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Abstract
Since many ecosystem services involve spatial scales beyond farm size, their preservation and management in agricultural systems depends on the interaction of the landowners. For the analysis of such interactive land use a dynamic generic land-use model is developed that considers different payoff structures in a systematic manner and relates land-use dynamics to payoff structure in a generic manner. A landowner's own payoff depends on the land use on neighbouring land parcels. The landowners' payoffs are interpreted in a game-theoretic manner which allows for a game-theoretic classification of the different land-use dynamics generated by the model. The model is analysed to determine the proportion, spatial aggregation and temporal turnover of land-use measures. The model results are applied to a number of cases from the literature in which the management of ecosystem services involves a regional scale, including pollinator conservation, pest control, and coordination incentives for the conservation of species in fragmented landscapes. Four main domains of model behaviour are identified, characterised by the proportions and temporal turnover of land-use measures, and whether the system has one or two stable equilibria. The borders between different domains are characterised by high behaviour-induced spatial aggregation of land-use measures.

Key words: ecosystem services, land use, simulation model, spatial externality.

JEL codes: C63, C65, Q20, Q57

1 Introduction

The conservation and management of ecosystem services (ESS) is probably the biggest current challenge in agricultural systems, because on the one hand, the intensification of agricultural land use threatens the persistence of ESS, while on the other hand the decline of ESS threatens agricultural productivity as well as human welfare in general (Millennium Ecosystem Assessment 2005).

Examples of ESS in agricultural landscapes include, among others, biodiversity, water quality, pest control, pollination, invasive species (as a disservice), and landscape aesthetics and recreation (Millennium Ecosystem Assessment 2005, Qiu 2019). The structure and dynamics of many, if not most, of these ESS operates on spatial scales extending those of single agricultural fields or even whole farms (Kremen et al. 2007, McKensie et al. 2013). This implies on the one hand that the management of these ESS involves multiple agents; while on the other hand, an agent's action affecting an ES will, due to the ES's spatial extent, affect the production conditions of other, neighbouring agents – causing a positive or negative spatial externality (Lewis et al. 2007). For instance, in half of the cases investigated by Lonsdorf et al. (2019), the positive externalities from pollinator conservation exceeded private costs.

A popular approach to the analysis of interactions between agents is game theory. Classical games include, e.g., the prisoners dilemma, stag-hunt, and chicken/snowdrift, and are able to characterise, in an abstract manner, environmental problems (Colyvan et al. 2011). Originally formulated for the interaction of two players, various games have also been analysed in a spatial context (Nowak and Simund 1994, Brauchli et al. 1999, Koella 2000). These studies provide important general insights, such as those about the emergence of cooperation in a population of selfish individuals, but are rather abstract, providing no direct linkage to real environmental problems.

On the opposite, a number of studies have analysed problems of ESS management in a game-theoretic framework, such as Grogan and Goodhue (2012), Bell and Zhang (2016) and Singerman and Useche (2019) for integrated pest management, Bareille et al. (2021) for pollinator conservation, and Larhsoukanh and Wang (2019) for the management of eco-cultural tourism. These studies, however, are specific and their general insights about the land-use dynamics induced by the specific agent interactions are limited. Even more, each application – and associated game structure – is considered in separation, ignoring possible relationships with other applications and game structures. What would be desirable is a comprehensive and systematic analysis of different game structures and related spatial ESS management problems.

The present study aims at the establishment of such a systematic, starting from the observation of Stark et al. (2008) that many 2-player games – in particular those mentioned above, can be formulated in a common framework, where each game is characterised by the values of three parameters. Here that framework is extended into an N-player framework that includes spatially explicit interactions among agents.

The obtained model is analysed through numerical simulation, focusing on the proportion of land parcels under ESS- preserving land use, their spatial aggregation, as well as the temporal turnover between the environmentally friendly land use and the “economic”, i.e. myopic and self-interested, land use. All the possible game structures included in Stark et al. (2008) are considered in a systematic manner. For the proportion of land parcels under ESS- preserving land use the simulation results are confirmed by a semi-analytical approximation.

The use of the framework is demonstrated in four applications. The first is the vase of pollinator conservation by Bareille et al. (2021) in which farmers can devote a certain share of their land to pollinator conservation. Due to their mobility, conserved pollinators benefit not only the conserving farmer but also neighbouring farmers.

The second application by Bell and Zhang (2016) considers the spraying of pests as well as the conservation of natural enemies in non-crop habitat. Among other things, the authors consider two opposing spatial externalities of pesticide use (Grogan and Goodhue 2012): a positive one that it reduces pest abundance both in the focal and neighbouring landholdings, and a negative one that it kills natural enemies both in the focal and neighbouring landholdings.

Third, area-wide pest management (Singerman and Useche 2019) considers only the positive externality of pesticide use but on a regional scale so that successful suppression depends on the sufficient number of participating farmers.

Fourth, many species require contiguous habitat for their survival. Coordination incentives (Nguyen et al. 2022) have been introduced to induce the spatial agglomeration of biodiversity conservation measures. The most popular scheme here is the agglomeration bonus by Parkhurst et al. (2002) in which conservation earns a base payment that is raised by a bonus if the conserved land is adjacent to other conserved land. For some species such as species with territorial behaviour the spatial dispersion of habitat can be beneficial. Bamière et al. (2013) introduced an agglomeration malus that penalises adjacency to conserved land.

The paper is structured as follows. In the next section the “land-use game” is introduced which models the land use of multiple agents under spatially explicit interactions. The interactions are represented by game-theoretic parameters. In the two following sections the behaviour of the model is analysed systematically in dependence of these game parameters. The four described applications are embedded in the results of the general analysis, before the paper concludes with a discussion of the general and application-specific results.

2 Methods

2.1 The land-use game

The analysis considers "land-use games" in which each player i has two choices x_i: an ESS-preserving land use $x_i = 1$ (henceforth termed *cooperative* land use), and a conventional land use $x_i = 0$ (henceforth, *uncooperative* land use). I start with the consideration of two players $i = 1, 2$. The interaction between the two players is symmetric, so that if both players choose the same land use, $x_1 = x_2$, each of them receives the same payoff; and if player 1 chooses some $x_1 = u$ and player 2 chooses some $x_2 = v \neq u$ then player 1 receives the same payoff as player 2 would receive if s/he chose $x_2 = u$ and player 1 chose $x_1 = v$.

Without loss of generality I scale all payoffs relative to that associated with both players choosing the uncooperative land use, $x = 0$. This is achieved formally by setting that payoff to $\mu = 1$ if it is positive and to $\mu = -1$ if it is negative. The associated payoff matrix is given in Table 1 with three continuous model parameters R, r_1 and r_2, and the binary parameter μ. Here r_1, is the payoff of choosing $x = 1$ while the other players chooses $x = 0$; r_2 is the payoff of choosing $x = 0$ while the other player chooses $x = 1$; and R_3 is the payoff if both players choose $x = 1$.

Table 1: Payoffs of player 1 (first number) and player 2 (second number) in a 2-player game, as a function of the chosen actions x_1 and x_2.

	$x_2 = 1$	$x_2 = 0$
$x_1 = 1$	R, R	r_1, r_2
$x_1 = 0$	r_2, r_1	μ, μ

In equation form, the payoffs can be written as

$$V_i(x_i) = Rx_i x_{2-i} + r_1 x_i(1-x_{2-i}) + r_2(1-x_i)x_{2-i} + \mu(1-x_i)(1-x_{2-i}) \tag{1}$$

Now I extend the 2-player game into an *N*-player game. Each player *i* (henceforth termed a landowner) now interacts with a number of landowners *j* within some neighbourhood M_i (which may be the Moore neighbourhood of the eight adjacent grid cells (land parcels) in a square grid: Bareille et al. (2023), or the von-Neumann neighbourhood of the four adjacent grid cells to the north, south, east and west: Parkhurst and Shogren (2007), or else).

The interactions between the landowners are assumed isotropic and independent. The former means that the interaction between two players depends on the distance between the two but is otherwise spatially homogenous. The latter means that the influences of neighbouring landowners on some focal landowners are additive. By these assumptions, the joint impact of the neighbours' land-use choices x_j on the payoff of landowner *i* can be modelled as dependent on the proportion q_i of landowners with $x_j = 1$ in the neighbourhood M_i:

$$q_i = \frac{1}{M}\sum_{j\in M_i} x_j \quad , \tag{2}$$

where *M* is the number of landowners or grid cells in the neighbourhood M_i (eight in the case of the Moore neighbourhood above, and four in the case of the von-Neumann neighbourhood). It is assumed assumed identical for all land parcels *i*. To allow for some non-linearity in the interactions, I consider that the influence of the neighbours depends on q_i^a, with α some positive real number. A value of $\alpha < 1$ represents a concave relationship with diminishing marginal influence; while $\alpha > 1$ represents a convex relationship with increasing marginal influence.

Analogous to eq. (1) I assume that if landowner i chooses $x_i = 1$, her payoff is given by $V_i = R$ if all neighbours choose $x_j = 1$, i.e. if $q_i = 1$; while it equals $V_i = r_1$ if all neighbours choose $x_j = 0$, i.e. if $q_i = 0$. The payoff for values of q_i between zero and one is given by linear interpolation between r_1 and 1.

And if landowner i chooses $x_i = 0$ her payoff is given by $V_i = r_2$ if all neighbours choose $x_j = 1$, i.e. if $q_i = 1$; while it equals $V_i = 1$ if all neighbours choose $x_j = 0$, i.e. if $q_i = 0$. And analogously, the payoff for values of q_i^{α} between zero and one is given by linear interpolation between 1 and r_2. Altogether, the payoff of landowner i is given by

$$V_i(x_i) = (R - r_1)x_i q_i^{\alpha} + r_1 x_i + (r_2 - 1)(1 - x_i)q_i^{\alpha} + \mu(1 - x_i) . \tag{3}$$

To take the possibilities of a negative and a positive payoff $V_i(x_i = q_i = 0)$ into account the last term in eq. (3) has the prefactor $\mu \in \{-1, +1\}$. To add realism to the present land-use model (and to go beyond trivial model results), a random component $\sigma\varepsilon_i$ is included in the payoff μ:

$$V_i(x_i) = (R - r_1)x_i q_i^{\alpha} + r_1 x_i + (r_2 - 1)(1 - x_i)q_i^{\alpha} + \mu(1 - x_i)(1 + \sigma\varepsilon_i) . \tag{4}$$

Here ε_i is as random deviate with mean zero and standard deviation one, so $\sigma > 0$ measures the relative variation in μ.

