



Emergence of cooperative behaviours in the management of mobile ecological resources[☆]



Julia Touza^{a,*}, Martin Drechsler^a, James C.R. Smart^{b,1}, Mette Tormansen^{c,1}

^aHelmholtz Center for Environmental Research – UFZ, Department of Ecological Modeling, Permoserstrasse 15, 04318 Leipzig, Germany

^bEnvironment Department, University of York, Heslington Road, York YO10 5DD, United Kingdom

^cSustainability Research Institute, School of Earth and Environment, University of Leeds, Leeds LS2 9JT, United Kingdom

ARTICLE INFO

Article history:

Received 29 March 2011

Received in revised form

23 March 2012

Accepted 24 March 2012

Available online 24 April 2012

Keywords:

Deer management

Evolutionary game theory

Cooperation

Spatially explicit model

ABSTRACT

Cooperation at neighbourhood and landscape scale is frequently advocated as a means of improving the management of ecological resources. Such management often involves multiple agents and takes place in spatially structured landscapes where interactions between management actions are mediated via spatio-temporal dynamics of the managed resource. Evolutionary game theory has sought mechanisms to explain the emergence of cooperation among selfish individuals in these complex socio-ecological contexts, and spatial implementations of standard games have shown that the development and persistence of cooperation is affected by spatial structure. However, existing game theoretic models do not incorporate the dynamics of the managed resource or cross-linkages between resource dynamics and management actions and payoffs. We use a spatial agent-based modelling approach to investigate how ecological dynamics, payoff structures, and their interdependencies, influence the emergence and persistence of cooperative behaviours in the management of red deer (*Cervus elaphus*) in Scotland. Simulation results for landscapes comprised of agents with (i) only sporting, and (ii) only biodiversity management objectives show significant differences in the spatial patterns of management action and cooperative behaviour which emerge as limit cycle attractors. Compact clusters of cooperative agents arise in the sporting scenario, culling at low intensity to maintain advantageously high deer densities. Cooperative behaviour in the biodiversity scenario emerges as a context-dependent function of deer density in filament-like structures along the boundaries between linear regions of high or low culling intensity. These findings suggest that mechanisms driving the emergence of cooperative behaviours can be complex and that the opportunities for, and benefits derived from, cooperation are likely to depend critically on both the management objectives and dynamics of the resource.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

1.1. General background and research questions

The use of natural resources often involves multiple actors and takes place in spatially structured landscapes where interactions among users, and the dynamics of the resource, are distance-dependent. The dynamics of such coupled socio-ecological

systems therefore result from spatially defined interactions between human management activities and the evolving natural resource. Social dilemmas arise because cooperation is prone to exploitation by “selfish” individuals which typically leads to a situation dominated by defectors, at a loss to all, as famously characterised by “the tragedy of the commons” (Hardin, 1968). There is much current interest in studying how individuals facing such social dilemmas overcome the strong temptation to defect and instead cooperate to deliver benefits (e.g. Ostrom, 1990; Fehr and Gächter, 2000; Janssen and Ostrom, 2006; Fehr and Gintis, 2007). The literature on evolutionary game theory has modelled such behaviours to explain the emergence of cooperation in biological and economic systems through mechanisms such as kin selection, punishment, reward, policing or direct/indirect/network reciprocity (Axelrod, 2006; Nowak, 2006; Noailly et al., 2007, 2009; Suzuki and Iwasa, 2009). The importance of spatial linkages and

[☆] Thematic Issue on Spatial Agent-Based Models for Socio-Ecological Systems.

* Corresponding author. Present address: Department of Applied Economics, School of Economics, University of Vigo, Lagoas Marcosende s/n, 36.310 Vigo, Spain. Tel.: +34 986813515; fax: +34 986812401.

E-mail addresses: julia.touza@uvigo.es (J. Touza), martin.drechsler@ufz.de (M. Drechsler), jcs@dmu.uk (J.C.R. Smart), mter@dmu.dk (M. Tormansen).

¹ Present address: Department of Environmental Science, University of Aarhus, Frederiksborgvej 399, 4000 Roskilde, Denmark.

structure in the development, extent and persistence of cooperation have been studied in evolutionary game theoretic work using spatial implementations of standard games like the prisoners dilemma or the snowdrift game (also referred to as the chicken game) in which four discrete payoffs are assumed to arise from an *a priori* binary choice of “cooperation” or “defection” strategies by a selected individual and their neighbours (e.g. Doebeli and Hauert, 2005; Ohtsuki et al., 2006; Nowak, 2006; Noailly et al., 2007; and references therein). Under the prisoners dilemma game agents benefit most if all were to cooperate but their individual interests leads them to defect. While under the snowdrift game, agents also prefer not to cooperate, but the worst possible outcome is one in which no other agent cooperates, so an agent will cooperate if he/she thinks that the others will not.

Previous game theoretic settings of cooperation do not, however, fully apply to the analysis of socio-ecological systems as they do not model the dynamics of the managed ecological resource. There is, in particular, no acknowledgement that the costs and benefits arising from management decisions may be dependent on the stock of the ecological resource; nor is it acknowledged that the ecological dynamic is, in turn, affected by the players' actions and evolves according to its own rules (e.g. regarding growth rate and movement). Furthermore, the usual consideration of only two actions, cooperation and defection, defined rigidly *a priori* is insufficient when management adapts in response to a resource which changes continuously in time.

In this paper, we address the emergence of behaviours in dynamic resource management which can be classified, *a posteriori*, as being cooperative. Our particular focus is on the influence which payoff structures and ecological dynamics exert over the evolution and persistence of such cooperative behaviours, and on the conditions under which these behaviours can emerge among “selfish” individuals. We adapt the spatially-specific, agent-based approach of Killingback et al. (1999) to make it more relevant to the practical management of ecological resources by (i) making the payoffs obtained from management dependent on the stock level of the managed resource, (ii) allowing management actions of agents to influence the ecological dynamics of the resource (temporal and spatial), (iii) using density-dependent movement of the resource between agent's landholdings as a means of transmitting the effects of management actions across the landscape, and (iv) reporting the level of *a posteriori* cooperation achieved within the local neighbourhood using an index which varies continuously between full cooperation and complete defection.

Our implementation is consistent with a wildlife management context in which cooperative behaviours (or their opposite) arise from varying levels of management effort affecting the temporal and spatial dynamics of the natural resource, which then in turn affect the payoffs from subsequent management actions. Agents are assumed to be motivated by their own net benefit (payoff), and cooperation is defined to be a behaviour that delivers benefits to neighbouring agents, irrespective of the level of self benefit achieved (West et al., 2007). Within this context, a continuous definition of cooperation at the neighbourhood scale (i.e. cooperation as benefit conferred to immediate neighbours) is used, similar to that of Killingback et al. (1999), Wahl and Nowak (1999) and Doebeli et al. (2004). The level of cooperation at the neighbourhood scale that is associated with a particular management action is quantified *a posteriori* using an intuitive index developed by Wahl and Nowak (1999).²

² It is important to appreciate that this local neighbourhood *a posteriori* quantification of cooperation does not relate directly to the maximum level of social welfare attainable across the entire landscape.

The socio-ecological dynamics of natural resource management are simulated using spatially-specific agent-based modelling, which is widely used to study complex system dynamics in ecology (e.g. Grimm et al., 2005; Monticino et al., 2007; Zhang et al., 2011) as well as the governance of socio-ecological systems, including the conditions that may foster cooperative behaviour (e.g. Janssen and Ostrom, 2006; Zhao, 2009; Souchère et al., 2010).

1.2. The management problem

The analysis is implemented using the example of deer management in the UK, loosely based on a bioeconomic parameterisation of the management of red deer (*Cervus elaphus*) in the Scottish Highlands (Smart et al., 2008). 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 *C. elaphus* and *Capreolus capreolus* with antler trophy heads. In some areas, notably the Highlands of Scotland, landowners can realise profits from these sport shooting activities. 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 (Forestry Commission, 2008). Deer management issues that have arisen against this background include: (a) calls for coordinated culling action to maximise delivery of sporting objectives in areas where deer are regarded primarily as a sporting resource (Association of Deer Management Groups, 2009), (b) calls for substantial reductions in deer densities in areas where grazing and browsing pressure is damaging biodiversity interests (Scottish Natural Heritage, 1994) and (c) attempts to coordinate the culling actions of private landowners to deliver meaningful reductions in deer density across wider areas and improve the net benefits of deer management (Scottish Government, 2008).

