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## Coupled ecological and social dynamics in a forested landscape: the deviation of individual decisions from the social optimum

Received: 13 January 2006 / Accepted: 31 January 2006 / Published online: 4 April 2006  
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**Abstract** We present a Markov chain model for land-use dynamics in a forested landscape. This model emphasizes the importance of coupling socioeconomic and ecological processes underlying landscape change. We assume that a forest is composed of many land parcels, each of which is in one of a finite list of land-use states. The land-use state of each land parcel changes stochastically. The transition probability is determined by two processes: the forest succession and the decision of landowners. The landowner tends to choose the land-use state which has a high expected discounted utility, i.e., the sum of the current and the future utilities of the land parcel. Landowners take the likelihood of future landscape changes into account when making decisions. We focus on a three-state model in which forested, agricultural, and abandoned states are considered. The land-use composition at equilibrium was analyzed and compared with the social optimum that maximizes the net benefit of all landowners in a society. We show that when landowners make a myopic choice focused on short-term benefits, their individual decisions tend to push the entire landscape toward an agricultural state even if the forested state represents the highest utility. This land-use composition at equilibrium is very different from the social optimum. A long-term management perspective and an enhanced rate of forest recovery can eliminate the discrepancy.

**Keywords** Markov chain · Land use · Expected discounted utility · Forest regrowth · Decision making

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### Introduction

Landscape change is the outcome of both natural and anthropogenic disturbances. Natural disturbances (e.g., forest fires, land slides, and floods) are episodic and stochastic events that occur across a wide range of spatial and temporal scales. Anthropogenic disturbances (e.g., forest clearance for agriculture, timber harvest, or pasture) also occur at various temporal and spatial scales, but often at a faster rate and a more extensive scale than natural disturbances (Millennium Ecosystem Assessment 2005).

Deforestation is especially an important environmental problem because of its impact on biodiversity (Matson et al. 1997; Cuarón 2000; Sala et al. 2000; Waldhardt et al. 2004), carbon cycling associated with global climate (Dixon et al. 1994; Grünzweig et al. 2004), biogeochemical cycling (Houghton et al. 2000; Priess et al. 2001), and other ecosystem functions (Lewis et al. 2004). Consequently, the changes in forest ecosystems may lead to the degradation of many ecosystem services (e.g., water purification, natural hazard protection, and regulation of erosion), and may enhance risks of non-linear changes to the global ecosystems (Millennium Ecosystem Assessment 2005).

Many attempts to model spatial and temporal processes of land conversion have been made to understand the causes and consequences of these changes, and to predict the role of landscape change in the functioning of ecosystems. Lambin et al. (2000) classified a range of land-cover/use models into four basic categories:

1. Empirical–statistical models which basically use the generalized linear models in analyzing land-cover/use data (e.g., Mertens and Lambin 1997; Müller and Zeller 2002).
2. Stochastic models such as Markov chains governed by simple transition rules in land-cover/use (Baker 1989; Thornton and Jones 1998; Cuarón 2000).

3. Optimization models originated from the land rent theory (von Thünen 1966).
4. Dynamic simulation models which imitate the biophysical and socioeconomic processes associated with land-cover/use conversion and follow their development through time (Boserup 1965, 1981; Chayanov 1966).

Lambin et al. (2000) stressed the need for more integrated modeling approaches that combine elements of different modeling techniques.

A key factor inducing landscape change is the human behavior that underlies these changes. The simplest way to consider this is to develop a model which traces the responses of landowners to the change of socioeconomic and ecological conditions. Conventional economic models of an individual's land-use decisions assume irreversible changes, e.g., conversion from natural vegetation to developed land (Bockstael 1996; Irwin and Geoghegan 2001; Bell and Irwin 2002; Irwin and Bockstael 2002; Vance and Geoghegan 2002). Consequently, the major question in these models is the timing of land development, such as "When do I develop?" (Batabyal 1996). However, abandonment of developed land may result in growth of secondary vegetation. Such reforestation helps to restore nutrient and water cycling, and leads to the development of a forest with an assemblage of species and rates of biomass accumulation that resemble the original forest. For example, natural regrowth of vegetation following agriculture or pasture abandonment has been reported in Amazonia (Moran et al. 1996), or the island of Puerto Rico (Aide et al. 2000; Pascarella et al. 2000; Grau et al. 2003), and globally (Rudel et al. 2005). Lugo and Brown (1993) estimate that at least 250 million ha are undergoing succession worldwide. In addition, small farmers who practice swidden agriculture in tropical countries strongly rely on the capability of the forest to recover following repeated cycles of cultivation (Batabyal and Lee 2003). Therefore modeling of landscape change occurring in a forest ecosystem needs to incorporate forest regeneration (i.e., ecological processes) in addition to forest exploitation (i.e., socioeconomic processes).