2.2 Model analysis

The land-use dynamics are simulated on a square grid with N grid cells (land parcels), $i = 1,\ldots, N$, each of which can be used cooperatively ($x_i = 1$) or uncooperatively ($x_i = 0$). To eliminate boundary effects, boundaries are periodic, so that the eastern border joins the western border and the northern border the southern border and the "model world" has the shape of a torus). The simulation starts by randomly sampling, with probability p_{init}, for each grid whether $x_i = 1$; otherwise $x_i = 0$.

Each landowner i observes the proportion q_i of land parcels with $x_i = 1$ in its (eight-cell) Moore neighbourhood M_i and builds the payoff function, eq. (4). The payoff difference between land use $x_i = 1$ and $x_i = 0$ equals

$$\begin{aligned}\Delta V_i &= (R - r_1)q_i^{\alpha} + r_1 - (r_2 - 1)q_i^{\alpha} - \mu(1 + \sigma\varepsilon_i) \\ &= g q_i^{\alpha} + r_1 - \mu(1 + \sigma\varepsilon_i) \\ g &= R - r_1 - r_2 + 1\end{aligned} \quad . \qquad (5)$$

For $r_1 = 0$, ΔV_i depends two parameters: g and σ. For $r_1 \neq 0$, both sides of eq. (5) can be divided by σ to obtain

$$\frac{\Delta V_i}{\sigma} = \frac{g}{\sigma} q_i^{\alpha} + \frac{r_1 - \mu}{\sigma} - \varepsilon_i \quad , \qquad (6)$$

where $\Delta V_i/\sigma$ depends on two quantities: the payoff g scaled in units of σ, and the difference between the payoffs r_1 and $\mu \in \{-1,+1\}$, also scaled in units of σ. Such scaling methods help reducing the set of model parameters to the set of truly independent one (here from three parameters (g, r_1, σ) to two). The interpretation of the influences of g and r_1 is not changed by the scaling, while an increase in σ by some factor has the same effect as a <u>decrease</u> in g <u>and</u> ($r_1 - \mu$) by the same factor.

To simulate the land-use dynamics, I assume that landowner i chooses $x_i = 1$ if $\Delta V_i > 0$, and $x_i = 0$ otherwise. In the next time step the landowners observe the adapted x_i, calculate their q_i and ΔV_i, adapt their x_i, and so on. The dynamics are simulated over 100 time steps (a highly conservative choice) to reach a steady state. For the final 20 time steps, a temporal average is calculated for three quantities that characterise the macroscopic behaviour of the model system. The first is the proportion p of cooperative land parcels, i.e. the grid cells with $x_i = 1$; henceforth termed *coop-proportion*:

$$p = \frac{1}{N} \sum_i x_i \quad . \tag{7}$$

The second quantity of interest is the average proportion of land parcels with $x_j = 1$ within the Moore neighbourhoods M_i of conserved land parcels i, where the average is taken over all land parcels in cooperative use, $x_i = 1$: $q_0 = \Sigma_i(x_i q_i)/\Sigma_i(x_i) = \Sigma_i(x_i q_i)/p$. However, this measure is confounded with the proportion p, because if a proportion p of all land parcels has $x = 1$ then for any land parcel the proportion of neighbours with $x = 1$ will, on average, be equal to p. To eliminate this "statistical agglomeration" and only keep the "behaviour-induced" aggregation (henceforth termed *bi-aggregation*), I subtract p from q_0 to obtain

$$q = \frac{\sum_i x_i q_i}{p} - p \tag{8}$$

A technical motivation for the use of q rather than q_0 is that, for the above reasons, q_0 quite strongly correlates with p. The results of the model analysis are presented below by coloured contour plots, and it turned out that these plots are for q_0 difficult to distinguish from those for p, so little understanding is gained from showing q_0.

The last quantity of interest is the land-use turnover between consecutive time steps. Denoting by x_i the current land use and by x_i' the land use in the next time step, this temporal turnover is calculated as

$$\tau = \frac{1}{N}\sum_i \left[x_i'(1-x_i) + (1-x_i')x_i \right] \tag{9}$$

The term in brackets equals 1 if $x_i' \neq x_i$ and 0 otherwise, so τ represents the proportion of land parcels changing their state between two consecutive time steps.

Each simulation is replicated 200 times and averages are taken to account for the randomness ε_i in the payoffs. As noted above, the decisions of the landowners only depend on the sign of the payoff difference ΔV_i. In the formulation if eq. (5) (used for the case of $r_1 = 0$) this depends, next to the binary parameter μ and the endogenous variable q_i, on the model parameters g and σ; while in eq. (6) it depends on g and $(r_1 - \mu)$, both scaled in units of σ.

To analyse the model in wide generality, I analyse it, for $\alpha = 0.5$, 1 and 2,

(i) via eq. (5) with $r_1 = 0$, systematically varying $g \in [-10, 10]$, $\sigma \in [0, 0.8]$, and $\mu \in \{-1, 1\}$, and

(ii) for $r_1 \neq 0$ via eq. (6), systematically varying $g/\sigma \in [-10, 10]$ and $(r_1 - \mu)/\sigma \in [-5, 0]$.

The bounds are motivated as follows. For analysis (i), the upper bound on the variation, $\sigma = 0.8$ represents a relative payoff variation of 80 percent, which may be regarded as large in an agricultural context. For σ within that range, ΔV_i of eq. (5) is of the order of magnitude of one, so raising g to its upper or lower bounds of 10 and –10, respectively represents a very strong change of ΔV_i.

For analysis (ii), at the upper and lower bounds of $g/\sigma = \pm 10$ a variation of q_i between zero to one affects ΔV_i much more than does the variation in the ε_i (which has standard deviation one). Regarding $r_1 - \mu$, at its upper bound of zero we have $\Delta V_i = \varepsilon_i$ and even $q_i = 0$ implies a 50-percent probability of landowner i choosing $x_i = 1$. So after the first simulation time step pN landowners have chosen $x = 1$. As argued above, this implies an aggregation of $q_0 = p = 0.5$. Since q_0 is the average over all q_i, in the next time step we have on average $\Delta V_i = 0.5 + \varepsilon_i$, implying even more landowners choosing $x = 1$, and after another few time steps all landowners will eventually choose $x = 1$. A the lower bound of $r_1 - \mu = -5$ we have, for $q_i = 0$, $\Delta V_i = \varepsilon_i - 5$, which is negative with an extremely high probability.

Preliminary analyses, motivated by Drechsler (in press) reveal that for some model parameter combinations there are two possible steady-state solutions, one with a rather high p and one with a rather low p – whose emergence depends on the initial proportion p_{init} of land parcels with $x = 1$. To detect this bistability in the model behaviour, I consider two levels for the initial proportion: $p_{\text{init}} = 0$ and $p_{\text{init}} = 1$.

To confirm the simulation results, the steady state behaviour of the model dynamics is determined semi-analytically via a mean-field approximation (Online Appendix A). By the nature of this kind of approximation, only the coop-proportion p can be determined and analysed.

2.3 Applications

2.3.1 Pollinator conservation

As the first example, Bareille et al. (2021) consider a public good problem that arises from the fact that conserving land for pollinators incurs local costs while benefits spread over a larger spatial scale. Their bio-economic model, based on Cong et al. (2014), considers that each landowner partitions their land for three mutually exclusive land-use types: fruit production (orchards), crop production (arable land), and land conserved for pollinators. While the share of land devoted to fruit production is exogenous, the landowner can choose how much land to devote for crop production (to gain economic benefits) and how much to set aside for pollinator conservation. The latter increases the abundance of pollinators and the fruit yield of the focal landowner as well as the fruit yield in the orchards of neighbouring landowners, providing a positive externality.

Since the present modelling framework allows only for two land-use types, I simplify the model of Bareille et al. (2021), still capturing its essence, i.e. the spatial interactions between the landowners, and adopting their terminology as far as possible for easy reference. The main change is that I ignore crop production and assume (may be somewhat unrealistically at least on short time scales) a varying extent of fruit production, so that in each time step landowner *i* reserves a share of land, e_i, for pollinator conservation and uses the rest, $1 - e_i$, for fruit production. The second simplification is that the choice of e_i is not continuous but binary, where e_i has either a positive value $0 < E \leq 1$ or is zero. The choice $e_i = E$ represents the cooperative land use $x_i = 1$ in the present framework, while the choice $e_i = 0$ represents the uncooperative use, $x_i = 0$.

According to Bareille et al. (2021), the fruit gross margin on farm *i* is given by

$$\Pi_i = (1 - e_i)\left(py(a + b\vartheta_i) - C\right) \tag{10}$$

where p is the fruit price, y the reference fruit yield and C the cost of fruit production. The total fruit yield is the product of the reference yield y and a linear function, $a + b\vartheta_i$ where

$$
\begin{aligned}
\vartheta_i &= \beta \sum_j e_j \exp\left\{-\lambda d_{ij}\right\} \\
&\approx \beta \sum_{j \in M_i} e_j \exp\left\{-\lambda \delta\right\} \equiv \gamma \frac{1}{M} \sum_{j \in M_i} e_j
\end{aligned}
\tag{11}
$$

is the immigration of pollinators into farm i (cf. the ecological metapopulation theory of Hanski (1999)) and a and b some positive coefficients. The first line of eq. (20) considers that pollinators emigrate from farms j, with their number proportional to the reserve size e_j. They reach farm i with probability $\exp\{-\lambda d_{ij}\}$, where d_{ij} is the Euclidean distance between farms i and j, and λ is the inverse of the mean dispersal distance of the pollinator (Hanski 1999).

The second line of eq. (20) is a simplification of the first line, assuming that pollinators can reach farm i only if they emigrate from a farm j within the neighbourhood M_i of farm i, and that these pollinators all have the same probability $\exp\{-\lambda\delta\}$ of reaching farm i. Parameter δ can be regarded as the mean of the distances d_{ij} over all farms in the neighbourhood M_i, and $\gamma = \beta M \exp\{-\lambda\delta\}$.