Substantive and lasting cooperation in deer management at the landscape scale has proved elusive in situations where deer are regarded as a resource which ranges across landownership boundaries, a pest which ranges across landownership boundaries, or as both a pest and a resource simultaneously by landowners with different management objectives operating in the same landscape (Nolan et al., 2001; Ramsay, 1997; Scottish Natural Heritage, 1994). In this respect, the management of deer has similarities with that of other mammal species such as foxes in Australia (Jones et al., 2006), elephants in southern Africa (Walpole, 2008) and seals in northern Europe (Bruckmeier, 2005). The present research aims to improve understanding of factors which act to increase or decrease cooperation at the neighbourhood scale, and to examine the implications which such increases or decreases in neighbourhood cooperation carry for coordinated resource management at the landscape scale. We therefore choose a modelling setting which recognises that interactions between landowners' management decisions and the ecological dynamics of the resource may influence the development of cooperative behaviour.

The paper proceeds as follows. Firstly, the model is specified, cooperation at the neighbourhood scale, and an appropriate index to measure this cooperation, are defined, and the functional forms used to depict benefits, costs, deer population dynamics and deer movement are described. Secondly, we present the results generated for two different specifications of the model representing landscapes dominated by sporting estates and biodiversity conservation respectively. Finally we draw conclusions on factors

which influence the development and evolution of cooperation and identify policy implications for management.

2. The model

2.1. Introduction to the model

We adopt a time-discrete grid-configured agent-based model (Nolan et al., 2009) for simulating management behaviour in a spatial setting. In building the model we follow the principles outlined by Grimm and Railsback (2005). The model depicts a set of landowners (agents) in a landscape grid managing a resource which can move from grid cell to grid cell across the landscape. The model portrays the evolution of management strategies and, consequently, the emergence of cooperation (or its opposite) among landowners. The model is based on deer management in a UK setting as outlined above, but simplifies the problem by considering only landscapes which contain landowners with the same interests (i.e. either a landscape containing only sporting owners or a landscape containing only biodiversity owners).

Each landholding is represented as a grid cell, and all landholdings are of the same size. The landscape grid is a torus (no boundary effects) and comprises 81 * 81 (6561) landholdings. 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 time step (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. deer population density, growth, movement). 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 net benefit (payoff) each landowner obtains from deer management in each year.

Spatial externalities arise from management through density-dependent movement of deer between neighbouring landownerships (Clutton-Brock et al., 2002). This means that if an agent culls deer heavily, deer density on their landholding will reduce and fewer deer from that cell will tend to move to neighbours'

landholdings as a consequence, while more deer from neighbouring cells may immigrate into the focal cell, depending on relative deer densities across cell boundaries. High intensity culling by the focal agent could thus impose a positive or negative externality on neighbouring agents, depending on whether neighbouring agents' payoffs are dominated by biodiversity damage costs or stalking revenues at their current level of deer density. Revenue, culling cost, damage cost and movement functions take the forms and parameterisations reported in Table 1, drawing from the literature as explained in the following sections and in the footnotes to Table 1.

2.2. Deer population dynamics and deer movement

In our model local populations of the resource (deer) evolve on the individual grid cells and animals can disperse among the grid cells. Dispersal is driven by deer density at the source cell, and this deer density-driven dispersal provides a spatial coupling between landholdings (grid cells) which transmits the consequences of agents' management decisions through to the payoffs of their neighbours. In each cell deer population dynamics is determined by natural growth, spatial movement and culling activities.

$$X_{k,t+1} - X_{k,t} = X_{k,t}(1 - X_{k,t}) - K_{k,t}(X_{k,t}, h_{k,t}) - eX_{k,t} + \frac{e}{N} \sum_{l \in L(k)} X_{l,t} \quad (1)$$

Here $X_{k,t}$ is the number of deer in focal cell k at year t . The first term on the r.h.s. describes logistic growth with carrying capacity and intrinsic growth rate scaled to 1. $K_{k,t}$ is the number of deer culled in cell k in year t , as determined by the culling effort applied by the landowner, $h_{k,t}$, and the size of the deer population in the cell, $X_{k,t}$. Culling effort is expressed in terms of culling intensity, i.e. the fraction of the resident deer population that is culled in year t , $h_{k,t} \in [0, 1]$. A constant proportion ($e = 0.2$; Table 1) of the resident deer population is assumed to emigrate from each cell in any year. This approximates the flat initial tail of the logistic density dependence in movement which Smart et al. (2008) applied based on the findings of Clutton-Brock et al. (2004) for red deer in Scotland. The final term on the r.h.s. of Eq. (1) describes immigration from the $L(k)$ neighbouring cells around cell k , where N is the number of neighbours (4 in the case of a von Neumann

Table 1
Model parameters and default values.^a

Parameter	Description	Default values	
		Sporting	Biodiversity
Landowners			
w	Unitary costs per culling effort: wages	10	10
r	Unitary benefits from culling	30	20
v	Unitary damage costs	2	30
α	Percentage change in cull size resulting from a 1% increase in culling effort	0.5	0.5
β	Percentage change in cull size resulting from a 1% increase in deer density	1.1	1.1
d	Maximum density difference for payoff comparison among neighbours	0.15	0.15
p_m	Mutation rate	0.01	0.01
σ	Standard deviation of mutation random error	0.3	0.3
Landholdings			
e	Movement parameter	0.2	
N	Number of neighbours	4	

^a Wage rate w assumes sporting and biodiversity owners utilise the same workforce for culling. The difference in the unitary benefit of culling r reflects the additional trophy revenues available to stalking owners (Milner et al., 2002). The substantial difference in unitary damage cost v reflects the strong differences in relative importance placed upon biodiversity outcomes by sporting and biodiversity owners (Beaumont et al., 1994; Ramsay, 1997). The α and β parameters relating to culling effort and deer density are those used by Smart et al. (2008) as estimated in Smart (2003). The movement parameter m is representative of the percentage movement of reported by Clutton-Brock et al. (2004). The choice of the mutation parameters is based on evolutionary game theory literature (e.g. Killingback et al., 1999; Hauert and Doebeli, 2004; Doebeli et al., 2004). The sensitivity of the results to variation in N ($N = 8$), $d = [0.15, 1]$, $p_m = [0.01, 0.1]$, and in $\sigma = [0.05, 0.3]$ were examined, and the qualitative results are robust to changes in these parameters. The results presented in the text are for the parameter settings shown in Table 1.

neighbourhood, and 8 in the case of a Moore neighbourhood). Altogether, the change in deer density $X_{k,t+1} - X_{k,t}$ from year t to year $t + 1$ is therefore determined by logistic growth, culling, movement of deer from the focal landholding to surrounding landholdings, and movement from surrounding landholdings into the focal landholding. Management (choice of culling intensity) in one landholding therefore influences deer population size, and hence the costs and benefits of deer presence, on neighbouring landholdings via spatial movement of deer between landholdings in the neighbourhood.

2.3. Benefits and costs from deer management for sporting and biodiversity owners

The payoffs which sporting and biodiversity owners are able to derive from any particular number of deer on their cell will typically differ. Both types of owners implement management through culling, but they receive and perceive different culling revenues and biodiversity damage costs. Both types of owners are assumed to share a common management objective in wishing to maximise the payoff from their management, using the relevant perceptions of culling revenues and biodiversity damage costs.

Sporting owners are portrayed to derive higher revenues per deer culled, in recognition of sporting and trophy income, and are assumed to regard biodiversity damage costs as being relatively unimportant (Milner et al., 2002; Wigan, 1993). Biodiversity owners are portrayed to regard biodiversity damage as a considerable cost and to realise no sporting or trophy revenues from culling³ (Ramsay, 1997; Scottish Natural Heritage, 1994).

Both types of owner incur culling costs. Based on Smart et al. (2008), culling cost changes to reflect changing culling effort which is dependent on the size of the pre-cull population, X , and the size of the total cull extracted, K . The total cull extracted is determined by culling intensity and population size, so culling cost can be expressed in terms of either cull size and population size, or culling intensity and population size:

$$C = wK^{\frac{1}{\alpha}}X^{\frac{\beta}{\alpha}} \quad (2)$$

Here w is the unitary cost of culling effort (wages); α and β define the percentage change in the size of the cull which follows from a 1% change in culling intensity and population size, respectively (Smart et al., 2008). With this deer-calibrated culling function, marginal culling costs increase rapidly with decreasing deer density for any particular level of culling intensity.

