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# Sinks, sustainability, and conservation incentives

"There is always an easy solution to every human problem – neat, plausible, and wrong."

H. L. Mencken (*The Divine Afflatus*)

## Summary

Sustainability of agro-ecosystems can be achieved if farming systems are both ecologically sound and economically viable. Therefore, it is critically important for conservation scientists to see wide-scale biodiversity policy as only one aspect of a complex socio-ecological system, in which independent land managers, subject to financial constraints, make choices subject to a range of objectives, most of which are only tangentially influenced by considerations of nature conservation. Conservation incentives are a policy instrument to reconcile conservation and land managers' objectives. Two broad approaches – payment for specific conservation actions (payment-for-activities), and payment for specific environmental outcomes (payment-for-results) – warrant particular attention. We investigate how undetected sinks might influence species persistence and richness in different policy and socio-economic contexts. To this end, we used a spatially explicit agent-based model of land use decision making, coupled with a spatially explicit metacommunity model. Our results show that, except when land managers are satisfied by low financial returns, the assumptions made by policy makers regarding habitat suitability of target species can have serious consequences on species' persistence when sinks are present but not detected. Sinks are more influential for species associated with habitat that does not tend to become rare, due to the profitability associated with land use conversion under free-market conditions. For other habitat types, habitat turnover due to market-driven land use change is more important for conservation.

## Background

Sustainable agriculture must be ecologically sound, economically viable, and socially responsible (Ikerd 2006). In many parts of the world, low-intensity farming has been ecologically sound, and important for the conservation of valuable habitats and species. A drive to increase economic returns, however, has led to the expansion and increasing intensity of modern agriculture, which has profoundly influenced landscapes and biodiversity worldwide (e.g., Mattison and Norris 2005; Secretariat of the Convention on Biological Diversity 2006). In most developed countries, intensive agriculture has become the dominant land use, landscapes in high intensity areas have been greatly simplified in structure, and most habitats have been replaced by rather uniform arable fields or improved grassland (e.g., Robinson and Sutherland 2002). Also, agriculture has become more specialized and spatially segregated (Warren *et al*. 2008). As a consequence, habitats have been lost, or their quality degraded, and functional landscape connectivity compromised, in large areas, due to fragmentation (e.g., Fischer and Lindenmayer 2007). At the landscape scale, the decline of farmland species such as birds (Gregory *et al*. 2004), bees (Kwaiser and Hendrix 2008), and plants (Hald 1999) is due to the combined effect of this marked loss of functional heterogeneity and of more intensive land management practices (e.g., Benton *et al*. 2003).

Given the extent of the areas involved, reserve-based conservation needs to be integrated with conservation of the "wider landscape." From a theoretical point of view, there are two principal reasons why a reserve-based conservation paradigm might not be sufficient to save a large number of species from extinction.

1. Firstly, a static conservation paradigm, based on saving some important areas, might – by itself – not be effective in the long run, due to the dynamic nature of landscapes.
2. Secondly, there is a risk that such areas might not be able to accommodate viable populations, because habitat area is an important functional property of landscapes, to which species richness is related (e.g., Rosenzweig 2003).

The conservation status of many species could be improved by spatially targeting conservation measures in agricultural landscapes, and by recognizing their highly dynamic state.

Conservation requirements, however, need to be reconciled with the fact that land managers' decisions are mainly financially – rather than biodiversity – oriented. This can be addressed through public policy, whose fundamental purpose is to resolve conflicts between interests of individuals and

the goals of society (Ikerd 2006). Ecological sustainability can, in principle, be achieved, but farming systems must also be made economically viable if they are to be sustainable. The public ultimately pays for the cost of conservation-friendly policies, either through availability and prices of agricultural products, or through government fiscal policy and expenditure for conservation incentives. Therefore, it is critically important for conservation scientists to see wide-scale biodiversity policy as only one aspect of a complex socio-ecological system, in which independent land managers make choices subject to a range of objectives, most of which are only tangentially influenced by considerations of nature conservation. Conservation incentives are therefore aimed at enhancing the sustainability of agro-ecosystems by paying for activities and land use practices that are thought to enhance the provision of biodiversity and other ecosystem services. However, for reasons which are often unclear, incentive schemes are not always effective, and the response varies among taxa (Kleijn and Sutherland 2003).

Particular challenges come from the fact that many populations have spatial dynamics at scales wider than the local management area (e.g., farm), so habitat value might be context-dependent (e.g., Robinson *et al*. 2001; Concepción *et al*. 2008), and connectivity time-dependent (Clergeau and Burel 1997). Also, some land uses can constitute a demographic sink (Pulliam 1988) for organisms such as birds (e.g., Hatchwell *et al*. 1996; Chamberlain and Fuller 2000; Arlt and Pärt 2007), small mammals (Tattersall *et al*. 2004), butterflies (Boughton 1999; Ockinger and Smith 2007), and bees (Ockinger and Smith 2007).

### The effect of sinks

The source–sink concept has been incorporated into conservation literature and management for two decades (e.g., Meffe and Carroll 1997) and has been used to explain the presence of species in low-quality habitat (Duguay *et al*. 2001; Tittler *et al*. 2001). Spatial linkages between local communities are thought to have strong effects on species sorting and coexistence (see also Benkman and Siepielski, Chapter 4, this volume). This is made more complex by the directionality of fluxes, as in source–sink cases.

Theory regarding sink effects in simple systems is freely available (e.g., Dunning *et al*. 1992; Doebli and Ruxton 1998; Amarasekare and Nisbet 2001; Gundersen *et al*. 2001; Namba and Hashimoto 2004), and the role of environmental variation and its temporal pattern has been recognized (Gonzalez and Holt 2002; Gonzalez and De Feo 2007). However, there has been no theoretical attempt (as far as we are aware) to explore the dynamic effect of sinks in systems where demographic processes are interacting in rather complex

ways with socio-economic processes which drive the temporal availability of habitat. Therefore for human-influenced systems (an increasing proportion of the Earth's surface), the theoretical long-term consequences of the existence of sinks have not yet been explored adequately because most models ignore the socio-economic factors that provide the context in which population dynamic processes are embedded, and drive habitat dynamics, which is usually ignored. This makes it more difficult to generate hypotheses explaining why policy measures, such as incentive schemes, are effective or otherwise.