With these assumptions, the payoff (fruit gross margin) of landowner i equals

$$
V_i(x_i) \equiv \Pi_i = \left(1 - x_i E\right)\left(u + v q_i E\right) \tag{12}
$$

with $u = pya - C$ the “unilateral” net revenue per unit orchard area if no neighbour conserves their pollinators ($q_i = 0$), and $v = pyb\alpha\gamma$ the added revenue per pollinator habitat area (E) if all neighbours conserve their pollinators ($q_i = 1$).

To add spatial variation, I assume that the net revenues vary among landowners with a relative variation of size σ, which is achieved by multiplying u by $(1 + \sigma\varepsilon_i)$. Since u can be positive or negative, I write it as the product $u = \mathrm{sgn}(u)|u|$ with $|u|$ the absolute value and $\mathrm{sgn}(u)$ the sign of u. Dividing both sides of eq. (12) by $|u|E$, i.e. measuring V_i in units of $|u|E$ then yields for the difference $\Delta V_i = V_i(x_i = 1) - V_i(x_i = 0)$:

$$\frac{\Delta V_i}{|u|\,E} = \mathrm{sgn}(u)(1+\sigma\varepsilon_i) - \frac{vE}{|u|}q_i \tag{13}$$

where the right-hand side is equivalent to eq. (5) with $g = -vE/|u|$, $r_1 = 0$ and $\mu = -\mathrm{sgn}(u)$.

2.3.2 Pest control

Bell and Zhang (2016) is an experimental study about integrated pest management in Southeast Asia. Each of the subjects in the game experiment manages a square of nine grid cells (agricultural fields) of size one, and choose for each grid cell one out of four options (Table 1 in Bell and Zhang (2016)): (i) planting crops without spraying (payoff $\Pi = 5$), (ii) planting crops with light spraying to kill pests ($\Pi = 6$), (iii) planting crops with heavy spraying ($\Pi = 10$), and (iv) non-crop habitat to protect natural enemies of the pests ($\Pi = 0$). Options (iii) and (iv) generate external effects to neighbouring grid cells, such that option (iv) raises the payoffs in all grid cells with distance up to two by a magnitude $\Delta\Pi = 2$ (positive externality), while option (iii) erases this non-crop externality in all adjacent grid cells (short-range negative externality).

Since the present framework considers only two land-use options, the model of Bell and Zhang (2016) has to be simplified by assuming that each 9-cell block is managed as a single entity; and each block is surrounded by eight blocks, each owned by a neighbouring farmers. Two "subgames" are considered:

1. No spraying and protecting enemies ($x = 1$) or not ($x = 0$)

To protect enemies, analogous to the previous application, landowner i can devote a share E of their land for non-crop habitat, which reduces the payoff from $\Pi = 5$ to $\Pi = 5(1 - E)$. Each neighbour who protects natural enemies raises the payoff of landowner i by $2E$. Variation among the landowners is introduced by multiplying the unilateral payoff, $5(1 - x_i E)$, by $(1 + \sigma\varepsilon_i)$, so that

$$V_i(x_i) = 5(1 - x_i E)(1 + \sigma\varepsilon_i) + 16 q_i E \tag{14}$$

and

$$\frac{\Delta V_i}{5E} = (16/5) q_i - (1 + \sigma\varepsilon_i), \tag{15}$$

and the right-hand-side of eq. (15) is equivalent to eq. (5) with $g = 16/5$, $r_1 = 0$ and $\mu = 1$.

2. Conserving a share E of land for natural enemies and use light sprayning (x = 1) or heavy spraying (x = 0)

According to the payoffs listed above, the local payoff of farmer i equals $6(1 - E)$ for light spraying and $10(1 - E)$ for heavy spraying. To introduce variation among the landowners, these two payoffs are multiplied by $(1 + \sigma\varepsilon_i)$. If all neighbours apply light spraying farmer i receives, analogous the previous case, an externality of size $16E$. As outlined above, Bell and Zhang (2016) assume the range of the positive externality larger than that of the negative one. Since the present framework considers only one spatial range (neighbourhood size), I consider the smaller range of the negative externality such that it does not erase the entire positive externality of the protecting neighbours in the neighbourhood, but instead if n_i farmers in the neighbourhood spray heavily this multiplies the magnitude of the positive externality with a factor $(1 - n_i/8) < 1$. Equivalently, if a proportion q_i of neighbouring farmers applies light spraying rather than heavy spraying (i.e., choose land use $x_i = 1$) the positive externality ($16E$) is multiplied by q_i.

The payoff of landowner i thus equals

$$V_i = (10 - 4x_i)(1 - E)(1 + \sigma\varepsilon_i) + 16q_i E \tag{16}$$

and

$$\frac{\Delta V_i}{4(1 - E)} = -(1 + \sigma\varepsilon_i) \tag{17}$$

so the right-hand side of eq. (17) is equivalent to eq. (5) with $g = r_1 = 0$ and $\mu = 1$.

2.3.3 Area-wide pest management

Singerman and Useche (2019) present a case of area-wide pest management (AWPM) in which a pest can be eradicated only if a sufficient number of landowners participates in the control effort. The authors model this by assuming that the payoff of a landowner i not participating in pest management ($x_i = 0$) equals z. The payoff of participation ($x_i = 1$) is zero if less than k_c landowners participate, and equal to π if at least k_c landowners participate. Note that in Singerman and Useche (2019), z does not differ among landowners. In the present framework I consider variation in z by multiplying it with $(1 + \sigma\varepsilon_i)$.

The type of management problem considered by Singerman and Useche (2019) is a threshold public good problem that slightly differs from the present framework in which payoffs depend on the neighbouring land use and not the land use in the entire region. To translate the essence of

Singerman and Useche (2019) into the present framework I approximate it by considering that it represents an extreme case of increasing marginal benefit of pest control effort: The benefit is very small if only few landowners participate in pest control but strongly increases as the number of participants grows towards the threshold. In the present framework this can be modelled by raising the proportion q_i to the power of α, with $\alpha > 1$. With this approximation the payoff of landowner i becomes

$$V_i = x_i \pi q_i^{\alpha} + (1 - x_i) z \,, \tag{18}$$

implying

$$\frac{\Delta V_i}{z} = \frac{\pi}{z} q_i^{\alpha} - (1 + \sigma \varepsilon_i) \,, \tag{19}$$

so that the right-hand side of eq. (19) is equivalent to eq. (5) with $g = \pi/z$, $r_1 = 0$ and $\mu = 1$.

2.3.4 Agglomeration bonus and agglomeration malus

The agglomeration bonus (Parkhurst et al. (2002) rewards biodiversity conservation ($x_i = 1$) by a base payment P_0 and incentivises the spatial agglomeration of conservation efforts by offering an additional bonus b for each conserved land parcel in some neighbourhood M_i. Economic use ($x_i = 0$) generates a payoff of size c, independent of the neighbours' land use. Variation among landowners is here included by multiplying c with $(1 + \sigma\varepsilon_i)$.The payoff of landowner i then is given by

$$V_i = \left(P_0 + bMq_i\right) + (1 - x_i)(1 + \sigma \varepsilon_i) c \,, \tag{20}$$

implying

$$\frac{\Delta V_i}{\sigma c} = \frac{(P_0 / c) - 1}{\sigma} + \frac{(b / c)}{\sigma} M q_i - \varepsilon_i \quad , \qquad (21)$$

so that the right-hand side of eq. (21) is equivalent to eq. (6) with $g = (b/c)M$ and $r_1 = P_0/c$ and $\mu = 1$.

In its original version of Parkhurst et al. (2002), the bonus b is positive. As a variant, Bamière et al. (2013) proposed an agglomeration *malus*, $b < 0$, to incentivise the spatial dispersion of conservation measures, addressing the conservation of territorial species.

3 Results

3.1 Major domains of model behaviour

As a reference for the results of the simulation analysis, note that the payoffs in Table 1 allow for four major types of model behaviour: (a) $R > r_2$ and $r_1 > \mu$: $x = 1$ is a dominant strategy ("cooperation game"); $R > r_2$ and $r_1 < \mu$: two Nash equilibria exist with either both players choosing $x = 1$ or both players choosing $x = 0$ (coordination game); $R < r_2$ and $r_1 > \mu$: two Nash equilibria exist with both players choosing opposite strategies (anti-coordination game); and $R < r_2$ and $r_1 < \mu$: $x = 0$ is a dominant strategy (for $R > \mu$ representing a prisoners dilemma).

Translating these distinctions into the space of g and r_1 leads to the behaviour shown in Fig. 1. For $g > 0$ and $r_1 > \mu$ (upper right quadrant) the model is a "cooperation game", while for $g < 0$ and small $r_1 < \mu$ (lower left quadrant) the choice of $x = 0$ is dominant. For $g < 0$ and $r_1 > \mu$ (upper left quadrant), there is a cooperation game for large r_1 above the diagonal and an anti-coordination game below it. And for $g > 0$ and $r_1 < \mu$ (lower right quadrant) $x = 0$ is dominant for small r_1 below the diagonal, while there is a coordination game for r_1 above the diagonal.

3.2 Model analysis

For the model simulation (i) with $\alpha = 1$ and $\mu = 1$, described in section 2.2, Figure 2 shows the upper steady-state solution in the upper panels and the lower steady-state solution in the lower ones (if both panels show the same value only one solution exists). For (large) positive g and large σ the coop-proportion p of land parcels is about one (upper right in Figs. 2a,d), while for negative g and small σ (lower left) it is near zero. The associated levels of bi-aggregation q Figs. 2b,e and temporal turnover τ (Figs. 2c,f) are small.

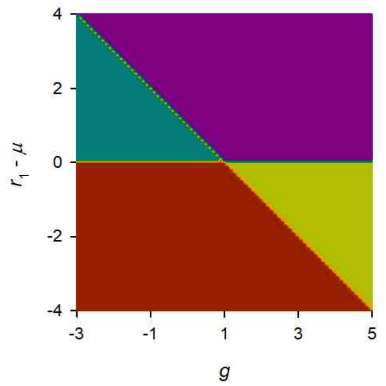

Figure 1: Major domains of model behaviour as a function of the payoffs g and $r_1 - \mu$, derived from the payoffs of the 2-player game of Table 1 and the transformation $g = R - r_1 - r_2 + 1$(cf. eq. (5)). Brown colour: $x = 0$ is a dominant strategy; light green colour: coordination game; dark green colour: anti-coordination game; purple colour: $x = 1$ is a dominant strategy.