The marginal revenue from culling is assumed to be a fixed amount per deer culled, i.e. $B = r * K$, with that marginal revenue, r , assumed greater for sporting owners than for biodiversity owners as explained earlier (Table 1).

Biodiversity-motivated landowners are portrayed to incur substantial biodiversity damage costs when deer population density rises. The relationship between biodiversity impact and deer density in the real world differs depending on the aspect of biodiversity concerned. In the cases of major current concern in the UK, biodiversity damage typically increases with deer density and, in some situations, that increase can be rapid, for example regarding the regeneration of native tree species (Palmer and Turcott, 2003), native ground flora (Kirby, 2001), or the diversity in insects, birds or mammals (Fuller and Gill, 2001). Here we capture these effects by assuming that biodiversity damage costs

rise proportionally with the square of deer density $D = v * X^2$, where v is a scaling factor to account for the different severities which biodiversity and sporting owners attach to these damages (Table 1).

2.4. Model scheduling, control updating, management imitation and stochastic perturbation

The model is initialised with a randomly chosen deer abundance per grid cell, varying between 0 (no deer) and 1 (full carrying capacity), and with landowners' initial culling intensities per grid cell randomly chosen to be between 0 and 1. The model then proceeds through simulated time using a 1 year time step as the period within which management actions are determined and evaluated. Each management year is sub-divided into four sequential sub-steps to depict the relative sequencing of culling, population growth, emigration and biodiversity damage events,⁴ each of which is dependent on the density of deer present in each grid at that time within the management year.

The first sub-step (autumn/winter) in the management year contains the cull. Each landowner culls the deer population [state variable] in their cell with a culling intensity [choice variable] influenced by the payoff [objective] which they achieved in the preceding management year, in comparison to the payoffs achieved by landowners in their cell neighbourhood whose cells held similar deer population sizes. A landowner will persist with the culling intensity they used in the preceding management year unless another landowner whose cell contained a similar deer population size in their neighbourhood achieved a higher net benefit. A neighbour with a similar deer population is defined to be a neighbour for which the magnitude of difference in deer population size = (deer population (neighbour) – deer population (self)) < d . If a 'similar' neighbour⁵ achieved a higher payoff the focal landowner will copy the culling intensity enacted by their more successful neighbour. We thus follow the perspective of evolutionary game theory, where this revision of management action, based on a landowner either sticking to their own strategy or imitating the culling strategy of a more successful neighbour, is interpreted in terms of imitation and learning (Nowak and Sigmund, 2004; Noailly et al., 2007; Sigmund et al., 2010). The deer cull, determined in each grid cell by multiplication of the chosen culling intensity and the resident deer population, is removed synchronously across all cells in the landscape grid.

In the second sub-step in the year (late spring), the deer population which remains in each cell after culling then grows (calves are born) according to the logistic growth function. In the third sub-step (early summer), the number of animals from the resident population which will emigrate from each cell is determined, knowing the number of deer (effectively deer density, since all cells cover the same area) present in a cell after growth and the (fixed) emigration proportion. The deer emigrating from each cell are dispersed equally among either 4 (von Neumann neighbourhood) or 8 (Moore neighbourhood) neighbours, and deer populations in cells across the landscape are updated to reflect these emigration and immigration movements.

⁴ 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 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.

⁵ The maximum deer population difference for payoff comparison among neighbours d was chosen arbitrarily, and the sensitivity of the results to variation in the d parameter ($d = [0.15, 1]$) was examined.

³ 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 in the UK.

In sub-step four (late summer), the level of damage which the post-cull, post-growth, post-movement deer population in each cell imposes on biodiversity in that cell is then calculated. When sub-steps one to four of the management year are complete, culling revenues, culling costs and damage costs for the whole management year are known. Owners can then calculate the payoff which they have achieved from the full year of deer management. These payoffs, which have been influenced by neighbours' management (culling) actions via density-dependent emigration/immigration, are then used to inform the culling intensity which individual owners will adopt at the start of the next management year (the next full time step) of the model. Less successful agents will attempt to copy the culling intensity of their most successful 'similar' neighbour as explained two paragraphs previously.

We explore management actions over a continuous culling intensity space by introducing stochastic errors into agents' culling intensities. This stochasticity may be thought of as representing the real-world uncertainty surrounding any one agent's ability to estimate the payoffs and/or observe the culling intensities of their neighbours,⁶ and the willingness of managers to explore alternative strategic options (Traulsen et al., 2009). It also reflects the landowners' practical difficulties in achieving cull targets in the real world due to e.g. bad weather, random deer movements, disturbance from hillwalkers, forestry felling, etc. Following Killingback et al. (1999), Doebeli et al. (2004) and Hauert and Doebeli (2004), this stochasticity is introduced into the model by assuming that whenever an owner attempts to copy a neighbour's culling intensity, or replicate their own culling intensity, for the following year there is probability of 0.01 (parameter " p_m ", Table 1) that the culling intensity which is actually adopted differs from that intended (i.e. the culling intensity of 1 out of 100 owners is disturbed by stochasticity). The stochastically perturbed imitated culling intensity is the desired culling intensity plus a random error, where the imitation or replication error is normally distributed with mean of zero and a standard deviation of 3.16% (i.e. variance 10%) of the desired culling intensity.

2.5. Using the attractor of the modelled system to provide insights into system behaviour

In our analysis we focus on system condition in the attractor of the modelled complex system, i.e. system condition in the states and dynamics to which the system converges after some transient time (e.g. Gandolfo, 1996; Auyang, 1998). If we were considering a linear deterministic system this would be equivalent to analysing system condition at the stable fixed (or equilibrium) points of the system, but in complex systems like the one studied here the concept of a fixed equilibrium is usually not appropriate. Our analysis therefore focuses on the level of, and variation in, the resource (deer density), management action (culling intensity) and cooperation between neighbouring agents across the landscape after convergence. We evaluate the level of cooperation between a landowner in a focal cell and one randomly selected neighbour.

⁶ The practical assumption underlying this portrayal of learning/imitation behaviour is that all landowners are equally skilled and knowledgeable regarding deer management within their business setting. Thus, by observing the deer density on a neighbour's property a landowner would be able to make a reasonable estimate of the marginal cost of culling deer on that property and also approximate the marginal benefit which their neighbour would realise from culling deer. Landowners here are assumed to produce a homogeneous output (sport shooting or regenerating biodiversity, in the relevant scenario) for which, in the UK at least, the value of a marginal unit produced remains relatively constant as the quantity of units produced varies. In this way, we assume that a landowner would be able to estimate a neighbour's net payoff by observing their culling practice.

We avoid using a measure of average cooperation – the mean or median level of cooperation across the Moore or von Neumann neighbourhood, for example – because this might obscure the full extent of variation in cooperation between individuals which occurs across the landscape. Our measure of cooperation is described in the following sub-section.

2.6. Degree of cooperation

Within the model described above, agents' management actions can be interpreted in the phraseology of evolutionary game theory literature as follows: agents *invest* in *management* action by choosing to cull a proportion, $h_{k,t}$, of the deer population in their grid cell. Culling proportion (cull intensity) can vary smoothly between 0 and 1. Culling incurs *costs* in accordance with cull intensity, the population size from which the cull is extracted and the wage cost of culling effort (Eq. (2) and Table 1), 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: $payoff = culling\ revenue - culling\ cost - biodiversity\ damage\ cost$. Differences in payoff between sporting and biodiversity owners arise *ceteris paribus* principally as a result of their different valuations of damage cost and to a lesser extent because of differences in the marginal revenue they receive from culling (Table 1).

In our model we make no *a priori* assumptions concerning the dependence of an agent's action on the level of cooperation with or by their neighbours. Instead, cooperation is quantified *a posteriori*, following the evolutionary game theory literature, as a behaviour on a continuous scale which arises from agents' self-interested choice of culling intensity. Consequently, there are no *a priori* assumptions about the type of game (prisoners' dilemma, snow-drift, assurance, etc.) played. Essentially, our model investigates whether cooperative behaviour emerges from imitation and learning among self-interested agents whose payoffs are sensitive to spatial and temporal resource dynamics, and whose actions affect their neighbours' payoffs via their impact on density-dependent movement of the managed resource.