A theoretical question that has received virtually no attention is what happens if conservation incentives – due to imperfect knowledge – promote the creation of habitats or the adoption of land uses that are actually sinks for the (set of) species of interest and whether this can be avoided by rewarding outcomes (species) rather than activities.

Studying this problem is interesting for the application of source–sink theory to conservation in managed landscapes, because it can help focus both theoretical and empirical efforts on situations in which sink effects are likely to be relatively important compared with other factors. We have developed tools to begin such an exploration.

### Research methods

#### A coupled human–natural system model

In agro-ecosystems, the landscape structure, which influences species diversity, emerges from the interaction of biophysical constraints and individual decisions influenced by factors such as crop prices, management input costs, and economic aspirations. Agent-based modeling seems a natural tool with which to model the human portion of such systems, as analytical models would be much more difficult to formulate and solve. Arthur *et al.* (1997) have listed several properties of complex adaptive systems, of which we see this as an example, that pose a challenge for traditional mathematical modeling techniques.

It has further been argued that agent-based modeling is particularly well suited to studying coupled human–natural systems (Hare and Deadman 2004). Boulanger and Bréchet (2005), highlighting the promise of agent-based modeling in the study of sustainable development, note that it allows an intuitive representation of the environment and the embedding of agents within it. Bousquet and Le Page (2004) conclude that researchers in ecology and the social sciences can use agent-based modeling to study the interactions between spatial, network and hierarchical levels of organization, a view supported by Huigen (2004).

FEARLUS (Polhill *et al*. 2001) is an agent-based modeling system designed to build models for studying land use change. This is a modeling tool flexible enough to capture differences between individual land managers but still able to produce relatively simple general models. It has been used to study various aspects of boundedly rational land use decision-making algorithms and their interaction with differing degrees of spatiotemporal heterogeneity in factors influencing economic returns, including imitation (Polhill *et al*. 2001) and aspiration (Gotts *et al*. 2003). We have coupled this model with a metacommunity model which is an extension of the stochastic patch occupancy model (SPOM) framework (Moilanen 1999, 2004). See Box 8.1 for details.

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**Box 8.1**

The sequence of events in FEARLUS is depicted on the left-hand side in Figure 8.B1.1, each cycle of which is intended to represent a year. (In what follows, we adopt the convention of giving entities in the model upper-case initial letters.) Starting from the top, Land Managers use their Land Use Selection algorithm to decide the Land Use of each Land Parcel they own. The Economy and Climate for the Year are then obtained (these are effectively exogenous time series) and, together with the Biophysical Characteristics of the Land Parcels (also exogenous, but varying spatially rather than temporally), are used to compute the Yield and Economic Return to the Land Manager (the latter in the "Harvest" step). A Government Agent (an optional component of the model) may then make some observations and issue grants or fine Land Managers according to Government Policy. After the Harvest, an optional Approval phase takes place, in which Managers may use rules to Approve or Disapprove of their neighbors for various reasons. Managers then learn from their experience of different Land Uses. At the end of the Year, those Managers with negative accumulated wealth in their Account are regarded as being bankrupt, and must sell all their Land Parcels to solvent neighbors or to in-migrant Managers. Parcels are sold in an auction, and Managers have rules determining how much to bid and which Parcels to bid for (Polhill *et al*. 2008).

The overall effect is to create an evolutionary environment in which Managers using more successful decision-making algorithms tend to accumulate more Land Parcels, and those using less successful algorithms tend to go bankrupt. These dynamics need not necessarily apply, however. If the amount of money required to prevent loss (a parameter of the model) is too low, Managers with even relatively poor decision-making algorithms will stay in business. Likewise, if this parameter is too high, it is not possible to
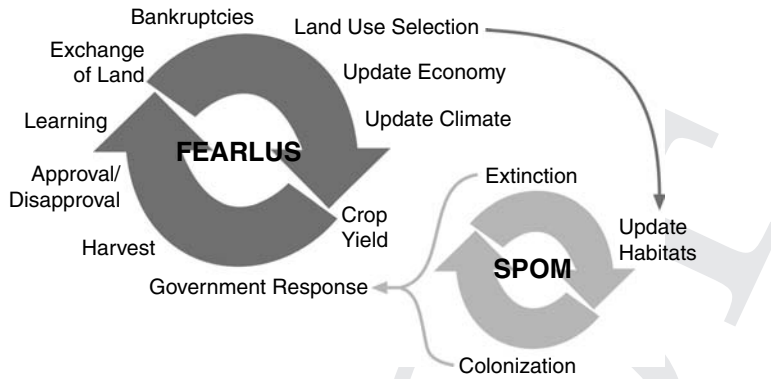
**Box 8.1.3** (*Cont.*)



FIGURE 8.B1.1.
The sequences of events in the agent-based model of land use change (FEARLUS) and the species metacommunity model (SPOM), and how each influences the other.

make enough money to stay in business, no matter how good the algorithm. Rapidly changing Climate or Economy can also make it difficult to stay in business, particularly if conditions in one Year offer no predictive basis for conditions in the following Year.

The right-hand side of Figure 8.B1.1 depicts the sequence of events in the SPOM. The SPOM is a metacommunity ecological model, which simulates populations on a lattice (in this case toroidal) in which each cell can be thought of as a landscape Patch. The SPOM models the presence or absence of Species on Patches of land, rather than recognizing individuals (as in classic individual-based ecological modeling). This is similar to Moilanen's (2004) SPOMSIM, in that it uses the same equations to model extinction and colonization, but has a number of extensions, the most significant of which are to allow for multiple Species and interactions between them, to allow for Habitat preferences, and modeling the effect of sink Habitat. There is a many-to-many relationship between Species and Habitats in the model; a Species may be configured to survive on several Habitats if it is adaptable, and a Habitat may be suitable for several Species. Each Year, the Species occupying a Patch compute a Local Extinction Probability, which is the chance of the Species ceasing to occupy the Patch. Patches providing Habitat for – but not occupied by – a Species, also represent a Colonization Probability, which determines the chance that the Patch will become occupied by the Species in that Year. The SPOM also provides the (optional) possibility that the availability of Habitats on each Patch may change once per

Year, before Extinctions and Colonizations are computed again in the next cycle.

