

Coping with spatial structure in the collaborative management of a mobile ecological resource

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Abstract

We study management of deer populations in a landscape where reciprocal externalities between landholders affect net benefits from management. The net benefits arising from deer populations at particular densities typically differ among landowners. Higher densities are preferred by landowners primarily interested in shooting revenues, whereas lower densities are generally required for biodiversity imperatives. An individual-based model is used to represent interactions among landholders' decisions in a mosaic landscape. Emergence of cooperative strategies is explored among each type of ownership and related to the interaction between the local density of the managed deer population and the costs and benefits which arise from management action.

Keywords: deer management, evolutionary game theory, cooperation, spatially explicit model.

1. Introduction

The use of natural resources often involves multiple actors and takes place in spatially structured landscapes where ecological interactions are distance-dependent. The dynamics of such ecological-economic systems result from an interaction of the human activities with the evolving natural resource. For instance, several fishermen usually harvest the same fish stock; the local density of fish is spatially heterogeneous and results from the interaction of the harvesting behaviour of the fishermen with the population dynamics of the spatially structured fish population.

One of the major questions arising in such coupled systems concerns the co-evolution of human behaviour alongside the spatial and temporal dynamics of the exploited resource. Analysing such co-evolution requires the integration of several fields, including bioeconomic modelling and game theory. Game-theoretic bioeconomic models have been used to study the effects of institutions and different types of human behaviour on the dynamics of the resource and the benefits of management which accrue to the human actors. The number of actors is often limited to two or three (e.g., Levhari and Mirman 1980, Lindroos and Kaitala 2001, Laukkanen 2003, 2005, Baht and Huffaker 2006), although multiplayer settings have also been considered in some studies (e.g., Hannesson 1997, Bischi et al. 2002). Some of the two-actor models consider simple spatial structure in that each actor harvests in a fixed compartment of the region considered, and the stocks in the two regions interact through dispersal of individuals (e.g., Laukkanen 2003, 2005). The multi-actor

bioeconomic models mentioned previously, in contrast, consider a single homogeneous stock and are thus non-spatial. Spatial structure has thus only been considered in bioeconomic game-theoretic models up to the analysis of two adjacent regions.

Literature on the evolution of cooperation has studied the evolution of decision making in a more realistic spatial setting using standard games like the prisoners dilemma or the snowdrift game implemented on a spatial grid and analysed analytically, or more frequently with the help of agent-based simulations (e.g., Doebeli and Hauert 2005, Ohtsuki et al. 2006, Nowak 2006, Noailly et al. 2007, and references therein). The payoffs arising from various behavioural strategies of agents, the persistence of strategies and cooperation among strategies are analysed in terms of the setting of the game, and particularly in terms of the ratio of costs and benefits incurred by a player in the game. In contrast to the above-mentioned game-theoretic bioeconomic analyses, these spatial game simulations typically assume four discrete payoffs depending on the actions of a focal individual and of his/her neighbours. The four discrete payoffs arise from the binary choice of “cooperation” or “defection” strategies by the individual and his/her neighbour. These game theoretic analyses do not acknowledge that the costs and benefits which arise from management decisions may be dependent on an underlying dynamic such as that of a managed ecological resource. Nor do they acknowledge that this ecological dynamic is, in turn, affected by the players’ actions and evolves according to its own rules (e.g. growth rate and migration rate). Continuous (i.e. non discrete) agent-based simulations have been implemented within the evolutionary cooperation literature, (e.g. Killingback et al. 1999, Wahl and Nowak 1999, Doebeli et al. 2004), but these too assume a fixed payoff structure indicative of a uniform resource base unaffected by agents’ management decisions.

We aim to address the problem of co-evolution of management behaviours and cooperation alongside the ecological dynamic of a managed mobile resource in a (relatively) realistic spatial setting. Like much of the cited literature we focus particularly on the evolution of cooperation, and ask in the presence of which payoff structures, and under which spatial and temporal dynamics, can cooperative behaviour evolve where an individual is prepared to accept some personal costs to deliver benefits to his neighbours. Here we develop a continuous game-theoretic analysis of the evolution of management strategies and cooperation among resource managers, following the approach of Killingback et al. (1999), in which (i) investment in cooperation through management action can vary smoothly between extremes, (ii) the payoffs obtained from management are dependent on the underlying stock level of the managed resource, and (iii) the ecological dynamics of that resource (temporal and spatial) are influenced by management actions of agents. This implementation is consistent with wildlife management strategies in real settings in which a continuously variable level of control or harvesting effort can be applied, and the level of control applied affects the temporal and spatial dynamics of the managed resource. The analysis is implemented using the example of deer management in the UK.

Under law in England, Wales and Scotland landownership confers the right to shoot resident deer (Parkes and Thornley 2000) and considerable revenue can be generated by leasing shooting rights for mature males of deer species such as *Cervus elaphus* and *Capreolus capreolus* with antler trophy heads. In some areas, notably the Highlands of Scotland, landowners can realise net profits from these sport shooting revenues. However, severe grazing and browsing pressure by high density deer populations is altering the ecological characteristics of woodland and moorland in many areas of the UK, with potentially severe adverse consequences for native biodiversity (Fuller and Gill 2001, Scottish Natural Heritage, 1994). Woodland management objectives are also changing to focus increasingly on recreation and biodiversity rather than timber production. Deer management issues that have arisen against this background include: (a) calls for substantial reductions in deer densities in areas where grazing and browsing pressure is damaging biodiversity interests; and (b) attempts to coordinate the management actions of private landowners to deliver meaningful reductions in deer density across wider areas and improve the net benefits of deer management by

restoring or enhancing the biodiversity of native woodland. Effective coordination among landowners has, however, proved elusive (Nolan, Hewison and Maxwell 2001) and substantial reductions in deer density have proved very difficult to achieve on a landscape scale. A desire to understand whether cooperative management is hindered by the interaction of landowners' deer management objectives with the underlying ecological dynamics of deer as a managed resource in a spatial setting motivated the research presented here.