The degree of cooperation which the management action (cull intensity) of one agent displays towards an agent in a neighbouring cell is quantified using an index of continuously variable cooperation developed from that proposed by Wahl and Nowak (1999). Wahl and Nowak used a cooperation index to denote the benefit arising to agent j through the action of agent i , irrespective of

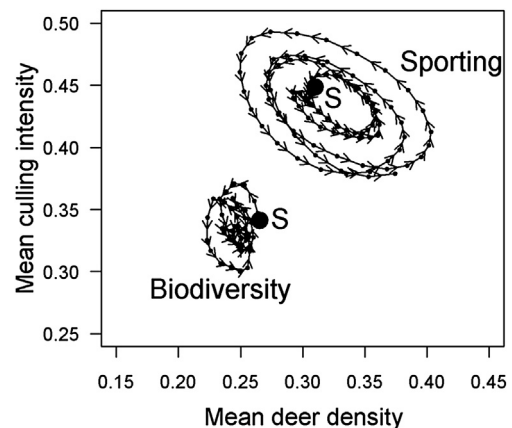


Fig. 1. Mean culling intensity vs. mean deer density for the sporting and the biodiversity scenarios. Each dot represents one time step (100 consecutive time steps in the sporting scenario and 50 consecutive time steps in the biodiversity scenario). The system evolves in the direction of the arrows from starting points labelled 'S'.

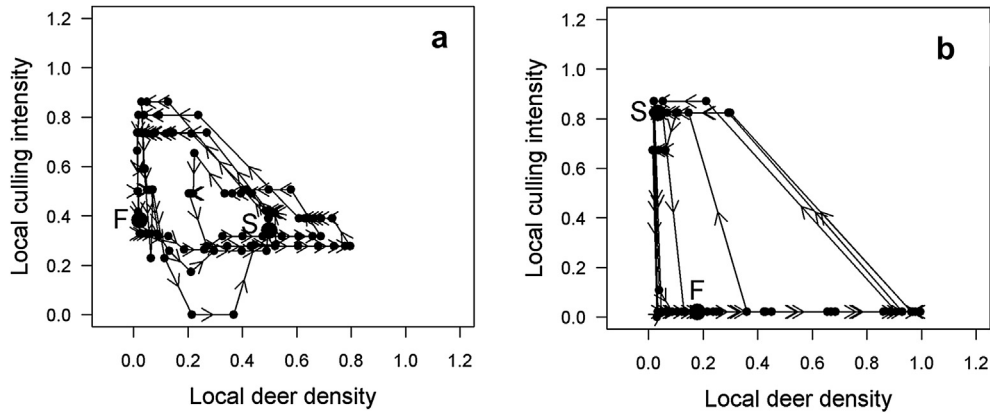


Fig. 2. Local culling intensity vs. local deer density for a randomly sampled landowner for the sporting (panel a) and the biodiversity (panel b) scenarios. Each dot represents one time step (100 time steps in panels a and 50 time steps in panel b). The system evolves in the direction of the arrows from point 'S' to point 'F'.

whether agent i incurs any self-cost in delivering the benefit to their neighbour j , as $b_j = a_i b$ where $a_i = 0$ denotes 'defection' by agent i (minimising the benefit which agent i delivers to agent j) and $a_i = 1$ represents 'cooperation' by agent i (maximising the benefit which agent i delivers to agent j). Therefore, b is the maximum benefit j can achieve under full cooperation from i . Wahl and Nowak also quantified the cost incurred by agent i in delivering their management action as $c_i = a_i c$ so that cooperation ($a_i = 1$) maximises the costs to agent i and defection ($a_i = 0$) minimises it. In our case we do not use this approach directly, because (a) our cost and benefit functions are non-linear (which could be considered though, as Wahl and Nowak (1999) argue), (b) the costs and benefits which result from management actions in our case are not fixed but depend on the evolving deer population density and spatial distribution of the deer, and (c) cooperation, or defection, in our model is not defined *a priori* by strategic choices made by agents, but instead emerges *a posteriori* through imitation and learning in pursuit of an agent's own management objectives. Nevertheless, we do take from Wahl and Nowak (1999) that *ceteris paribus* 'cooperation' is a behaviour which maximises the other agent's payoff while 'defection' minimises it. On this observation we define an index to measure cooperation *a posteriori* as follows. We denote the *maximum* level of cooperation which agent i could deliver by h_i^+ so that management action $h_i = h_i^+$ maximises the neighbour's payoff. Accordingly, we denote the *minimum* level of cooperation which agent i could deliver by h_i^- , so that the neighbour's payoff would be minimised by management action $h_i = h_i^-$. The *actual* level of cooperation which agent i affords to their neighbour j at any other culling intensity h_i is then defined as:

$$\text{Coop}_i(h_i) = \frac{h_i - h_i^-}{h_i^+ - h_i^-} \quad (3)$$

This cooperation index ranges from 0 (full defection, i.e. delivering as little benefit to neighbour as possible) to 1 (full cooperation, i.e. delivering as much benefit to neighbour as possible). To evaluate a representative level of the cooperation delivered by agent i , *a posteriori* of that agent's choice of management action at any point in the simulations, one neighbour j is chosen randomly and the value of the cooperation index between that pair of agents is evaluated at that point in time. *A posteriori* cooperation can thus be evaluated across the whole landscape grid and depicted graphically as a filled contour map. Under this definition, *a posteriori* cooperation is quantified at the neighbourhood scale, and does not directly relate to the maximum level of net benefit attained across the whole landscape grid.

3. Results

We present the results in two parts. The first part focuses on the resource economic dimensions of the deer management problem. This includes the evolution of deer density and culling intensity, and their inter-relation, in landscapes under the different management regimes. In the second part we turn to the game theoretic dimension of the problem and present results concerning the dynamics of cooperation at the neighbourhood scale and how this neighbourhood cooperation relates to culling intensity. The results presented are representative of those obtained from multiple simulation runs using the model parameter values shown in Table 1. They also hold, with minor quantitative differences, (i) for a Moore neighbourhood ($N = 8$ neighbours), (ii) across a range of values for the maximum density difference for the payoff comparison among 'similar' neighbours ($d = [0.15, 1]$) which limits the scope of learning by imitation, (iii) across a range of values for the mutation probabilities ($p_m = [0.01, 0.1]$) which dictates the frequency at which random errors occur, and (iv) across a range of values for the standard deviation of the random mutation error ($\sigma = [0.05, 0.3]$). The 500 year simulation timeframe was easily sufficient to ensure that the system locked itself into the repetitive cyclic patterns illustrated, from all initialisation states modelled. The nature of the emerging patterns is not determined by spatial grid size; this was tested from grid sizes as small as $25 * 25$ holdings.

3.1. Dynamics of deer and culling intensity

The mean deer density in the landscape and the mean culling intensity develop over time in cycles in both types of landscapes; sporting and biodiversity (Fig. 1).⁷ Starting from a relatively high mean deer density and low mean culling intensity, culling intensity gradually increases bringing about a gradual decrease in deer density. This continues until a relatively high culling intensity and low density is reached. At this stage, landowners realise that it becomes advantageous to reduce the culling intensity, and this is then followed by a subsequent increase in deer density. As

⁷ Mean culling intensity and mean deer density are means across all the land-holdings for one run of the model. For clarity issue, only 100 and 50 consecutive points were plotted for the sporting and biodiversity scenarios, respectively. Fig. 1 uses points 360:460 from the sporting scenario and points 410:460 from the biodiversity scenario. Fig. 2 plots points 210:310 from the sporting scenario and points 180:230 from the biodiversity scenario.