Whilst the Local Extinction Probability depends on parameters of the Species (and, optionally, also on the presence of competitor Species) and the amount of Habitat on the Patch, the Colonization Probability depends also on the occupancy of the Species in other Patches in the Environment. As a consequence, the long-term survivability of a Species depends on the pattern of Habitats at the landscape scale.

The fact that FEARLUS and the SPOM operate at the same spatial and temporal scale, and at similar levels of abstraction, allows them to be integrated more easily. Land Uses chosen by Land Managers in FEARLUS translate into Habitats in the SPOM.

A feedback to Land Managers is provided through the Government Agent, which pays for conservation incentives.

Scheduling is indicated by the two sets of arrows in Figure 8.B1.1. The Update Habitats step in the SPOM takes place after the Land Use Selection step in FEARLUS, and the Extinction and Colonization steps in the SPOM following the Habitat change take place before the Government Response step in FEARLUS.

Together, FEARLUS and the SPOM present a socio-ecological system in which Species distributions adjust to changes in Land Use arising from Land Managers' decisions and any demographic changes in Land Manager populations. Land Managers' decisions, insofar as they depend on Government grants or fines, are affected in turn by Species distributions. This creates a modeling system in which some explorations of biodiversity Policy can be made.

In the description below we use capital initial letters to indicate entities that are part of our model (e.g., Land Managers).

### Land Managers' decisions, incentive strategies and sinks

This coupled modeling tool permitted us to build stylized models to investigate the space-time dynamics of a socio-economic system. In this particular application, the objectives were to investigate the interaction between undetected sink Habitats and incentive-based Policies.

We set up simulations of a relatively simple system, where some Species of conservation interest share Habitat with other "less interesting" Species and in which conservation incentives reward either the choice of Land Uses providing the appropriate Habitat, or the occurrence of target Species on a Parcel of land.

Species, Habitats and landscape

Land Use here incorporates notions both of crop and management *practices* (as these partly determine the level of intensity) which have an effect on Habitat suitability for Species of interest. In this model system, we made available two main land cover types "G" and "A," at three levels of intensity (from "1" – low, to "3" – high) giving Land Uses labeled GL1, GL2, GL3, AL1, AL2, and AL3. Six corresponding Habitats were specified in the SPOM model: GH1, GH2, GH3, AH1, AH2, and AH3. The more intense the Land Use, the fewer Species were able to use the corresponding Habitat.

One possible interpretation of this model configuration (although by no means the only one) is a landscape where arable and grassland patches coexist due to the land use system, with the grassland patches hosting a wider pool of species. Practices of increasing intensity are different in the two types of patches but both have the effect of excluding some of the species.

Ten Species were specified, G1–6, A1–3, and a competitor Species C1, which was able to outcompete and exclude some of the Species (G1–3) if present on the same Patch. This was intended to simulate a situation in which a complete lack of management would result in lower alpha diversity (patch species richness) with respect to a moderately intense regime. This is the case for many grassland systems, where grazing can promote diversity (e.g., Wallis de Vries *et al.* 1998). The Species parameters were such that they represent functional groups tolerating an increasing amount of land use intensity.

All Species were characterized by a Dispersal Distance, a Probability of Extinction, given Habitat occupied, and a Probability of Colonization which depended on the configuration of occupied Patches in the landscape (see Box 8.2). Table 8.1 shows which Species could live on which Habitats. To create a potential refuge from competition, Land Uses GL1, GL3, AL1, AL2 and AL3 provided Habitats GH1, GH3, AH1, AH2 and AH3, respectively, while Land Use GL2 provided two Habitat types: GH1 (20% of the Patch area) and GH2 (80% of the Patch area). Only GH1 was available to the superior competitor C1. The relatively more vulnerable Species were G5, G6 and A2, A3, having more specialized Habitat requirements and shorter average dispersal distances.

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**Box 8.2**

Dispersal, Colonization, and Local Extinction are modeled as in Moilanen (2004). Local Extinction can also be caused by competition (see below). All Patches have unit area.

For each Species *s* and Patch *i* the following equations were used:

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*Connectivity*

$$S_{is}(t) = A_{is}^{c} \sum_{j \neq i} O_{js}(t) D\left(d_{ij}, \alpha_s, \ldots\right) A_{js}^{b}$$

where $j$ denotes Patches that are not the focal Patch $I$, $c$ and $b$ are parameters, $A_{is}$ is the available area (i.e., the amount of Habitat area made available by the present Land Use for Species $s$), $O_{js}(t)$ is an indicator variable assuming the value 1 if the Patch is occupied by the Species, 0 otherwise. $D_s(d_{ij}, \alpha_s) = \exp(-\alpha_s d_{ij})$, and $d_{ij}$ is the distance between two Patches.

*Colonization*

At each time step $t$

$$C_{is}(t) = \frac{[S_{is}(t)]^2}{[S_{is}(t)]^2 + y^2}$$

where $S_{is}(t)$ is the connectivity of Patch $i$ at time $t$, for Species $s$ and $y$ is a parameter.

*Local Extinction*

$$E_{is} = \frac{\mu_s}{A_{is}^{x}}$$

where $\mu$ is the Extinction Probability of a Patch of unit size, $A$ is the available area of the Patch, and $x$ is a scaling parameter (always set to 1 in our simulations).

In addition (in this exercise) when a competitor is present this can cause Local Extinction of inferior competitors within $n$ time steps (here $n = 3$).

The parameter values used in the simulation are shown in Table 8.B2.1.