In contrast to the spatial game-theoretic models mentioned earlier, we do not know a priori, and make no assumption about, what level of management (culling) corresponds to "cooperation" and what level does not. Instead we simulate the coupled ecological-economic dynamics and then classify the cooperation level of the emerging actions of the players. Cooperation is quantified by an intuitive index developed from Wahl and Nowak (1999). This cooperation index provides a measure of the level of cooperation in the system.

We adopt a grid-configured agent-based model in this paper for simulating management behaviour in a spatial setting. This approach follows the principles outlined by Grimm and Railsback (2005) and uses two types of agents; sporting landowners and biodiversity landowners, to portray two polar characteristics of deer management in the UK. We explore the evolution of management strategies and cooperation in the sporting and biodiversity contexts separately, i.e. within landscapes which contain only one type of owner; sporting or biodiversity. (Simulations from a landscape of mixed ownerships will follow in a subsequent publication). Both types of agents implement management through culling, but they pursue different deer management objectives and perceive different culling benefits and biodiversity damage costs. Sporting owners are portrayed to derive higher revenues per deer culled, in recognition of sporting and trophy income, and to ignore biodiversity damage cost. Biodiversity owners are portrayed to regard biodiversity damage as a considerable financial cost, and to realise no sporting or trophy revenues from culling¹. Both types of owner incur culling costs on the same basis where a strong stock effect increases marginal culling cost as deer density falls. Spatial externalities arise from management through density-dependent emigration of deer between neighbouring landownerships. If an agent culls deer heavily on his land, fewer deer will tend to emigrate from his landholding to his neighbours landholdings. Heavy culling by the focal agent could thus impose a positive or negative externality on neighbouring agents, depending on whether their particular management objective requires an increase or decrease deer in density on their own land.

The paper proceeds as follow. First, the model is specified following the ODD protocol (Grimm et al., 2006). Simulation methodologies, a cooperation index, and the functional forms used to depict benefits, costs and emigration are described. Second, we use an agent-based simulation of management in this landscape grid to investigate reciprocal externalities among the management actions of each type of landowner, and to explore how these reciprocal externalities affect the evolution of cooperative management. Third, we present a description of the results generated for both, sporting dominated and biodiversity conservation landscapes. Finally we draw some conclusions on the evolution of cooperation.

2. Methods

The model is individual-based and spatially explicit. It models the evolution of management strategies and cooperation among landowners based on deer management in a UK setting as described above, but simplifies the problem by considering only worlds which contain landowners with the same interests (i.e. either a world containing only sporting owners or a world containing only biodiversity owners). A description of submodels is included in the Appendix.

¹ Deer management for biodiversity protection is akin to pest control and it is uncommon for sporting and trophy revenues to be realised from biodiversity protection culls.

2.1. Purpose

The purpose of the model is to understand how ecological-economic factors (e.g. culling costs, deer damages, deer movement), and their interactions, influence the success and persistence of management strategies and the evolution of cooperation in deer management at a landscape level. The model thus attempts to address the empirical challenge currently posed by collaborative deer management in the UK.

2.2 State variables

The model depicts a set of landowners (agents) in a landscape grid. Each landholding is represented as a grid cell, and all landholdings are of the same size. The landscape grid comprises 80*80 landholdings, and we simulate management over a timeframe of 500 years.

Each agent ‘owns’ and manages one cell in the grid and can decide what proportion of the deer population in that cell should be culled in every timestep (year) of the simulation. Agents choose the intensity of their culling with the aim of maximising their payoff based on their own cost and benefit functions. Landholdings are characterised by deer dynamics variables (e.g. growth, emigration); and landowners’ management is characterised by culling intensity, the revenues accruing from culling activities, the costs incurred in culling and the biodiversity damage costs caused by deer on their landholding. These elements are combined appropriately for each type of landowner to determine the total payoff each landowner obtains from deer management. The payoffs of sporting and biodiversity owners differ for the reasons described below. Revenue, culling cost and damage cost functions use forms and parameterisations from Smart, White and Termansen (2008), as reported in Table 1.

Agents’ management actions can be interpreted in the phraseology of the evolutionary game theory literature as follows: agents *invest* in *management* action by choosing to *cull* a proportion (k) of the deer population in their grid cell. Culling proportion k can vary smoothly from 0 to 1. Culling incurs *costs* in accordance with cull size, population density and the wage cost of culling effort following the Cobb-Douglas-form relationship shown in the Appendix, and delivers *benefits* to the focal agent as quantified by the *payoff* function. Payoffs for sporting and biodiversity agents differ, but the general form is: $payoff = culling\ revenue - culling\ cost - biodiversity\ damage\ cost$. Sporting agents realise higher marginal revenues from culling, in recognition of sporting and trophy income, but do not account for any biodiversity damage costs from deer presence in their landholding. Biodiversity agents obtain lower marginal revenues from culling, lacking the sporting and trophy revenues, but they do account for biodiversity damage costs. Both sporting and biodiversity agents incur culling costs in accordance with cull size, population density and the wage cost of culling effort (Appendix).