For negative g and large σ (upper left in Fig. 2) the coop-proportion p is of medium size, bi-aggregation q is small but there is also some turnover τ. A large negative g means that in a neighbourhood of many sites with $x = 1$ (large q_i in eq. (5)) choosing $x = 1$ is disadvantageous. In contrast, in a neighbourhood of sites with many $x = 0$ (small q_i) a sufficiently large random payoff $\sigma\varepsilon_i$ can render the choice of $x_i = 1$ advantageous (eq. (5)). Thus, for sufficiently large σ the landowners are in an anti-coordination game, as in the upper left of Fig. 1. The positive turnover indicates that some land parcels switch their land use between time steps: If landowners observe a small q_i they choose $x_i = 1$. This implies an increased q_i for some of those who had chosen $x_i = 1$ before, who therefore switch to $x_i = 0$, and so on.

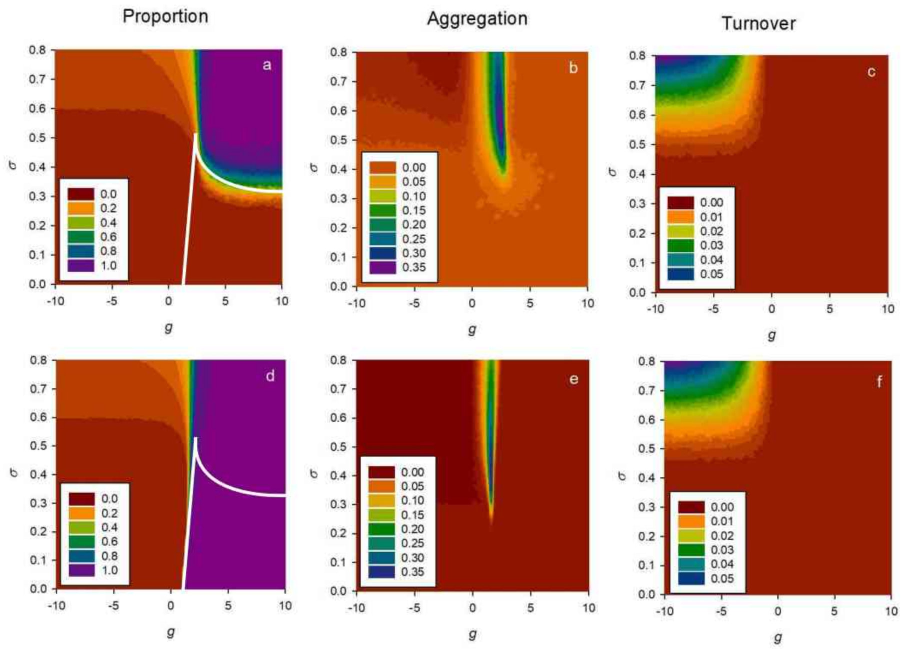

Figure 2: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (5) with $\alpha = 1$, $r_1 = 0$ and $\mu = 1$, as functions of the payoff parameter g and the payoff variation σ. Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists). The white lines mark the boundary between the existence of one and two solutions.

For positive g and small σ (lower right in Fig. 2) the model behaviour depends on the initial condition. If initially there are only very few or zero land parcels with $x_i = 1$, $gq_i << 1$, for most i and large random payoffs $\sigma\varepsilon_i$ would be required to render $x_i = 1$ profitable (eq. (5)). These, however, are excluded by small σ, so the land use choice $x_i = 1$ cannot spread in the landscape and p stays small. In contrast, if there are many land parcels with $x_i = 1$, gq_i is large for many i and a high coop-proportion p of land parcels is sustained. The landowners are thus in a coordination game, as in the lower right of Fig. 1.

As is argued in section 2.2, the average proportion q_0 of cooperative land parcels around cooperative land parcels strongly correlates with the coop proportion p. Thus, the parameter combinations that lead to high/medium/small p also lead to high/medium/small q_0. To gain additional understanding, Figs. 2b and 2e therefore focus on the behaviour-induced (bi-) aggregation q. As the figures show, this is small where the coop-proportion is large or small, but quite high for g around 1–4 and σ above 0.4, i.e. at the boundary between the two domains of anti-coordination game on the one side ($g < 0$)and the dominance of land use $x = 1$ o the other side ($g > 4$).

The model behaviour changes substantially when the value of μ is changed from +1 to –1 (Fig. 3). The payoff variation σ here has only a minor effect while the model behaviour strongly depends on the payoff g: If that is larger than about –1 the land use is stable with all land parcels in cooperative use ($p = 1$), and with small little bi-aggregation and zero turnover. For large negative g the coop-proportion p is about 0.5, bi-aggregation q is small and turnover very high – an extreme case of an anti-coordination game. As in Fig. 2, the two domains are separated by a region around $g \in [1, 4]$ with quite high bi-aggregation (Figs. 3b,d).

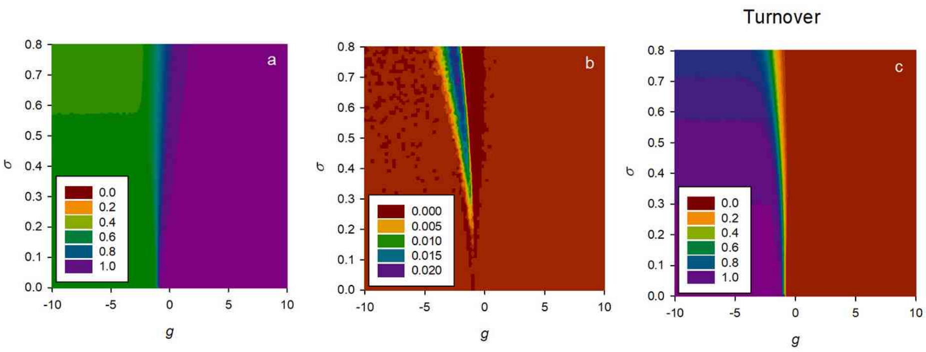

Figure 3: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (5) with $\alpha = 1$, $r_1 = 0$ and $\mu = -1$, as functions of the payoff parameter g and the payoff variation σ. In contrast to Fig. 2, only a single solution for p, q and τ exists.

Now turn to the case of $r_1 \neq 0$ which is considered in eq. (6). Similar to Figs. 1 and 2, Fig. 4 shows four major domains. For large payoffs g/σ and $(r_1 - \mu)/\sigma$ (upper right in the panels) the coop-proportion p is high, while bi-aggregation q and turnover τ are low. Reducing from here the payoff g (for given σ) leads into the domain (upper left) of reduced p but increased τ – again the case of an anti-coordination game. Reducing, from the upper right, the payoff $(r_1 - \mu)$ (for given σ) leads into a coordination game (lower right in the panels) with two solutions (a large p and a small p, depending on the initial proportion of land parcels with $x_i = 1$). Reducing, from the upper right, both payoffs (which is equivalent to increasing the payoff variation σ) leads into the domain (lower left) with small or zero p, q and τ. Similar to the analyses above, the domains are separated by areas of increased bi-aggregation q.

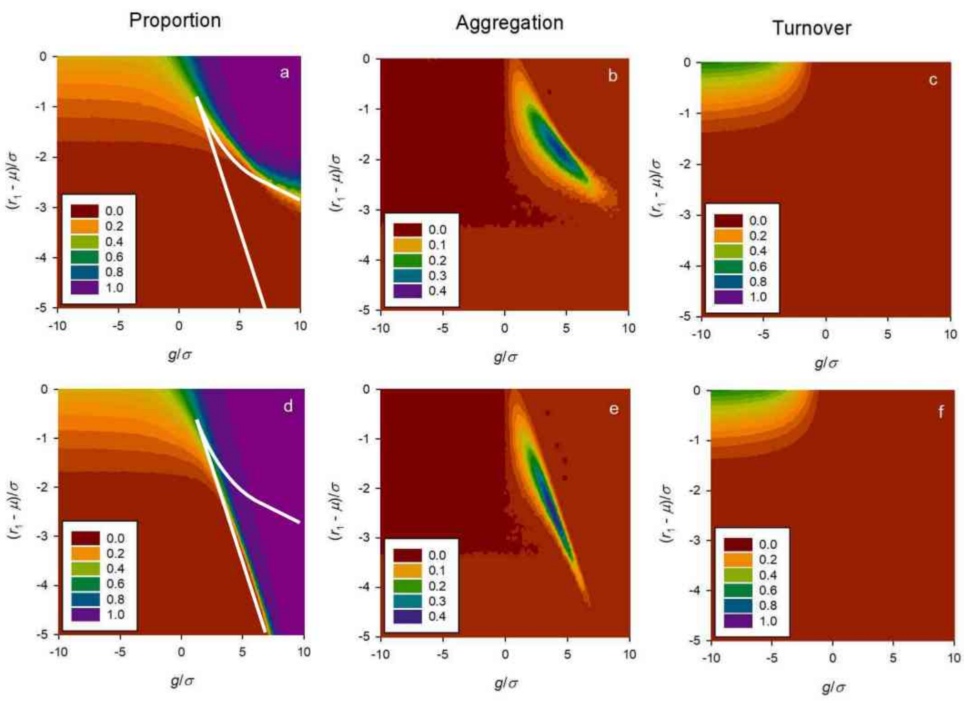

Figure 4: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (6) with $\alpha = 1$, as functions of the scaled payoffs g/σ and $(r_1 - \mu)/\sigma$. Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists). The white lines mark the boundary between the existence of one and two solutions.

The analyses above assumed a value of $\alpha = 1$ for the exponent at the proportion q_i (eq. (4)). A change in α does not change the general behaviour of the model but shifts the locations and sizes of the discussed domains of model behaviour. The results for the coop-proportion p are shown for α = 2 in Fig. 5 (for α = 0.5 and for bi-aggregation q and turnover τ, see Online Appendix B).