TABLE 8.B2.1. Parameter values used in the simulation.

| Species | $c$ | $B$ | $\alpha$ | $\mu$ | $\beta$ |
|---------|-----|-----|----------|-------|---------|
| G1 | 1.0 | 1.0 | 0.8 | 0.1 | 1.0 |
| G2 | 1.0 | 1.0 | 0.9 | 0.1 | 1.0 |
| G3 | 1.0 | 1.0 | 1.1 | 0.1 | 1.0 |
| G4 | 1.0 | 1.0 | 1.3 | 0.1 | 1.0 |
| G5 | 1.0 | 1.0 | 1.3 | 0.1 | 1.0 |
| G6 | 1.0 | 1.0 | 1.3 | 0.1 | 1.0 |
| A1 | 1.0 | 1.0 | 1.3 | 0.1 | 1.0 |
| A2 | 1.0 | 1.0 | 0.9 | 0.1 | 1.0 |
| A3 | 1.0 | 1.0 | 0.8 | 0.1 | 1.0 |
| C1 | 1.0 | 1.0 | 1.3 | 0.05 | 1.0 |

TABLE 8.1. *Species–Habitat matrix used in the demonstration experiments. Habitats are the columns and Species are the columns. A letter "Y" in a cell indicates that the Species can occupy a Patch having the Habitat in the row, and disperse from it. An "S" in a cell indicates that the Habitat in the row can be configured to be a sink Habitat; open to occupation by the column Species, but the Species cannot disperse from it. In runs where sink Habitats were not specified, "S" behaves as "Y."*

| Habitat | Species | | | | | | | | | |
|---------|---------|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|         | G1 | G2 | G3 | G4 | G5 | G6 | A1 | A2 | A3 | C1 |
| GH1 | Y | Y | Y | Y | Y | Y | – | – | – | Y |
| GH2 | Y | Y | Y | Y | Y | – | – | S | S | – |
| GH3 | Y | Y | Y | – | – | – | – | – | – | – |
| AH1 | – | – | – | – | S | S | Y | Y | Y | – |
| AH2 | – | – | – | – | – | – | Y | Y | – | – |
| AH3 | – | – | – | – | – | – | Y | – | – | – |

All Species were assumed to have relatively short dispersal distances due to the nature of the study, which was aimed at investigating the vulnerability of Species to fragmentation. An average Dispersal Distance (i.e., $1/\alpha$, see Table 8.B2.1) between 0.8 and 1.3 cells was therefore assumed.

For Species with higher dispersal distance, 99% of dispersal events were set within five cells, while they were within three cells for Species with the shorter dispersal distance. This choice of dispersal parameters is therefore oriented to represent species such as herbaceous plants (excluding weeds), small mammals and less mobile invertebrates, especially non-flying taxa.

Local (intrinsic) Extinction rate was set to 10% per Year. This is within the range of values reported by reviews from, e.g., Fahrig and Merriam (1994) and Schoener (1983). The first study, regarding plants and animals, reported rates between 5% and 30%; the second reported rates of 1–10% for vertebrates and plants, and 10–100% for invertebrates. Given that all Patches had the same (unit) area, we set parameters scaling immigration and emigration with area equal to 1 ($c$ and $b$ in Table 8.B2.1). Landscape structure was determined at each time step by the collective decisions of Land Managers, given their objectives.

All runs were initialized with a random distribution of 50% AL1 and 50% GL1, and maximum Species occupancy (this was to maximize the probability of Species surviving while the initial Land Managers were still learning), and then run for 300 time steps.

### Sinks

Additional Habitat was provided for the vulnerable Species, simulating a situation in which the populations of some A*x* Species are able to survive on

Habitat types provided by GL*y* Land Uses, and vice versa. In half of the simulation runs, however, these Habitat types were sinks for those Species. This is indicated as S in Table 8.1.

Because our population model has no internal Patch dynamics, but only tracks occupancy, sinks are simulated as Patches that do not contribute to colonization of other Patches in the next time step. They are therefore "black-hole" sinks, simulating a situation in which individuals do not contribute to the next generation. Neither the Government Agent issuing a financial reward, nor the Land Managers were aware of the existence of sinks.

### Land Managers

For these experiments, Land Managers were implemented with a satisficing approach (Simon 1955) to decision making (rather than aiming at making the maximum possible profit). Satisficing is a commonly used heuristic approach to representing human decision making. Departure from profit maximizing is known to occur. Parker *et al.* (2007) cite evidence of various factors that lead to farmers not making fiscally optimal decisions, such as meeting subsistence requirements and cultural norms. To this may be added questions of identity as a farmer, from qualitative social research (Burton and Wilson 2006), in which "keeping the name on the farm" and being recognized by one's peers as a "good farmer" (Burton 2004) are also motivating influences on decision making orthogonal to purely pecuniary concerns.

Land Managers reviewed their choice of Land Uses on all their Parcels if the mean Profit per unit area did not meet their financial Aspirations for a specified number of consecutive Years (this number was taken from a uniform distribution in the range 0–9). When deciding whether to change Land Use, Managers consulted their experience, i.e., employed case-based reasoning (Aamodt and Plaza 1994) to choose a Land Use based on their expectations of the Climate and Economy in the coming Year, and their experience of the Land Use in the past, which includes its Economic Return. Managers with no experience of a Land Use were given the opportunity to ask neighbors for their experience of it, and use that as a basis for decision making. If neighbors had no experience of a Land Use either, then Managers assumed that that Land Use would meet their Aspirations; when other Land Uses had poorer expected outcomes, this allowed the Land Managers to experiment. Expected outcomes (Profit) were obtained for each Land Use, and a selection made at random from those Land Uses with equal maximum expected Profit. Land Managers are therefore satisficing regarding the decision to change Land Use, but maximizing once they have decided to change. Since Profit includes any subsidies from the Government, Policy has an influence on Land Use Selection by Managers.

TABLE 8.2. *Gross Economic Return per unit area to Land Managers for each Land Use under an unchanging Economy (denoted by U).*

| Land Use | Yield | Price U | Return U |
|----------|-------|---------|----------|
| GL1 | 4 | 5.5 | 22 |
| GL2 | 5 | 5.5 | 27.5 |
| GL3 | 6 | 5.5 | 33 |
| AL1 | 4.5 | 5.0 | 22.5 |
| AL2 | 5.5 | 5.0 | 27.5 |
| AL3 | 6.5 | 5.0 | 32.5 |
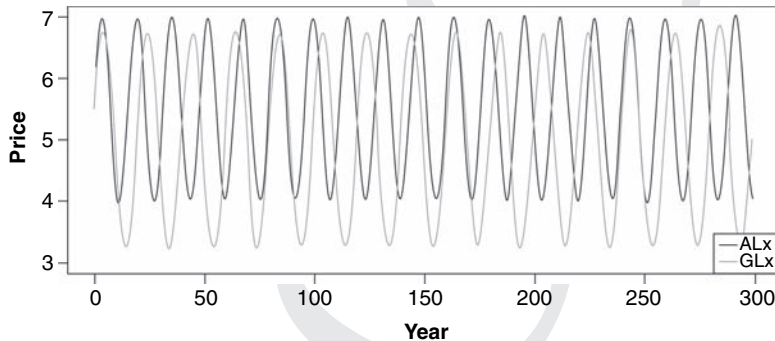


FIGURE 8.1.
Time series of price fluctuations per unit Yield in the Economy for the "G" (light curve) and "A" (dark curve) Land Uses with a variable Market.