The degree of cooperation which the management action (culling decision) of the agent in the focal cell affords to the payoff accruing to an agent in a neighbouring cell is defined by drawing on the index of continuously variable cooperation proposed by Wahl and Nowak (1999). Wahl and Nowak denote the benefit arising to individual j through the action of individual i as $b_j = a_i b$ where $a_i = 0$ denotes ‘defection’ by individual i (minimising the benefit to individual j) and $a_i = 1$ represents ‘cooperation’ by individual i (maximising the benefit to individual j). The cost to individual i is modelled as $c_i = a_i c$ so that cooperation ($a_i = 1$) maximises the costs of individual i and defection ($a_i = 0$) minimises it. In our case we cannot use this approach, because (a) our cost and benefit functions are non-linear (which could be considered though, as Wahl and Nowak (1999) argue), and crucially (b) the costs and benefits in our case are not fixed but depend on the evolving population density and spatial distribution of the deer. Nevertheless we do take from Wahl and Nowak (1999) that *ceteris paribus* ‘cooperation’ maximises the other player’s payoff while ‘defection’ minimises it. On this observation we define cooperation as follows. Let the *maximum* level of cooperation of

land user i , a_i^+ be defined as: $a_i^+ = \arg \max_{a_i} \Pi_j(a_i)$, where Π_j is the benefit accruing to land user j which depends on the culling level a_i of land user i . The *minimum* level of cooperation is defined as: $a_i^- = \arg \min_{a_i} \Pi_j(a_i)$. The *actual* level of cooperation which land user i affords to his neighbour j at any other culling level a_i is then defined as:

$$Coop_i(a_i) = \frac{a_i - a_i^-}{a_i^+ - a_i^-}$$

This cooperation index ranges from 0 (full defection) to 1 (full cooperation). To evaluate the level of cooperation of a land user i in the simulations, a neighbour j is chosen randomly and the value of cooperation between that pair of agents is evaluated. Cooperation can thus be evaluated across the whole landscape grid and depicted graphically as a filled contour map.

Table 1: Model parameters and default values

Parameter	Description	Default values	
Landowners		Sporting	Biodiversity
w	Unitary costs per culling effort: wages	10	10
r	Unitary benefits from culling	30	20
v	Unitary damages costs	2	30
α	Output elasticity of culling effort	0.5	0.5
β	Output elasticity of deer density	1.1	1.1
d	Diference in deer density for interaction among neighbours	0.15	0.15
p_m	Mutation rate	0.01	0.01
Landsholdings			
e	Emigration parameter	0.2	
N	Number of neighbours	4	

2.3 Process overview, scheduling and culling updating

The model proceeds sequentially through seasonal stages within an annual management cycle. At the start of each year landowners implement culling activities at a level influenced by the payoff they achieved in the preceding year. The deer population is updated synchronously across all cells in the landscape grid to allow for the cull removed from each landholding. The remaining deer population then grows according to a logistic growth function, and the deer density present on a landholding after this growth stage then determines the number of animals from the resident population which will emigrate. Simple linear density dependence is assumed for emigration, with 20% of the population emigrating at neighbouring lands. This approximates the flat initial tail of the logistic density dependence in emigration which Smart et al. (2008) applied based on the findings of Clutton-Brock et al. (2004) across a wide range of deer densities for a representative UK deer species². Emigrating deer disperse equally among either 4 (Moore neighbourhood) or 8 (von Neumann neighbourhood) neighbours. Deer populations are updated once more to allow for this immigration before the level of damage which this post-cull, post-emigration/immigration deer population imposes on biodiversity in each landholding is calculated. Knowing culling revenues, culling costs and damage costs for the whole year, owners can now calculate their annual payoff from deer management³. Finally, at the end of the year, owners compare the payoffs they achieved

² Red deer (*Cervus elaphus*) resident on the Isle of Rum off the west coast of Scotland.

³ The relative sequencing of events in the annual management cycle enacted here is broadly representative of deer management in the UK where autumn and winter culling precedes the birth of calves, which precedes density-driven emigration of immature individuals (especially males). Grazing damage to biodiversity can occur at different

with those of neighbours whose land holds deer at ‘similar’ densities to decide whether or not to change their culling strategy. If no ‘similar’ neighbour achieved a higher payoff then landowners will implement their culling strategy from the preceding year again in the year following. If, however, a ‘similar’ neighbour achieved a higher payoff then a landowner will attempt to imitate that neighbour’s culling strategy. In order to explore the continuous culling strategy space, we assume small errors in the selection of culling strategy, i.e. we allow mutations to occur. Following Doebeli et al. 2004 and Hauebert and Doebeli (2005) the model assumes that whenever an owner chooses his strategy for the following year there is small probability of 0.01, i.e. one mutation in the culling rate of 100 owners) that landowners adopt their desired strategy with some random error, which is normally distributed with mean equal to the desired culling level and a standard deviation of 0.1 of the mean.

2.4 Design concepts

Emergence: Deer population dynamics and culling intensity change with time from initial random settings, and converge toward a steady distribution that characterises the emergent level of cooperative behavior in the landscape.

Fitness: The landowners’ objective is to obtain the maximum economic payoff from deer management activities by choosing their culling intensity.

Interactions: Deer populations in each landholding interact by movement effects, and the level of emigration is dependent on the deer density (higher density holdings send more emigration to nearby holdings). The interaction among landowners’ behaviour is associated with the deer population dynamics. If a property owner culls deer on his land, animals from neighbouring ownerships will tend to immigrate into his less-populated, controlled parcel, this consequently will influence the owner’s payoffs and future culling strategy. Additionally, each landowner may be influenced by the actions of their successful neighbours, as we assume that neighbours observe each other’s behaviour and replicate successful actions.

Stochasticity: Stochasticity is introduced into the selection of the culling strategy for next year both as a means of increasing the rate of convergence towards equilibrium culling levels and also in recognition that stochasticity and imperfect knowledge are pervasive in real world deer management.

Observation: The spatial and temporal pattern of cooperation across the landscape is tracked along with spatial and temporal patterns of the other two key variables of interest: the deer density and culling intensity in each grid cell in order to observe how the level of cooperation depends on the rules and parameters of the simulation game.