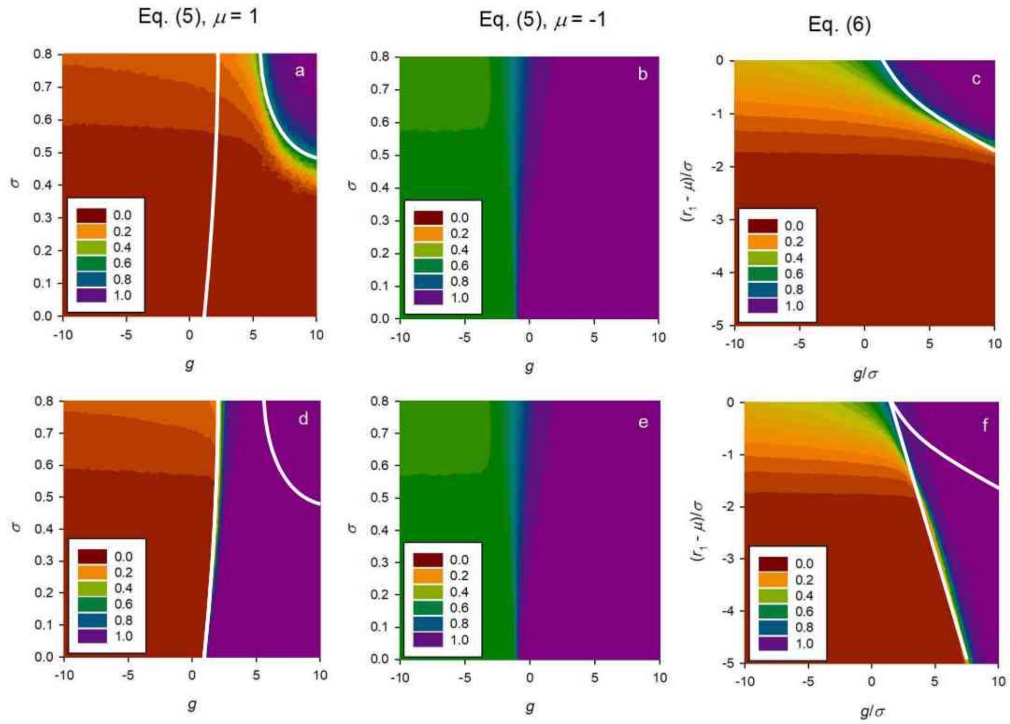

Figure 5: Coop-proportion of land parcels p as a function of the payoff g and the payoff variation σ (panels a,b,d,e) and as a function of the scaled payoffs g/σ and $(r_1 - \mu)/\sigma$ (panels c,f). Panels a and d refer to eq. (5) with μ = 1, panels b and e refer to eq. (5) with μ = –1, and panels c and f refer to eq. (6). Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists). The exponent at the proportion q_i of neighbours with x = 1 (eq. (4)) is set to α = 2. The white lines mark the boundary between the existence of one and two solutions.

Comparing Figs. 5a,d with Figs. 2a,d (which represents eq. (5) with μ = 1) reveals that the domain in the lower right with two solutions of p has expanded both upwards and leftwards, so that bi-stability occurs already at smaller g and larger σ than at α = 1. Comparing Figs. 5b,e with Figs. 3a,d (which represent eq. (5) with μ = –1) reveals no measurable influence of α. And comparing Figs. 5b,f with Figs. 4a,d (which represent eq. (6)) reveals an expansion of the b-istability upwards, so that it occurs already at larger payoffs $(r_1 - \mu)/\sigma$ than at α = 1. Altogether, increasing α seems to turn some areas of the parameter space associated with high coop-proportions p into parameter combinations associated with bi-stability.

The results of Fig. 5, as well as those for the coop-proportions shown in Figs. 2–4, are confirmed by the semi-analytical analysis in Online Appendix A. Even in a quantitative sense, deviations between numerical simulation and semi-analytical analysis are small.

3.3 Applications

3.3.1 Pollinator conservation

According to eq. (13), g is negative and its magnitude given by $vE/|u|$ which is the ratio of the externality from neighbours' pollinator conservation (v) and the focal landowners net revenue in the absence of pollination service. If $u > 0$, represented by $\mu = 1$ (Figs. 6a,d), the benefit of fruit production *ceteris paribus* exceeds the costs, so it is beneficial for the landowner to maximise the fruit production area by choosing $x = 0$. If the neighbours behave the same, everybody looses the externality from pollinator conservation, so the landowners are in a prisoners dilemma and the coop-proportion p of landowners conserving their pollinators is zero or very small. Non-zero p are obtained only where a large payoff variation σ leads to negative u for some landowners – for whom pollinator conservation then can be beneficial (see below).

If $u < 0$, represented by $\mu = -1$ (Figs. 6b,e), fruit production without the externality from neighbours' pollinator conservation is associated with a negative net revenue. Thus it is profitable to minimise the fruit production area by choosing $x_i = 1$ and conserve the pollinators. However, if all landowners behave the same, they generate a large positive externality which pushes the net revenue per fruit production area of some landowners to a positive value. For these landowners it is then profitable to maximise their fruit production areas by disengaging from pollinator conservation ($x_i = 0$) – which turns the revenue u to a negative value and favours pollinator conservation. The landowners are thus in an anti-coordination game with medium levels of p and high turnover τ (Figs. 3c,f).

This outcome "softens" a little if the magnitude of g is small, i.e. if the externality v is small and/or the magnitude of the net benefit, $|u|$ very large. Here the turnover is reduced and there is a small level of bi-aggregation q.

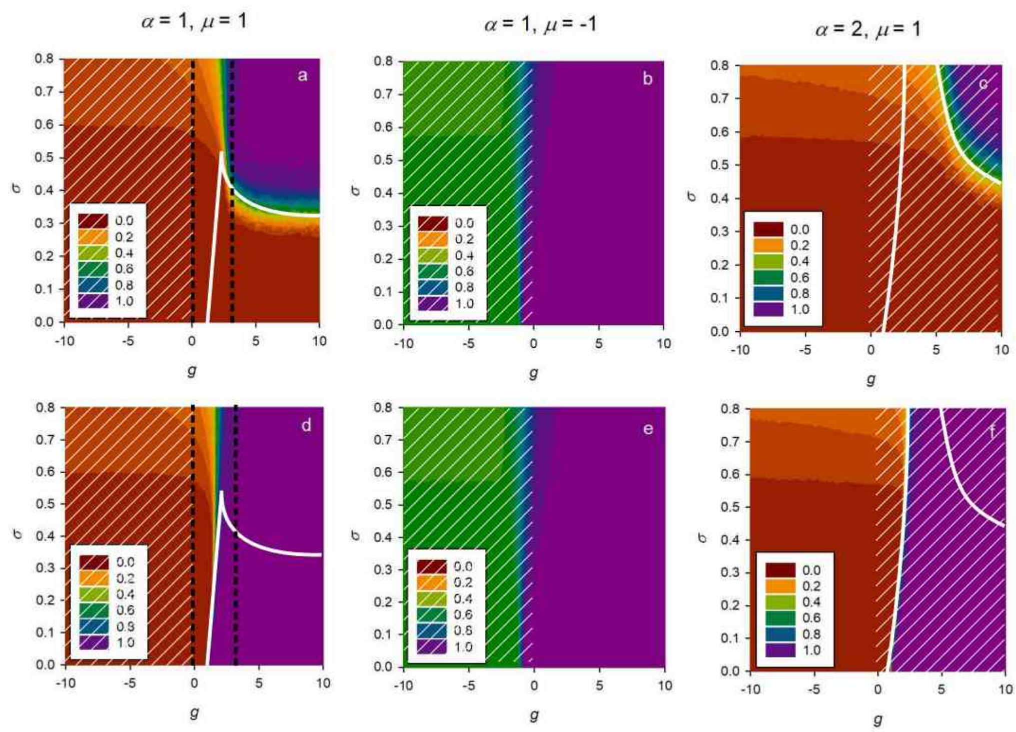

Figure 6: Coop-proportion p of landowners as a function of the payoff g and the payoff variation σ, for different levels of α and μ (compiling Figs. 3a,b, 4a,b, and 5a,b). For the shaded areas and the black dashed lines, see the text. The white lines mark the boundary between the existence of one and two solutions.

3.3.2 Pest control

The two cases outlined in section 2.3.2 are represented by the vertical black dashed lines in Figs. 6a,d. For the first variant with $g = 16/5$, the landowners protect the natural enemies ($x_i = 1$), implying high p, if the payoff variation σ exceeds about 0.4. For smaller σ the landowners are in a coordination game, so that if only few landowners protect the natural enemies it is profitable to reduce the area for enemy protection ($x_i = 0$), while if many landowners protect the natural enemies it is profitable to protect the own natural enemies, as well. A high payoff variation obviously unlocks the landowners from their coordination problem. In the second case of pest control, with $g = 0$, it is profitable to use heavy spraying, so the coop-proportion p of landowners using light spraying is zero or very small.

3.3.3 Area-wide pest management

As derived in section 2.3.3, the payoff g is positive and increases with increasing ratio π/z, where π is the landowner's benefit of cooperation (participating in pest control) if sufficiently many landowners participate, too (while $\pi = 0$ if there are not enough participants); and z is the unilateral landowner's benefit of not participating in pest control. The exponent at the proportion q_i of neighbours engaging in pest control is assumed $\alpha = 2$ (Figs. 6c,f).

For small ratios π/z the landowners are in a prisoners dilemma with small or zero p. For large π/z the situation is similar to that in the previous section: At small payoff variation σ the landowners are in a coordination game between a large and a small possible proportion of landowners participating in pest control; at large σ they all participate in pest control.

3.3.4 Agglomeration bonus and agglomeration malus

In this application the payoff r_1 is non-zero (so eq. (6) is used for the model analysis) and given by the ratio of the base payment P_0 and the mean economic profit c (associated with $x = 0$). A value of $(r_1 - 1)/\sigma = k$ means that the base payment is k standard deviations below the mean economic profit. The payoff g measures the additional payment if neighbours conserve their land parcels, too.

If that additional payment is positive (agglomeration bonus, $g > 0$) three outcomes are possible. If base payment and bonus are small the landowners use their land economically (small coop-proportion p). At large base payments and large bonuses they conserve their land (large p). And for large bonuses and small base payments (lower right of Figs. 7a,b) the landowners are in a coordination game where conservation is profitable if and only if sufficiently many other neighbouring landowners conserve, too.