The Economic Returns for Land Uses depend on their Yield per unit area (which increases with intensity), and Price per unit Yield. We simulated two contrasting Price time series for the Economy: one unchanging, the other variable. The settings for the unchanging Economy are shown in Table 8.2. For the variable Market, we used an approximately sinusoidal time series with a period of 16 Years, an amplitude of 1.5 and a mean of 5.5 for the "G" Land Uses, and a period of 20 Years, an amplitude of 1.75 and a mean of 5.0 for the "A" Land Uses. Figure 8.1 shows the time series of price fluctuations per unit Yield in the Economy, with a variable Market, and Table 8.3 shows the minimum and maximum Gross Economic Returns. The Climate and Biophysical Characteristics were kept constant.

Box 8.3 briefly characterizes FEARLUS and shows a summary of the parameterization used to characterize Land Managers' behavior, and their consequences for the landscape-scale abundance of Habitats, as well as its justification.

TABLE 8.3. *Gross Economic Returns per unit area to Land Managers for each Land Use under a variable Economy (denoted by V).*

| Land Use | Yield | Price V (min) | Return V (min) | Price V (max) | Return V (max) |
|---|---|---|---|---|---|
| GL1 | 4 | 3.0 | 12.0 | 7.0 | 28.0 |
| GL2 | 5 | 3.0 | 15.0 | 7.0 | 35.0 |
| GL3 | 6 | 3.0 | 18.0 | 7.0 | 42.0 |
| AL1 | 4.5 | 3.25 | 14.625 | 6.75 | 30.375 |
| AL2 | 5.5 | 3.25 | 17.875 | 6.75 | 37.125 |
| AL3 | 6.5 | 3.25 | 21.125 | 6.75 | 43.875 |

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**Box** 8.3

FEARLUS has been classed as a "typification" by Boero and Squazzoni (2005), i.e., a model focused on a particular class of phenomena, in contrast to "case-based models" fitted to a specific scenario. In such a modeling paradigm, one is concerned more with stylized scenarios of "life as it could be" than with particularities of "life as it is." Thus the absolute values of the parameters are less important than the dynamics caused by the relationships between them. Before running the experiments, exploratory runs were made to find sets of parameters covering the continuum of dynamics in the simulated social and ecological systems: from situations in which there is no economic pressure on Land Managers – and so no Land Use change, to those in which the pressure is so great that it is impossible for Managers to stay in business; from cases where all Species survive, to cases where all rapidly become extinct. From these explorations, we derive parameters for the reported experiments trading off covering the full range of dynamics with demands on computational power by eliminating those generating particularly unrealistic outcomes (e.g., where the bankruptcy rate is too high).

The Profit returned to Land Managers in each time step is given by the Gross Economic Return per unit Yield, less a Break-Even Threshold (representing input costs), on each Land Parcel they own:

$$R_{m,t} = \Sigma_{p \in Pm} \left[ g\left(E_t, U_{p,t}\right) y\left(U_{p,t}\right) - b \right.$$

where $R_{m,t}$ is the profit of Manager $m$ at time step $t$, $P_m$ is the set of Parcels owned by Manager $m$ (iterated over by $p$), $E_t$ is the state of the Economy at time step $t$ (determined from the exogenous time series as input to the model: "flat" or "var2"), $U_{p,t}$ is the Land Use applied by Manager $m$ to Parcel $p$ in time step $t$, $g()$ is a lookup table returning the gross income per unit Yield

**Box 8.3.3** (*Cont.*)

for the Economy state and Land Use (see Tables 8.2 and 8.3), *y*() is a lookup table returning the Yield per Parcel of the Land Use (see Tables 8.2 and 8.3), and *b* is the Break-Even Threshold.

The Aspiration Threshold (ASP) was set to 0.5, 1, and 5 units. The Break-Even Threshold (BET) per unit area was set at 25 and 30. This number is subtracted from a Land Manager's Gross Economic Return. Thus, from Table 8.2, when there is an unchanging Economy ("flat"), GL1 and AL1 are never profitable for either BET used (i.e., they are less than 25), and for the higher BET, only the most intensive Land Uses, GL3 and AL3 are profitable (i.e., more than 30). By contrast, when the variable Economy ("var2") is used, from Table 8.3 we see that all of the Land Uses are sometimes unprofitable. Thus, the less intensive Land Uses, in particular, require Government incentives if Land Managers are to deploy them. The parameters used in the simulations are listed and described in Table 8.B3.1.

TABLE 8.B3.1. *Parameters explored in the simulation experiments.*

| Parameter | Description | Values |
|---|---|---|
| Government | Specifies the set of rules used to reward Land Managers for biodiversity. | *RewardSpecies*: Give a reward to each Land Manager for the presence of any awardable Species on each Land Parcel; *RewardActivity*: Give a reward to each Land Manager for using any awardable Land Use on each Land Parcel. |
| Sink | Specifies whether or not certain Habitats are sinks for some Species (i.e., the Species can be present on Patches with this Habitat, but cannot disperse from them). | Yes; No |
| Market | Exogenous time series providing the level of Economic Return to Land Managers per unit Yield of each Land Use. | *Flat*: The Economic Returns for each Land Use do not change, and are 5.5 for the "G" Land Uses and 5.0 for the "A" Land Uses; *Variable*: The Economic Returns for each Land Use have a sinusoidal time series with a period of 16 Years, |

| Parameter | Description | Values |
|-----------|-------------|--------|
|  |  | amplitude of 1.5 and mean of 5.5 for the "G" Land Uses, and a period of 20 Years, amplitude of 1.75 and mean of 5.0 for the "A" Land Uses. |
| Break-Even Threshold | The amount of Economic Return per unit area that a Land Manager needs to make to avoid making a loss. | 25; 30 |
| Aspiration Threshold | The amount of Profit per unit area that the Land Manager hopes to make. If this is not achieved, the Land Manager will review the Land Uses allocated to all Parcels they own. | 0.5; 1.0; 5.0 |
| Reward | The amount the Government gives to Land Managers per awardable Species or Land Use | 0.0; 5.0; 10.0 |
| Ratio | An amount by which to divide the Reward when the Government awards by Species. | 1; 2; 3 |
| Stop C1 | Designs the incentives to stop C1 from causing extinction of non-target species. In activity-based policies, this amounts to not rewarding for Land Use GL1; in outcome-based policies, this amounts to rewarding for Species G3. Since this had no effect on the reported results, it is not discussed in the main text. | Yes; No |

