Both species are structured as metapopulations, i.e. can go locally extinct while empty habitats can be recolonised by local populations on neighbouring habitats. Combining a spatially explicit and dynamic ecological-economic simulation model with cluster analysis we investigate how the coexistence of both species depends on the design of the tradable permit scheme, and how the effective scheme design (i.e. the scheme design that maximises coexistence) depends on the biological characteristics of the two species. We show that scheme designs that are effective for the conservation of single species may be ineffective for the conservation of two competing species and that the effectiveness of a scheme with regard to coexistence strongly depends on the relative performances of the two species with regard to their colonisation abilities and local extinction risks.

Highlights

- We analyse an ecological-economic model of tradable permits
- The survival of two competing species strongly depends on the scheme design
- Metacommunities should get more attention in the analysis of policy instruments

Key words: competition, conservation, ecological-economic model, metacommunity, tradable permits.

1. Introduction

The biodiversity in agricultural systems is continuing to decline worldwide (Barnosky et al., 2011; Pereira et al., 2012). Reasons include the intensification of agriculture such as increased use of machinery, fertilisers and pesticides, as well as synchronization and homogenization of land use (Drechsler et al., 2007; Pe'er et al., 2014), drainage of lands, expansion of monocultures and destruction of natural landscape elements like solitary trees and hedge rows. All these measures have contributed to reduce the abundance of many taxa like insects (Bourn and Thomas, 2002) and birds (Pe'er et al., 2014).

To counteract the loss of biodiversity in agricultural landscapes, agri-environmental schemes have been introduced e.g. to reduce the use of chemicals or to establish hedges (Primdahl et al., 2003). Such agri-environmental schemes are implemented mostly in the form of market-based instruments like compensation payments and tradable permit schemes (European Commission, 2005; OECD, 2012).

The introduction of agri-environmental schemes, however, has not lead to the expected results. Instead, their success has been mixed (e.g. Kleijn et al., 2006). There are many potential reasons why existing agri-environmental schemes are not effective (failing to reach desired biodiversity outcomes) nor cost-effective (failing to achieve outcomes at minimum costs). One issue that has been discussed in the recent past is spatial heterogeneity and spatial interactions. Both the costs and the effectiveness of conservation measures may vary in space which affects the cost-effectiveness of conservation policies (Mouysset et al., 2014; Naidoo et al., 2006). Furthermore, the effectiveness of a conservation measure at a particular location may depend on conservation activities in the neighbourhood: For instance, agricultural land parcels are often too small to sustain a viable local species population, so many species can only survive in a region if such local populations can interact through dispersal of individuals (the so-called metapopulation theory: Hanski (1998)); since many species have limited dispersal abilities, the habitats of these local populations must be close enough to each other, which requires conservation measures to be spatially aggregated. Acknowledgement of this issue has lead, e.g., to the introduction of the agglomeration bonus approach that rewards spatial clustering of conservation measures (Parkhurst and Shogren, 2007; Parkhurst et al., 2002).

The agglomeration bonus concept can be employed in various types of conservation instruments, including payment schemes (where higher payments are offered to land users if they conserve land in the vicinity of other conserved land) and tradable permit schemes (where the conservation of land close to other conserved land earns more land-use permits while the destruction of habitats close to other habitats requires more permits than that of isolated habitats (Drechsler and Wätzold, 2009). Both applications of the agglomeration bonus concept lead to a higher degree of spatial clustering of conserved land patches (habitats). The cost-effectiveness gains of the agglomeration bonus with regard to species conservation has been analysed in both settings (tradable permits and payment schemes) by Drechsler et al. (2010), Hartig and Drechsler (2009) and Wätzold and Drechsler (2014).

A shortcoming of the above-mentioned and other studies on the cost-effectiveness of conservation instruments is that only the conservation of single species (Drechsler et al., 2010; Hartig and Drechsler, 2009; Wätzold and Drechsler, 2014) or multiple but non-interacting species (Armsworth et al., 2012; Mouysset et al., 2014; Nelson et al., 2008) were considered. It has, however, been shown that the interaction between species can considerably affect the cost-effective allocation of conservation resources (Baumgärtner, 2004; Probert et al., 2011).

Main types of species interaction include "predator-prey" (one species feeds on the other), "competition" (species compete for the same environmental resources) and "mutualism" (species positively influence each other) (Begon et al., 2006). Growing ecological research deals with the interaction of interacting species in a spatially structured environment. The most popular paradigm in this context is the metacommunity concept (Leibold et al., 2004). It is an extension of metapopulation theory (Hanski, 1998) and considers an ecosystem as an ensemble of interacting local communities. Each local community consists of a number of interacting local populations. Local communities interact with each other through the dispersal of individuals and the colonisation of neighbouring habitat patches. Species within a local community can go extinct either due to harming influences of other species in the habitat patch or adverse environmental conditions such as too high or too low temperature or too much or too little precipitation.