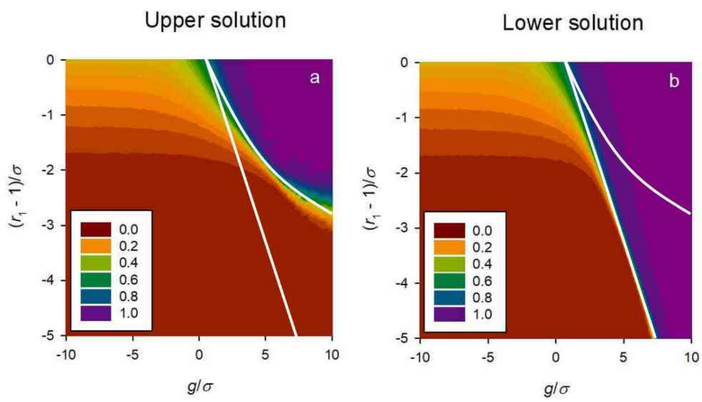

Figure 7: Coop-proportion p of landowners as a function of the scaled payoffs g/σ and $(r_1 - 1)/\sigma$ (adopting Figs. 4a,b).

Between these domains of model behaviour there is a boundary of high bi-aggregation where the size of the bonus b sensitively affects both the coop-proportion p and the bi-aggregation q.

If the additional payment is negative (agglomeration malus, $g < 0$) a small base payment implies – not unexpectedly – that the landowners use their land economically (lower left in Figs. 7a,b). In contrast, if the base payment is high and near the mean economic profit (upper left) the landowners are in an anti-coordination game with medium coop-proportion p and high turnover τ (cf. Fig. 4e,f).

4 Discussion

Land use often creates spatial externalities, so that it affects the decision environment of neighbouring landowners and in particular the profitabilities of their land-use measures. Such externalities include, among other things, the economic benefits from pollinators, benefits from (collaborative) pest management, as well as payments for the conservation of land for biodiversity.

A generic model is constructed that captures these interactions. It starts from a general game-theoretic classification of possible interactions between two agents and extends this into a multi-agent system. This also involves the introduction of heterogeneity among the different agents or landowners.

The model is analysed for a wide range of environmental conditions to determine the steady-state proportion of landowners engaging in cooperative land use, and the spatial aggregation and temporal turnover of land-use measures. Cooperative land use here is defined as a land use that (generally positively) affects the profitability of the neighbours' land-use measures.

Four major domains of system behaviour are identified: (i) with a low proportion and aggregation of cooperative land use and a low turnover between land-use measures (related to the prisoners dilemma in game theory); (ii) with a high proportion (and necessarily also aggregation) of cooperative land use and a low turnover between land-use measures (related to cooperation games); (iii) with the existence of two steady states: one with a low and one with a high proportion and aggregation of cooperative land use (related to coordination games); and (iv) with a medium (temporal average) proportion of cooperative land use, low aggregation and high turnover (related to anti-coordination games).

Often the boundaries between the different domains are characterised by a high level of "behaviour-induced" spatial aggregation, i.e. where the spatial aggregation exceeded the level that can be expected for mere statistical reasons (the latter meaning that a comparatively high proportion of cooperative land use implies a comparatively high spatial aggregation of this land use).

The boundaries between the domains are determined by the relative payoffs of the land-use measures and their dependence on the proportion of neighbours engaging in cooperative land use, as well as the spatial variation between the landowners' payoffs. The practical meanings of these payoffs are demonstrated on a number of applications from the literature, covering pollinator conservation, pest control (through spraying or the conservation of natural enemies), area-wide pest management where management success requires a minimum number of participating landowners, and the agglomeration bonus and agglomeration malus that reward or penalise, respectively, the spatial aggregation of conservation measures.

In particular, in the case of pollinator conservation the landowners were either in a state of low proportion of cooperative land use or in an anti-coordination game with high turnover between land-use measures. Similar was found for the case of pest control. The landowners in the area-wide pest management, in contrast, where either in a state of low proportion of cooperative land use, a state of high proportion of cooperative land use, or in a coordination game. Similar was found for the landowners in an agglomeration bonus scheme; while in an agglomeration malus scheme the landowners were either in a state of low proportion of cooperative land use, a state of high proportion of cooperative land use, or in an anti-coordination game with low spatial aggregation and high turnover of conservation efforts. In particular the results for the agglomeration bonus agree with previous studies like Parkhurst and Shogren (2007), Drechsler (2023) and Drechsler (in press) that landowners are confronted with a coordination problem because conservation of costly and spatially connected sites is beneficial only if a sufficiently many other landowner conserve, too.

To allow for a general and systematic analysis, the model involves a number of simplifying assumptions that may be relaxed in future research. Obvious limitations include that only two land-use measures are considered (cooperative use and uncooperative use), the landowner interactions are based only on a single factor (ecosystem service or conservation payment), ignoring the presence of multiple factors with multiple spatial ranges, as well as spatial correlations and temporal changes in payoff parameters.

The interactions between landowners are symmetric, so that the influence of one landowner on another landowner equals that of the latter landowner on the former. Dynamic and strategic decision behaviour are ignored, as well as evolutionary aspects and learning and risk aversion. The landowners are rational in the sense that they maximise their profit under complete information of their neighbours' land use (although their decisions are myopic).

Lastly, ecological dynamics are considered only as far as they determine the payoffs g, r_1 μ in eq. (4). The explicit consideration of the dynamics of ecosystem services and species populations would considerably complicate the model and its analysis but can also be expected to deliver important insights. Nevertheless, viewing problems of interacting land use and management of ecosystem service through the lens of (spatial) game theory appears to be a helpful approach to identify differences and similarities between different types of spatial environmental problem and develop a general understanding of the management of spatial ecosystem services.

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Appendix A: Semi-analytical model analysis

The temporal average of the coop-proportion p of land parcels with $x = 1$ can be determined using a so-called man-field approximation. It is frequently used to analyse complex spatially structured physical systems like magnetic materials in which the atomic spins can be ordered (magnetic state) or disordered (non-magnetic state) Schinckus 2018), but also social systems (Phan et al. 2003) like voter models in which individuals can choose between two (political) opinions and are influenced by their neighbours or peers (Grabowski and Kosiński 2006). For the agglomeration bonus it has been applied by Drechsler (in press).

In a mean-field approximation (Phan et al. 2003) the interaction of an agent with its neighbours is simplified by assuming that the agent does not react on each neighbour individually but only on the average behaviour of all neighbours (the "mean field" that the focal agent is subjected to), and that this field is identical for all agents. By this, the approach is unable to detect small-scale heterogeneities but focuses on the average behaviour of the macroscopic system (magnetic or non-magnetic; opinion A outweighs opinion B; large or small proportion of conserved land parcels).

Considering eq. (5), the probability of landowner i choosing $x_i = 1$ is the probability of ΔV_i being positive:

$$\begin{aligned}\Pr(x_i = 1) &= \Pr(\Delta V_i > 0)\\ &= \Pr\left(g q_i^{\alpha} + r_1 - \mu(1+\sigma\varepsilon_i)\right)\\ &= \Pr\left((g/\sigma) q_i^{\alpha} + (r_1 - \mu)/\sigma > -\varepsilon_i\right).\end{aligned} \tag{A1}$$

As described in section 2.1, the ε_i are normally distributed with mean zero and standard deviation one. This normal distribution can be approximated by the logistic distribution,

$$\Pr(\varepsilon_i \le z) = \frac{1}{1+\exp\{-\beta z\}}, \tag{A2}$$

with $\beta = \pi/3^{(1/2)}$ (Phan et al. 2003), so eq. (A1) becomes

$$\Pr(x_i = 1) = \frac{1}{1+\exp\left\{-\frac{\pi}{3^{1/2}}\left(\frac{g}{\sigma} q_i^{\alpha} + \frac{r_1 - \mu}{\sigma}\right)\right\}} \tag{A3}$$

The mean-field approximation is now represented by the assumption that q_i of eq. (A3) is identical for all i, and equal to the proportion p of land parcels with $x_i = 1$ in the model region. Due to the identity of the q_i for all land parcels, eq. (A3) further applies to all landowners i in the same manner and gives the probability of any land parcel i having $x_i = 1$. On the other hand, if the probability of a land parcel being in state $x_i = 1$ is the same for all land parcels, the proportion of land parcels with $x_i = 1$ equals $p = \Pr(x_i = 1)$. So we have $q_i = p = \Pr(x_i = 1)$ and eq. (A3) becomes

$$p = \frac{1}{1+\exp\left\{-\frac{\pi}{3^{1/2}}\left(\frac{g}{\sigma} p^{\alpha} + \frac{r_1 - \mu}{\sigma}\right)\right\}} \tag{A4}$$

An analytical solution of eq. (A4) for p is impossible, so the solution p^* is determined numerically by determining the roots of the equation $1/(1 + \exp\{\ldots\}) - p = 0$. Depending on the values of the model parameters g, r_1, μ and σ there can be one or two stable roots. They are determined for the same parameter ranges as in the simulation described in section 2.2. The results are given in Figs. A1–A3 for $\alpha = 0.5$, $\alpha = 1$ and $\alpha = 2$. They are, even quantitatively, nearly identical to their simulation counterparts (Figs. B1a,d, B2a,d, B3a,d for $\alpha = 0.5$; Figs 2a,d, 3a, 4a,d for $\alpha = 1$; and Fig. 5 for $\alpha = 2$) – with one exception: In the simulation analysis (i) (eq. (5) with $\mu = 1$, $\alpha = 2$: Figs. 5a,d) a large g and σ is leads to a single solution with large coop-proportion; while the mean-field approximation (Fig. A3a,b) has a large and a small solution. Interestingly, this bi-stability occurs in the mean-field approximation only for $\alpha > 1.9$, while for smaller α there is only a single solution, too.