Conservation incentives

When an activity-based Policy was simulated, Managers received a payment for each Parcel in which they deployed GL1, GL2, or AL1. When a results-based Policy was in place, Managers received a payment for *each* occurrence of
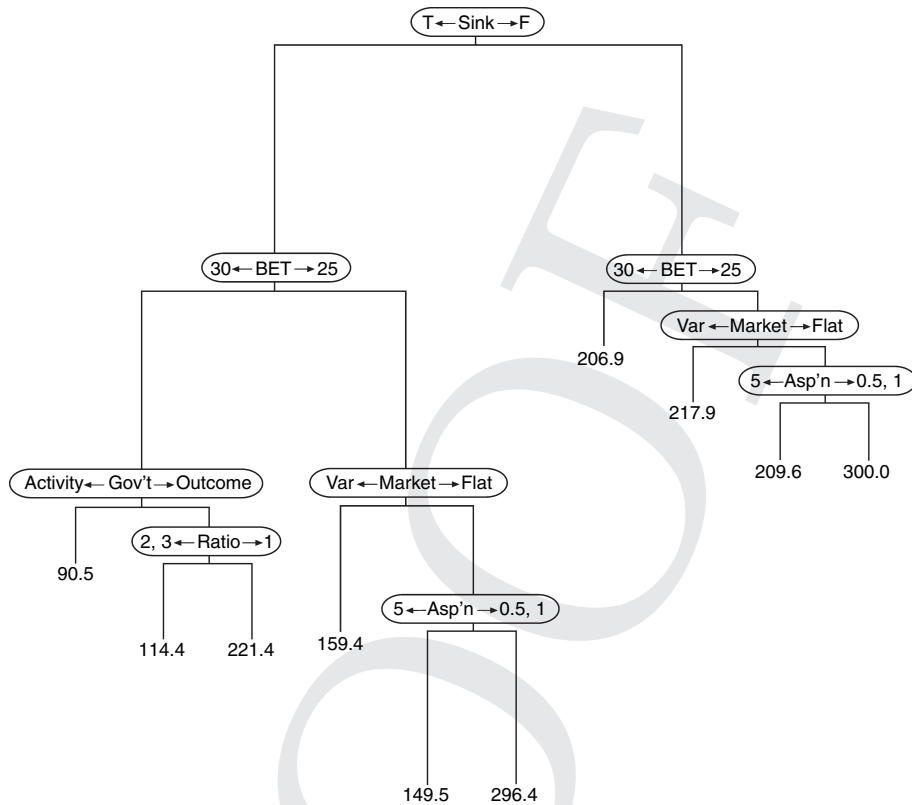
FIGURE 8.2.
A regression tree relating model parameters to extinction time of Species A3 in all the 11,800 runs. The "leaves" of the tree show the (fitted) average extinction time.

Species G5, G6, A2, or A3 on a Parcel they owned. Three Rewards levels were implemented: 0 (as a control), and 5 and 10 income units.

Analysis of results

The results are summarized in the regression trees (Breiman *et al*. 1984) in Figures 8.2, 8.3 and 8.4, which are based on 20 replicate runs (using different seeds for the pseudo-random number generator) for each combination of parameters, resulting in 16,800 runs. We analyzed persistence time and total species richness at the landscape level as a function of parameter values. Only variables useful for explaining the data appear in a tree. The "leaves" of each tree are the fitted values, while the "knots" show which variable best explained a particular split in the dataset. In the simulations, 70% of the runs were used to build statistical models, and 30% of the runs were used as a validation set. We ensured that the fitted values (e.g., persistence time) predicted by a tree, using
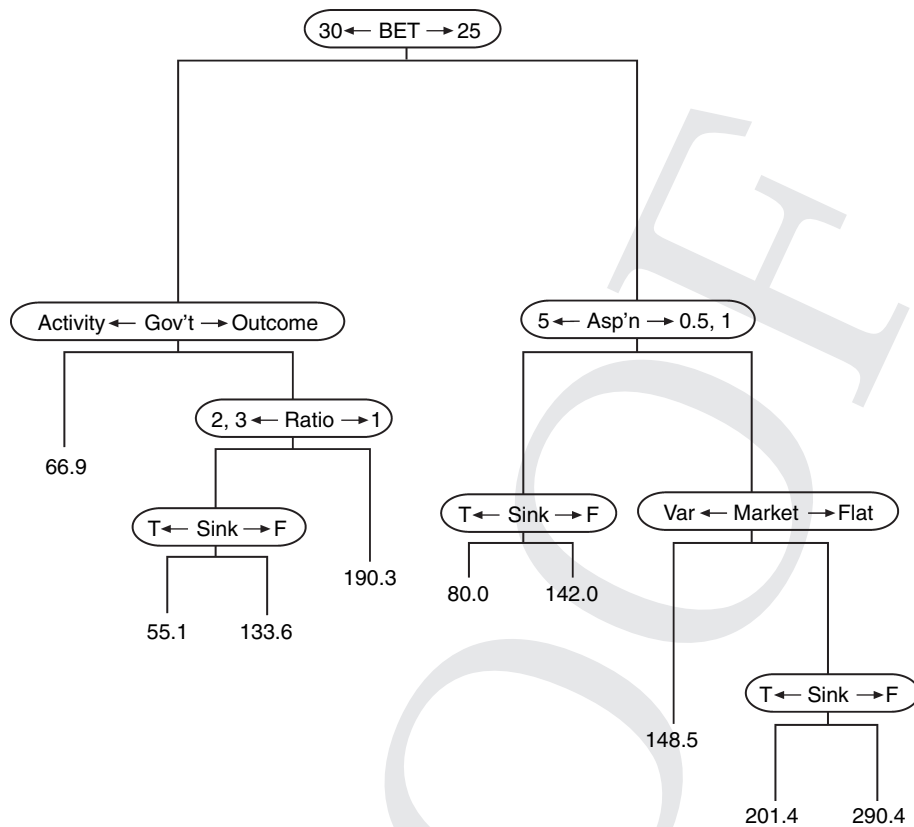
FIGURE 8.3.
A regression tree relating model parameters to extinction time of Species G6 in all the 11,800 runs. The "leaves" of the tree show the (fitted) average extinction time.