To improve instruments such as agri-environmental schemes for the conservation of biodiversity it is important to understand the circumstances under which species can co-exist, and how these circumstances are shaped by these schemes. To encompass the spectrum of species competition, in the one extreme, species occupy different ecological niches (i.e. have different requirements regarding temperature, precipitation, food resources, etc.), so the presence of one species in a local habitat has no or only a small influence on the other species and both species can co-exist locally. Here the species can be treated independently, as done in the studies mentioned above. In the other extreme both species occupy the same ecological niche. Here coexistence of both species is impossible (an effect termed the competitive exclusion principle (Begon et al., 2006)), but the superior competitor which utilises resources more efficiently, e.g., to transform given resources into a higher population growth rate, locally outcompetes the inferior competitor (Begon et al., 2006; Giller 1984), with an empirical example by Mackie et al. (1978). Various mechanisms that facilitate the co-existence of competing species have been identified, one of them being spatial heterogeneity and spatial structure. Spatial structure implies that the superior species generally cannot occupy the entire landscape, which leaves space for the inferior species to survive. Of particular relevance here is the so-called competition-colonisation trade-off, which states that in a disturbed environment an inferior competitor can coexist together with a superior competitor if it has a higher ability to colonise empty habitat patches (Tilman, 1994; Cadotte, 2007). The higher colonisation ability allows the inferior competitor to continuously escape from becoming outcompeted in the entire landscape – even though locally (i.e. on individual habitat patches) it is always outcompeted by the superior species.

Species communities subject to the competition-colonisation trade-off are likely to be affected by the spatial land-use pattern, which in turn is affected by the existing (economic) constraints of the land use and conservation instruments. Conversely, species communities subject to the colonisation-extinction trade-off are likely to respond to conservation instruments differently from single or independent species. While the response of single species by conservation instruments is quite well understood (see references above) the response of interacting species still needs to be analysed.

The present study for the first time links an economic model with a metacommunity model to investigate which policy designs facilitate the survival and coexistence of two competing species in a region. For the economic model we choose the above-mentioned tradable permit model by Drechsler and Wätzold (2009). The land-use pattern induced by the permit market affects the survival of two competing species where the presence of one species (the superior competitor) locally inhibits the presence of the other (the inferior competitor). Both species are spatially structured as metapopulations, i.e. each habitat patch may be occupied by a local population, local populations can go extinct by chance and empty habitat patches can be recolonised by neighbouring local populations.

The ecological-economic model and the way in which it is analysed are presented in the next section which is followed by the Results section. The paper concludes with a discussion of the results in section 4.

2. Methods

The following section describes the economic module and the integration of the ecological module into the economic module. The section concludes with a description of the way in which the combined model is analysed.

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 required 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. generation of habitat for endangered 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).

Conservation of a land parcel *i* generates an amount of land-use permits of

$$v_i = 1 + w m_i$$

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. A zero value implies that 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 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). The agency now demands from each land user to generate a certain proportion of this maximum. The proportionality factor is denoted as $\lambda \in [0,1]$, so each land user has to generate an amount of $\lambda(1+w)$ land-use permits. To interpret the two extreme values of λ, a value of λ=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 to conserve less and instead carry 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

Different spatial allocations of the habitats may have different effects on the survival and coexistence of competing species. We assume that the dynamics of both species can be described by the metapopulation concept (Hanski, 1998). Each habitat patch may harbour a local population. Local populations may go extinct at rates (probabilities per time step) E_1 and E_2 for species 1 and species 2. A local population of species 1 or species 2 colonises empty habitat patches in its Moore neighbourhood at rate C_1 and C_2, respectively.

The competition between the two species is considered as follows: one species, called “winner”, can colonise any habitat patch regardless of whether it is occupied by the other species, called “loser”, or not; and if the loser is present it disappears from the habitat patch when it is colonised by the winner. In contrast, the loser cannot colonise any habitat patch occupied by the winner. Note that the terms winner and loser characterise only the local interaction within single land patches and do not imply any statement on the regional level, i.e. the loser species can well outcompete the winner species on the regional scale if, e.g., it has a higher colonisation rate C (the above-mentioned competition-colonisation trade-off).

To conclude the model description, a land parcel that turns from economic use to conservation is empty until it becomes occupied through colonization by one of the two species, and a conserved land parcel that is turned into economic use becomes empty. Economically used land parcels cannot become occupied by any species.

2.3 Model analysis

In the analyses of the model we systematically vary the policy parameters λ and w within their ranges between 0 and 1 (the consideration of values $w>1$ turns out to provide no additional insights). For each combination of λ and w we investigate the coexistence probability of 6084 pairs of species. Each species pair consists of a winner and a loser; the colonization and local extinction rates of the two species are systematically varied in steps of 0.1 from $C=0.1$ to 1 and from $E=0$ to 0.9, keeping only those species that are able to survive individually, i.e. in the absence of the other species. This leads to 78 candidate species and $78^2=6084$ pairs of species.

The coexistence probability is determined as follows. First we run the economic module for 40 time steps to ensure that the land-use dynamics are in a steady state. Then we include the ecological module, starting with 50% of conserved land parcels occupied, and running for another 60 time steps. To encompass the stochasticity in the ecological-economic dynamics we run the model 40 times and count how often both species are present in the region at the end of the simulation.