In this article, we develop a Markov chain model for land-use dynamics in a forested landscape. The model emphasizes the importance of coupling socioeconomic and ecological processes underlying landscape change. Our objectives are:

1. To model the decision making of a landowner associated with land conversion.
2. To explore how individual decisions come to influence macroscopic patterns of land-use and how these patterns are different from the social decision that maximizes the net benefit of all the landowner in a society.
3. To identify key factors that can facilitate the agreement between individual and social decisions.

## Model

### Decision making of landowners

We assume that a forest is composed of many land parcels. Each parcel is in one of a finite list of land-use states. In this section we describe a general model in which there are  $m$  different land-use states (e.g., forested, agricultural, pasture, residential, or abandoned land). The landowner of each parcel may be a single person, a household, or a group of people. The land-use states of each land parcel may change stochastically from one to another. The transition probability is determined by both ecological processes (i.e., forest succession or natural disturbances) and socioeconomic processes (i.e., decisions of the landowners). Landowners' decisions depend on the change in the expected discounted utility associated with land conversion (Fig. 1).

The expected discounted utility is given as the cumulative sum of the current and the future utilities that are discounted over time. Let  $V_i$  be the expected discounted utility of a land parcel in the  $i$ th land-use state at time  $t$ .  $V_i$  is formalized as follows:

$$V_i = \sum_{n=0}^{\infty} \omega^n U_i(n), \quad (1)$$

where  $U_i(n)$  is the expected utility to be received after  $n$  time steps in a future when the land parcel is in  $i$ th land-use state at the present time and  $\omega$  is the discount factor ( $0 \leq \omega < 1$ ). The land-use state may change in the future due to the decision of the landowner or forest succession. Therefore  $U_i(n)$  includes all the contributions from different land-use states that can be realized after  $n$  time steps. The utility of a land parcel in the  $i$ th land-use state is consistent with the total revenue received minus the costs incurred when the land is in the  $i$ th state. For example, an agricultural land parcel will provide the landowner with monetary benefits over time, e.g., by crop sales. On the other hand, we need to consider costs pertaining to land management, harvesting, and

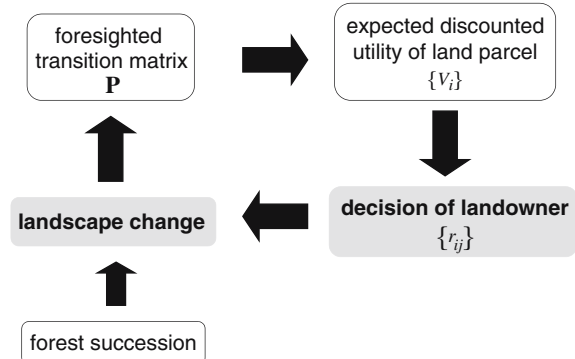


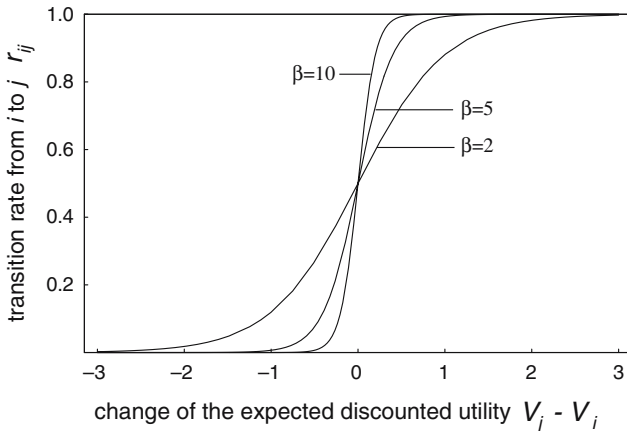
Fig. 1 A land-use model: flow chart of the major interactions

transportation. The distant future utility would be of less importance to the decision than the utility expected in the near future. This time discounting is expressed by the discount factor  $\omega$ .  $\omega$  is defined as  $1/(1 + \hat{r})$  where  $\hat{r}$  is the interest rate. When  $\omega$  is close to 1, the landowner identifies the future utility of the land to be as important as the current utility. In contrast, if  $\omega$  is close to 0, the landowner attaches most importance to the current utility.