70% of the cases, correctly predicted the values in the validation set ($R^2 > 0.8$). All the regression trees presented are also tenfold cross-validated. This means that the observations were split into ten groups and, recursively, one group was left out while the other nine groups were used to grow trees of various sizes. The final tree is the one which gives the minimum cross-validation error.

## Results and discussion

We concentrate mainly on the effect of sinks, and will report more fully on the effects of policy strategies in future work. We concentrate on species with narrower habitat preference and affected by sinks, which better serve to illustrate how various factors vary in importance according to species traits.

The regression trees show, in order of strength of influence (measured by decrease in variance) starting at the top, the parameters that affect average persistence time of the most vulnerable Species types in AL*x* (Fig. 8.2: Species
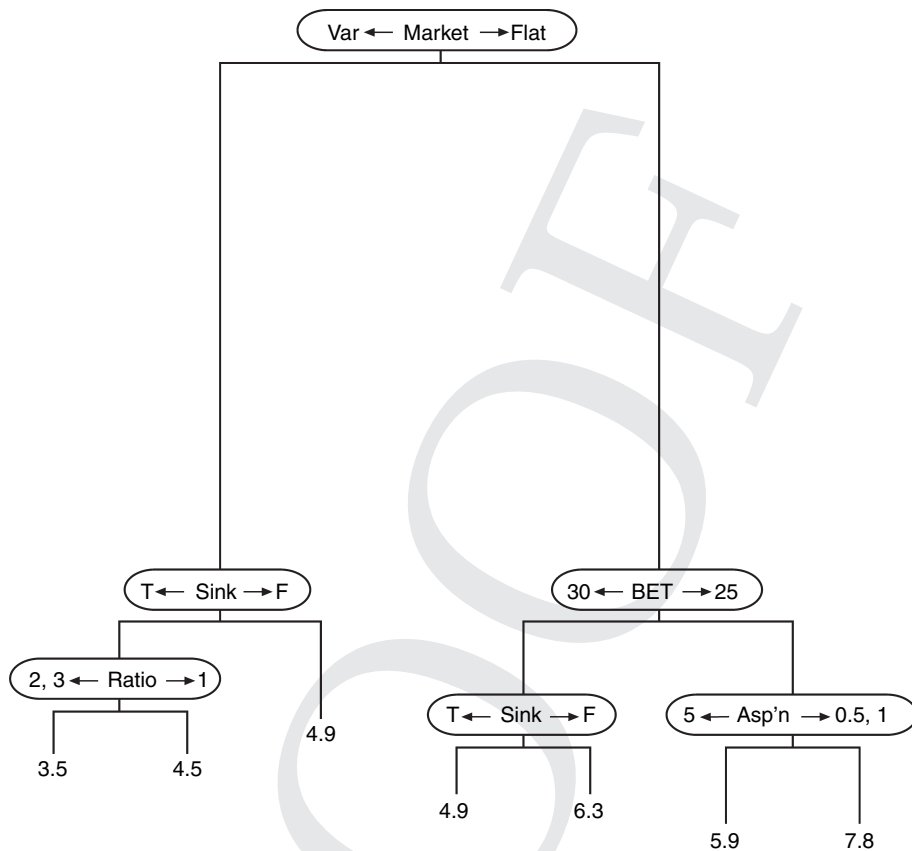
FIGURE 8.4.
A regression tree relating model parameters to species richness in all the 11,800 runs. The "leaves" of the tree show the (fitted) average landscape-scale species richness.

A3) and GL*x* (Fig. 8.3: Species G6) Land Uses, and landscape species richness (Fig. 8.4). Although the importance of source–sink dynamics for biodiversity conservation has been widely recognized, the results confirmed our hypothesis that its practical significance must be understood in the context of Land Use decisions.

In general, rewarded sinks compete with sources for Land Use allocation. Sinks are the most important factor affecting persistence time for a Species, such as A3 (Fig. 8.2), living in Habitats which do not tend to become very rare because they are associated with Land Uses of moderate profitability (including any Government incentive). In this case, GL2, which is more profitable than AL1 (the Land Use providing A3's primary Habitat), is also rewarded when activity rather than outcome qualifies, hence Land Managers are more likely to

adopt GL2 than AL1. Sinks (left-hand sub-tree of Fig. 8.2) have an effect because they "outcompete" sources in the marketplace, lowering the effective number of Patches and therefore persistence time. In this situation, BET = 30 (left-hand sub-tree of the left-hand sub-tree of Fig. 8.2). Here, rewarding for outcome allows A3 to persist, on average, for longer than when rewarding per activity. However, since multiple Species can survive on some Parcels, this effect could be due entirely to larger total subsidies. To test this, we introduced the "ratio" parameter (see Table 8.B3.1), which is aimed making absolute rewards for outcome and activity comparable when set to 1, and observed that for higher values of ratio explored, with consequent lower per-Species Rewards, the effect is reduced (see Fig. 8.2; average persistence for 114.4 with ratios 2 and 3 versus 221.4 steps with ratio 1).

