Modelling the effectiveness and permanence of a compensation payment scheme for the conservation of a public environmental good

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Joint Abstract:

The present submission consists of two rather short papers that deal with the performance of compensation payment schemes, employing game-theoretical approaches within a grid-based dynamic ecological-economic model. The first paper introduces the environmental problem: the trade-off between the selfish maximization of agricultural profit and the conservation of pollinators that benefit the entire farming community. In their individual land-use decisions, famers decide to either spray their land with pesticides to eliminate pests – with the unintended but unavoidable adverse side effect that this also eliminates beneficial pollinators, or to accept pest-induced losses but conserve the pollinators. The pollinators are assumed to be mobile, representing a public good, and their elimination on a particular land parcel leads to negative spatial externalities to neighbouring farmers.

Three behavioural strategies are considered for each farmer: Cooperate (i.e. do not spray), defect (spray) and tit-for-tat (spray if neighbours sprayed previously and do not spray otherwise). The present model is used to analyse, among others, the circumstances under which a compensation payment that is paid to cooperating farmers, can induce cooperation in the farming community. The results highlight the relevance of the tit-for-tat strategy for yielding effectiveness of the payment scheme.

The second paper relativises this result by employing an evolutionary game-theoretic approach. While in the first paper the famers are either all cooperative, all defecting, or all tit-for-tat players, in the second paper each famer can in any time step choose one of these three strategies, and s/he does so in a way that maximizes his/her expected profit.

The analysis of this model reveals that even at rather low payment levels, a considerable proportion of the farmers plays tit-for-tat, which confirms the well-known result that tit-for-tat is a viable strategy even if a considerable proportion of the other players defects. What has not yet been tested, however, is whether tit-for-tat also leads to the protection of the public good. The model analysis reveals that this is not the case. Instead, tit-for-tat players appear as opportunists: their frequency of cooperation is precisely determined by the proportion of cooperators in the population, and if – due to low payment levels – the defectors are in the majority compared to the cooperators, a correspondingly large majority of the tit-for-tat players effectively defects. I conclude that the tit-for-tat strategy, even though it is commonly understood as a model for overcoming selfishness and developing altruism, fails in the protection of a public good.

Key words: conservation, public good, ecological-economic model, game theory

JEL codes: C63, C72, C73, Q24, Q28, Q57, Q59.

The impact of conservation payments and landowner behaviour on conservation when conservation costs at the local level but pays at the regional level

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Abstract

Biodiversity and ecosystem services are in decline worldwide. One reason for this is that private interests of landowners are often at conflict with public interests. Payments for environmental services as well as spatial externalities together with a cooperative attitude among landowners may alleviate this conflict. A grid- and agent-based simulation is used to investigate the effects of payments and landowner behaviour on the levels of conservation and social welfare in a region, as well as the permanence of conservation, i.e. whether conservation is maintained even after payments have been reduced or ceased. Results indicate that the proper choice of payment levels is a delicate balance between achieving conservation goals and maximizing social welfare, and permanence is possible if conservation leads to positive spatial effects and landowners respond to conservation in their neighbourhood with conservation on their own land.

Highlights

A model is presented for the conservation of spatially interacting ecosystem services

Conservation payments must balance ecological effectiveness and social welfare

Externalities together with reciprocal altruism enhance permanence of conservation

Key words

Cooperation, conservation, externality, payments for ecosystem services, permanence, pollination, social dilemma.

1. Introduction

Biodiversity and ecosystem services are in dramatic decline worldwide (Millennium Assessment, 2005). Often these losses are not compensated by sufficient increases in other forms of capital and – even under the concept of weak sustainability - imply a net loss in human welfare. A major reason for the loss of ecosystem services is that private interests of landowners are often at conflict with public interests (Pannell, 2008). If property rights allow, landowners will generally maximise their private profits even if this comes at a net loss in public goods and welfare.

A solution for this problem exists when public interests can be aligned with private interests. Such an alignment can occur due to biophysical conditions, such that a landowner has own benefits from the protection of ecosystem services. This may be direct in that the ecosystem services protected on the own property lead to private benefits on that property. Or it may be indirect in that neighbouring landowners benefit from the protection of ecosystem services (positive spatial externalities). In the latter situation, reciprocal altruism where a landowner responds with cooperative behaviour to cooperative behaviour in neighbouring landowners may lead to overall cooperation. If cooperation is understood as protection of an ecosystem service, reciprocal altruism may lead to protection of the ecosystem service on the regional scale with positive aggregated net benefits for all landowners.

Reciprocal altruism is a major paradigm for the evolution of cooperation (Trivers, 1971; Nowak, 2006). A model environment in which this evolution has been studied experimentally and theoretically is the prisoners' dilemma (Kollock ,1998), a theoretical game in which two players are confronted with a situation where defection leads to private benefits (the own reward) but reduces public benefits (the summed rewards of both players). A frequently cited strategy to overcome selfish behaviour is Tit-for-tat (Stephens, 1996) where cooperation is responded to with cooperation and defection is responded to with defection.

Reciprocal altruism and Tit-for-tat have been extensively studied in spatial settings (e.g., Nowak, 1992; Brauchli et al., 1999; Koella, 2000). Many of these studies investigate under which circumstances altruistic behaviour can spread into and survive in a spatially structured population of egoists (defectors) and altruists (cooperators).

Next to the direct and indirect benefits of cooperation, an alternative to induce cooperative behaviour beneficial to the whole of all landowners are environmental instruments like payments for environmental services (PES) (Engel et al., 2008; Gómez-Baggethun et al., 2010; Engel, 2016). The application of PES rises world-wide to encounter biodiversity loss and the degradation of ecosystems. A problem with these instruments, however, is that they are associated with substantial costs to society. Therefore it is questioned whether PES can be financed forever, and the issue of permanence, i.e., “do participants of PES carry on with environmentally friendly land use even after the PES has been ceased?”, attracts increasing attention. For this question a game-theoretic approach like the one discussed above may help to investigate the circumstances under which altruistic behaviour can survive in a population.

To address the problem of inducing cooperative, environmentally friendly behaviour in a population of selfish landowners and ensuring its permanence even in the absence of financial incentives I combine both approaches and present a model of landowners which to some extend are interested in their short-term economic profits but also act according to the paradigm of reciprocal altruism. The model is based on the problem of pollinator conservation (Faegri and Van Der Pijl, 2013) but applicable to similar environmental problems. Pollinators are an important economic factor in agricultural production, providing about 10 percent of the value of the world’s agricultural production for food (Gallai, 2009). Pollinator management leads to a sensitive trade-off. On the one hand the spraying of pesticides reduces pest abundance in agricultural fields, raising harvests and income. On the other hand it harms pollinators whose absence reduces harvests and income. In addition, losses caused by the absence of pollinators may not only occur on the sprayed field itself but also on neighbouring fields which would have benefitted from dispersing pollinators. Therefore, even though for the individual farmer it may be on net beneficial to spray (depending on the relative effects of pest species and pollinators on harvest and income) it may be adverse to the entire farming community, and we face the trade-off between individual (local) and aggregated (regional) benefits outlined above.

The model used for the analysis is a grid- and agent-based simulation model for the spatio-temporal land-use dynamics emerging from the landowners’ preferences and decisions. Each landowner can choose between two land-use measures: conservation (not spraying) and spraying. In the game-theoretic setting of the above-mentioned prisoners’ dilemma, the former land use is identified with cooperation and the latter with defection. As noted above, the landowners’ decisions are based both on the landowners’ own benefits and the behaviour of their neighbouring landowners. For the latter I consider the above-mentioned Tit-fot-tat strategy and another frequently discussed strategy, termed “Pavlov” (Kraines and Kraines, 1988). Under the Pavlov strategy, a player keeps the current action if the other player(s) cooperate(s) and shifts to the other action (cooperation to defection or vice versa) if the other player(s) defect(s).

With the model I analyse the following two questions: (1) How does the level of cooperation (conservation / not spraying) in the model region depend on model parameters, in particular the initial proportion of cooperators in the region?, and (2) How can a payment to conserving landowners influence the level of cooperation and how does this affect the associated aggregated profit of the landowners and the regional social welfare?

2. Methods

2.1 Model structure

I consider a stylized landscape with 10 by 10 grid cells, each representing a land parcel *i* that can be managed with pesticides (x_i=0) or without (x_i=1) (following the usual notation that 1 represents "conservation" and 0 "economic use"). Not spraying (x_i=1) implies more pests on parcel *i* and ceteris paribus reduces harvest, modelled by an opportunity cost *c*. Not spraying (x_i=1) further provides habitat for pollinators in the parcel. A sprayed parcel (x_i=0) does not provide habitat for pollinators but can be pollinated by pollinators dispersing from neighbouring parcels.