2.5 Initialization

The model tests a homogeneous deer density, i.e. each landholding has a deer density of 0.5, and a random deer-populated landscape where the initial deer abundance per holding is randomly chosen between [0,1]. Landowners have a fifty-percent chance of apply initially a low (random number between 0 and 50) and high (random number between 50 and 100) culling intensity level. Simulation runs always start on the first day of a hunting season, and thus on start-up, owners have already taken their initial management decision.

3. Results

Figures 1 and 2 show snapshot configurations at a moment of time during the “steady-state” equilibrium for both spatial games in biodiversity and sporting worlds, respectively. The biodiversity world is characterized by filament-like structures, within which landholdings maintain high culling rate (fig 1a). This means that owners of these holdings behave similarly and intensively cull the resource to reduce the damage costs. Due to the inherent population dynamic of the

times in the year depending on the ecological setting. Damage inflicted by the post-cull, post-growth, post-emigration population implemented here is more representative of wooded lowland ecosystems than upland ones.

resource, deer density is low (high) in those areas where a large (small) culling rate has been maintained over several periods. This means that as these structures of heavy cullers are formed with time, deer density will start decreasing at the center of the cluster formation (fig. 1b). Equivalently, areas of low culling intensity tend to evolve towards a high level of deer density. Our measure of cooperation (fig. 1c) indicates that for this case, cooperative behaviour can be defined as maintaining high culling, because in the filament-like structures the cooperation index is higher than in the surrounding areas where the culling level is low. Interestingly, the highest level of cooperation occurs at the “edges” of the dendritic areas of heavy-culling. Since cooperation is defined as generating a benefit to ones neighbours (at a cost to the focal individual), it is at these interfaces where the high levels of culling undertaken by cooperative individuals generate the highest payoffs for their neighbours.

In the sporting world landowners form compact, circular clusters with similar culling strategies (fig. 2a). Deer density also forms clusters (fig. 2b) which results from the response of the deer population to the culling level maintained in the cluster. If the culling level is high (low) deer density is low (high). Figure 2c shows that compact clusters of cooperators (light grey-white) correspond to locations where clusters of light-culling landowners (dark grey-black) are present. This indicates that, contrary to the biodiversity case above, a sporting owner is cooperating when he undertakes light culling.

This spatial structure of cooperative behavior in the sporting world delivers a higher mean level of cooperation than in the biodiversity scenario above where compact clusters do not form (sporting owners world has mean cooperation = 0.6; biodiversity world has mean cooperation = 0.2). Furthermore, there is lower mean deer density in the biodiversity scenario than in the sporting scenario, and interestingly mean culling level is higher in the second situation. Figures 1a and 1b also show that in the biodiversity world strategies evolve toward an equilibrium where there is higher polarization of culling behavior (either high or low), while in the sporting world there is a mixture of all strategies, including high, low and medium culling levels.

The evolution of deer density over time is significantly different in both scenarios. Figures 3 and 4 show, respectively, the deer density from the initial time. After some transition time, mean deer density in the biodiversity world reaches a steady level where it remains practically constant. In contrast, in the sporting scenario mean deer density remains cyclical, characteristic of a culling rate which evolves gradually over time within the clusters until it reaches a certain level (influenced by the deer density), whereupon the cluster becomes vulnerable to different culling behavior. When we look two random landholdings in the landscape we see that the equilibrium cycles are larger for the sporting scenario due to the difference in payoff structure in both worlds. The biodiversity damage function is a relatively steep function of deer density. Biodiversity damage only appears in the payoff function of biodiversity owners. Biodiversity owners' payoffs therefore respond more rapidly to changes in deer density than do those of sporting owners, and this effect acts to limit the excursions in deer density which develop in the biodiversity world.

4. Summary and Conclusions

This paper investigates the emergence of cooperation in natural resource management at a landscapes scale. In particular, it studies the spatio-temporal evolution of cooperative behavior in two types of deer management systems: a landscape dominated by sporting estates and a landscape predominantly used for biodiversity conservation. We followed an evolutionary game theory approach, where individual owners occupy sites on a spatial lattice. The landowners' payoffs from deer management are a function of the changing level of deer in their land holding. The deer population depends on biological characteristics (population growth and movement across the lattice), and on the mutually interacting management actions of the landowners. The landowners' decisions depend on their expected payoffs involving a mechanism of imitation and learning from

nearest neighbours. The modelled game is continuous because cooperation is defined as a continuous variable - in contrast to the classical “all” or “nothing” strategies that predominate classical games. There are no a priori assumptions on the dependence of a landowner’s action on the level of cooperation with or by his/her neighbours. Instead cooperation is defined a posteriori, following the literature, as a function of the culling strategy. Consequently, there are therefore no *a priori* assumptions about the type of game (prisoners’ dilemma, snow drift, etc.) played.

The results show that spatial structure promotes cooperation in the sporting world, where the cooperative landowners form clusters to obtain the benefits from mutual cooperation. In the biodiversity world however, cooperators form filament-like features, but are unable to form compact clusters. Cooperation level is lower, on average, in the biodiversity world than in the sporting world. In both worlds, cooperative strategies evolve with time and cooperators are not fixed in location, i.e. individuals alternate cyclically between cooperation and defection. This is associated with two effects: (i) once cooperation reaches a certain level it becomes more vulnerable to invasion by defectors, as has been shown in continuous games (Wahl and Nowak 1999); (ii) the benefits derived from cooperation change as the deer population changes. In the biodiversity world, landowners are more distinctively polarised into those carrying out very high and very low levels of culling (cooperation).

The difference in the spatial patterns of management action, cooperation and resource density between the two worlds (filaments versus compact clusters) is striking. It will be a matter of future research to understand these differences and explain them fully in terms of the payoff functions of the two types of land owners. Different types of games have been demonstrated to produce different spatial structures of cooperators and defectors within a landscape (Doebeli and Hauert 2005). Future research will identify which type of game the land owners are actually playing either in the biodiversity or the sporting worlds, and when, so that the results of this study can be better understood in the context of spatially explicit evolutionary game theory.