The model analysis consists of two steps. The first one focuses on the global influence of the policy parameters (λ and w) on species coexistence on the one hand and the global influence of the species characteristics (C and E) on the other. The second step considers the interacting influences of the two policy parameters and species characteristics.

In the first step, for each combination of policy parameters we determine the coexistence probability for each species pair and take the arithmetic mean of these coexistence probabilities over all species pairs, delivering for each combination of λ and w an average coexistence probability. This will give a first idea of the suitability of policy schemes to deliver coexistence. Complementarily to this, we calculate for each species pair the arithmetic mean of its coexistence probability over all combinations of λ and w. This delivers a first idea of the likelihood of coexistence of each species pair in dependence of its characteristics C_{winner}, C_{loser}, E_{winner} and E_{loser}.

The second step of the analysis aims at understanding in detail how the influence of the policy scheme (λ and w) on species coexistence depends on the characteristics (C and E) of the two species. The analysis is based on a contingency table telling for each policy scheme and each species pair the coexistence probability. We do not consider the species pairs that are not viable under any policy scheme, or those that only survive for a single policy scheme, to obtain robust results.

Based on this table we carry out a correspondence analysis (CA) (using the FactoMineR package) (Lê et al., 2008) in order to find patterns in our data set and thus group species pairs that respond in the same way to the land-use dynamics in the region, and group the policy schemes that have similar influences on the species coexistence. The correspondence analysis leads to a number of isolated policy schemes in CA-space. A closer look reveals that all of these policy schemes lead to scattering of habitat patches in the region while the other policy schemes lead to clustered habitat patches. Those isolated policy schemes are removed from the main CA analysis. At the same time we remove the species pairs that are specific to these policy schemes. Thereafter, we consider two different CAs:

- one with the removed policy schemes and the species pairs that can survive only under these policy schemes;

- one with the remaining policy schemes and those species pairs that can survive under these policy schemes.

The final choice of the groups for both CAs is performed by a hierarchical cluster analysis (using the Euclidian distance and the Ward method). We keep for the first CA seven axes, and for the second CA five axes, which represent 90% of the variance in the data. We finally keep 2 respectively 3 groups for each CA.

For the analysis of these five groups we determine the mean coexistence probability over all included species pairs for each policy scheme. In order to understand which species pairs are included in each group we count the number of each species characteristics (colonisation and extinction rates) in each group.

3. Results

3.1 First step of analysis

Figure 1 shows the mean coexistence probability over all species pairs as a function of the two policy parameters λ and w. The most adverse policy schemes (low λ and low w) never allow coexistence because they are associated with a low level of spatial clustering and a high turnover (destruction and recreation) of habitats (Fig. 2). Quite unexpected though is that the highest coexistence probability is not obtained for maximum λ and w but for intermediate values of about $0.5 \leq \lambda \leq 0.9$ and $w \approx 0.3$. One should note, however, that here the mean coexistence probability is still rather low – below 0.15, meaning that one or the other species of a lot of pairs do not survive under these conditions.

The influence of the species characteristics on coexistence is shown in Fig. 3. The following conclusions can be drawn from the figure. (i) an increase in the colonisation probability C_{winner} decreases the coexistence probability until some pairs cannot coexist any more, (ii) if the local extinction probability E_{winner} increases, the coexistence probability increases, (iii) the coexistence probability increases with increasing C_{loser}, and (iv) if E_{loser} increases the coexistence probability decreases and an increasing number of species pairs becomes not viable. In sum, coexistence is highest (with coexistence probabilities up to 0.8) when the winner has high C and/or low E and the loser has low C and/or high E. We conclude that for the coexistence of the two species their C/E

ratios a decisive in that for coexistence the loser must have a higher C/E than the winner. To simplify the following elaborations we term species with high (low) C/E *strong* (*weak*) species.

Finally we can note that as the winner becomes weaker (higher E and/or lower C), the number of characteristics (combination of C and E) for the loser that allow for coexistence increases. For instance, for C_{winner}=0.7 and E_{winner}=0.8 coexistence is possible for all loser's characteristics, while only one combination of C_{loser} and E_{loser} enables coexistence in the case of C_{winner}=0.9 and E_{winner}=0.

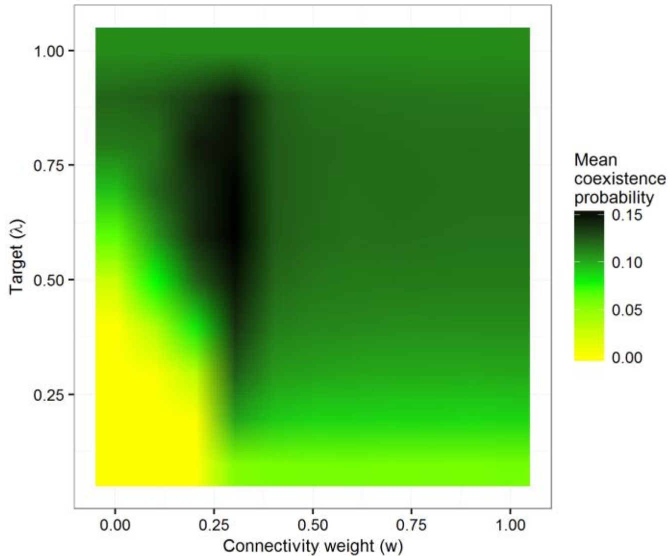

Figure 1: Suitability of the policy schemes for species coexistence. Colours represent the mean coexistence probability over all species pairs.