An isolated sprayed parcel (x_i=0) generates, without loss of generality, a profit of zero. Compared to this, in an isolated parcel that is not sprayed (x_i=1) the profit is reduced by *c*, as argued above, but at the same time increased by some amount β which measures the positive impact of the pollinators. So the profit becomes $\pi_i = \beta - c$. Altogether, an isolated parcel generates a profit of

$$\pi_i = (\beta - c)x_i \,. \qquad (1)$$

In a land parcel connected to other land parcels the number of pollinators depends on the number of parcels in the neighbourhood that are not sprayed. As neighbourhood I regard the so-called Moore neighbourhood of the eight adjacent land parcels. The profit increase due to the presence of pollinators on a land parcel *i* then can be modelled as βn_i where n_i is the number of conserved land parcels in the Moore neighbourhood plus the focal land parcel. By this, n_i can range between zero (all parcels in the neighbourhood as well as parcel *i* are sprayed) and nine (all parcels are conserved, i.e. not sprayed).

The profit of a parcel *i* then is

$$\pi_i = \beta n_i - c x_i , \tag{2}$$

which includes the case of an isolated parcel as a special case, since for an isolated parcel $n_i = \beta x_i$.

Above, all parcels have been assumed to have the same productivity. Productivity, however, may vary among parcels, e.g. due to different soil qualities. To consider this spatial heterogeneity in the landscape the parcel's profit π_i is multiplied with some factor k_i:

$$\pi_i = k_i (\beta n_i - c x_i) \tag{3}$$

The values k_i are sampled randomly from a uniform distribution with bounds $1+\sigma$ and $1-\sigma$.

2.2 Management decisions / strategies

If $\beta < c$ and for given land-use choices on the neighbouring land parcels it is always profitable to spray. However, since the parcels are not isolated, not spraying not only increases the local number of pollinators but also the number of pollinators on other parcels. Therefore, depending on the relative magnitudes of β and c, not spraying any parcel may increase the aggregated profit of all land parcels compared to the case where all parcels are sprayed. This is similar to the situation of a two-player prisoners dilemma where the aggregated profit of both players is maximised when both players cooperate (not spraying their parcels) but the individual profit of each player is maximised by defecting (spraying the parcel).

Two main strategies have been discussed in the literature to overcome the prisoners' dilemma and induce cooperation even though ceteris each player's profit is maximised by defecting:

1. Tit-for-tat: Each landowner cooperates (does not spray) if in the previous time step the proportion q of cooperating (not sprayed) land parcels in the neighborhood exceeds a certain threshold. If only a proportion q below the threshold cooperated in the previous time step the landowners defects (sprays the land parcel).

2. Pavlov: Each landowner keeps the management of the previous time step if in the previous time step the proportion q of cooperating neighbours exceeded a certain threshold, and switches the management (from cooperation to defection and vice versa) otherwise.

To combine these strategies with the profit model above I build a utility function as a weighted sum of the profit above and the preference for cooperation according to the two models Tit-for-tat and Pavlov. For this I first rescale the profits of all land parcels to a range between zero and one and consider four extreme land-use patterns:

(i) all land parcels except for parcel *i* are sprayed but parcel *i* is not sprayed,

(ii) all land parcels, including parcel *i*, are sprayed,

(iii) land parcel *i* is sprayed but all other land parcels are not sprayed, and

(iv) none of all land parcels is sprayed.

The land-use pattern that maximizes respectively minimizes the profit of parcel *i* are among those four. I numerically identify the maximising and minimsing land-use pattern and denote the associated maximum and minimum profits as $\pi_i^{(\max)}$ and $\pi_i^{(\min)}$. For a given land-use pattern, the profits $\pi_i(x_i)$ are then rescaled via

$$\pi_i'(x_i) = \frac{\pi_i - \pi_i^{(\min)}}{\pi_i^{(\max)} - \pi_i^{(\min)}} . \tag{4}$$

The utility for strategy 1 (Tit-for-tat) then is modelled as

$$u_i = \begin{cases} w\pi_i'(1) + (1-w)q, & x_i = 1 \\ w\pi_i'(0) + (1-w)(1-q), & x_i = 0 \end{cases} \tag{5}$$

By this, an increasing profit from conservation and/or an increasing proportion of conserved land parcels in the neighbourhood increase the utility from conservation while the utility from spraying increases with increasing profit from spraying and/or increasing number of sprayed land parcels in the neighbourhood. The influence of the profit π_i’ on the utility relative to the influence of the land-use in the neighbourhood is given by the weight *w*, where *w*=1 represents the extreme case where only the profit is relevant, and *w*=0 represent the case where only the land-use in the neighbourhood is relevant.

For strategy 2 (Pavlov) the profits of keeping the previous land-use respectively changing to the other are

$$\pi_i(stay) = \begin{cases} \pi_i'(1) - \pi_i'(0), & x_i = 1 \\ \pi_i'(0) - \pi_i'(1), & x_i = 0 \end{cases} \tag{6}$$

and

$$\pi_i(shift) = \begin{cases} \pi_i'(0) - \pi_i'(1), & x_i = 1 \\ \pi_i'(1) - \pi_i'(0), & x_i = 0 \end{cases} \tag{7}$$

and the utilities are

$$u_i(stay) = w\pi_i(stay) + (1-w)q \tag{8}$$

and

$$u_i(shift) = w\pi_i(shift) + (1-w)(1-q) \tag{9}$$

By this, an increasing profit from staying (keeping the current land use) and/or an increasing proportion of conserved land parcels in the neighbourhood increase the utility from staying while the utility from changing the current land use (shifting) increases with increasing profit from shifting and/or increasing number of sprayed land parcels in the neighbourhood. The relative influences of the two factors are given by the weight *w*.

2.3 Agricultural policy

Two policy scenarios are considered: (i) absence of any policy intervention, and (ii) a payment of magnitude *p* is offered to each land owner who does not spray his/her parcel. These landowners' profits are increased by *p* accordingly.

2.4 Initial conditions and simulation

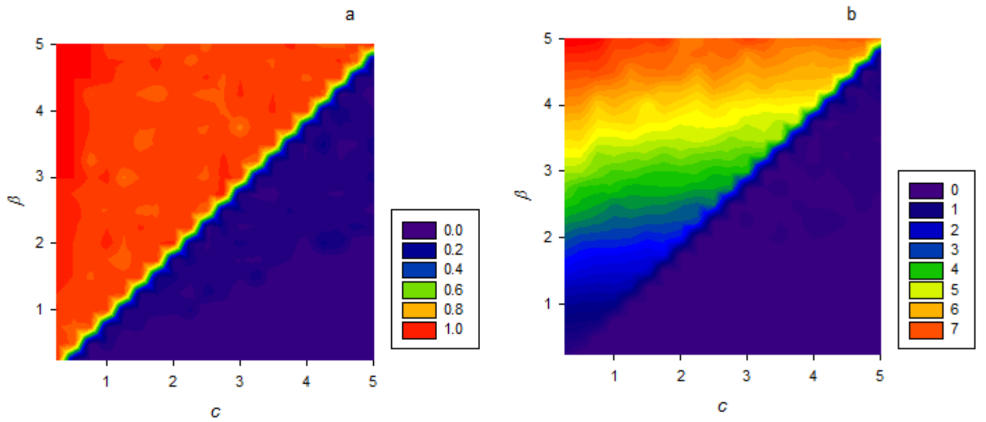
A number of different initial conditions, ranging from the case where all land parcels are sprayed to the case where no land parcel is sprayed are considered through a parameter *z* which is the probability of a land parcel being conserved (not sprayed). Varying z between zero and one leads to different initial land-use patterns, ranging from the case in which all land parcels are sprayed (z=0) to the case in which none is sprayed.

The land-use dynamics are simulated over 100 time steps, which has been checked to be sufficient for the dynamics to reach a steady state. The proportion of conserved (not-sprayed) land parcels is recorded for the final time step. For non-zero payments, $p>0$, in addition the aggregated profit of all landowners, $\Pi = \sum_i \pi_i$, the required budget for the policy maker, $B = \sum_i px_i$, and social welfare, W=Π-B are calculated. For each parameter combination the simulation is repeated 50 times and averages over the output variables are taken.