We find that this analysis has important implications for the role of policy intervention to promote specific forms of management. The analysis would suggest that landscapes with a high level of conservation effort are likely to require active intervention even though private benefits from cooperation exist. In contrast, if the outcomes generated from sporting estate landscapes are in line with broader objectives for provision of ecosystem good and services from the landscape, our analysis suggests that such systems are more likely to persist without intervention.

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APPENDIX

1. Submodels

1.1 Deer population dynamics

In the grid-configured agent-based model in this paper local populations of the resource (deer) evolve on the individual grid cells and animals can disperse among the grid cells. Dispersal is driven by resource density at the source cell and this dispersal produces a spatial coupling between landholdings (grid cells) which transmits the consequences of agents’ management decisions through to the payoffs of their neighbours. In each landholding deer population dynamics is determined by natural growth, spatial movement and culling activities. After culling at the beginning of the season, the change deer density dX in each time step is determined by growth following a logistic distribution, minus emigration and plus immigration from nearby lands:

$$\frac{dX_k}{dt} = X_k(1 - X_k) - eX_k + e \sum_{l \in L(k)} X_l$$

Here $L(k)$ is the set of neighbouring cells around focal cell k and the neighbourhood can be of either von Neumann (8 neighbours) or Moore (6 neighbours) type. In each year season, deer can move up to one neighbour distant from the focal source. We use a simple linear relationship between deer density at the source site and the proportion of the population emigrating. The proportion of deer density emigrating is determined by parameter e , which assumed to be equal for all landholdings. Thus, the emigration is density driven, and low density patches, where deer is been culled heavily, emigration is lower than in high density patches.

1.2 Benefits and costs from deer management

We use a Cobb-Douglas production function to represent the deer culling process.

$$\begin{aligned} K &= AE^\alpha X^\beta \\ \Rightarrow E &= A^{\frac{-1}{\alpha}} K^{\frac{1}{\alpha}} X^{\frac{-\beta}{\alpha}} \\ \Rightarrow C &= wE = wA^{\frac{-1}{\alpha}} K^{\frac{1}{\alpha}} X^{\frac{-\beta}{\alpha}} \\ \Rightarrow C &= c(K, X) \\ \Rightarrow \frac{\partial C}{\partial K} &= \frac{1}{\alpha} \frac{C}{K} \quad \text{and} \quad \frac{\partial C}{\partial X} = \frac{-\beta}{\alpha} \frac{C}{X} \end{aligned}$$

with K is cull size, E is culling effort (hours of culling contractor time), X is density of population before culling begins, A is a constant, w represents wage rate (per hour of culling contractor's time), and the relationship between α and β define the intensity of the returns to scale. This implies that culling cost changes depending on the size of the pre-cull population and the size of the total cull extracted. Thus, culling costs increase rapidly in low deer density patches, and this makes the net culling benefit (culling benefits-culling costs) density dependent. Benefits from culling are simply assumed to be a fixed amount per deer culled, i.e. $B = r * K * D$. Unit profits, r , are assumed greater for the sporting owners as explained in the main text. Biodiversity-motivated landowners also incur biodiversity damage. Damage costs increase with deer density, and we assumed this relationship to be a quadratic $D = v * X^2$.

1.3 Updating of culling strategies

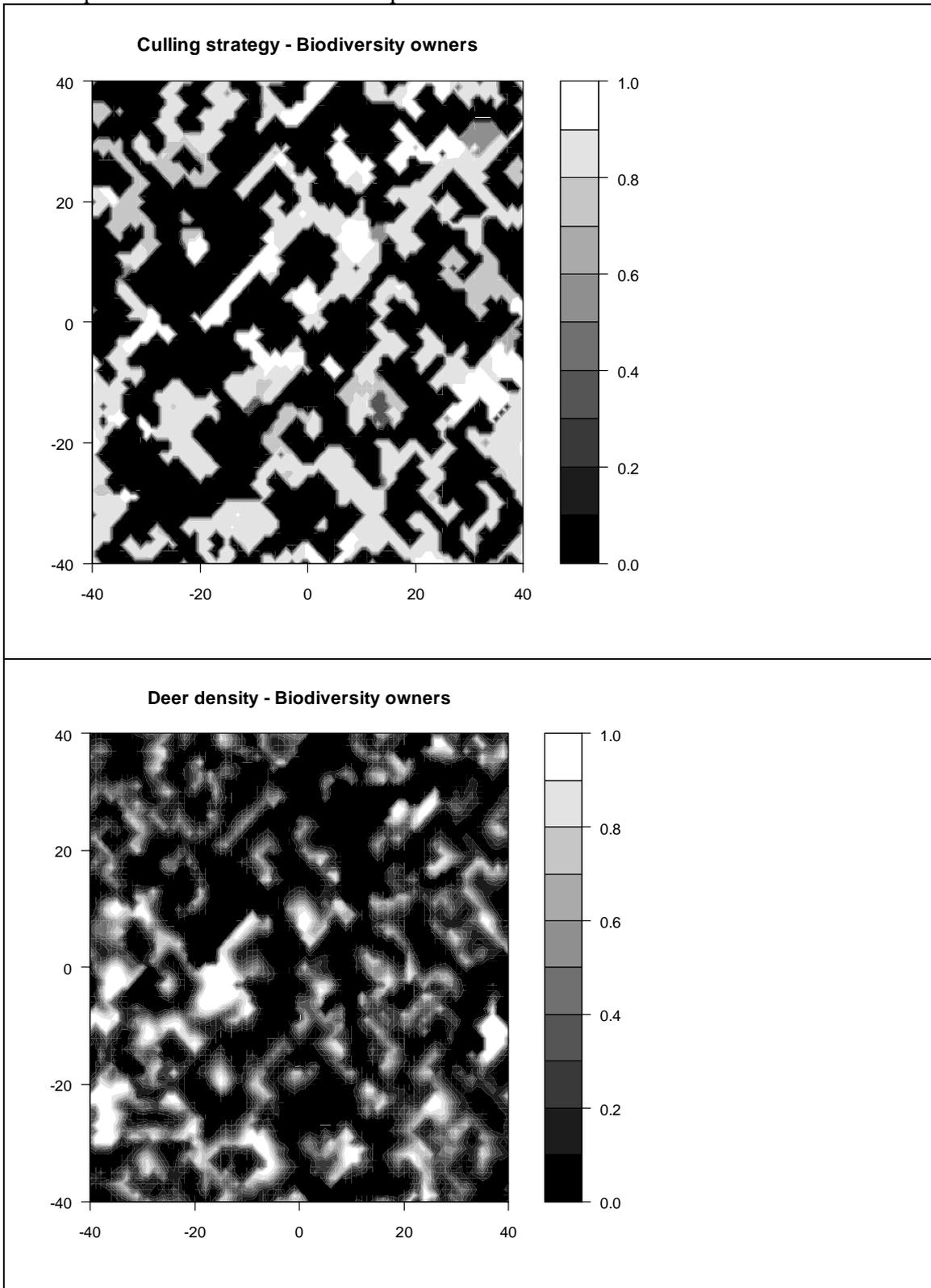
All strategies are evaluated simultaneously. We first compare the deer density of a focal landowner with those of his neighbours whose land holds deer populations of similar density (see Table 1 for the default value of 'similar'). The model determines the neighbour with the highest payoff. If the payoff of this neighbour is higher than that of the focal owner, then the strategy of the successful neighbour is imitated by the focal landowner in the next culling season. Mutations occur by assuming that there is a 1% probability that the strategy selected for the following year is adopted with a small, normally distributed error.