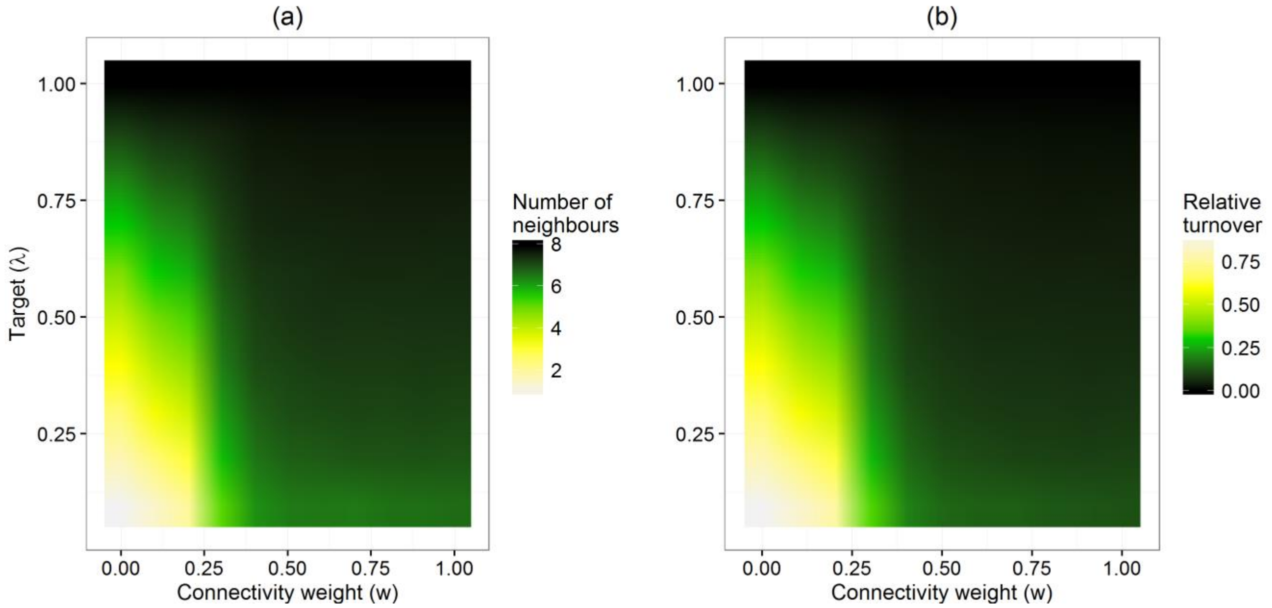

Figure 2: Mean number of habitat neighbours around a habitat (panel a) and relative habitat turnover in the landscape (proportion of destroyed habitats between two consecutive time steps) (panel b). Since the target (λ) is the same every time step, the numbers of destroyed and created habitats are always equal.