The landowner makes a decision about whether to change the land-use state of his/her land parcel. The land conversion from the  $i$ th state to the  $j$ th state at time  $t$  produces the change in the expected discounted utility, denoted by  $V_j - V_i$ . The transition rate from  $i$ th state to  $j$ th state at time  $t$ , denoted as  $r_{ij}$ , is given as a function of  $V_j - V_i$  as follows:

$$r_{ij} = \frac{s}{1 + e^{-\beta(V_j - V_i)}}, \quad (2)$$

where  $s$  and  $\beta$  are positive constants. The above equation indicates that land conversion from the  $i$ th state to the  $j$ th state occurs more frequently if it results in a larger increase in the expected discounted utility (i.e., larger  $V_j - V_i$ ; see Fig. 2).  $s$  represents the degree of conservative attitude ( $0 < s \leq 1$ ).  $s$  becomes smaller as the landowners become more conservative (i.e., even if  $V_j - V_i$  is large, the landowners do not convert the land from the  $i$ th to the  $j$ th land-use state quickly).  $\beta$  is a parameter that controls the degree of stochasticity (Fig. 2). As  $\beta$  becomes infinitely large, the landowner makes a deterministic decision by choosing the best land-use state that represents the highest expected discounted utility (Hofbauer and Sigmond 2003). However, it is likely that different landowners have different attitudes regarding land conversion, because landowners differ in their need for an immediate income, preferred level of risk, and degree of conservatism. Assuming attitudinal heterogeneity exists among landowners, sto-



**Fig. 2** The transition probability from land-use state  $i$  to  $j$ , denoted by  $r_{ij}$ .  $V_i$  Expected discounted utility of the land parcel in state  $i$ ,  $V_j$  expected discounted utility of the land parcel in state  $j$ ,  $\beta$  positive constant,  $s = 1$

chastic decision making is more realistic than deterministic dynamics. In addition, an accurate evaluation of the utility of the land parcel may be very difficult and therefore the valuation system of a landowner may always include some degree of error, which is another source of stochasticity.

It is important to emphasize that the decision dynamics in Eq. 2 are closely related to the decision models in a theoretical game setting. Recently the quantal response equilibrium (QRE; McKelvey and Palfrey 1995) has been used to describe probabilistic responses of players under imperfect, or noisy, rational expectations rather than best responses assuming perfect foresight. The dynamic version of QRE is based on logit dynamics in which the probability of players choosing option  $j$  is given by  $e^{\beta V_j} / \sum_l e^{\beta V_l}$  (Hofbauer and Sigmond 2003). This means that better responses are more likely to be observed than worse responses, but best responses are not played with certainty. When there are only two choices (i.e.,  $i$  and  $j$ ), and when  $s = 1$ , Eq. 2 is the same as the logit dynamics.

#### Transition matrix for future landscape dynamics

When landowners make decisions about land conversion, they may take into account the landscape change that could occur in the future. For example, agricultural land may be abandoned, and after several decades an abandoned parcel may revert back to secondary forest that is equivalent in structure, functioning, and value to old growth forest. Future episodic events of natural disturbance, e.g., landslides and forest fires, may perturb the forest partly or completely. The landowner who has the foresight to consider future landscape dynamics would employ the following calculus: (1) anticipate the future transition path, (2) compute the expected discounted utility of different land-use states, and (3) choose the land-use state expected to yield the higher expected discounted utility. This type of decision-making is sometimes called the “perfect foresight dynamics” in game dynamics theory (Matsui and Matsuyama 1995; Oyama 2002).