3. Results

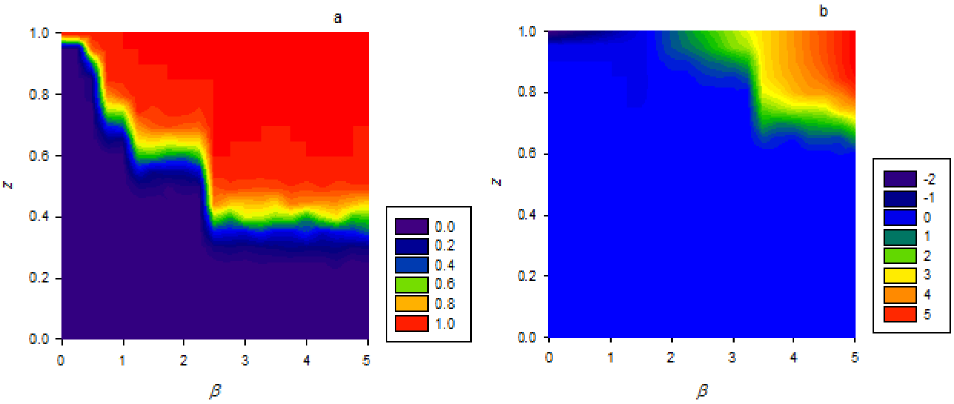
I start with the land-use dynamics when landowners decide according to eq. (5) (Tit-for-tat). Figure 1a shows that the proportion of conserved (not sprayed) land parcels is close to one if $\beta > c$ and close to zero if $\beta < c$. For $\beta \approx c$ there is a sharp transition between these two outcomes. In the case of $\beta > c$ where all landowners turn out to cooperate and conserve their land parcels the aggregated profit is higher than in the case of $\beta < c$ without conservation. In the former case the aggregated profit increases with increasing β due to the profit equation (eq. 2).

Figure 1: Effect of the profit parameters β and c on the proportion of conserved land parcels (panel a) and the aggregated profit (panel b). The two dependent variables are shown by colour scale. Land use is chosen according to eq. (5) (Tit-for-tat). Other model parameters: σ=0.5, w=0.5, p=0, z=0.5.



According to Fig. 2, the proportion of conserved land parcels increases with increasing β and increasing initial proportion of conserved land parcels (z) (Fig. 2a) and is close to one for large β and/or large z and close to zero for small β and/or small z. The transition between the two outcomes is rather sharp. Like in Fig. 1, the aggregated profit is positively related to the proportion of conserved land parcels (Fig. 2b).

Figure 2: Effect of the profit parameter β and the probability z of a land parcel being conserved in the beginning of the simulation on the proportion of conserved land parcels (panel a) and the aggregated profit (panel b). The two dependent variables are shown by colour scale. Land use is chosen according to eq. (5) (Tit-for-tat). Other model parameters: c=2.5, σ=0.5, w=0.5, p=0.



A relevant parameter for the land-use dynamics is the weight w attached to the profit compared to the proportion of conserved land parcels in the neighbourhood. Figure 3 shows that the steepness of the yellow transition line that separates the outcomes where all respectively no land parcels are conserved increases with increasing w. In particular, for w=0 the value of β has no effect on the proportion of conserved land parcels (Fig. 3a) while for w=1 the initial proportion of conserved land parcels has no effect (Fig. 3d). This is plausible because the impact of β on the decision to conserve a land parcel increases with increasing w. Conversely, the initial proportion of conserved land parcels has a strong impact on the proportion of conserved land parcels at later time steps, and the impact of the proportion of conserved land parcels (in the neighbourhood) increases with decreasing w.

Lastly, Fig. 4 shows that an increasing payment p increases the proportion of conserved land parcels (Fig. 4a) and the aggregated profit (Fig. 4b). Of course, at the same time a higher payment leads to higher expenses for the agency (Fig. 4c). Altogether, social welfare which is the difference between aggregated profit and agency's expenses decreases with increasing payment p – but only in those cases of sufficiently high initial proportion of conserved land parcels (z) so that most landowners cooperate and conserve their land parcels. If z is too small and no land parcel is conserved the payment has no effect on social welfare.

Figure 3: Proportion of conserved land parcels as a function of the profit parameter β and the probability z of a land parcel being conserved in the beginning of the simulation for four levels of the weight w: (a) w=0, (b) w=0.2, (c) w=0.8, (d) w=1. Land use is chosen according to eq. (5) (Tit-for-tat). Other parameters as in Fig. 2.

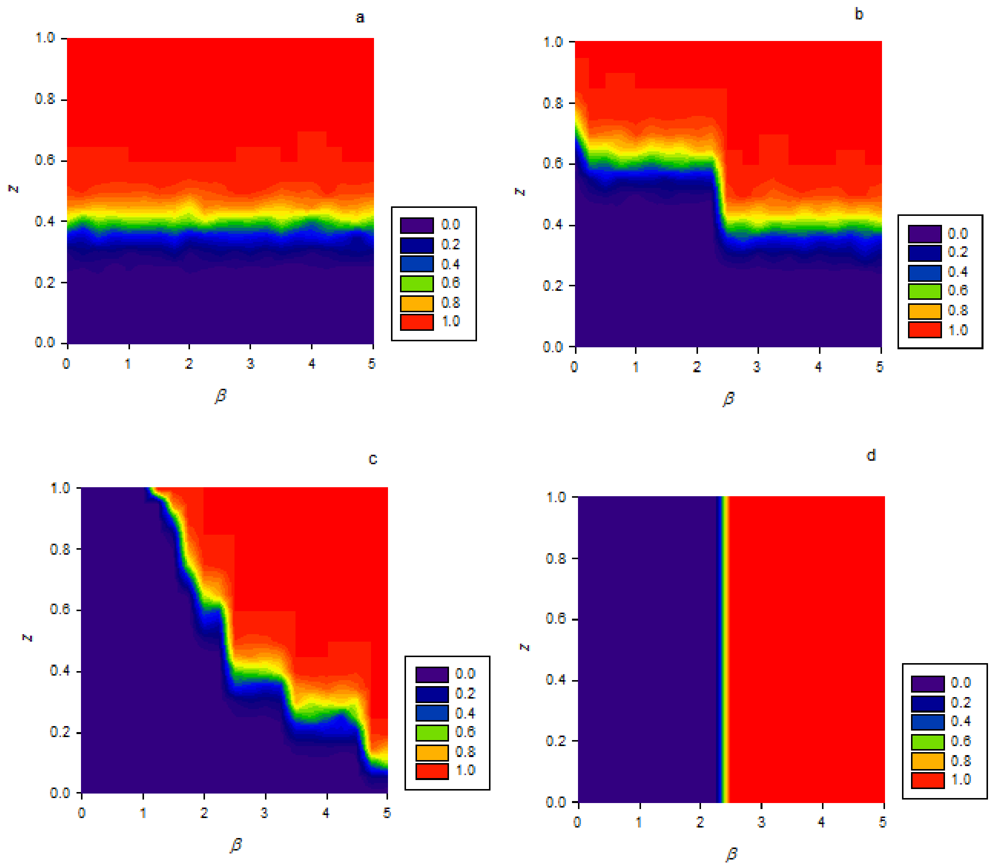
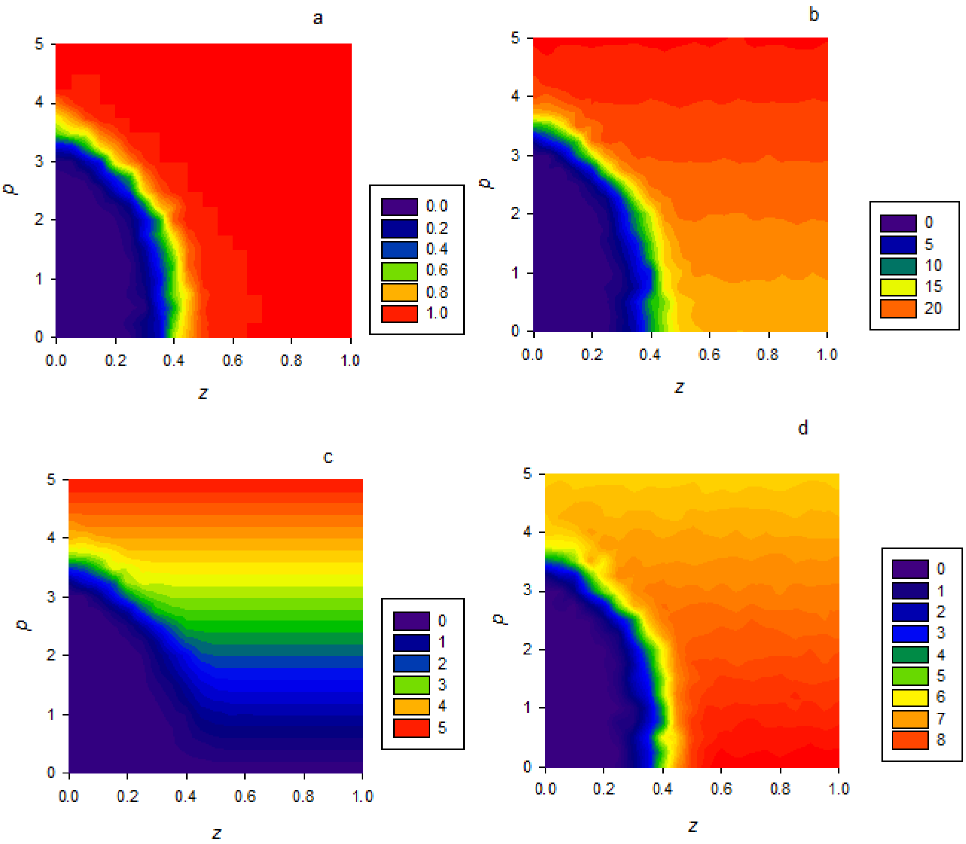
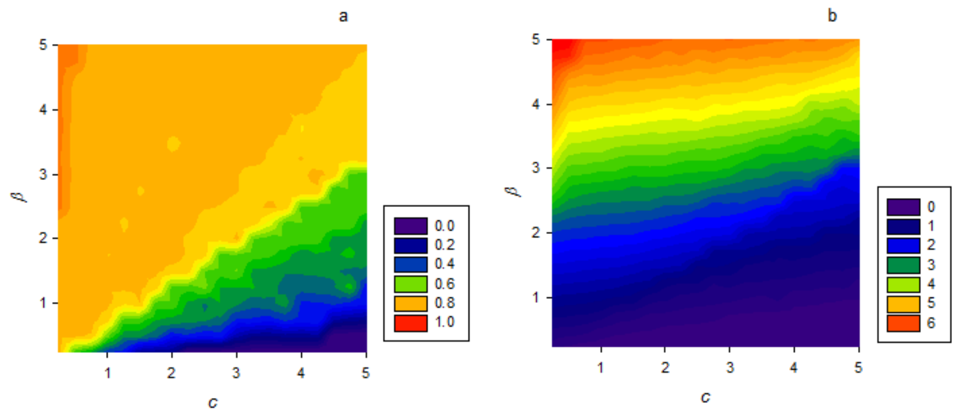