For Species such as G6 (Fig. 8.3), living in Habitats associated with Land Uses having higher opportunity costs (AL1 and GL1), the effect of sinks is dwarfed by other factors. In these cases, persistence time is not influenced *principally* by sinks, although these play a role, but the combination of input costs (BET, root node of the tree in Fig. 8.3) and Land Managers' Aspirations (right-hand sub-tree of Fig. 8.3) led to different levels of Land Use intensity, and therefore to different relative abundances of source Habitat (GH1, principally from GL1, but to a small extent from GL2). In other words, Species living on Habitats associated with less profitable Land Uses, when these can easily be converted into more profitable ones, are vulnerable, independently of the presence of sinks. Their persistence is influenced more by Land Manager's Aspirations and Market fluctuations. If Land Managers have high Aspirations relative to the Returns from such Land Uses (left sub-tree of the right sub-tree of Fig. 8.3), the Habitat becomes rare, sometimes disappearing altogether, and the Species is likely to become extinct. With high input costs (left-hand sub-tree of Fig. 8.3), the outcome-based strategy works better. Though, again, this is partly because the outcome Policy leads to higher overall expenditure and reward, the fact that sinks have a significant effect only when there is a lower per-Species Reward ("ratio" 2 or 3) suggests that large incentives, or regulation, can preserve these Habitats for longer. Even though the activity-based Policy rewards for GL1, the main provider of the source Habitat for G6, it also rewards for the more profitable GL2, and Managers have no incentive to adopt GL1. Here too, there are good reasons to believe that there are contexts in which outcome-based incentive schemes would be more successful.

Habitat availability over time is therefore the main driver of persistence in the modeled system. Sinks are more influential for Species living in Habitats associated with sufficiently profitable or incentivized Land Uses (which do not tend to become very rare). In this case Land Managers allocate to sinks when the

combination of incentives and profitability make them attractive. For these Species, Policy incentives improve persistence only when there are high input costs to be repaid, meaning that non-awardable Land Uses become less attractive. In such cases, landscape-level persistence time is enhanced only when enough subsidies are provided, while "black-hole" sinks, as expected, shorten this time.

As far as species richness is concerned (Fig. 8.4):

1. market variability, by inducing land use (and hence habitat) turnover on the land parcels, has the highest effect on richness;
2. when the market is variable, the effect of incentives is subordinate to that of sinks (left sub-tree of left sub-tree, Fig. 8.4);
3. when the market is invariant the effect of sinks is subordinate to that of input costs (left sub-tree of right sub-tree, Fig. 8.4), which, together with profit orientation, drive intensification of land use.

Finally, it is worth noting that extinction of some non-target species, and thus decline in diversity, could not be avoided because the target species are not acting as "umbrella" species. This means that if landscape-scale species richness is the policy goal, incentive schemes will have to be designed carefully.

To summarize, sinks are an important issue, and worth considering for the conservation of species associated with habitats that remain moderately abundant. In other cases the disappearance of sources due to opportunity cost and land managers' profit orientation is the main cause of concern.

The consequences of modeling species abundance rather than occupancy have not been explored in this framework. Models show that sinks can stabilize population dynamics, thus avoiding density-dependent crashes in patches where there is a high growth rate (e.g., Kawecki 2004) by acting as a sort of buffer (see also Morris, Chapter 3, this volume). In the context of agro-ecosystems, this situation is likely to be relevant for populations that thrive and rapidly grow in local patches, e.g., of pests, but less so for most species of conservation concern. Also, this study was concerned with regional rather than local effects. Our results show conditions in which sinks matter, and it is here that the results might provide a lower limit to persistence times.

It is worth noting that in models tracking abundance, when dispersal involves individuals that do not contribute to the next generation in source communities, local coexistence is not influenced by dispersal (Amarasekare and Nisbet 2001). This is implicitly assumed by our model. Also, our model did not examine the effects of density dependence on dispersal rates (Amarasekare 2004a, 2004b).

Finally, as in population viability analysis, persistence time and richness should be considered as currencies used to compare scenarios rather than as stand-alone quantities.

### Conclusions

Source–sink theory (Shmida and Ellner 1984; Pulliam 1988) is supported by empirical evidence (e.g., Thomas *et al*. 1996; Boughton 1999; Cousins and Lindborg 2008), and is considered to be one of the theories at the foundation of landscape ecology (Wiens *et al*. 1993). This work contributes to understanding the details of its relevance to managed landscapes.

We have explored the effect of sinks in situations that have received virtually no attention so far, namely in a system in which economic factors, policy factors, and land managers' aspirations are allowed to interact and to influence landscape structure, and therefore population persistence.

Our results show that the assumptions made by policy makers regarding habitat suitability can have serious consequences on species' persistence. If many of the lower land use intensity patches (e.g., fields with field margins) are undetected sinks, these might lead to the "wrong" policy. The problem facing policy makers, however, is not simple. Because persistence depends on landscape-scale attributes of a whole population, and is realized (or not) over a relatively long time period, it cannot be measured or predicted easily. Often, the presumed habitat quality (*sensu* Van Horne 1983) of individual patches composing the landscape mosaic is what is used to decide whether a habitat type or land use practice should be incentivized. This might result in perverse incentives, causing land managers to adopt land uses that are supposedly conservation-friendly but which might compete with the source habitat of target species for financial support.

Our results are consistent with studies suggesting that environmental variation plays an important role in determining community composition. The temporal structure of variation, for example, can influence extinction risks (Heino 1998), population dynamics (e.g., Gonzalez and Holt 2002), and coexistence (Holt *et al*. 2003).

In the system simulated, as in many semi-natural landscapes, local communities are assembled through dispersal, and species are "filtered out" by local environmental conditions and competition in some habitats. However, the disturbance regime can be severe, especially when market-driven signals translate into frequent land use change, and often local disappearance of habitat. Market-driven landscapes therefore appear to be prone to biodiversity crises when market conditions change. If we consider such disturbance as a type of "environmental variation" which is known to impact appreciably population

processes (e.g., Gonzalez and De Feo 2007), we can notice that, in this system too, the internal structure of environmental variation is a major driver of diversity. Such disturbance depends on market prices and land managers' attitudes, and is altered by incentives, which interact with "black-hole" sinks.

To understand how present and future (e.g., due to climate change) natural environmental variation is likely to impact on communities in managed landscapes, and what role sinks might have in future species extinction or persistence, it is necessary to devote attention to how socio-economic factors are likely to drive the dynamics of habitat availability and quality at the landscape level.

### Acknowledgments

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