Here we introduce the  $m \times m$  transition matrix  $\mathbf{P}$  that presents future landscape changes. The elements of  $\mathbf{P}$ ,  $p_{ij}$ , represent the transition probability that the land parcel initially in the  $i$ th state will change to the  $j$ th state in the future.  $p_{ij}$  is determined either by the decision of the landowner (i.e., the transition rate  $r_{ij}$ ) or the rate of forest succession (Fig. 1). An example of the transition matrix is given later.

Let  $\mathbf{u} = (u_1, \dots, u_m)^T$  be a column vector composed of the utilities for each land-use state  $y [y \in (1, \dots, m)]$ . We simply consider that  $\mathbf{u}$  is time invariant although this assumption can be relaxed easily. Let  $\mathbf{U}(n) = [U_1(n), \dots, U_m(n)]^T$  be a column vector composed of the utilities attained after  $n$  time steps in a future when the land parcel is in state  $y [y \in (1, \dots, m)]$  at the present time.

$\mathbf{U}(n)$  changes according to  $\mathbf{U}(n+1) = \mathbf{P}\mathbf{U}(n)$ . Because the utility attained at the present time,  $\mathbf{U}(0)$ , is simply given by  $\mathbf{u}$ , we have the following relationship:  $\mathbf{U}(n) = \mathbf{P}^n \mathbf{u}$ . Using this relationship, the expected discounted utilities for each land-use state  $y[y \in (1, \dots, m)]$ , denoted by a column vector  $\mathbf{V} = (V_1, \dots, V_m)^T$ , is given as:

$$\begin{aligned} \mathbf{V} &= \mathbf{U}(0) + \omega \mathbf{U}(1) + \omega^2 \mathbf{U}(2) + \omega^3 \mathbf{U}(3) + \dots \\ &= \sum_{n=0}^{\infty} \omega^n \mathbf{P}^n \mathbf{u}, \end{aligned} \quad (3)$$

where  $\omega$  is the discount factor ( $0 \leq \omega < 1$ ) as given in Eq. 1. The landowner who has foresight regarding future landscape dynamics makes the decision to convert his/her land according to Eqs. 2 and 3.

Note that the expected discounted utility  $\mathbf{V}$  and the transition matrix  $\mathbf{P}$  are dependent on each other (Fig. 1)—the transition rate  $r_{ij}$  is a function of  $V_i$  and  $V_j$  (Eq. 2);  $V_i$  and  $V_j$  in turn depend on  $\mathbf{P}$  (Eq. 3); but elements of  $\mathbf{P}$  include  $r_{ij}$ . To cope with this interdependence between  $\mathbf{V}$  and  $\mathbf{P}$ , we performed a recursive calculation (see Appendix).

### Social welfare function

In a previous section, we described the land-use dynamics which resulted from the decisions made by “individual” landowners who have a propensity to choose the land-use state expected to generate the higher expected discounted utility. However, society as a whole should employ a perspective to maximize the sum of the expected discounted utility over all land parcels included in a society rather than maximizing the expected discounted utility of one particular land parcel. The latter approach will maximize the net benefits of all the landowners in a society.

In this section, we consider the social welfare function, which is defined as (Lerner 1944):

$$\Phi(t) = \sum_{n=0}^{\infty} \omega^n \mathbf{x}(t+n) \mathbf{u}, \quad (4)$$

where  $\mathbf{x}(t) = [x_1(t), \dots, x_m(t)]$  is a row vector composed of the fractions of land parcels in each land-use state  $y[y \in (1, \dots, m)]$  and  $\mathbf{u} = (u_1, \dots, u_m)^T$  represents a column vector composed of the utilities of each land-use state  $y[y \in (1, \dots, m)]$ . Equation 4 indicates that the social welfare function is given as the weighted sum of the current and the future utilities of all the land parcels included in the whole forest. When there are  $m$  different land-use states,  $\mathbf{x}(t)$  changes according to the following dynamics:

$$\mathbf{x}(t+n) = \mathbf{x}(t) \mathbf{P}^n, \quad (5)$$

where  $\mathbf{P}$  is the transition matrix introduced in Eq. 3. Using Eq. 5, Eq. 4 is rewritten as follows:

$$\Phi(t) = \mathbf{x}(t) \mathbf{V} = \sum_{i=1}^m x_i(t) V_i, \quad (6a)$$

where  $V_i$  is the expected discounted utility of the land parcel in state  $i$  (Eq. 3). The state composition,  $\mathbf{x}(t)$ , converges to the equilibrium distribution (i.e.,  $\lim_{t \rightarrow \infty} \mathbf{x}(t) = \hat{\mathbf{x}}$ ). If we replace  $\mathbf{x}(t)$  by  $\hat{\mathbf{x}}$  in Eq. 6a, we have the following:

$$\hat{\Phi} = \sum_{i=1}^m \hat{x}_i V_i, \quad (6b)$$

The equilibrium state composition,  $\hat{\mathbf{x}}$ , that maximizes the social welfare function (Eq. 6b) is called “the social optimum” and is denoted by  $\mathbf{x}^*$ . The problem is to seek the solution for  $\mathbf{x}^*$ .

If  $\hat{\mathbf{x}}$  is freely chosen,  $\mathbf{x}^*$  is easily calculated:  $\mathbf{x}^*$  is the one in which the land-use state with the highest expected discounted utility occupies the entire system. Therefore for any pair of land-use states  $i$  and  $j$ , the following relation must be satisfied in the social optimum:

$$\frac{x_i^*}{x_j^*} = \begin{cases} \infty, & \text{if } V_i > V_j \\ 0, & \text{if } V_i < V_j \end{cases} \quad (7)$$

This social optimum,  $\mathbf{x}^*$ , can be very different from the equilibrium land-use composition generated from individual decisions as explained later.

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### Forested, agricultural, and abandoned lands

To illustrate characteristics of land-use dynamics, we focus here on a simple landscape composed of only three land-use states, namely forested land, agricultural land, and abandoned land. These three land-use states are defined as follows:

#### Forested land

Forested land provides multiple ecosystem services, e.g., biodiversity conservation, air and water purification, generation and renewal of soil and soil fertility, and ecotourism. Environmental economists have developed methods for valuing ecosystem services, even when they are not traded in conventional markets (Goulder and Kennedy 1997; Heal 2000; Armsworth and Roughgarden 2001). In our modeling framework, we assume that the utility of the forested land encompasses the many ecosystem services provided by intact forests. This can be interpreted as the situation in which individual landowners receive a subsidy equivalent to the value of ecosystem services.

#### Agricultural land

A land parcel is considered as agricultural land if it is used for crop or timber production. The utility of agricultural land is mainly influenced by the monetary benefits from crop or timber sales and the costs of land management, harvesting, and transportation.

Abandoned land

If agriculture becomes uneconomical (for example, because of alternative more profitable jobs or a drop in crop/timber prices), landowners may stop an agricultural or logging operation, which would result in the abandonment of agricultural land. The abandoned land lacks many of the ecosystem services of the forested land. In addition, there are few plant species that can be a source of economically valuable timber or of non-timber products. Therefore abandoned land produces a low short-term profit. But it has the potential to revert back to forested land in the future. Aide et al. (2000) reported that in the Island of Puerto Rico lands abandoned after agricultural use had been restored after approximately 40 years to secondary forests that resembled the old growth forest in terms of density, basal area, aboveground biomass, and species richness. Consequently the abandoned land produces a significant long-term profit.

**Land-use composition at equilibrium: quick recovery after abandonment**

We first investigate the simple cases in which all the transitions between different land-use states occur only due to the decisions of landowners. Natural processes, such as forest succession, do not influence the transition probability. We focus on the decisions of myopic landowners who place the highest importance on the current utility and neglect the contribution of the future utility when making decisions (i.e.,  $\omega=0$ ). We analyze the land-use composition when the system reaches the equilibrium. Since  $\omega=0$ , the expected discounted utility is equal to the utility for each land-use state (i.e.,  $\mathbf{V}=\mathbf{u}$ ).