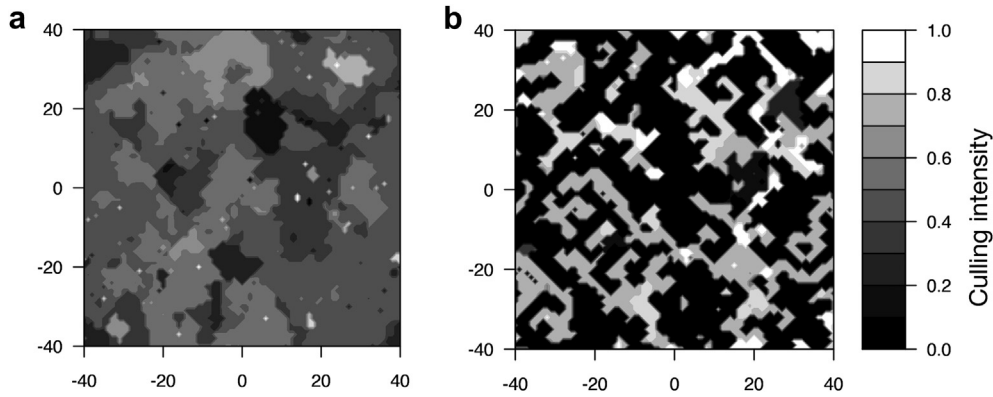


Fig. 3. Filled contour plots of representative culling intensities in 'limit cycle' attractor quasi-equilibrium on a 81×81 square landscape lattice ($t = 500$). Panel a: sporting scenario. Panel b: biodiversity scenario.

a consequence of this dynamic we observe a negative relationship between deer density and culling intensity in both scenarios.

Fig. 2 shows phase diagrams of deer density and culling intensity for a randomly selected single cell. Similar to the dynamics of the mean values (Fig. 1) we observe cycles (including a negative relationship between deer density and culling intensity) whose shapes however differ considerably from those in Fig. 1. The first

difference is that the observed local culling intensity and deer density both span almost their entire feasible range $[0, 1]$. Secondly, in both scenarios the cycles display a pronounced triangular shape which arises as a consequence of the fact that heavy culling can reduce the population size more rapidly than natural population growth can restore it. Starting from relatively high deer density and low culling intensity, an increase in culling intensity is followed

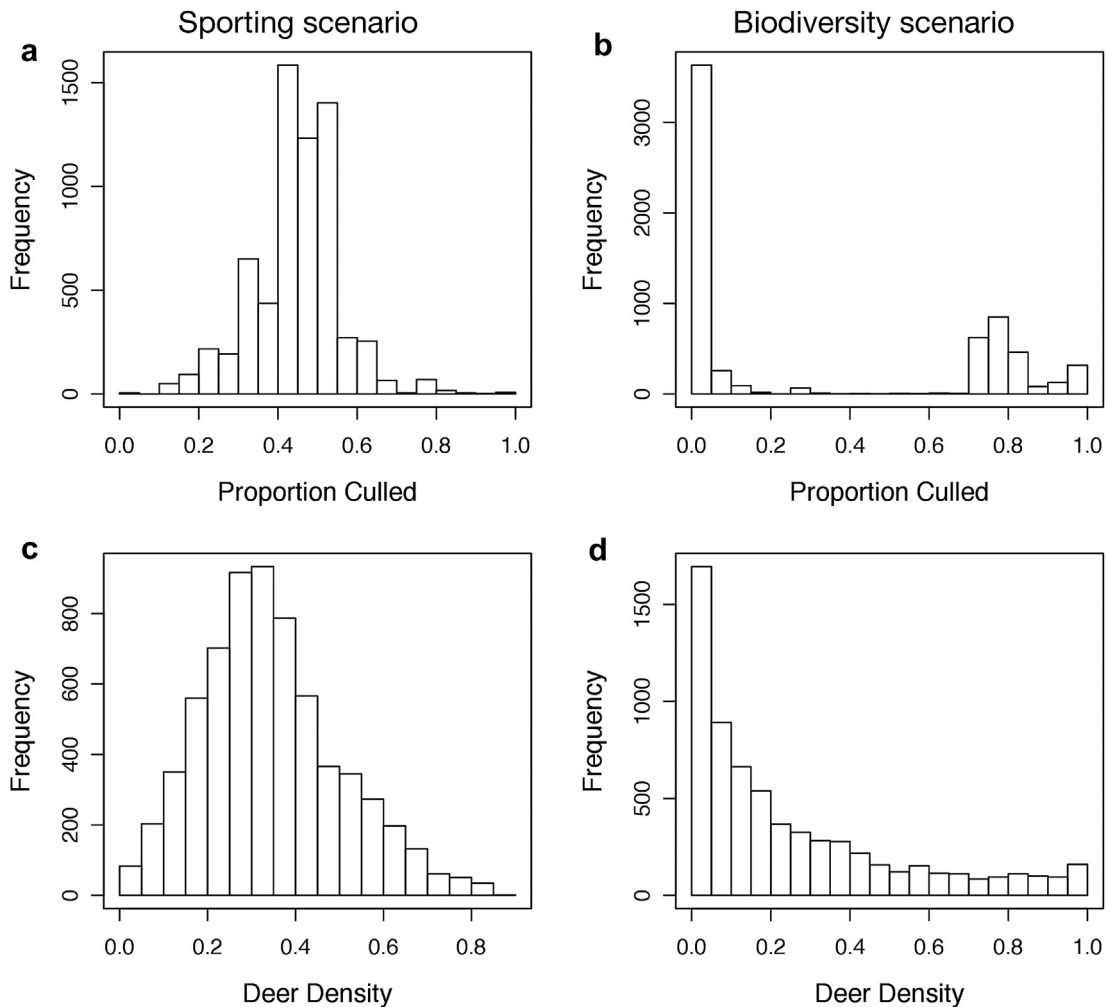


Fig. 4. Frequency of culling intensity and deer density sampled overall cells at time $t = 500$. Panel a: culling intensity, sporting scenario. Panel b: culling intensity, biodiversity scenario. Panel c: deer density, sporting scenario. Panel d: deer density, biodiversity scenario.

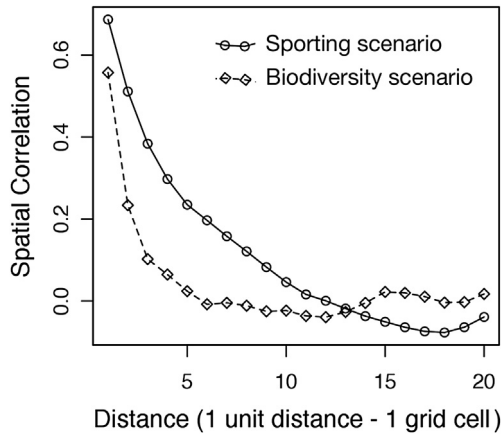


Fig. 5. Correlation length of culling intensities. A measure of spatial correlation with respect to distance under the assumption that 1 unit distance is one cell in the landscape. The line with circles shows results for the sporting scenario, the line with diamonds shows results for the biodiversity scenario.

rapidly by a decrease in deer density (similar to Fig. 1). The landowner responds to the decline in the deer density and associated increase in culling cost by reducing their culling intensity to maximize their payoff. However, it is only after low culling has been applied for some time that the deer population increases once again to a sufficiently high density for the cycle to repeat.

Although both sporting and biodiversity scenarios share this feature, they do differ markedly in that in the sporting scenario culling intensity is seen to take practically all values within the feasible interval, whilst in the biodiversity scenario it takes only very high or very low values. Furthermore, in the biodiversity scenario the culling intensity jumps between high and low levels within only very few (often a single) time steps, while in the sporting scenario it generally changes more gradually. Overall, in the biodiversity scenario the dynamics of local culling intensity are more polarised in terms of applied culling intensities and run on a faster cycle than in the sporting scenario.

Differences between the sporting and biodiversity scenarios can also be seen in the spatial structure of the landscape. Fig. 3 shows representative spatial distributions of culling intensities in filled contour plots of the sporting and biodiversity landscapes. The structural features illustrated are representative of those observed across the landscape grid in the limit cycle attractor. The location of these structural features on the landscape grid changes from year to year, but the basic spatial features recur (at different locations)

across the grid, year on year. In both scenarios the landscape is structured into patches consisting of cells with similar culling intensities. In the sporting scenario almost the full range of culling intensities can be observed across the grid. In the biodiversity scenario, however, the landscape is comprised only of patches with either very low culling intensity or very high culling intensity. This is further emphasized in the frequency distributions of culling intensities (Fig. 4). Fig. 4 also shows that in the sporting scenario the deer density tends to be higher than in the biodiversity scenario. The second marked difference between the two scenarios is in the spatial correlation of the culling intensities (Fig. 5). In the sporting scenario the spatial correlation length, which measures the distance at which cells with similar culling density can be observed, is much higher than in the biodiversity scenario. Culling intensity in a particular cell in the biodiversity scenario therefore changes not only on a shorter time scale than in the sporting scenario, but it also varies among cells across a much shorter spatial scale. As a consequence, individual patches of similar culling intensity spread over larger areas in the sporting landscape and these patches typically have a higher edge-to-area ratio than those observed in the biodiversity scenario, whereas similar culling intensities exist in smaller, more linear areas in the biodiversity landscape (Fig. 3).