Figure 4: Effect of the probability *z* of a land parcel being conserved in the beginning of the simulation and the payment *p* on the proportion of conserved land parcels (panel a), the aggregated profit (panel b), the agency's expenses (panel c) and social welfare (panel d). The four dependent variables are shown by colour scale. Land use is chosen according to eq. (5) (Tit-for-tat). Other model parameters: c=2.5, β=0.5, σ=0.5, w=0.5.



For landowners choosing their land use according to eqs. (8) and (9) (Pavlov) the results are similar with a few differences. As in the Tit-fot-tat scenario, the proportion of conserved land parcels and the aggregated profit increase with increasing β and/or decreasing c (Fig. 5). In contrast to Fig. 1, however, there is no sharp transition between full conservation and no conservation but the proportion of conserved land parcels increases gradually.

Figure 5: Effect of the profit parameters β and *c* on the proportion of conserved land parcels (panel a) and the aggregated profit (panel b). The two dependent variables are shown by colour scale. Land use is chosen according to eqs. (8) and (9) (Pavlov). Other model parameters: σ=0.5, *w*=0.5, *p*=0, *z*=0.5.



The role of the initial proportion of conserved land parcels is more complex under Pavlov than under Tit-for-tat (Fig. 6). As in Fig. 2, for z>0.5 the proportion of conserved land parcels increases with increasing *z* (Fig. 6a). However, for z<0.5 it does not decrease with decreasing z, but instead there is another maximum in the number of conserved land parcels for very small *z* (red colour at the bottom of Fig. 6a). The reason for this is that if z is very small, most landowners have few cooperating neighbours around them, inducing them to change their land use (eqs. (8) and (9)). Thus, in the next time step very many landowners conserve their land parcels and they keep doing so according to eqs. (8) and (9). This pattern is reflected in the aggregated profit (Fig. 6b) which is maximal for large β and for large or small *z*.

The influence of β and *z* on the proportion of conserved land parcels changes with varying weight *w* (Fig. 7). While the patterns in Fig. 7 differ from those in Fig. 3, the dependence on *w* can be explained in the same way as in Fig. 3. For small *w* (Figs. 7a and 7b) the local land-use choice is mainly affected by the proportion of conserved land parcels in the neighbourhood and so the profit parameter β has only a small effect while the initial proportion of conserved land parcels (*z*) has a strong effect on the proportion of conserved land parcels. In the opposite extreme of large *w*, *z* has little effect while β has a strong effect on the proportion of conserved land parcels (Figs. 7c and 7d).

Figure 6: Effect of the profit parameter β and the probability z of a land parcel being conserved in the beginning of the simulation on the proportion of conserved land parcels (panel a) and the aggregated profit (panel b). The two dependent variables are shown by colour scale. Land use is chosen according to eqs. (8) and (9) (Pavlov). Other model parameters: c=2.5, σ=0.5, w=0.5, p=0.