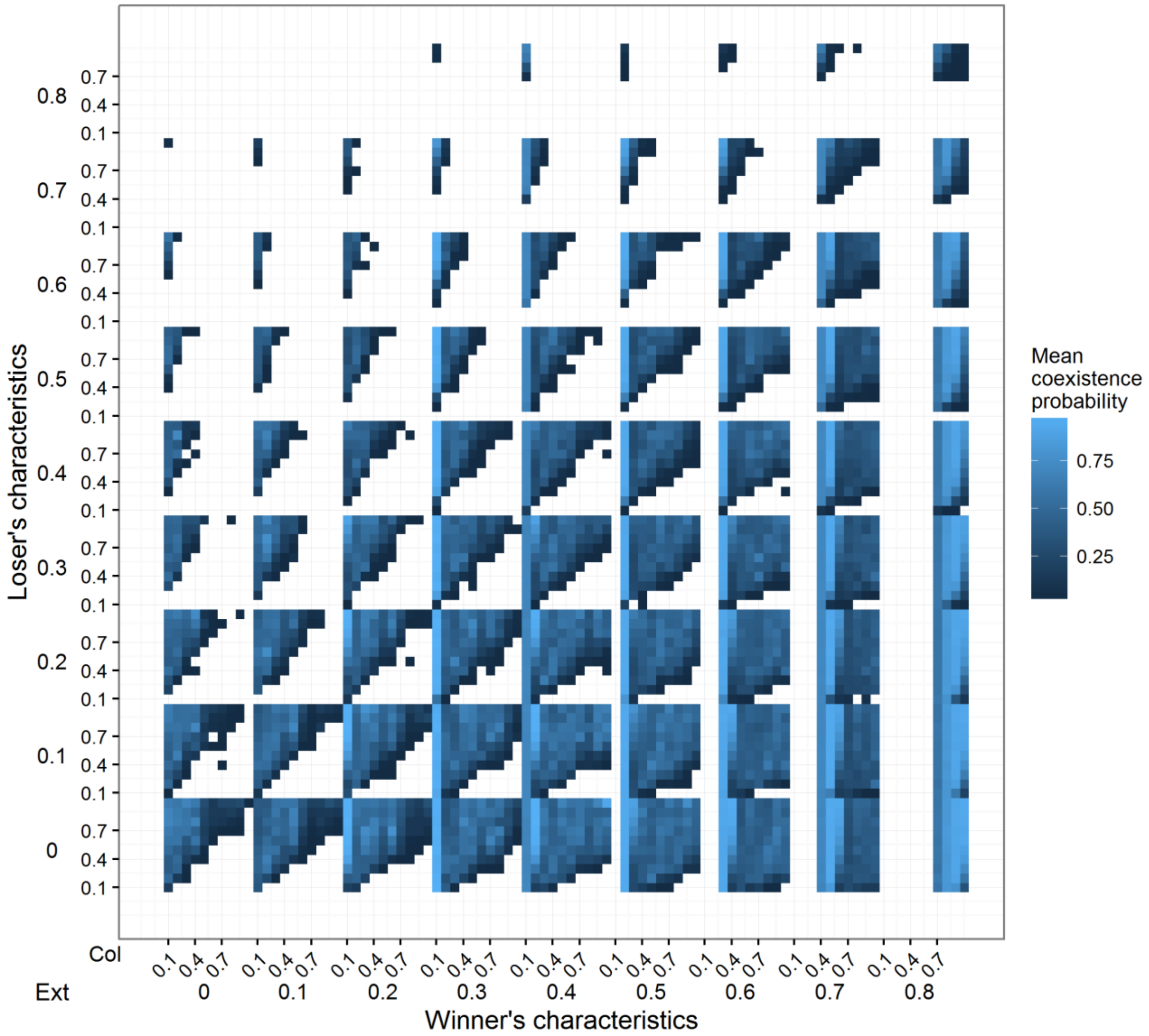

Figure 3: Coexistence of species pairs as a function of species characteristics (*C* and *E*). The colours represent the arithmetic mean of the coexistence probability over all policy schemes (λ and *w*). Note that the policy schemes where the species pairs do not survive (coexistence probability equal to 0) are not considered in the average to improve the readability of the plot. This does not change the interpretations.

3.2 Second step of analysis

In the correspondence analysis we identified five groups of species so that within each group the policy parameters λ and w have similar influences on species coexistence. Groups 1 and 2 originate from the first CA and groups 3-5 from the second. Figure 4 shows for each of the five groups the frequency of species characteristics for the winner and the loser. The first group (upper left panel) altogether contains rather few species (in total 77 pairs) and most species are strong, i.e. have a high colonisation (C) and a low local extinction rate (E), implying that almost all habitats are occupied. In contrast, the winner species contained in group 5 are all weak, so that species survival is low and the number of occupied habitats is small (lower right margin in the upper right panel of Fig. 4). The total number of species pairs in this group is 820. In between we have the groups 2-4. In these groups the winner has medium survival abilities and the loser again tends to have higher C and/or lower E than the winner. The groups 2-4 comprise most of the species pairs (1280, 64 and 1032, respectively).

Losers tend to have higher C and lower E than the winner, which was noted above as a condition for coexistence, also known as the competition-colonisation trade-off. As the winner's strength decreases, more combinations of C and E for the loser are lead to coexistence.

The coexistence probability in the species groups follows a slightly different trend (Fig. 5). Groups 1-3 survive only for those policy schemes (low λ and low w) that are associated with habitats that are scattered and subject to high turnover (Fig. 2). The opposite behaviour is found in group 5, where coexistence is rather likely and occurs in those regions of the policy parameter space (high λ and/or high w) that are associated with clustered and stable habitats (Fig. 2). In between, the species of group 4 coexist if the land-use dynamics induced by the policy parameters are in a transitional state, showing some level of clustering but still a high turnover.