3.2. Analysis of cooperation

Fig. 6 shows filled contour plots of the cooperation index for both scenarios. Broadly, clusters of similar levels of cooperation are found in the sporting scenario (Fig. 6a). Cooperative behaviour in the sporting scenario is characterised by a uni-modal frequency distribution with most individuals displaying medium levels of cooperation index (Fig. 7a). Fig. 8a shows that the cooperation index in the sporting scenario is strongly negatively correlated with culling intensity, i.e. cooperative individuals are those that undertake low culling, while defecting individuals are those that apply high culling intensities. This leads to the conclusion that in the sporting scenario clusters of cooperative behaviour are formed by individuals culling at low intensity. This low culling intensity will allow the deer population, which sporting owners regard primarily as a resource, to increase. Defecting individuals in the sporting scenario will be those that free-ride on the cooperative individuals by culling higher proportions of the deer population.

In the biodiversity scenario, where deer are regarded primarily as a pest because of the high damage cost which they impose on landowners' payoffs, the cooperation index is high only at the boundaries between the high-culling and low-culling clusters. This

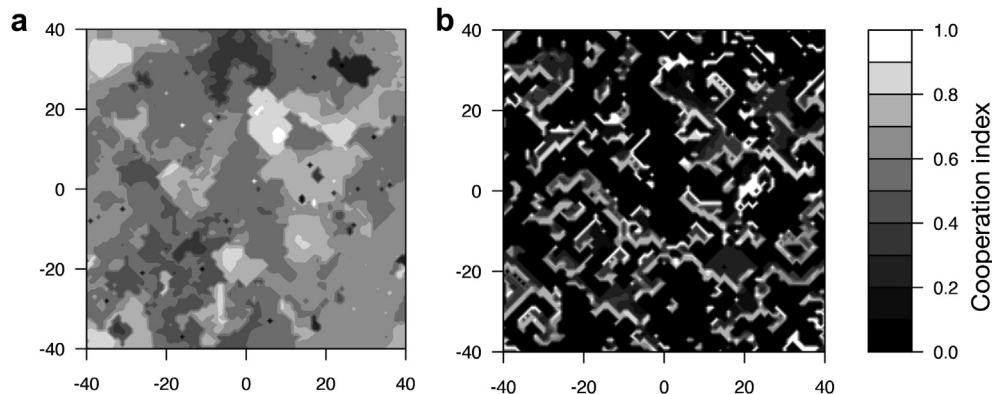


Fig. 6. Filled contour plots of representative cooperation indices in 'limit cycle' attractor quasi-equilibrium on a 81 * 81 square lattice ($t = 500$). Panel a: sporting scenario. Panel b: biodiversity scenario (Culling intensities are those shown in Fig. 3).

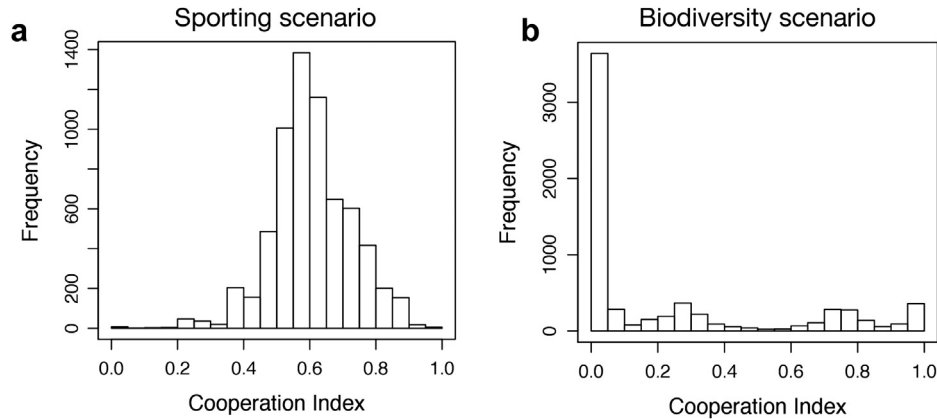


Fig. 7. Frequency distribution of landowners' cooperative behaviour. Panel a: sporting scenario. Panel b: biodiversity scenario.

can be seen by comparing Figs. 6b and 3b. The cooperation index is very low inside larger areas where culling is very low and also moderately low inside areas where culling is relatively high. Compact clusters of cooperating landowners have therefore failed to form in the biodiversity scenario. The small number of cooperators are located in filament-like structures along the boundaries between areas in which low and relatively high culling dominates. Fig. 7b shows that a low level of cooperative behaviour is very common in the biodiversity landscape, and corresponds with the many grid cells where culling intensity is very low (Figs. 3b, 4b and 6b).

Fig. 8b shows that there is a more complex relationship between cooperation index and culling intensity in the biodiversity scenario, compared with the sporting scenario (Fig. 8a). The correlation between culling intensity and cooperation is not consistently of the same polarity.

Given that deer are primarily regarded as a pest in the biodiversity scenario, we would anticipate a positive correlation: heavier culling would be expected to benefit the neighbour. However, Fig. 8b suggests that both positive (Mode 1) and negative (Mode 2) correlations may exist. These different modes of behaviour are related to the culling intensity of the neighbour selected for calculation of the cooperation index. Mode 1 mainly occurs when the selected neighbour of the focal individual is culling at low intensity, while Mode 2 occurs mainly when the focal individual's selected neighbour applies high culling intensity (Fig. 9).

According to this finding, the cooperation index of an owner in the biodiversity scenario increases with increasing culling when the neighbour applies low intensity culling (Mode 1), but decreases with increasing culling when the neighbour is undertaking high intensity culling (Mode 2). Cooperative behaviour in the biodiversity scenario appears to be characterised by doing the opposite to your neighbour (A and B, Fig. 8b); whereas defecting implies applying similar strategies, i.e. either both culling at high intensity, or both culling at low intensity (C and D, Fig. 8b). At Point B, the focal agent culls at high intensity, while the neighbour is culling at low intensity (Mode 1 behaviour, Fig. 8b, Fig. 9). The focal agent is cooperative here because heavy culling reduces deer emigration to the neighbour's land with positive consequences for damage reduction. In this instance the neighbour is free riding on the heavy culling of the owner in the focal cell. At Point A, the focal agent culls at low intensity while their neighbour culls at high intensity (Mode 2 behaviour, Fig. 8b, Fig. 9). Low intensity culling in the focal cell increases emigration onto the neighbour's land. This emigration would increase the neighbour's payoff, and hence be regarded as cooperative, if the consequent reduction in culling cost exceeded the increase in damage cost. Culling cost and damage cost respond strongly, but oppositely, to increasing deer density. Therefore, the incremental reduction in a neighbour's culling cost which results from higher emigration is only likely to exceed the associated incremental increase in damage cost when the neighbour has a low deer density and is applying high culling levels. This suggests that the neighbour may not have reduced culling optimally as their

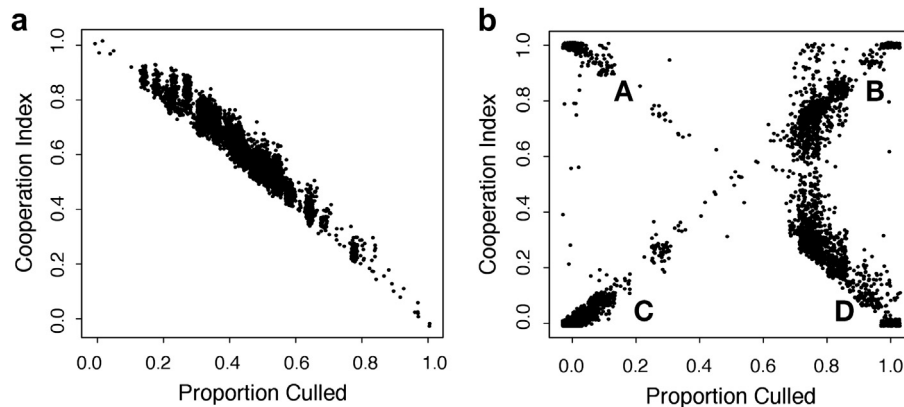


Fig. 8. Correlation between landowners' culling intensity and cooperative behaviour. Panel a: sporting scenario. Panel b: biodiversity scenario. Note: A jitter function was used to avoid overlapping and make visible all the data-points.