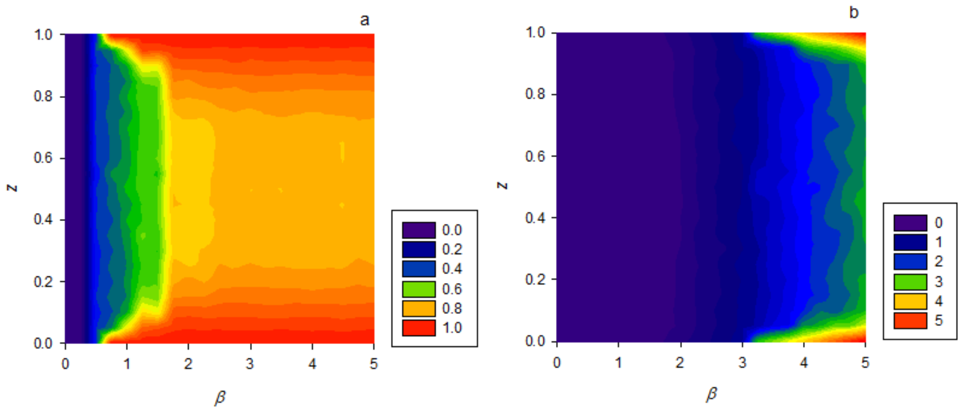
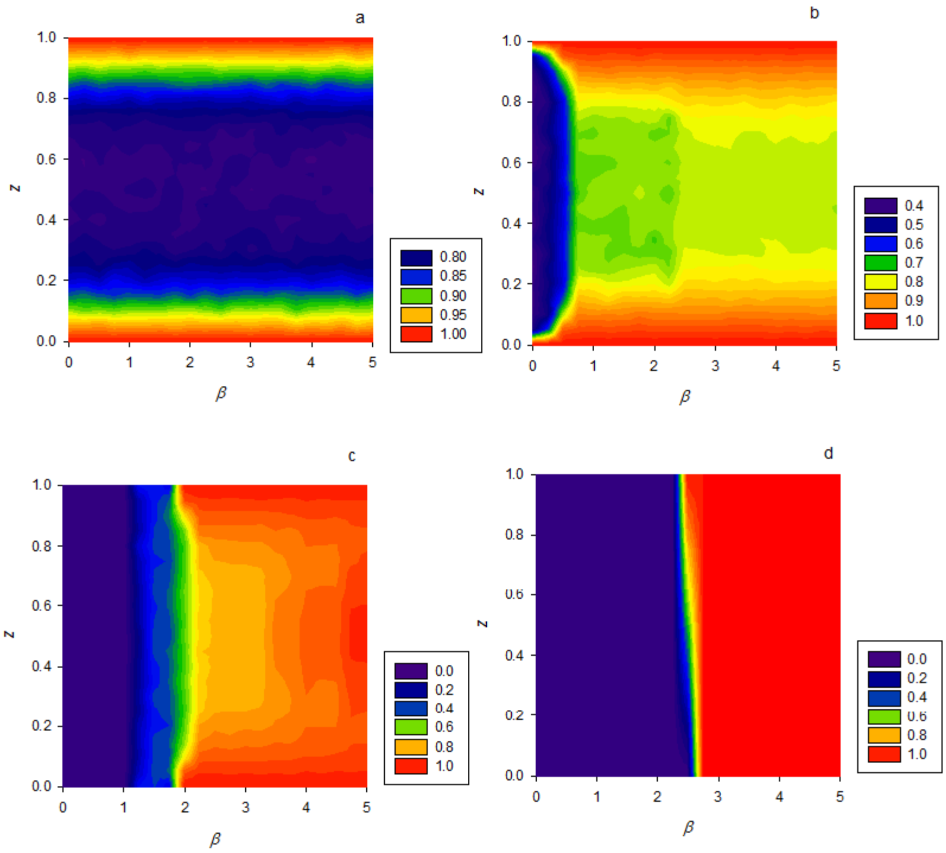
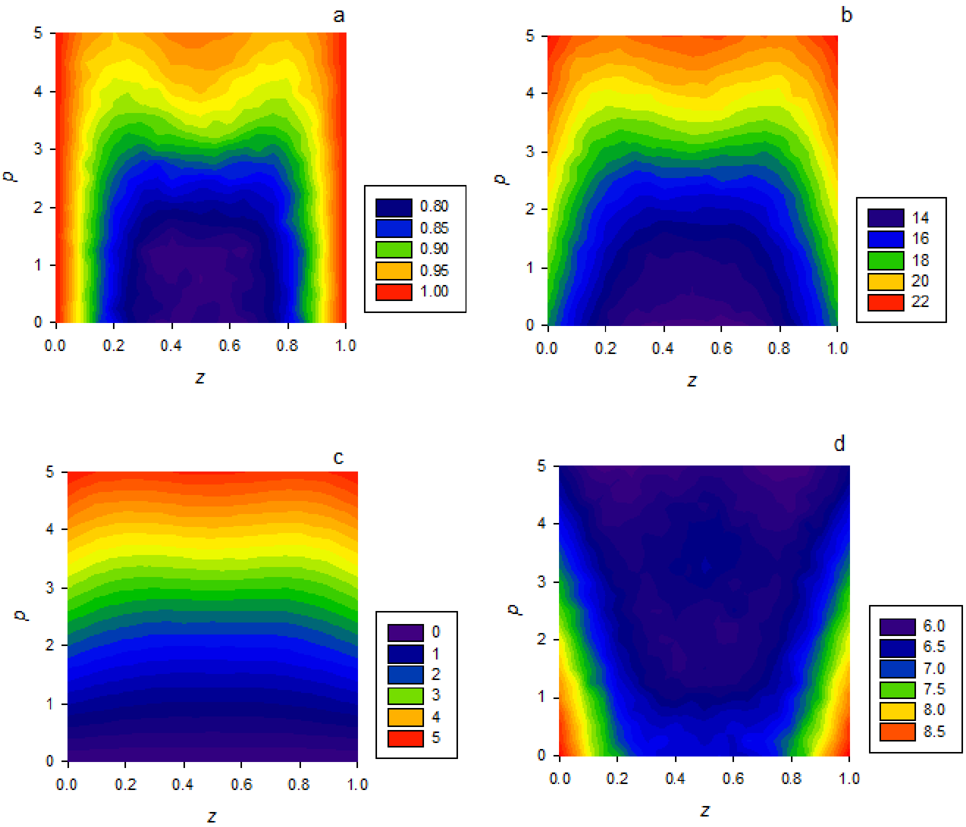


Figure 7: Proportion of conserved land parcels as a function of the profit parameter β and the probability z of a land parcel being conserved in the beginning of the simulation for four levels of the weight w: (a) w=0, (b) w=0.2, (c) w=0.8, (d) w=1. Land use is chosen according to eqs. (8) and (9) (Pavlov). Other parameters as in Fig. 6.



The effect of the payment *p* is similar as in the Tit-for-tat scenario. Increasing *p* increases the proportion of conserved land parcels and the associated aggregated profit as well as the budget required for the agency (Figs. 8a-c). Similar to Fig. 4d for large *z*, social welfare is maximised by small *p* (Fig. 8d). However, in contrast to Fig. 4d, small *p* maximise social welfare independent of *z*, and there is no critical minimum the payment *p* must exceed to induce a non-zero proportion of conserved land parcels.

Figure 8: Effect of the probability *z* of a land parcel being conserved in the beginning of the simulation and the payment *p* on the proportion of conserved land parcels (panel a), the aggregated profit (panel b), the agency's budget (panel c) and social welfare (panel d). The four dependent variables are shown by colour scale. Land use is chosen according to eqs. (8) and (9) (Pavlov). Other model parameters: c=2.5, β=0.5, σ=0.5, w=0.5.



4. Discussion

A major reason for the decline of biodiversity and ecosystems services is that private interests of landowners are at conflict with public interests. Even if conservation does not maximise the profit of an individual landowner the aggregated profit of all landowners may be maximised if they all conserve. In such a case the difficulty is to induce the landowners to conservation and shift the regional land use from a selfish to a cooperative regime. An instrument for this can be payments for environmental services. Once conservation has been established in a majority of land parcels as a response to such payments, a conservation agency may consider reducing or ceasing these payments because it is in the landowners' own interest to maintain conservation. Such a behaviour in the landowners community may be regarded as a form of permanence.

With the help of a simulation model, based on the case where conservation of pollinators is costly locally (i.e., for an individual landowner) but beneficial regionally (i.e. for all landowners if all landowners conserve), I investigate the influence of payments on the level of conservation in a region and the influence of the behaviour of the landowners on the permanence of conservation.

For the first question I find that a sufficiently large payment leads to large scale conservation in the region. In the case where landowners act according to the Tit-for-tat strategy, the payment must exceed a particular threshold whose magnitude depends on other ecological and economic factors. Within this constraint, from a welfare point of view (considering the difference between the landowners' aggregated profit and the conservation agency's expenses) the payment level should be choses as low as possible.

For the second question, if landowners respond to conservation on neighbouring land parcels with conservation (Tit-for-tat strategy) or with a continuation of their current land use (Pavlov strategy) conservation is permanent, i.e. a sufficiently large number of conserving landowners implies that these landowners will keep conserving their land parcels. In addition, in the case where the landowners decide according to the Pavlov strategy, even an extremely small initial level of conservation leads to a high level of conservation because realising that their neighbours do not conserve, all landowners switch their land use to conservation and then stay in that land-use regime.

The model analysis makes a number of assumptions. An important assumption is that the landowners behave myopically, i.e. consider only their short-term profits and the land use in the immediate neighbourhood, and they have no memory. Further simplifying assumptions are that each landowner can choose only between two land-use measures (conservation / not spraying pesticides, and no conservation / spraying); local land use is made dependent on whether the majority of neighbouring land parcels is conserved; dispersal of the pollinator is only to adjacent land parcels. While the assumption of "smarter" landowners may have an influence on the model results, a relaxation of the other assumptions will probably not change the model results significantly.

In addition to a relaxation of the above assumptions, future research may consider other conservation instruments than payments, such as tradable land-use permits; consider the spatial allocation of conservation (e.g., agglomeration of conservation activities); and explicitly model the population dynamics of the pollinator species. Furthermore, it might be worthwhile considering other land-use problems where cooperation and the trade-off between local and regional benefits play a role, such as water management issues, and applying the model to a real case study.

Nevertheless, the present study already points to two important issues: that the proper payment level for environmental services is a critical issue, since too small payments will not induce conservation while to large payments may reduce social welfare; and that once conservation has been established through a payment, it is likely to persist in a region even after reduction or cessation of the payment if (i) conservation has positive spatial external effects and (ii) landowners respond to conservation in their neighbourhood with the decision to conserve their own land, too.

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Modelling the evolution of cooperation under payments for environmental services

Abstract

Payments for environmental services (PES) are an effective instrument to induce environmentally friendly behaviour. A spatially explicit game-theoretical simulation model is developed to explore the effectiveness of a PES. To assess the effectiveness of PES, the classical game-theoretical approach that focuses only on strategies must be extended to the consideration of the landowners' actions (cooperate, i.e., use the land in an environmentally friendly manner, or defect) determined by these strategies. Systematic exploration of the model reveals that Tit-for-tat ("do what the other player did before") that is commonly viewed as a model of altruism and cooperation is not sufficient to ensure cooperation under a payment scheme, but its positive influence on the scheme's effectiveness heavily relies on the presence of other strategies (in particular the strategy to always cooperate) in the population of landowners.