References

- Bhat, M. G. and R. G. Huffaker, (2007) Management of a Transboundary Wildlife Population: A Self-Enforcing Cooperative Agreement with Renegotiation and Variable Transfer Payments *Journal of Environmental Economics and Management*, 53: 54-67.
- Bischi, G.I., Lamantia F., and Sbragia L. (2004) Competition and cooperation in natural resources exploitation: An evolutionary game approach. in: "Game Practice and the Environment" (C.Carraro and V.Fragnelli Eds.) - Edward Elgar Publishing (2004) pp. 187-211.
- Clutton-Brock T.H, Coulson T, and Milner J.M. (2004) Red deer stocks in the Highlands of

- Scotland. *Nature*, 429: 261–262.
- Doebeli, M., and Hauert, C. (2005) Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. *Ecology Letters* 8, 748-766.
- Doebeli M., Hauert C. and Killingback (2004) The evolutionary origin of co-operators and defectors. *Science*, 306: 859-862.
- Fuller, R.J. & Gill, R.M.A. (2001) Ecological impacts of increasing numbers of deer in British woodland. *Forestry*, 74, 193-199.
- Grimm V. et al. (2006) A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198: 115-126.
- Grimm V. and Railsback S.F. (2005) *Individual based modelling and ecology*. Princeton University Press.
- Hannesson, R. (1997): 'Fishing as a Supergame'. *Journal of Environmental Economics and Management*, 32, pp. 309-322.
- Hauert C. and Doebeli M. (2004) Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature*, 428: 643-646.
- Killingback T, Doebeli M. and Knowlton N (1999). Variable investment, the continuous prisoner's dilemma and the origin of cooperation. *Proceedings of Royal Society B* (266): 1723-1728.
- Laukkanen M. (2003) Cooperative and Non-cooperative Harvesting in a Stochastic Sequential Fishery. *Journal of Environmental Economics Management*, 45(2), Supplement 1.
- Laukkanen M., (2005) Cooperation in a Stochastic Transboundary Fishery: The Effects of Implementation Uncertainty versus Recruitment Uncertainty. *Environmental and Resource Economics* 32, 289-405.
- Levhari, D. & L.J. Mirman (1980): 'The great fish war: an example using a Dynamic Cournot-Nash solution'. *Bell Journal of Economics*, Vol. 11, pp. 322-334.
- Lindroos, M., Kaitala V. (2001) Nash Equilibria in a Coalition Game of the Norwegian Spring-spawning Herring Fishery. *Marine Resource Economics* 15, 321-339.
- Noailly, J., Withagen, C.A., van den Bergh, J.C.J.M. (2007) Spatial Evolution of Social Norms in a Common-Pool Resource Game. *Environmental and Resource Economics* 36, 113-141.
- Nowak, M.A. (2006) Five rules for the evolution of cooperation. *Science* 314, 1560-1563.
- Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M.A. (2006) A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441, 502-505.
- Parkes, C. & Thornley, J. (2000) *Deer: Law & Liabilities*, Swan Hill Press, Shrewsbury, UK.
- Scottish Natural Heritage (1994) 'Red Deer and the Natural Heritage', SNH Policy Paper, Scottish Natural Heritage, Perth U.K.'
- Smart, J.C.R, White, P.C.L. & Termansen, M. Modelling conflicting objectives in the management of a mobile ecological resource: red deer in the Scottish Highlands. *Ecological Economics*, 64(4):881-892.
- Wahl, L.M., Nowak, M.A. (1999) The Continuous Prisoner's Dilemma: I. Linear Reactive Strategies. *Journal of Theoretical Biology* 200, 307-321.

Figure 1: Snapshots of equilibrium configurations of culling strategy, deer density and cooperators on a square lattice. See Table 1 for parameter values.