Two-state model

The process of forest recovery after abandonment of agricultural land may be very fast. In this case, we can neglect the abandoned state, and then the three-state model is reduced to the two-state model that represents a direct transition between forested (F) and agricultural (A) lands (Fig. 3a). The equilibrium state

of the two-state model satisfies the following (Feller 1968):

$$\hat{x}_F r_{FA} = \hat{x}_A r_{AF}, \tag{8}$$

where  $\hat{x}_F$  and  $\hat{x}_A$  are densities of forested and agricultural land at equilibrium.  $r_{FA}$  and  $r_{AF}$  are transition rates from forested to agricultural land and vice versa (see Eq. 2 with  $V_i = u_i$ ). From Eqs. 2 and 9, we have,

$$\hat{x}_F / \hat{x}_A = e^{\beta(u_F - u_A)}. \tag{9}$$

This indicates that the ratio of equilibrium densities of forested and agricultural lands is determined by the difference between the utilities of both land-use states (i.e.,  $u_F - u_A$ ). When  $\beta$  is sufficiently large, the equilibrium land-use composition approaches the following:

$$(\hat{x}_F, \hat{x}_A) \approx \begin{cases} (1, 0) & \text{if } u_F > u_A \\ (0, 1) & \text{if } u_F < u_A \end{cases}. \tag{10}$$

If the utility of forested land is greater than that of agricultural land (i.e.,  $u_F > u_A$ ), all of the land parcels should be in a forested state at equilibrium, while if  $u_F < u_A$ , the agricultural state dominates the entire system. Therefore the equilibrium land-use composition generated by the decisions of myopic landowners (i.e.,  $\omega=0$ ) is dominated by the state with the larger utility. This is close to the social optimum that maximizes the social welfare function (Eq. 7).

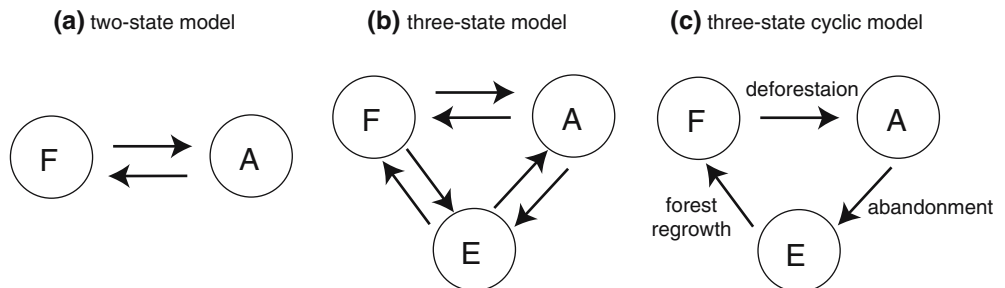
Multiple-state model with detailed balance condition

We can extend the results of the two-state model to the multi-state model that includes  $m$  land-use states in general. In order to perform this extension, a ‘‘detailed balance’’ condition needs to be satisfied, which is defined as:

$$\hat{x}_i r_{ij} = \hat{x}_j r_{ji}, \quad \text{for all pairs of } i \text{ and } j, \tag{11}$$

where  $\hat{x}_i$  and  $\hat{x}_j$  are the equilibrium density of the land parcel in the  $i$ th and  $j$ th state and  $r_{ij}$  and  $r_{ji}$  are the transition rate from the  $i$ th to  $j$ th state and vice versa that are given in Eq. 2. Equation 11 means that, for each transition, there is a reverse transition, and they have the same net probability flux at equilibrium as exemplified by the model with  $m=3$  (Fig. 3b). If any two states in the system are connected either directly by transition or

**Fig. 3a–c** A diagram of a Markov chain model for land-use dynamics [forested land (F), agricultural land (A), and abandoned land (E)]. **a** Two-state model in which land abandoned after agricultural use rapidly reverts back to F. **b** Three-state model that satisfies a ‘‘detailed balance’’ condition. **c** Three-state cyclic model



indirectly by a chain of transitions, the system is called “strongly connected” (Feller 1957). If the system is strongly connected, and if the detailed balance condition is satisfied, we can apply the same argument as for the two-state model. When  $\beta$  is sufficiently large, the equilibrium land-use composition under a detailed balance condition is given by:

$$\lim_{\beta \rightarrow \infty} \frac{\hat{x}_i}{\hat{x}_j} = \begin{cases} \infty, & \text{if } u_i > u_j \\ 0, & \text{if } u_i < u_j \end{cases} \quad (12)$$

meaning that the land-use state representing the largest utility dominates the entire system. This result again is close to the social optimum (Eq. 7).