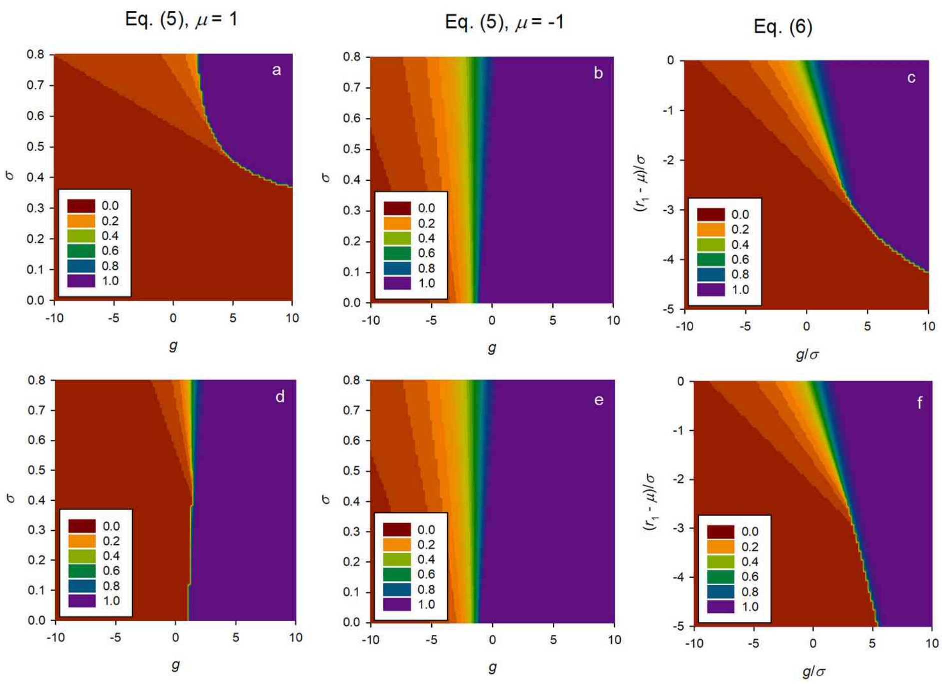

Figure A1: Coop-proportion of land parcels (solution p^* of eq. (A4) as a function of the payoff g and the payoff variation σ (panels a,b,d,e) and as a function of the scaled payoffs g/σ and $(r_1 - \mu)/\sigma$ (panels c,f). Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists). The exponent at the proportion q_i of neighbours with $x = 1$ (eq. (4)) is set to $\alpha = 0.5$.

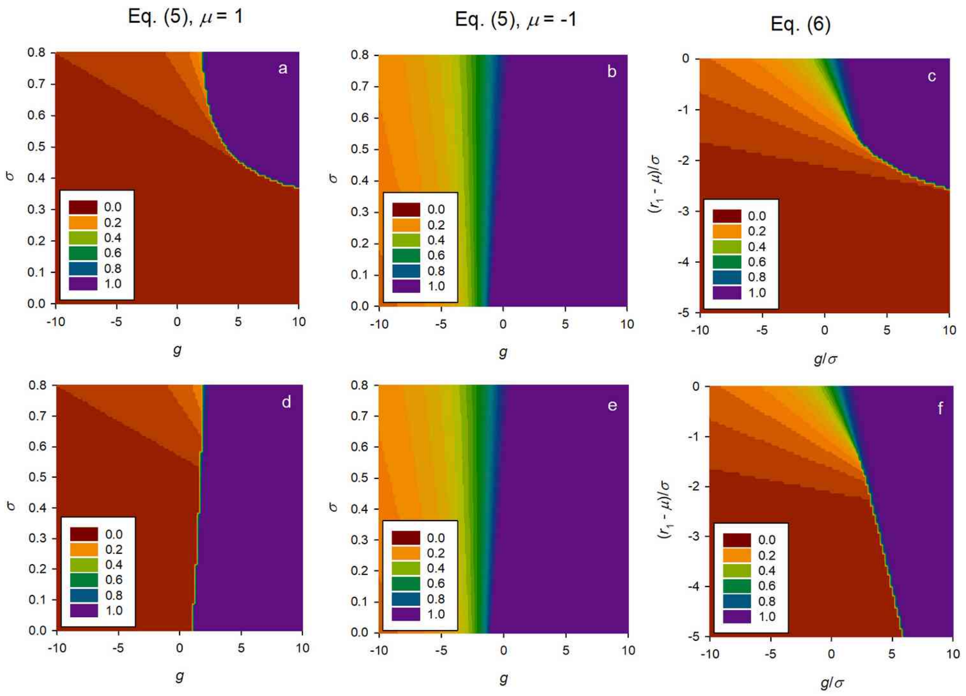

Figure A2: Coop-proportion of land parcels (solution p^* of eq. (A4) as a function of the payoff g and the payoff variation σ (panels a,b,d,e) and as a function of the scaled payoffs g/σ and $(r_1 - \mu)/\sigma$ (panels c,f). Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists). The exponent at the proportion q_i of neighbours with $x = 1$ (eq. (4)) is set to $\alpha = 1$.

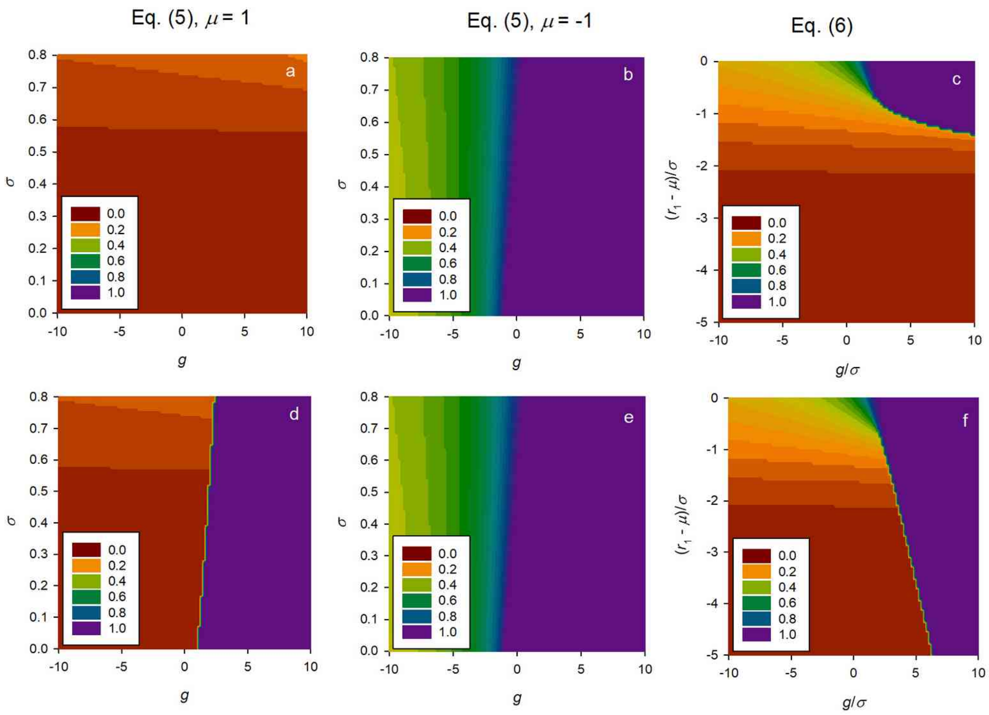

Figure A3: Coop-proportion of land parcels (solution p^* of eq. (A4) as a function of the payoff g and the payoff variation σ (panels a,b,d,e) and as a function of the scaled payoffs g/σ and $(r_1 - \mu)/\sigma$ (panels c,f). Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists). The exponent at the proportion q_i of neighbours with $x = 1$ (eq. (4)) is set to $\alpha = 2$.

Appendix B: Simulation results for $\alpha = 0.5$ and $\alpha = 2$

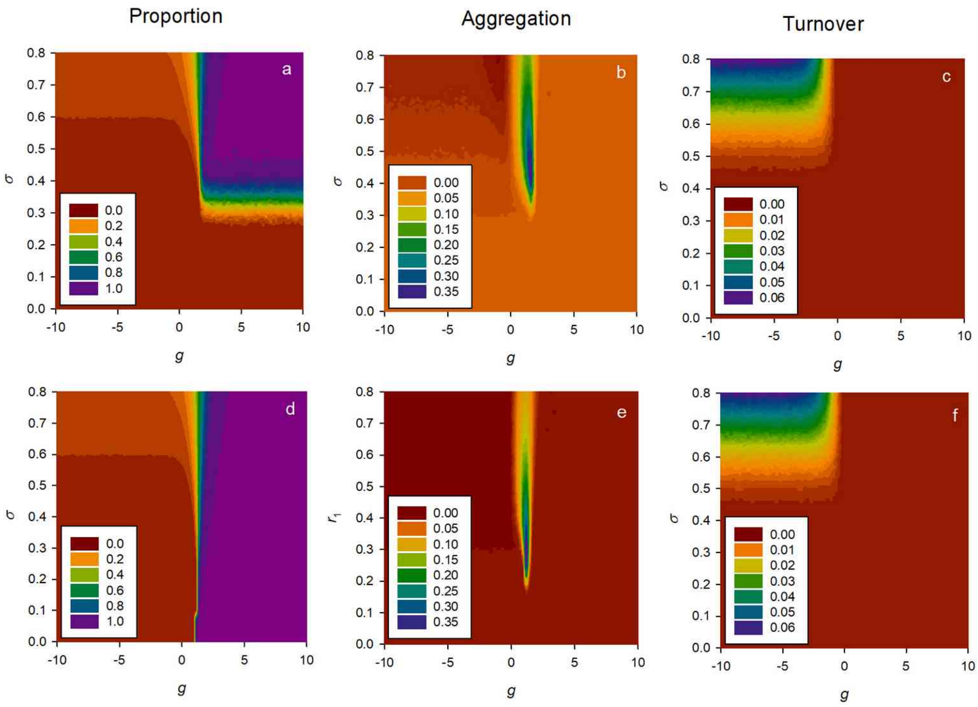

Figure B1: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (5) with $\boldsymbol{\alpha} = \mathbf{0.5}$, $r_1 = 0$ and $\mu = 1$, as functions of the payoff parameter g and the payoff variation σ. Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists).

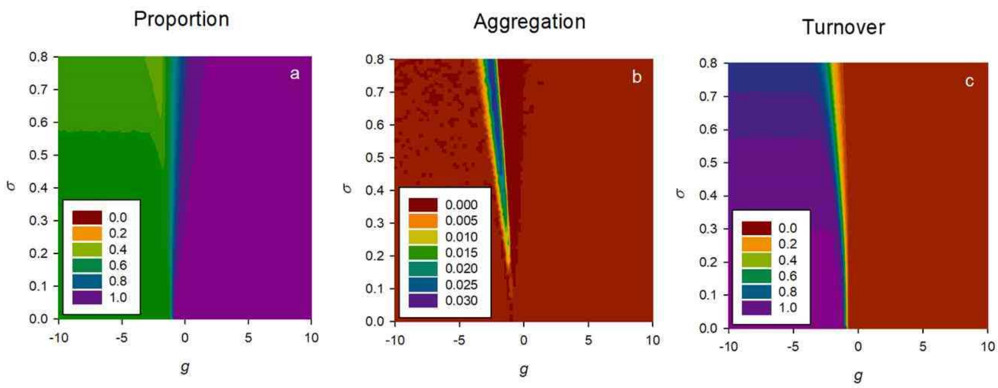

Figure B2: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (5) with $\boldsymbol{\alpha} = \mathbf{0.5}$, $r_1 = 0$ and $\mu = -1$, as functions of the payoff parameter g and the payoff variation σ. In contrast to Fig. B1, only a single solution for p, q and τ exists.