Key words

Cooperation, environmental policy, evolutionary game theory, payments for environmental services, simulation model, tit-for-tat.

Introduction

Ecosystem services and biodiversity are in dramatic decline worldwide (MA 2005, WWF 2014). A major reason for this is the dilemma between private and public interests (Pannell 2008), such that even though the protection of the public good biodiversity and related ecosystem services (such as pollination, water quality, soil quality and carbon sequestration) maximizes overall welfare it is often profitable for the individual to exploit these services unsustainably and cause their deterioration.

This problem of freeriding is typical in public good problems (Baumol 1952, Varian 2009) and can be elegantly formalized in a game-theoretical setting through the prisoners' dilemma (Kollock 1998): Although the joint payoff of both players in the prisoners' dilemma is maximised when both players cooperate, the payoff of each individual players is maximised if s/he defects.

One factor that can help overcome this dilemma is reciprocal altruism (Trivers 1971, Nowak 2006). It assumes an iterated interaction between the players and rewards cooperation of the other player with cooperation. In a game-theoretical setting it is represented by the well-known Tit-for-tat strategy (Stephens 1996) which initially cooperates but in the next rounds copies the other players' action (cooperates if the other player has cooperated previously and defects if the other player has defected). By this, Tit-for-tat is "immune" against exploitation by defectors (Axelrod 1984, Nowak and Sigmund 1994).

The main approach for analyzing strategies like Tit-for-tat in games like the prisoners' dilemma is evolutionary game theory (Maynard-Smith and Price 1973, Easley and Kleinberg 2010). In this approach different strategies compete against each other in a kind of tournament. A population of players is assumed, each with a certain initial strategy, who play against each other in a 2-player game so that the player with the lower reward adopts the strategy of the opponent with the higher reward. By this, superior or dominant strategies become more abundant in the population while inferior strategies go extinct.

While the first studies of evolutionary game theory were non-spatial such that each player could encounter any other player in the population, later research also considered local interactions in which a player interacts only with the players within some neighbourhood (e.g., Nowak, 1992; Brauchli et al., 1999; Koella, 2000). Again, a prominent question has been whether a given strategy could invade and/or survive within a population of other strategies.

Although these studies provided important contributions to a better understanding of public-good problems and strategies to overcome them, their practical applicability in the solution of environmental problems is limited. In the context of the protections of ecosystem services, a deficiency of the mentioned approaches is that they focus on the strategy, i.e the rule set that tells under which conditions to cooperate (protect the ecosystem service) or defect (unsustainably exploit the ecosystem service) but not which of these actions is actually chosen in the course of the system dynamics. For instance, while Tit-for-tat includes cooperation in its set of actions it also includes defection and it is not clear whether players actually cooperate even if Tit-for-tat is abundant in the population.

To address this issue in the present paper I slightly extend the above-mentioned classical game-theoretical approach and explicitly consider the players' actions. The particular question I want to study is the impact of a payment offered by an agency to those players (landowners) who cooperate (protect the ecosystem service(s) under consideration). Under the name "payments for ecosystems services (PES)" such payments have become very popular as market-based instruments for inducing landowners to adopt environmentally friendly land-use measures (Engel et al., 2008, Engel 2016). The question here is how the presence of a PES affects both the frequencies of strategies in the population of landowners as well as those of the two actions.

For the analysis I consider a stylized grid-shaped landscape with players selecting from a set of strategies and actions and simulate the evolution of the strategies and actions. Although numerous strategies have been defined in the literature (Wikipedia 2017), I focus on the two extreme strategies of always cooperating and always defecting, and Tit-for-tat because of its above-described special role for overcoming public-good problems.

Methods

Model description

The purpose of the model is to analyse the effect of a payment for environmental services on a spatially structured population of interacting landowners. Each landowner can conserve his or her land parcel or use it for economic purposes like intensive agriculture or forestry, and each landowner interacts with his/her neighbours. This interaction is modelled using approaches from evolutionary game theory. The particular question analysed with the model is how the proportion of landowners playing a particular strategy, and how the proportion of landowners conserving their land develops over time. The model is a dynamic spatially explicit simulation model as it is used commonly in the field of spatial evolutionary game theory.

The model extends the classical spatial models of evolutionary game theory as they have been introduced, e.g., by Nowak and Sigmund (1994) (cf. references above). The present model modifies those models in three aspects: (i) it considers the process of interaction between neighbouring players in a slightly different way, (ii) it not only considers the evolution of strategies over time but also the dynamics of the players' decisions (to cooperate or to defect in a particular simulation step), and (iii) it introduces an exogenous payment, mimicking a payment for environmental services (PES) offered by an agency to players (landowners) who cooperate (conserve their land).

The model considers a stylized landscape structured as a square grid where each grid cell *i* is owned by a single landowner who can cooperate (conserve the grid cell for environmental purposes) or defect (use the grid cell for economic purposes). The payoff from each of these two actions depends on the actions of neighbouring players. As usual in game theory, considering the interaction of two neighbouring players, these payoffs can be arranged in a matrix with four entries corresponding to the four combinations of the players' actions (Table 1).

Table 1: Payoff matrix for a two-player game. The parameters *R*, *S*, *T* and *P* represent the payoff of player 1 as a function of player 1's and player 2's actions.

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	*R*	*S*
	Defect	*T*	*P*

Without loss of generality one may set *R*=1 and *P*=0, assuming (cf. Introduction) that cooperation of both players leads to a higher payoff (for each player) than defection. The magnitudes of parameters *S* and *T* can take any positive or negative values. Different combinations of these values are associated with different game types, such as Prisoners' Dilemma, Hawk-Dove, etc. (Stark et al. (2008); see below).

As noted above, regardless of the neighbour's action, cooperation may be additionally rewarded by an exogenous payment *p*, so the payoff matrix becomes

Table 2: Payoff matrix with scaled payoffs (*R*=1 and *P*=0) and an exogenous payment *p* offered to player 1 if s/he cooperates.

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	$1+p$	$S+p$
	Defect	T	0

Based on the payoff matrix, classical spatial models of evolutionary game theory describe the interaction of a player with his or her neighbours as follows. A sequential game is carried out individually with each neighbor within the neighbourhood (usually the Moore neighbourhood of the eight adjacent grid cells). The game starts with both players (focal player versus neighbour) cooperating. Then each player applies his/her strategy to decide on the action (cooperate or defect) for the next round. This game is repeated for a random number of rounds. For each player, in each round the payoff is recorded and summed over all rounds. Having played this sequential game with all neighbours, the focal player compares his/her total payoff with those of the neighbours. For the next simulation step s/he adopts the strategy of the neighbor with the highest payoff (or stays with the own strategy if that lead to the highest payoff). In this manner the strategy for the next simulation step is determined for each player on the grid.

A spatio-temporal simulation is carried out by assigning each player (grid cell) an initial strategy, then updating this as described above for the next simulation step, doing the same for the following step, and so on. A common question is how the proportion of players with a particular strategy evolves over time, and in particular, if a certain strategy can invade into the system, and/or if a strategy can survive.

A disadvantage of the above-described interaction of a player with his/her neighbours is that it appears rather academic, since in the real world nobody will play a certain strategy against someone else for a certain number of "fictitious" rounds to decide whether it is a good strategy or not. Another disadvantage is that the players' actions (cooperation or defection) do not appear explicitly in the simulation but only implicitly in those fictitious rounds. Given that the purpose of the present paper is to analyse the performance of payments for environmental services, it is necessary to know in each simulation step the action of each player (cooperation/conservation or defection/economic use).

To address these two disadvantages, I slightly modify the above-described interaction procedure of a player with his/her neighbours. In a given simulation step I randomly select *only one* of the eight neighbours. Based on the current strategies and the current actions (cooperation or defection) of the focal player and his/her selected neighbor I determine both players' actions for the next round (as in the classical approach, except that the current actions are considered rather than starting with both players cooperating) and evaluate these with the payoff matrix, Table 2, to obtain a payoff for each player. The focal player then adopts the strategy with the highest of the two payoffs (i.e., copies that of the neighbouring player if that had the higher payoff, and stays with the own strategy otherwise), which is selected for the next simulation step. Based on the current actions of the two players and the new chosen strategy, the focal player then also selects the action for the next simulation step.

Many models of evolutionary game theory assume that players may make slight mistakes when choosing their strategy. To test the impact of such errors I additionally simulate the model dynamics after introducing a small "mutation" probability of 0.01 by which a player does not choose the new strategy as described above but chooses a random strategy (with probability 1/3 for each) from the set of the three possible strategies. The player's action then is chosen according to that strategy as described above.