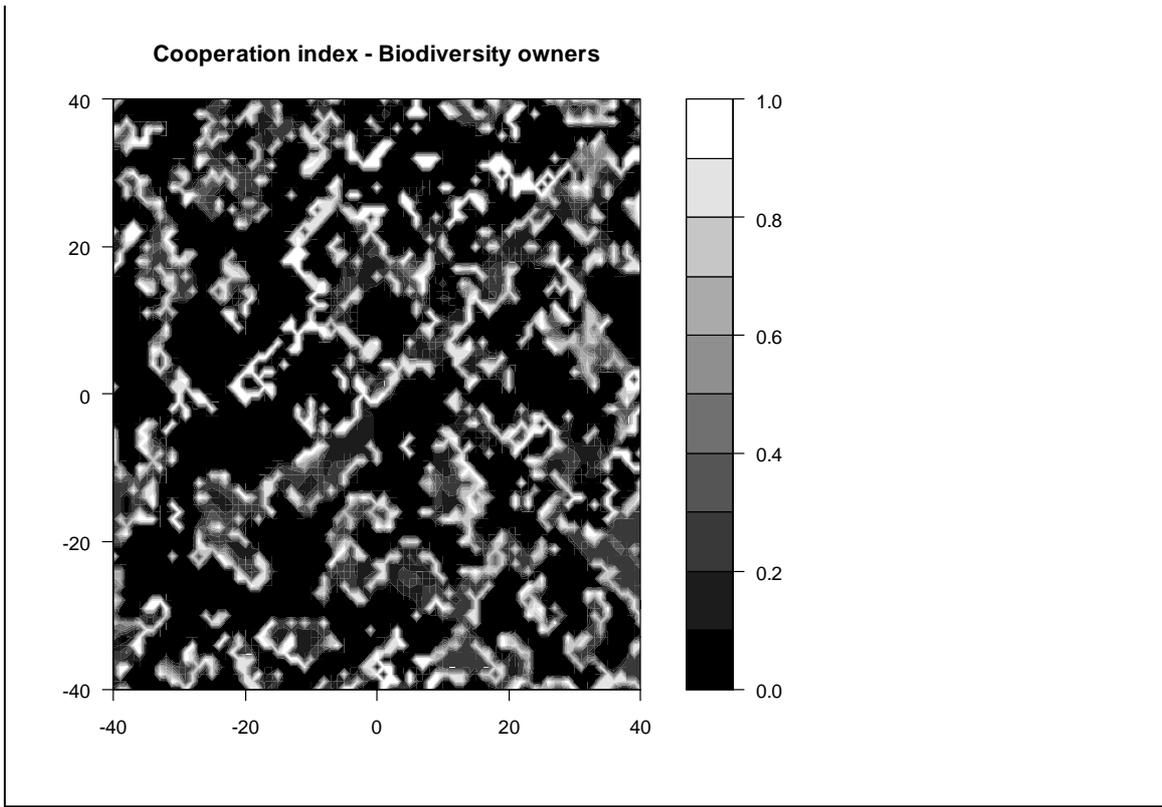
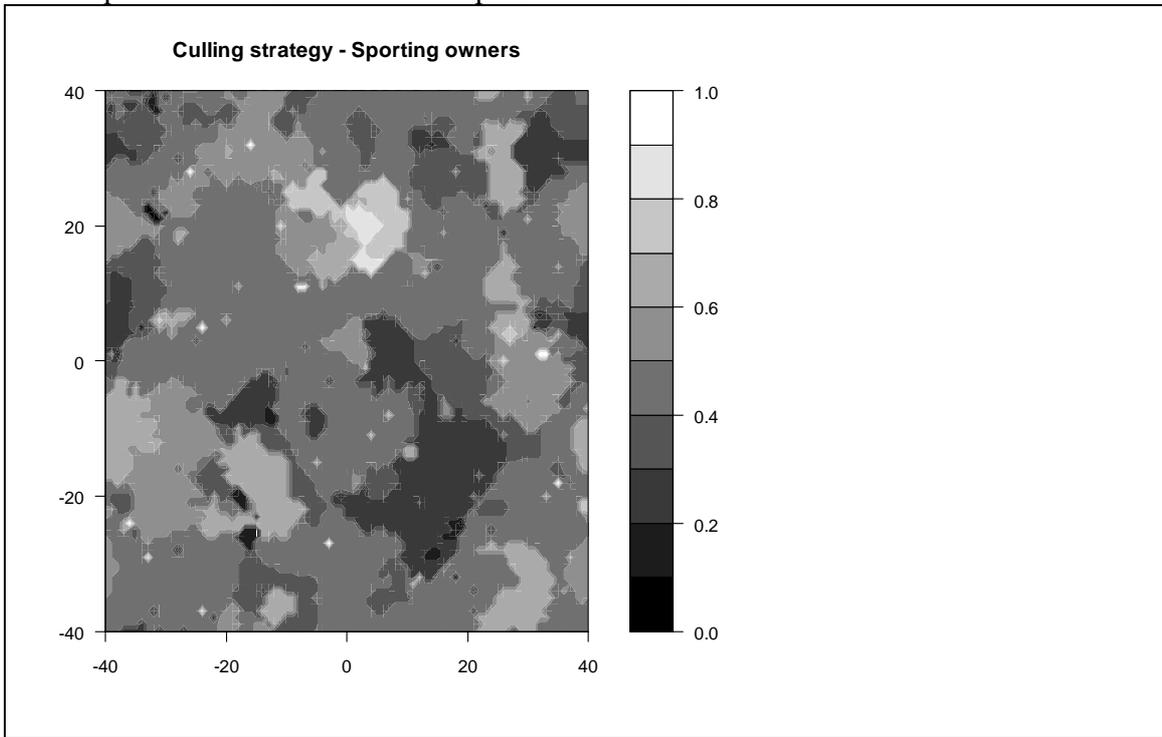