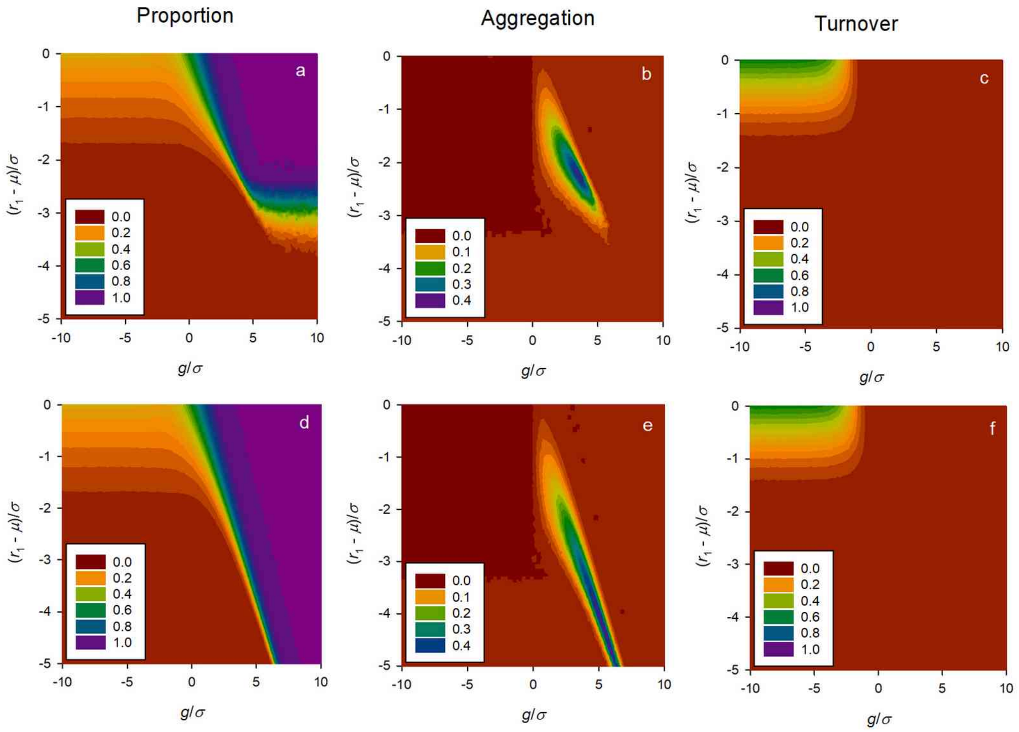

Figure B3: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (6) with $\boldsymbol{\alpha} = \mathbf{0.5}$, as functions of the scaled payoffs g/σ and $(r_1 - \mu)/\sigma$. Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists).

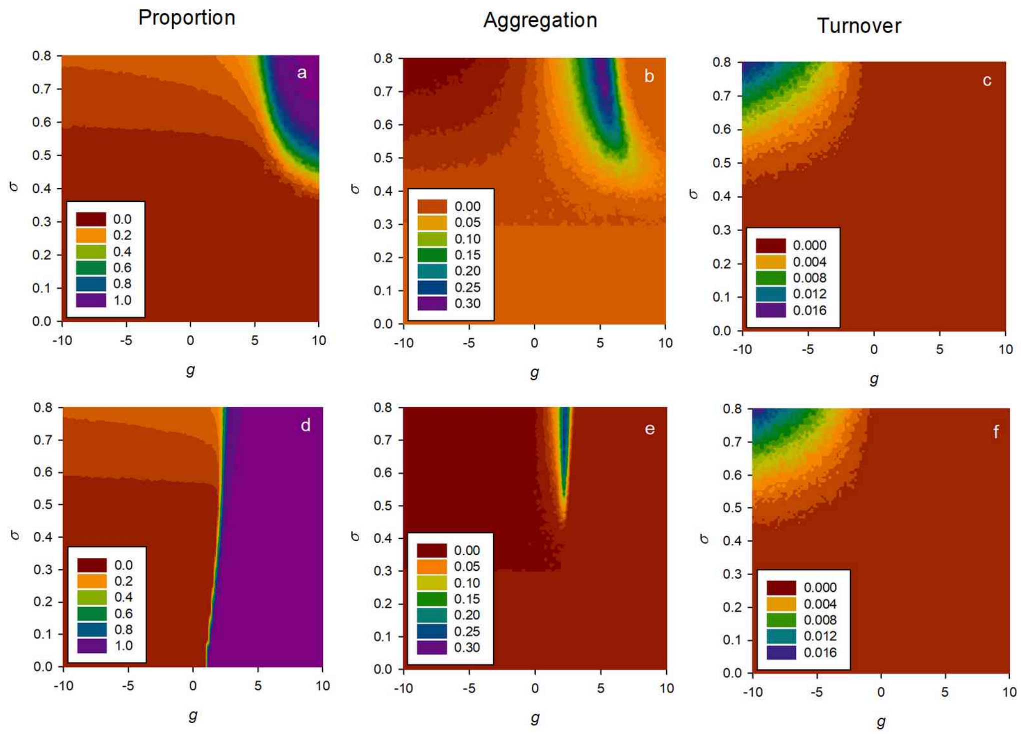

Figure B4: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (5) with $\boldsymbol{\alpha} = \mathbf{2}$, $r_1 = 0$ and $\mu = 1$, as functions of the payoff parameter g and the payoff variation σ. Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists).

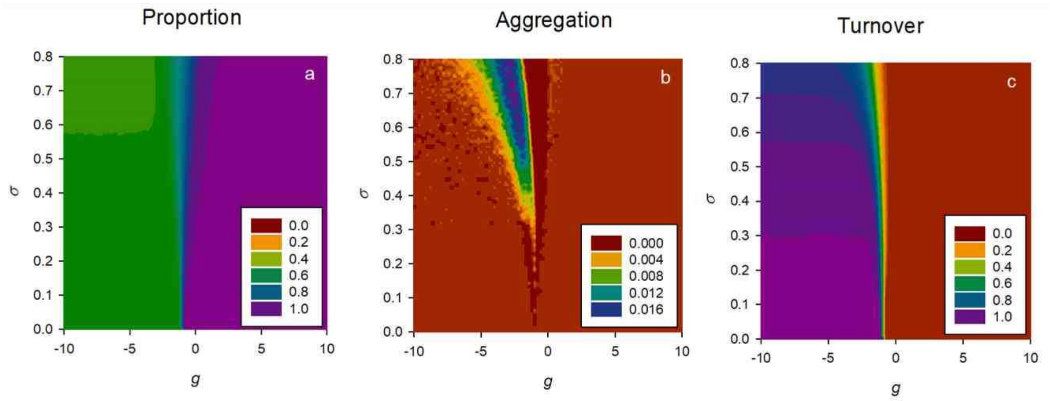

Figure B5: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (5) with $\boldsymbol{\alpha} = \mathbf{2}$, $r_1 = 0$ and $\mu = -1$, as functions of the payoff parameter g and the payoff variation σ. In contrast to Fig. B5, only a single solution for p, q and τ exists.

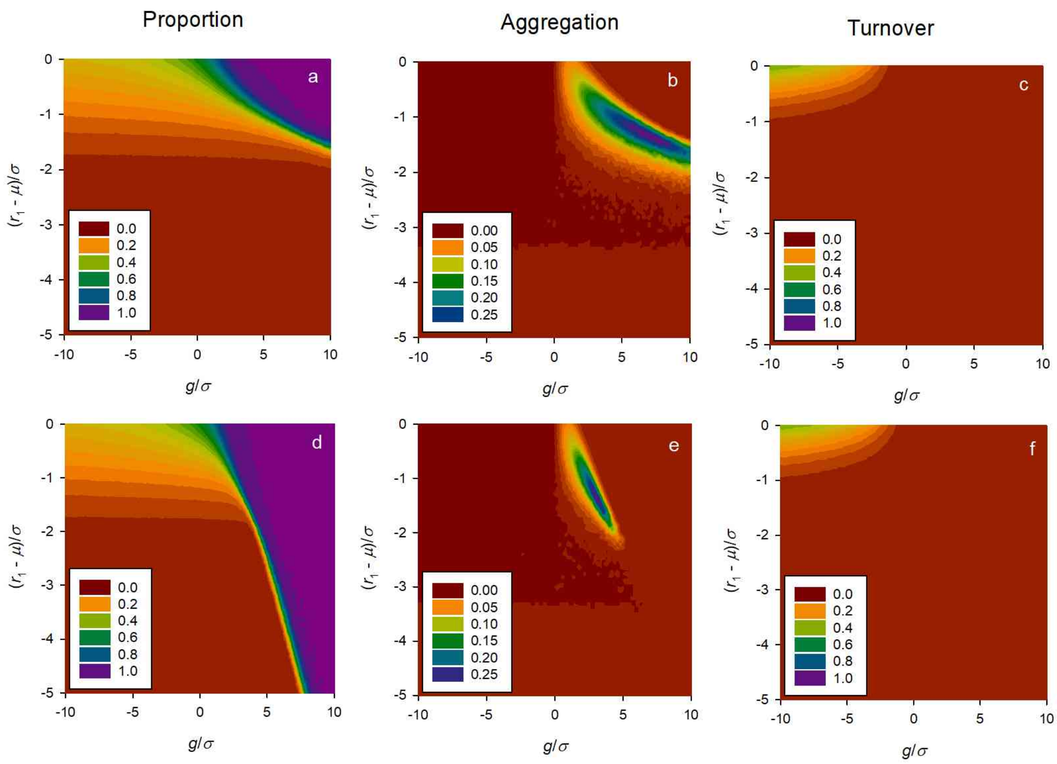

Figure B6: Coop-proportion p (left panels) bi-aggregation q (middle panels) and temporal turnover τ (right panels) in the steady state of simulations based on eq. (6) with $\boldsymbol{\alpha} = \mathbf{2}$, as functions of the scaled payoffs g/σ and $(r_1 - \mu)/\sigma$. Upper solution in the upper panels and lower solution in the lower panels (if both panels show the same value, only a single solution exists).

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