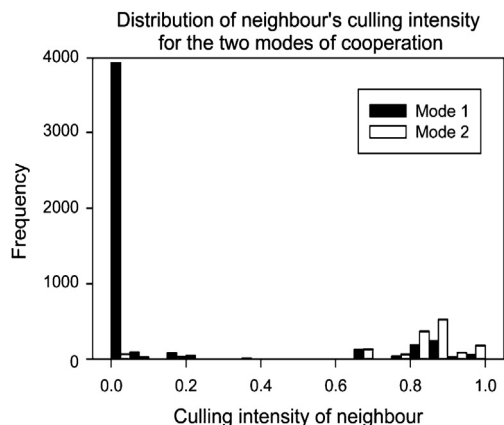


Fig. 9. Frequency distribution of selected neighbour's culling intensity for the two modes of cooperation (biodiversity scenario).

resource stock has decreased, presumably due the adaptation inertia in the system. Therefore in the cooperation snapshot of the biodiversity scenario (Fig. 6b) unhelpful behaviour dominates within both the high (D, Fig. 8b) and low (C, Fig. 8b) culling intensity clusters (Fig. 3b), where neighbouring landowners are pursuing similar culling strategies. The cooperation index is only high in the filament-like structures at the edges of these like-culling clusters, where landowners are doing the opposite to their neighbours.

4. Discussion and conclusions

In this paper we use an evolutionary game theory approach to investigate the influence which payoff structures and ecological dynamics exert over the emergence, evolution and persistence of cooperative behaviours among a population of “selfish” individuals managing an ecological entity which can be regarded as either a resource or a pest. The spatio-temporal evolution of cooperative behaviour is investigated in two types of deer management systems: a landscape composed only of sporting estates whose owners regard deer as a resource, and a landscape used only for biodiversity conservation in which landowners regard deer primarily as a pest. Individual landowners occupy sites on a spatial lattice. Landowners' payoffs from deer management are a function of the changing level of deer density on their landholdings. The deer population depends on biological characteristics (population growth and movement across the lattice) and on the mutually interacting management actions of the landowners. Landowners' culling decisions depend on their expected payoffs, and evolve through a mechanism of imitation and learning from nearest neighbours. The modelled game is continuous because an agent's action (culling intensity) is defined as a continuous variable in contrast to the “all” or “nothing” strategies that predominate in classical games. There are no *a priori* assumptions concerning the dependence of a landowner's action on the level of cooperation with or by their neighbours. Cooperation is, instead, defined *a posteriori*, following the evolutionary game theory literature, as a function of the outcome which a particular culling intensity confers on a neighbour. We acknowledge that our notion of cooperation might be classified rather as a positive externality arising from selfish behaviour (West et al., 2007). Nevertheless, situations in which cooperation – following our definition – evolves to become widespread would be more likely to carry lower potential for conflict between neighbours, and therefore to be more conducive to joint/consensual management. In the context of landscape

scale management it is therefore an applicable definition as management initiatives in real landscapes usually involve joint agreements between independent parties.

The results show a significant difference in the spatial patterns of the limit cycle attractor which emerges with regard to management action and cooperative behaviour in the sporting and biodiversity scenarios. In the sporting scenario cooperation emerges through the formation of compact clusters of cooperative agents surrounded by defecting individuals. In the biodiversity scenario, by contrast, strong cooperators do not form compact clusters but exist mainly in filament-like structures along the boundaries between zones of high or low culling intensity. Cooperative behaviour in the biodiversity scenario is context dependent, because it is a function of the neighbours' actions: cooperation turns out to mean taking the opposite action to your neighbour.

When neighbours in the biodiversity scenario are finding it advantageous to cull at a low intensity, a focal landowner will show cooperative behaviour by culling at high intensity because this decreases immigration of deer onto neighbours' landholdings and reduces neighbours' damage costs. The benefit provided by the focal owner's high intensity culling here could be substantial if the deer population density in their cell is high relative to that in neighbouring cells, since in these circumstances considerable numbers of deer could emigrate from the focal cell to neighbouring cells and thereby increase neighbours' damage costs significantly. In this situation the neighbours are free riding on the culling efforts of the focal ‘cooperator’. The neighbours will find that their low intensity culling, assisted by the high intensity culling of the cooperative ‘focal’ owner, is the best strategy for maximizing their payoffs until the deer population recovers sufficiently to impose prohibitive damage costs, whereupon it will become advantageous to switch back to a higher culling intensity. The location of the switchover point between high and low intensity culling will depend on the relative steepness of the culling cost and damage cost curves with respect to deer population density at the current level of culling intensity. By contrast, when neighbours implement high intensity culling, low culling intensity by a focal individual will be regarded as cooperative behaviour because this increases deer movement onto neighbouring landholdings which reduces neighbours' culling costs. Again, the ‘opposite’ culling strategy of the focal cooperator here would be appropriate if deer population density in their cell was markedly lower than that of their neighbours. This explains why in the biodiversity scenario cooperative individuals are those who implement either high or low intensity culling along the edges of clusters of low and high intensity culling landowners.

In both the sporting and biodiversity scenarios, cooperative behaviours evolve with time and cooperators are not fixed in location, i.e. agents alternate cyclically between cooperation and defection. This gives rise to two effects in our modelled landscapes: (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, and the costs incurred, from cooperation change as the deer population changes under its intrinsic dynamic. Both of these features suggest that, unless applied culling effort is exactly sufficient to hold population density fixed, considerable effort will typically be required to facilitate and support adaptive cooperation in real world resource management and pest control situations. This is exemplified by the existence of government-funded bodies such as the Deer Initiative in England whose main objective is to facilitate and support coordinated deer management (Deer Initiative, 2011).

In the biodiversity scenario, primarily as a consequence of the strong influence which deer density exerts over biodiversity damage costs and over culling costs, landowners are distinctively

polarised into those culling at very high and very low intensities. The model suggests that landowners in the biodiversity scenario will switch between very heavy and relatively light culling depending on the level of damage being incurred. This indicates that ‘pulse culling’ might be an optimal strategy for pest control, and, indeed, in the real world intensive pest control is often applied only periodically when pest densities increase sufficiently to impose significant welfare losses.

In the sporting scenario, however, the span of culling intensities applied is lower. As a consequence of this, modelled local deer densities are significantly lower in the biodiversity scenario than in the sporting scenario. This mirrors the situation found in the Scottish Highlands where deer densities are typically much higher in areas dominated by sporting estates than in areas where biodiversity conservation is a major priority (Scottish Natural Heritage, 1994; Wigan, 1993).

The results also suggest that the loss inflicted by cooperative culling in the sporting scenario, i.e. by culling somewhat less heavily than the (self-) optimum, will be small. This loss is also likely to be of similar magnitude to the gain which neighbours obtain from the cooperation. Management evolves when it becomes apparent that a neighbour’s strategy is more profitable. Thus, given the small differences in performance between ‘cooperative’ landowners and their free-riding neighbours, there is little stimulus for sporting estates’ management to adapt to the changing resource stock. In the absence of a strong stimulus to adjust culling intensity, relatively steady management of the resource emerges. The opposite situation holds in the biodiversity scenario, where the consequences of adopting a cooperative culling strategy could rapidly become very severe and the comparative cost of ‘cooperation’ would soon become evident. This provides biodiversity managers with a much stronger stimulus to change their management; faster adjustments occur as a result, leading to a rapidly fluctuating stock of the pest with periodically severe losses.

These findings suggest that the potential for actually realising the benefits of cooperation might not in itself be enhanced by learning. Considering the collected results from the model experiments, the findings suggest that successful adaptive management at the landscape scale may only be likely to emerge under fairly restricted conditions. The current modeling framework could usefully be applied to explore which conditions might best engender, or impede, the emergence of cooperation and also investigate how public intervention could best support the emergence of cooperative outcomes. Further work could usefully consider a wider range of owner characterisations in the landscape and also analyse how interactions between landowners with different interests affect the dynamics of, and the potential for, cooperation.