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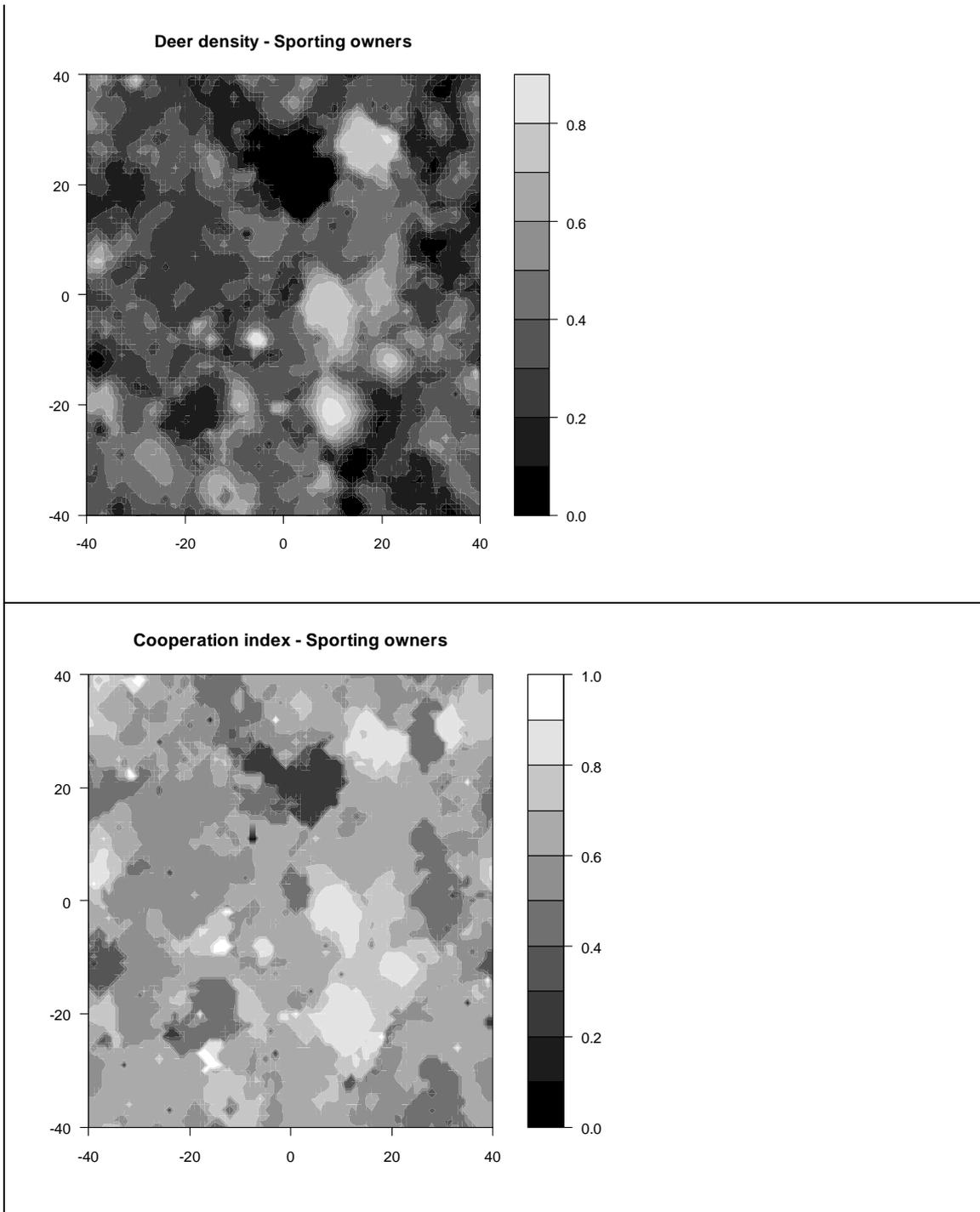


Figure 4: Evolution of mean deer density at the landscape level, and in two random landholdings in the biodiversity world.

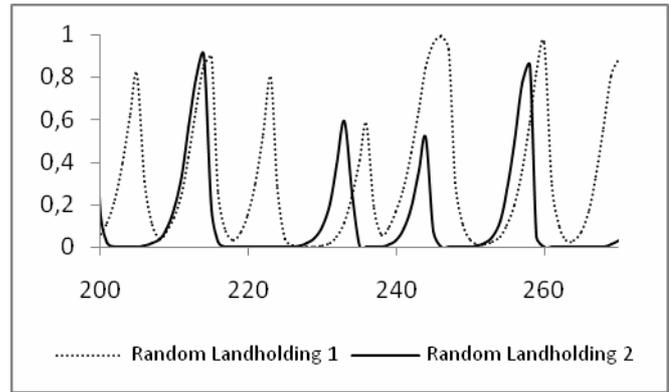
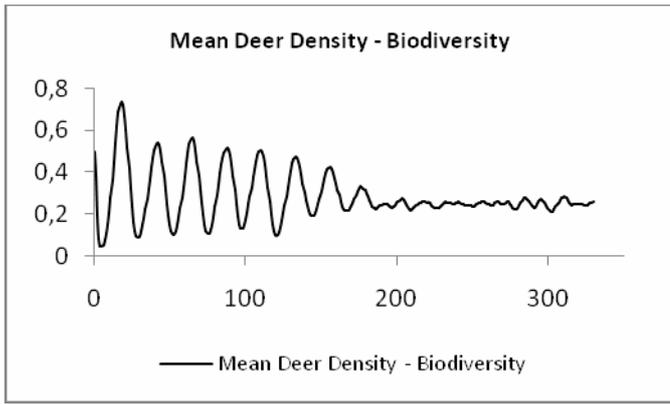


Figure 5: Evolution of mean deer density at the landscape level, and in two random landholdings in the biodiversity world.