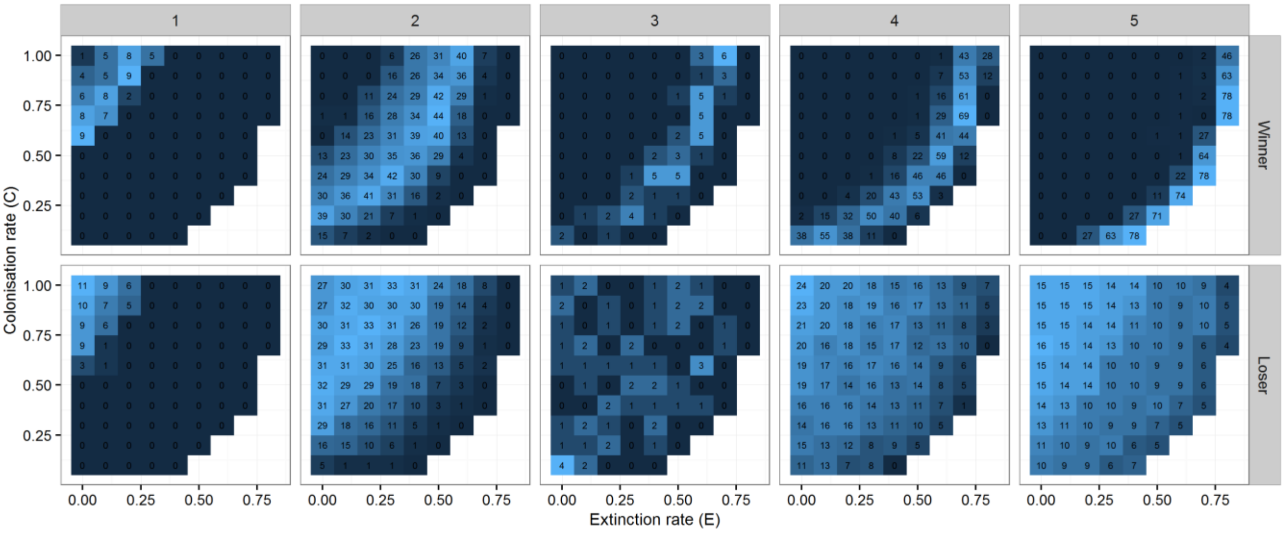

Figure 4: The five groups obtained in the correspondence analysis and the contained species. Upper row: characteristics of the winner, lower row: characteristics of the loser. Each panel shows the frequency of species characteristics (combinations of colonisation rate *C* and local extinction rate *E*) contained in the group. For instance, in group 1 (left panel in second row) most of the contained losers have high *C* and low *E*. In particular, 11 loser species have *C*=1 and *E*=0 (upper left corner of the panel).

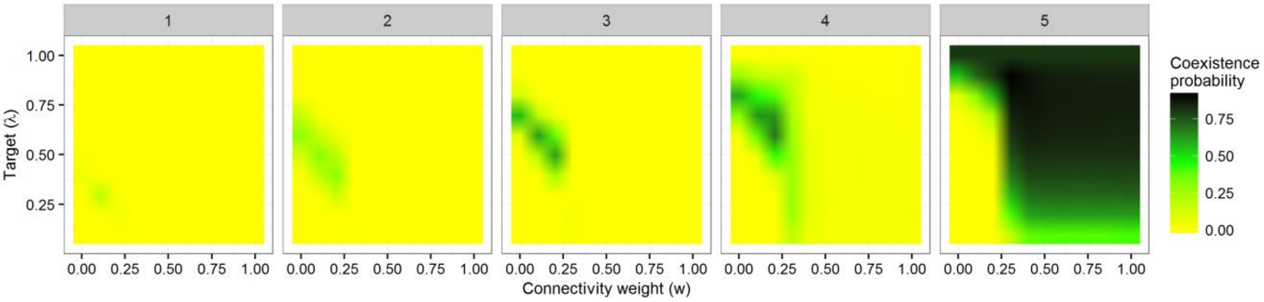

Figure 5: Coexistence probabilities (by colour) as functions of the policy parameters target (λ) and connectivity weight (w). Each panel represents one of the five groups of Fig. 4. The coexistence probability for each group and each combination of λ and w is the arithmetic mean of the corresponding coexistence probabilities of all species pairs contained in the group.

The figures show that coexistence of the two species is always determined by three factors: first, the winner must be strong enough so it can survive in the landscape. Second, however, the winner must be weak enough under the particular land-use dynamics (sufficiently low strength for given λ and w) so it leaves space for the loser. Lastly, the loser must have higher C and/or lower E than the winner (competition-colonisation trade-off). This has the following implications for the impact of the policy parameters on species coexistence.

If the winner is very strong, as in group 1, it will outcompete the loser for almost all policy schemes. Similarly, when λ and w are very low and the habitats highly scattered, even the winner cannot survive, implying zero coexistence probability, too. Coexistence is possible for slightly higher values of λ and w with sufficiently many and moderately scattered habitats and rather high level of habitat turnover (Fig. 2). Only under these circumstances the winner is neither too strong nor too weak so it neither goes extinct nor occupies all habitats and outcompetes the loser regionally. The behaviour of groups 2 and 3 can be explained in the same way.

If the winner is weak (group 5), it cannot survive in scattered habitats subject to high turnover. It can only survive at a low occupancy level (with about 5-60% occupied habitats, not shown) in clustered and temporally stable habitats induced by high λ and/or high w. In these cases, the landscape is stable enough to be easily colonised and the competition pressure is low, allowing the looser to be present in a lot of habitats. The coexistence probability is high.

Group 4 is an interesting transition that shows an in-between behaviour. For $w<3$ the winner has a medium viability that allows for coexistence based on the same processes as described for groups 1-3. However, coexistence is also observed in a new area of the policy parameter space (with slightly higher λ and w). The reason for this new area of coexistence will be explained in the Discussion below.

4. Discussion

4.1 Summary of objectives and methods

We analysed the influence of a market-based conservation instrument – tradable land-use permits – on the survival of two interacting species. By varying the weight w attached to the number of habitats in the neighbourhood of a habitat the regulator can control the degree of spatial clustering of habitats and the habitat turnover (rate of habitat destruction and recreation) (cf. Fig. 2). By varying the target λ for the proportion of habitats in the region the regulator can in addition control the amount of habitat in the region. Varying both policy parameters, λ and w, allows inducing a large range of different types of land-use patterns and dynamics.