Model analysis

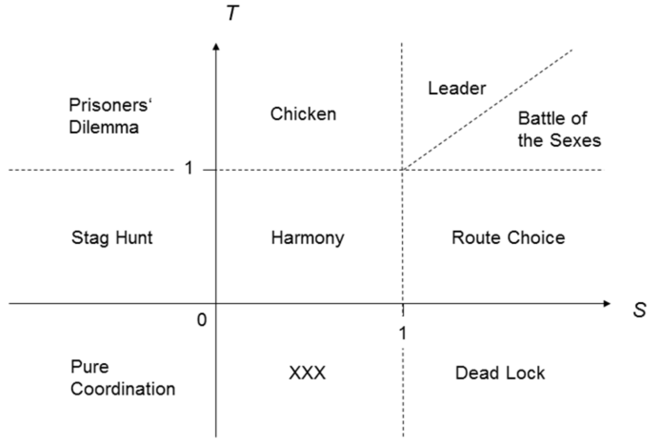
For given values of *S* and *T* (cf. Table 2) the dynamics are simulated on a square grid with 10 by 10 grid cells. For the initial state of the system, each grid cell is randomly assigned one of the three strategies AllC (always cooperate), AllD (always defect) and TFT (Tit-for-tat: cooperate if the neighbor cooperated and defect if s/he defected previously) with probability 1/3 each. In addition, the initial action on each grid cell is C (cooperate) with probability 0.5, and D (defect) otherwise. Other strategies than the three mentioned ones could be considered, but I chose those, since they represent unconditional egoism (AllD), unconditional altruism (AllC) and reciprocal altruism (TFT) which are most relevant in the present environmental-economic context of public good protection.

A simulation experiment consists of three phases. Starting from the described initial state the dynamics on the grid are simulated as described in the previous section for 2000 time steps (phase 1). In the final time step I record four system state variables: the proportions of cells with the strategies AllC, AllD and TFT and the proportion of cells with action C. After that a payment of magnitude *p* is added which changes the payoffs according to Table 2. Starting from the state (strategies and actions on the grid cells) of simulation step 2000, the dynamics are simulated for another 2000 time steps (phase 2) and in the final time step the four state variables are recorded again. To explore what happens when the payment is ceased, *p* is set to zero again and, starting from the state of simulation step 4000 the dynamics are simulated for another 2000 steps (phase 3) followed by the final recording of the four state variables.

To evaluate the simulation over the three phases I calculate the absolute and relative differences in the four state variables between the end of phase 2 compared to the end of phase 1 (to detect impacts of the payment) and between the end of phase 3 and the end of phase 1 (to detect possible permanent impacts even after cessation of the payment). To assess the impact of the payment on these differences I vary *p* in steps of 0.5 from 0 to 2. For each payment level I systematically vary the payoffs *S* and *T* randomly between -1 and 2. To account for stochasticity in the dynamics, each simulation run (for given *S*, *T* and *p*) is replicated 100 times and averages are taken.

I consider 10000 random combinations of *S* and *T* and sort them into 10 different classes according to Fig. 1. This figure was constructed after Fig. 8 of SDtark et al. (2008) which assigns all possible combinations of *S* and *T* into different types of games. For each game type I take the mean over the above-mentioned state variables (and their differences) over the (*S*,*T*) combinations within each game type.

Figure 1: Types of 2-player games after Stark et al. (2008) as functions of the payoffs *S* and *T*. Game XXX was not considered in Dtark et al. (2008) and is included in the present analysis for comprehensiveness.



Results

The presentation of the simulation results starts with the first phase before the payment is offered. With altogether N_{tot}=100 players, the observed frequencies of the three strategies, after 2000 time steps are about (for the exact values see Table A1 in the Appendix):

- N_{AllC}=0, N_{AllD}=50, N_{TFT}=50 for the Prisoners' Dilemma, the Chicken Game and Stag Hunt (i.e. for the upper left triangle of the matrix in Fig. 1)
- N_{AllC}=25, N_{AllD}=25, N_{TFT}=50 for Pure Coordination and Harmony (i.e. the diagonal of the matrix in Fig. 1 running from the lower left to the centre)
- N_{AllC}=50, N_{AllD}=0, N_{TFT}=50 for Route Choice, XXX and Dead Lock (i.e. for the lower right tgriangle of the matrix in Fig. 1).
- The two games in the upper right of the matrix in Fig. 1, Leader and Battle of the Sexes, behave like the games in the two triangles so that the results for Leader equal those found for the upper left triangle and the results for Battle of the Sexes equal those found for the lower right triangle.

The numbers of players cooperating are about (for the exact values see Table A1 in the Appendix):

- N_{Coop}=1 for the Prisoners' Dilemma, the Chicken Game and Stag Hunt (i.e. for the upper left triangle of the matrix in Fig. 1)
- N_{Coop}=50 for Pure Coordination and Harmony (i.e. the diagonal of the matrix in Fig. 1 running from the lower left to the centre)
- N_{Coop}=99 for Route Choice, XXX and Dead Lock (i.e. for the lower right triangle of the matrix in Fig. 1)
- N_{Coop}=1 and 99 for Leader and Battle of the Sexes, respectively.

An obvious relationship exists between the frequencies of the strategies and the number of cooperating players:

$$N_{\mathrm{Coop}} \approx N_{\mathrm{AllC}} + N_{\mathrm{TFT}} \frac{N_{\mathrm{AllC}}}{N_{\mathrm{AllC}} + N_{\mathrm{AllD}}},$$

which means that landowners playing AllC and a proportion q of TFT players cooperate. The proportion q is given by the proportion of AllC players in the population of landowners playing AllC or AllD. For instance, if the number of AllC players and AllD players are equal, 50 percent of TFT players cooperate and 50 percent do not; or, if there are twice as many

AllC players than AllD players, two third of the TFT players cooperate and one third do not. That means the TFT players cooperate only to a degree determined by the proportion of AllC players in the population.

Now turn to the second phase where a payment of magnitude *p* is offered to all players who cooperate (i.e. conserve their land). One can observe that this increases N_{AllC} by some ΔN_{AllC} whose magnitude is positively related with *p*. At the same time, N_{AllD} declines by the same amount, and N_{TFT} remains constant (cf. Tables A2-A6 in the Appendix).

The change in the number of cooperating players can be calculated from the changes in the frequencies of the strategies in the population by

$$\Delta N_{\text{Coop}} \approx \Delta N_{\text{AllC}} - \Delta N_{\text{AllD}} \approx 2\Delta N_{\text{AllC}},$$

which means that N_{Coop} increases due to $\Delta N_{\text{AllC}}=\Delta N_{\text{Coop}}/2$ players switching their strategy from AllD to AllC and the associated proportion of TFT players switching from defection to cooperation.

As a result the number of cooperating players increases with increasing payment *p* as shown in Table 3. Next to the influence of *p*, for given level of *p* the number of cooperating players increases from the lower right of each corresponding sub table to the upper left.

To conclude with the third phase of the dynamics, the frequencies of the strategies and the numbers of cooperating players switch back to their values from the first phase when the payment *p* is set back to zero.

Introducing a mutation rate of 0.01 does not change the results qualitatively. The main effect of the mutation rate is that the frequency of the AllC strategy and thus the proportion of cooperating players is increased (Tables A6 and A7 in the Appendix). The reason is probably that the AllC strategy is generally superior to the AllD strategy but in the mutation process is given the same likelihood (1/3) and thus draws a comparative advantage from the mutation.

Table 3: Number of players cooperating (N_{Coop}) for five levels of payment p for the ten games in Fig. 1 (the two numbers in the upper right cell of each sub table, separated by the slash, refer to Leader and Battle of the Sexes, respectively) (cf. the tables in the Appendix).

p=0		
1	1	1/99
1	50	99
49	99	99
p=0.5		
0	12	78/100
12	87	100
87	100	100
p=1		
0	49	100/100
49	100	100
100	100	100
p=1.5		
13	89	100/100
89	87	100
87	100	100
p=2		
51	100	100/100
100	100	100
100	100	100

Discussion

The paper presents an evolutionary game-theoretical simulation model to explore the effectiveness of a market-based environmental instrument: a payment offered to players (landowners) who cooperate (carry out biodiversity conservation measures on their land). While previous studies of evolutionary game theory focused only on the players' strategies (i.e., the rules that tell under which circumstances a player cooperates and under which circumstances s/he defects) the present model considers both the players' strategies and their resulting actions (cooperation or defection). The reason for this extension is that for the evaluation of an environmental instrument it is less relevant to know the behavioural rules (strategies) of the landowners but rather whether they actually carry out environmentally friendly measures (cooperate) or not.