Acknowledgements

We are grateful to Volker Grimm, Joseph Murphy, Klaus Hubacek and two anonymous reviewers for their helpful comments and suggestions. JT gratefully acknowledges funding from the EU Marie Curie project EcolEconMod at the Helmholtz Center for Environmental Research – UFZ; and Conselleria de Economía e Industria-Xunta de Galicia (08MDS032300PR).

References

Association of Deer Management Groups, 2009. www.deer-management.co.uk (accessed April 2009).

Auyang, S.Y., 1998. Foundations of Complex System Theories in Economics, Evolutionary Biology, and Statistical Physics. Cambridge University Press, New York.

- Axelrod, R., 2006. Agent-based modeling as a bridge between disciplines. In: Tesfatsion, L., Judd, K.L. (Eds.), 2006. Handbook of Computational Economics, vol. 2, North-Holland, Amsterdam, 1565–1584 pp.
- Beaumont, D., Dugan, D., Evans, G., Taylor, S., 1994. Deer management and tree regeneration at the RSPB reserve at Abernethy Forest. In: Aldhous, J.R. (Ed.), Our Pinewood Heritage. Forestry Commission, Edinburgh UK, pp. 186–195.
- Bruckmeier, K., 2005. Interdisciplinary conflict analysis and conflict mitigation in local resource management. *Ambio* 34, 65–73.
- Clutton-Brock, T.H., Coulson, T.N., Milner-Gulland, E.J., Thomson, D., Armstrong, H.M., 2002. Sex differences in emigration and mortality affect optimal management of deer populations. *Nature* 415 (6872), 633–637.
- Clutton-Brock, T.H., Coulson, T., Milner, J.M., 2004. Red deer stocks in the Highlands of Scotland. *Nature* 429, 261–262.
- Deer Initiative, 2011. www.thedeerinitiative.co.uk (accessed 24.11.11.).
- Doebeli, M., 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., Killingback, T., 2004. The evolutionary origin of co-operators and defectors. *Science* 306, 859–862.
- Fehr, E., Gächter, S., 2000. Cooperation and punishment in public goods experiments. *American Economic Review* 90 (4), 980–994.
- Fehr, E., Gintis, H., 2007. Human motivation and social cooperation: experimental and analytical foundations. *Annual Review of Sociology* 33, 43–64.
- Forestry Commission, 2008. Delivery Plan 2008 – 2012: England’s Trees, Woods and Forests. Report by the Forestry Commission, Edinburgh UK.
- Fuller, R.J., Gill, R.M.A., 2001. Ecological impacts of increasing numbers of deer in British woodland. *Forestry* 74, 193–199.
- Gandolfo, G., 1996. *Economic Dynamics*. Springer, Berlin.
- Scottish Government, 2008. Scotland’s Wild Deer: a National Approach. Report to the Scottish Government by the Deer Commission for Scotland Forestry Commission Scotland and Scottish Natural Heritage. UK.
- Grimm, V., Railsback, S.F., 2005. *Individual Based Modelling and Ecology*. Princeton University Press, Princeton, N.J.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310, 987–991.
- Hardin, G., 1968. The tragedy of the commons. *Science* 162, 1243–1248.
- Hauert, C., Doebeli, M., 2004. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature* 428, 643–646.
- Janssen, M.A., Ostrom, E., 2006. Governing social-ecological systems. In: Tesfatsion, L., Judd, K.L. (Eds.), 2006. Handbook of Computational Economics, vol. 2, North-Holland, Amsterdam, 1465–1509 pp.
- Jones, R., Saunders, G., Balogh, S., 2006. An Economic Evaluation of a Pest Management Control Program: ‘Outfox the Fox’. Economic Research Report No. 29. New South Wales Department of Primary Industries, Orange, New South Wales, Australia.
- Killingback, T., Doebeli, M., Knowlton, N., 1999. Variable investment, the continuous prisoner’s dilemma and the origin of cooperation. *Proceedings of Royal Society B* 266, 1723–1728.
- Kirby, K.J., 2001. The impact of deer on the ground flora of British broadleaved woodland. *Forestry* 74, 219–229.
- Milner, J.M., Alexander, J.S., Griffin, A.M., 2002. A Highland Deer Herd and Its Habitat. Red Lion House, Letterewe Estate, Achnasheen, Ross-shire, UK.
- Monticino, M., Acevedo, M., Callicott, B., Cogdill, T., Lindquist, C., 2007. Coupled human and natural systems: a multi-agent-based approach. *Environmental Modelling & Software* 22 (5), 656–663.
- 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.
- Noailly, J., Van den Bergh, J.C.J.M., Withagen, C.A., 2009. Local and global interactions in an evolutionary resource game. *Computational Economics* 33, 155–173.
- Nolan, A.J., Hewison, R.L., Maxwell, T.J., 2001. Deer Management Groups: Operation and Good Practice. Report to the Deer Commission for Scotland. Inverness, U.K.
- Nolan, J., Parker, D., von Kooten, C.G., Berger, T., 2009. An overview of computational modeling in agricultural and resource economics. *Canadian Journal of Agricultural Economics* 57, 417–429.
- Nowak, M.A., 2006. Five rules for the evolution of cooperation. *Science* 314, 1560–1563.
- Nowak, M.A., Sigmund, K., 2004. Evolutionary dynamics of biological games. *Science* 303, 793–799.
- 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.
- Ostrom, E., 1990. *Governing the Commons: The Evolution of Institutions for Collective Action*. Cambridge University Press, New York.
- Palmer, S.C.F., Turscott, A.-M., 2003. Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris* L.) and its effects on sapling growth. *Forest Ecology and Management* 182, 31–47.
- Parke, C., Thornley, J., 2000. *Deer: Law and Liabilities*. Swan Hill Press, Shrewsbury, UK.
- Ramsay, P., 1997. *Revival of the Land*. Scottish Natural Heritage, Perth, UK.
- Scottish Natural Heritage, 1994. *Red Deer and the Natural Heritage*. SNH Policy Paper. Scottish Natural Heritage, Perth, UK.
- Sigmund, K., De Silva, H., Trauslen, A., Hauert, C., 2010. Social learning promotes institutions for governing the commons. *Nature* 466, 861–863.
- Smart, J.C.R., 2003. *Conflicts of Interest Surrounding the Management of Red Deer in Scotland*, PhD. Thesis, University of York Environment Department, York, UK.

- Smart, J.C.R., White, P.C.L., Termansen, M., 2008. Modelling conflicting objectives in the management of a mobile ecological resource: red deer in the Scottish Highlands. *Ecological Economics* 64 (4), 881–892.
- Souchère, V., et al., 2010. Co-constructing with stakeholders a role-playing game to initiate collective management of erosive runoff risks at the watershed scale. *Environmental Modelling & Software* 25, 1359–1370.
- Suzuki, Y., Iwasa, Y., 2009. Conflict between groups of players in coupled socio-economic and ecological dynamics. *Ecological Economics* 68 (4), 1106–1115.
- Traulsen, A., Hauert, C., De Silva, H., Nowak, M.A., Sigmund, K., 2009. Exploration dynamics in evolutionary games. *Proceedings of the National Academy of Sciences of the United States of America* 106 (3), 709–712.
- Wahl, L.M., Nowak, M.A., 1999. The continuous Prisoner's dilemma: I. Linear reactive strategies. *Journal of Theoretical Biology* 200, 307–321.
- Walpole, M., 2008. Sharing experiences in human–elephant conflict mitigation. *Oryx* 42, 325–326.
- West, S.A., Griffin, A.S., Gardner, A., 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology* 20 (2), 415–432.
- Wigan, M., 1993. *Stag at Bay: the Scottish Red Deer Crisis*. Swan Hill Press, Shrewsbury, UK.
- Zhang, B., Zhang, Y., Bi, J., 2011. An adaptive agent-based modeling approach for analyzing the influence of transaction costs on emissions trading markets. *Environmental Modelling & Software* 26 (4), 482–491.
- Zhao, L., 2009. Model of collective cooperation and reallocation of benefits related to conflicts over water pollution across regional boundaries in a Chinese river basin. *Environmental Modelling & Software* 24, 603–610.