While most studies on market-based conservation instruments consider only single or non-interacting species we focused on two competing species – a winner and a loser species where the winner species excludes the loser locally, i.e. from any habitat patch it occupies. Both species can only coexist on the regional scale if the loser is stronger than the winner in some biological characteristics, for instance – as in our case – if it has a higher rate of colonising empty habitat patches and/or a lower rate of becoming locally extinct on individual habitat patches (the competition-colonisation trade-off).

In the present paper we developed an ecological-economic model and analysed it through sensitivity and correspondence analyses to evaluate the influence of a tradable permit scheme (represented by the two policy parameters λ and w) on the coexistence of two competing species, and how this influence depends on the characteristics (colonisation and local extinction rates) of the two species.

4.2 Summary and discussion of results

The above-mentioned competition-colonisation trade-off is confirmed by Fig. 3: if the loser has a higher colonisation rate and/or lower local extinction rate it can more easily colonise empty habitat patches before the winner can colonise and occupy them.

Intuitively, this coexistence mechanism is rather ineffective if all habitat patches are well-connected and if there is no habitat turnover, since in this case the winner can easily colonise most or all habitat patches, leaving no space for the loser which is eventually outcompeted and goes extinct regionally even if it has a higher colonisation rate and/or lower extinction rate than the winner. This explains our finding of Fig. 1 that the coexistence of two competing species is generally maximised at medium values of λ and w: if λ and w were large (which would maximise the survival of both, winner and loser, if the other species was not present) there would be much well-connected habitat with no or little turnover (cf. Fig. 2), so the winner could easily colonise and occupy all habitat and outcompete the loser in the model region. If, in contrast, both λ and w were small the loser would have a chance to resist the winner in the model region but habitat would be too scarce and spatially fragmented and there would be too high habitat turnover so that none of the two species could survive even in the absence of the other species.

More detailed results were obtained from the correspondence analysis in which all species were classified into five groups. Within each group the response of the species coexistence to the policy parameters is similar, between groups it differs. These differences are explained by the different biology of species contained in the different groups. The most important predictors for the response of the species to different policy designs were the ratios of their colonisation rates to their local extinction rates while the absolute magnitudes of these rates were not decisive. For groups 1-3 (Figs. 4 and 5) and for group 4 in the case of $w<0.3$, coexistence is possible because the winner species “looses” enough habitats due to habitat turnover while a sufficient number of empty habitats is created at each time step that can be colonised by the loser species. By this the loser can “escape” from being regionally outcompeted by the winner. For group 5, the winner has a low colonisation and/or a high local extinction rate, so it places sufficiently low pressure on the loser which can always find a sufficient number of empty habitats.

Additional arguments are required to understand the behaviour of group 4. For $w< 0.3$, the induced land-use patterns are homogeneous with regard to habitat turnover (i.e., in every part of the landscapes the same level of turnover is observed). For slightly higher w around 0.3, however, we observe a rather clustered pattern of habitats which falls into two different parts: a stable core with no habitat turnover and unstable edges that are clustered but subject to high turnover (Fig. A1). These edges are unsuitable for the winner with its rather low colonisation rate and high local extinction rate but suitable for the loser which has a higher colonisation rate and lower local extinction rate than the winner. In this case we observe a partition in the presence of the competitors, which might be regarded as some kind of competitive exclusion.

4.3 Assumptions and future research

The present results are based on a number of assumptions that may be relaxed in future research. First, we assumed myopic land users who base their decisions only on the land-use pattern of the current time step and consider only the land-use decisions of their neighbours. Furthermore, they consider only their expected profit in the next time step and not in the more distant future.

Second, we assumed that the land use can be switched between conservation and economic use instantaneously and at no cost. While there exist such land-use types (e.g. shifting the mowing of grassland from the profit-maximising date to a species-friendly one: see, e.g., Drechsler et al. 2007) often it takes time and management effort to create a habitat, or reverse the decision and turn a natural area into intensively used agricultural land.

Third, the dispersal of individuals is only short-ranged (to adjacent habitats). Longer-ranged dispersal, e.g. with an exponential decay of immigration with increasing distance between source and target habitats, is likely to affect the coexistence between the species and thus the effectiveness of the policy scheme.

Fourth, we assumed that the conservation costs (*z*) are spatially and temporally uncorrelated. Correlations in the conservation costs affect the cost-effectiveness of tradable permit schemes for single species (Hartig and Drechsler 2009) and can be expected to affect also the effectiveness of permit schemes for the conservation of interacting species.

Fifth, the interaction between the two species was modelled in a rather simple manner, such that the superior (“winner”) species always locally excludes the inferior (“loser”) species. In contrast, the competition could be weaker, so that e.g. the presence of the winner species only increases the local extinction rate of the loser species but does not automatically replace it. That would allow for temporary co-existence of both species even on the local scale, although in the long run the inferior competitor would still locally outcompete the inferiour competitor. Furthermore the two species could act in a predator-prey manner where the predator can survive only if it eats enough prey per time step, or in a mutualistic manner where the presence of one species facilitates the presence of the other. And, of course, three or more interacting species could be considered.