### Land-use composition at equilibrium: slow recovery after abandonment

Three-state cyclic model: myopic landowners

The process of forest recovery after abandonment of agricultural land may be slow (Aide 2000). In order to incorporate the process of forest regrowth, we consider a three-state cyclic model (Fig. 3c). In this model, instead of direct transition from an agricultural to a forested state (Fig. 3a), an agricultural land parcel needs to pass through an abandoned state that has a very low utility until the abandoned parcel undergoes succession to secondary forest. Consequently the detailed balance condition does not hold in the three-state cyclic model. Here we consider that land abandoned after agricultural use reverts back to secondary forest with the probability  $q_{EF}$  per unit time (i.e.,  $0 < q_{EF} < 1$ ).

The transition from an abandoned to a forested state may occur through forest succession initiated by natural processes such as seed dispersal, colonization of pioneer species, and stem branching or root sprouting. In addition, human activities can modify the speed of forest succession. For instance, forest conservation efforts, such as enhanced regeneration or enrichment tree planting, and agricultural operations with intensive maintenance that reduce detrimental impacts on land quality may accelerate the rate of forest succession. In contrast, intensive land uses prior to abandonment may slow the succession rate. The magnitude of  $q_{EF}$  can be influenced by these processes. It is important to emphasize that the transition from an abandoned to a forested state is basically a natural process (i.e., forest succession) rather than a socioeconomic process that can be perfectly controlled by the decision of a landowner.

The equilibrium density of forested, agricultural, and abandoned lands are given by  $\hat{x}_F, \hat{x}_A$ , and  $\hat{x}_E$ , and are calculated from the following condition:

$$\hat{x}_F r_{FA} = \hat{x}_A r_{AE} = \hat{x}_E q_{EF}. \quad (13)$$

The first term in Eq. 13 indicates the fraction of land parcels that are converted from forested to agricultural land. Similarly, the second and the third terms in Eq. 13

represent the fraction of land parcels that are converted from agricultural to abandoned land, and from abandoned to forested land. Since these three fluxes of converted land parcels must be balanced at equilibrium, we have

$$\hat{x}_F : \hat{x}_A : \hat{x}_E = \left(1 + e^{\beta(u_F - u_A)}\right) : \left(1 + e^{\beta(u_A - u_E)}\right) : s/q_{EF}, \quad (14)$$

from Eqs. 2 and 13. It is plausible to assume that the utility of abandoned land is less than that of other two states (i.e.,  $u_E < u_F, u_A$ ). In addition, it is also reasonable to assume that the rate of forest regrowth,  $q_{EF}$ , has some positive value. Under this assumption, there are two cases depending on the relative magnitude between  $u_F$  and  $u_A$ .

*Case 1. The utility of agricultural land is the largest;  $u_A > u_F > u_E$*

When the utility of agricultural land is the largest, the equilibrium state is given as a simple composition (Fig. 4a). From the inequality of  $u_A > u_F > u_E$ , the signs of  $u_A - u_F$ , and  $u_E - u_A$  are positive and negative, respectively. Therefore, when  $\beta$  is sufficiently large, the equilibrium state approaches the following (see Eq. 14):

$$(\hat{x}_F, \hat{x}_A, \hat{x}_E) \approx (0, 1, 0). \quad (15)$$

This implies that when landowners are myopic (i.e.,  $\omega = 0$ ), the land-use state representing the highest utility dominates the entire system. This is again the same as the social optimum (Eq. 7).

*Case 2. The utility of forested land is the largest;  $u_F > u_A > u_E$*

When the utility of forested land is the largest, there are two different equilibrium states. When  $\beta$  is sufficiently large, the equilibrium state approaches;

$$(\hat{x}_F, \hat{x}_A, \hat{x}_E) \approx \begin{cases} (1, 0, 0), & \text{if } |u_F - u_A| > |u_A - u_E| \\ (0, 1, 0), & \text{if } |u_F - u_A| < |u_A - u_E| \end{cases}. \quad (16)$$