Three strategies were considered: AllC (always cooperate), AllD, (always defect) and TFT (Tit-for-tat: cooperate if the neighbor has cooperated in the previous simulation step and defect otherwise). The analysis of the model reveals the decisive role of the TFT players whose actions depend on the proportion of AllC players (who by definition always cooperate) in the population. The more players choose their actions according to AllC compared to the number of players with strategy AllD, the higher the proportion of TFT players that actually cooperate. In that manner, the TFT players are indeed necessary for the evolution of cooperation and altruism as they are usually presented in the literature, but for the evolution of cooperation their presence is not sufficient but relies on the sufficient presence of "true" altruists like the AllC players. Or in other words, if one wishes to see the glass half full, TFT players a potentially beneficial for the conservation of public goods, but if one sees the glass empty they are mere opportunists who go with the majority.

This is also observed when exploring the impact of the payment on the level of cooperation. While with increasing payment the proportion of AllD players in the population declines and that of AllC players increases (and by that increasing the proportion of players cooperating), the proportion of TFT players stays constant and the actions of the TFT players change according to the above rule: if, e.g., the ratio of AllC players to AllD players doubles so does the proportion of cooperating TFT players within the subpopulation of TFT players.

For the analysis I considered ten different types of games, according to their values of S (reward of a cooperating player if the other player defects) and T (reward of a defecting player if the other players cooperates) in the 2-players payoff matrix (Table 1). Not unexpectedly, it turned out that the level of the payment required to induce cooperation increases with increasing difference T-S, since large T imply that players have a strong "temptation" to defect – which can only be overcome by a large payment for cooperation, while small S represent a large loss if one cooperates and the neighbour defects – which also can only be overcome by a large payment.

In the simulation I considered three phases: a "burn-in" phase of 2000 time steps with a zero payment, followed by a payment phase of another 2000 time steps with a non-zero payment, which again was followed by a phase of 2000 time steps in which the payment is set back to zero. The proportions of the strategies and the level of cooperation in the population were recorded at the end of each phase to ensure stationarity. To explore the effect of transients in the dynamics I considered two alternative simulation scenarios in which the lengths of the second and third phases where reduced to 100 time steps, respectively. These modifications, however, changed the results not qualitatively and only marginally. Also, in all the analysis no “memory effect” could be observed, i.e., the proportions of the strategies and the level of cooperation at the end of the third phase equaled those observed at the end of the first phase.

To conclude, presence of TFT players in a population of landowners does not automatically imply cooperation in the conservation of a public good like biodiversity. Instead, the proportion of TFT players actually cooperating is determined by the ratio of AllC players (who by definition always cooperate) and AllD players (who always defect). Thus, in the context of environmental policy, the reported advantage of the TFT strategy that it is immune exploitation by defectors and thus can survive even in an environment of defectors does not automatically translate into higher effectiveness of environmental instruments unless there are sufficiently many (cooperating) AllC players in the population of landowners.

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Appendix

Table A1: Number of players with strategies AllC, AllD and TFT, and number of cooperating players (N_{Coop}) for the ten game types considered (1=Prisoners' Dilemma, 2=Chicken, 3=Leader, 4=Battle of the Sexes, 5=Stag Hunt, 6=Harmony, 7=Route Choice, 8=Pure Coordination, 9=XXX, 10=Dead Lock). The numbers are averages over the 100 replications considered for each combination of *S* and *T*, and over all the combinations of *S* and *T* belonging to the same game type (cf. Fig. 1). The payment level is p=0 (first phase of the dynamics).

	1	2	3	4	5	6	7	8	9	10
N_{AllC}	0.3	0.3	0.3	49.8	0.3	24.7	49.9	25.5	49.8	49.8
N_{AllD}	49.9	49.8	49.8	0.3	49.9	25.4	0.3	24.6	0.3	0.3
N_{TFT}	49.9	49.9	49.9	49.9	49.9	49.9	49.9	49.9	49.9	49.9
N_{Coop}	0.6	0.5	0.6	99.5	0.5	49.2	99.5	51.0	99.5	99.5

Table A2: Changes in the number of players with the three strategies (ΔN_{AllC}, ΔN_{AllD}, ΔN_{TFT}) and change in the number of cooperating players (ΔN_{Coop}) when the payment is increased to p=0.5 (second phase). Other details as in Table 1.

	1	2	3	4	5	6	7	8	9	10
N_{AllC}	-0.3	6.0	38.5	0.3	5.8	17.5	0.3	18.7	0.2	0.3
N_{AllD}	0.3	-6.0	-38.5	-0.2	-5.8	-17.5	-0.3	-18.6	-0.2	-0.3
N_{TFT}	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N_{Coop}	-0.5	11.9	76.9	0.5	11.6	34.8	0.5	37.2	0.5	0.5

Table A3: Changes in the number of players with the three strategies (ΔN_{AllC}, ΔN_{AllD}, ΔN_{TFT}) and change in the number of cooperating players (ΔN_{Coop}) when the payment is increased to p=1 (second phase). Other details as in Table 1.

	1	2	3	4	5	6	7	8	9	10
N_{AllC}	-0.3	24.3	49.8	0.3	24.5	25.4	0.2	24.6	0.3	0.3
N_{AllD}	0.3	-24.3	-49.8	-0.3	-24.5	-25.4	-0.3	-24.6	-0.3	-0.2

N_{TFT}	0.0	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0
N_{Coop}	-0.5	48.5	99.4	0.5	48.9	50.7	0.5	49.0	0.5	0.5

Table A4: Changes in the number of players with the three strategies (ΔN_{AllC}, ΔN_{AllD}, ΔN_{TFT}) and change in the number of cooperating players (ΔN_{Coop}) when the payment is increased to p=1.5 (second phase). Other details as in Table 1.

	1	2	3	4	5	6	7	8	9	10
N_{AllC}	6.0	44.4	49.8	0.2	44.2	25.7	0.3	24.8	0.3	0.3
N_{AllD}	-6.0	-44.4	-49.9	-0.3	-44.2	-25.7	-0.3	-24.9	-0.2	-0.3
N_{TFT}	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N_{Coop}	12.0	88.6	99.4	0.5	88.2	51.3	0.5	49.5	0.5	0.5

Table A5: Changes in the number of players with the three strategies (ΔN_{AllC}, ΔN_{AllD}, ΔN_{TFT}) and change in the number of cooperating players (ΔN_{Coop}) when the payment is increased to p=2 (second phase). Other details as in Table 1.

	1	2	3	4	5	6	7	8	9	10
N_{AllC}	25.1	49.8	49.8	0.2	49.8	24.9	0.2	25.4	0.2	0.2
N_{AllD}	-25.1	-49.8	-49.8	-0.2	-49.9	-24.9	-0.3	-25.4	-0.3	-0.2
N_{TFT}	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
N_{Coop}	50.2	99.4	99.4	0.5	99.4	49.7	0.5	50.7	0.5	0.5

Table A6: Number of players with strategies AllC, AllD and TFT, and number of cooperating players (N_{Coop}) for the ten game types considered (for further details, see Table A1). In contrast to Table A1, the mutation rate is non-zero with a magnitude of 0.01.

	1	2	3	4	5	6	7	8	9	10
N_{AllC}	2.0	2.0	2.1	58.7	2.0	31.1	58.7	31.5	58.7	58.7
N_{AllD}	58.7	58.7	58.7	2.0	58.7	29.6	2.0	29.2	2.0	2.0
N_{TFT}	39.2	39.3	39.2	39.3	39.3	39.3	39.3	39.3	39.3	39.2
N_{Coop}	3.6	3.6	3.8	96.4	3.6	51.2	96.4	51.9	96.4	96.4

Table A7: Changes in the number of players with the three strategies (ΔN_{AllC}, ΔN_{AllD}, ΔN_{TFT}) and change in the number of cooperating players (ΔN_{Coop}) when the payment is increased to p=1 (second phase). Other details as in Table 1, except that the mutation rate is 0.01.

	1	2	3	4	5	6	7	8	9	10
N_{AllC}	-0.3	27.9	56.9	0.3	28.1	27.9	0.3	27.5	0.3	0.3
N_{AllD}	0.3	-27.9	-56.9	-0.3	-28.1	-27.9	-0.3	-27.5	-0.3	-0.3
N_{TFT}	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N_{Coop}	-0.5	45.7	93.0	0.5	46.0	45.6	0.5	45.0	0.5	0.5