Lastly, our conceptual model approach should be applied to real cases, which would require determining the spatial distribution and temporal dynamics of the conservation costs, the species colonisation and local extinction rates and dispersal ranges as well as the parameters of their interaction.

4.4 Policy implications and conclusions

Our results show that the effectiveness of policy instruments for the conservation of species strongly depend on the interactions between these species. While for the conservation of single or non-interacting species special survival is maximised when the policy parameters λ and w are largest, this is not true when two competing species are conserved (Fig. 1). Furthermore, the most effective combination of policy parameters that maximises species coexistence substantially depends on the characteristics (colonisation and local extinction rates) of the species (Fig. 5). This implies that before a policy scheme for the conservation of multiple interacting species can designed, i.e. before the choice of the policy parameters, (i) information about the conserved species including their interactions need to be gathered carefully, and (ii) a normative choice must be taken on which species to prioritise.

Our conclusions are based on the analysis of a tradable permit scheme with an agglomeration incentive as introduced by Drechsler and Wätzold (2009). However, they are not restricted to this policy instrument. Instead, our agglomeration incentive exactly equals the agglomeration bonus proposed by Parkhurst et al. (2002) where land users receive a base payment when the land is conserved and a bonus on top of it when the conserved land is contiguous to other habitat. While in our study the total amount of habitat is controlled by the policy parameter λ, in a payment scheme this is controlled by the levels of base payment and agglomeration bonus. Thus, the landscape dynamics induced by a tradable permit scheme can be equally induced by a payment scheme, such as a payment for ecosystem services (Engel et al. 2008).

5. References

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Appendix A. Patterns of land use and species occupancy

Figure A1 shows a number of screen shots of the model landscape. Comparing columns (a)-(c) one can see that increasing connectivity weight *w* leads to more clustering of habitats (cf. Fig. 2). In each panel, especially in panel (b), one can further see that the old habitats with ages above 100 time steps are found in the centres of habitat cluster(s) while the young habitats with ages below 10 time steps are at the edges. The age of a habitat is defined as the number of time steps a habitat patch has been conserved since its creation.

The expected habitat age is inversely related to the habitat turnover. For instance, the high turnover in panel (a) (*w*=0.2) leads to the destruction of one third of all habitats every time step, whereas with *w*=0.5 (panel (c)) this rate drops to 6%. Comparing the upper and lower rows of panels one can clearly see that the old habitats in the centres of the cluster(s) are mainly occupied by the winner while the young habitats at the edges are mainly occupied by the loser.

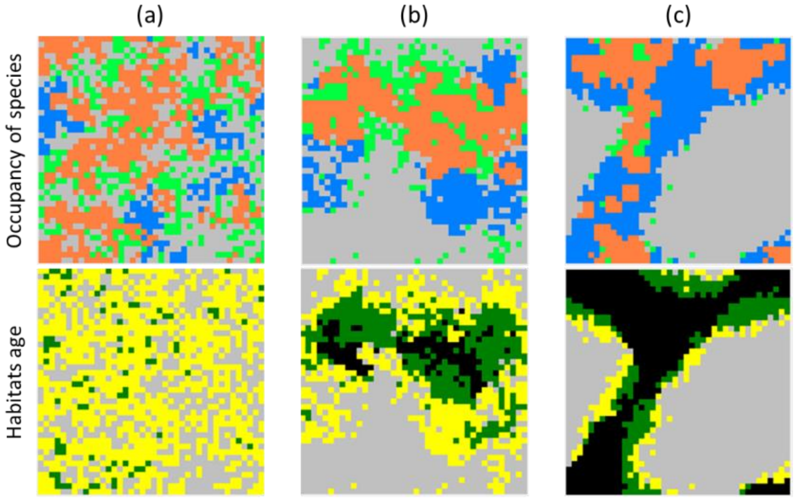

Fig A1: Spatial views of the landscape for three policy schemes at time step 110 for a single simulation run. Grids on the upper row represent the landscape (grey: *economic use*, green: *empty habitats*, orange: *winner presence*, blue: *loser presence*) and grids on the lower line represent the age of the habitats (yellow: *less than 10 time steps*, green: *between 10 and 100 time steps*, black: *more than 100 time steps*). Columns (a), (b) and (c) represent the outcomes of three policy schemes, represented by $\lambda=0.5$ and $w=0.2$, 0.3, 0.5, respectively. The species characteristics are chosen in the groups that allow coexistence on the respective policy schemes, namely: (a) $C_{\text{winner}}=0.7$, $E_{\text{winner}}=0.5$, $C_{\text{loser}}=1$ and $E_{\text{loser}}=0.1$; (b) $C_{\text{winner}}=0.7$, $E_{\text{winner}}=0.7$, $C_{\text{loser}}=1$ and $E_{\text{loser}}=0.1$; (c) $C_{\text{winner}}=0.9$, $E_{\text{winner}}=0.8$, $C_{\text{loser}}=0.8$ and $E_{\text{loser}}=0.1$.