The equilibrium land-use composition is dominated by the forested state if  $u_F - u_A$  is larger than  $u_A - u_E$  (Fig. 4b).  $u_F - u_A$  is interpreted as the loss of the utility associated with the land conversion from forested to agricultural land (in other words, deforestation).  $u_A - u_E$  is similarly interpreted as the loss of the utility associated with the land conversion from agricultural to abandoned land (i.e., abandonment). Therefore the forest-dominated state is realized when the loss of utility due to deforestation is larger than that of abandonment of agricultural land. In this case, the equilibrium land-use composition is the same as the social optimum. However if  $u_F - u_A$  is smaller than  $u_A - u_E$  (Fig. 4c), the equilibrium land-use composition does not converge with the one

dominated by the forested state but rather approaches the agriculture-dominated state (Eq. 16). In this case, even if forested land has the highest utility, the landowner who manages agricultural land would not abandon it because the cost of abandonment is large (i.e., the utility of abandoned land,  $u_E$ , is very low). As a consequence, most of the land parcels accumulate in an agricultural state which has less utility than the forested state (Fig. 4c). This equilibrium composition of land-use state is different from the social optimum (Eq. 7).

Finally we note the importance of stochasticity in making decisions (Eq. 2). Starting from a sub-optimal state (i.e., an agricultural state), it is impossible to reach the optimal state (i.e., a forested state) if there is no stochasticity (i.e.,  $\beta$  is infinitely large) because the abandoned state has a lower utility than the agricultural state. Therefore, to achieve the equilibrium composition in Eq. 16,  $\beta$  must be finite.

### Impact of a long-term management perspective

In this section, we show the importance of taking a long-term management view in order to eliminate the discrepancy between individual and social decisions, and how this perspective can alter the dynamics described above. We consider the case in which the discount factor  $\omega$  is positive, which means that a landowner takes the future value of the land into account when making his/her decision.

We investigate how the projection of regrowth of abandoned land affects the decision making of landowners. The transition matrix for future landscape change,  $\mathbf{P}$ , introduced in Eq. 3 is given by,

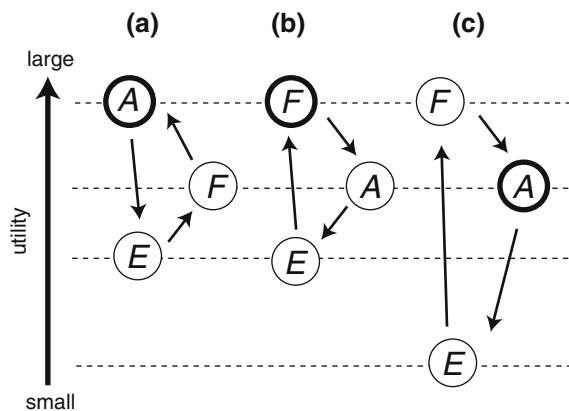
$$\mathbf{P} = \begin{pmatrix} & \text{F} & \text{A} & \text{E} \\ \begin{pmatrix} 1 - r_{\text{FA}} & r_{\text{FA}} & 0 \\ 0 & 1 - r_{\text{AE}} & r_{\text{AE}} \\ q_{\text{EF}} & 0 & 1 - q_{\text{EF}} \end{pmatrix} & \text{F} \\ & \text{A} \\ & \text{E} \end{pmatrix}, \quad (17)$$

where  $r_{\text{FA}}$  and  $r_{\text{AE}}$  are transition rates from forested to agricultural land and from agricultural to abandoned land.  $q_{\text{EF}}$  represents the rate of forest regrowth.

The utility of each of the three land-use states was assumed to satisfy  $u_{\text{F}} > u_{\text{A}} > u_{\text{E}}$ —forested land ( $u_{\text{F}}$ ) generates a larger utility than agricultural land ( $u_{\text{A}}$ ), which has a larger utility than abandoned land ( $u_{\text{E}}$ ). We chose the value of utilities so as to satisfy the inequality,  $|u_{\text{F}} - u_{\text{A}}| < |u_{\text{A}} - u_{\text{E}}|$ , with which the agriculture-dominated state is realized when landowners are myopic (i.e.,  $\omega = 0$ ). Under this assumption, we calculated the expected discounted utility (Eq. 3), and then simulated the decision of individual landowners using Eq. 2: 1,000 land parcels are considered. Starting from equally distributed land-use patterns for each land-use state, we performed the computer simulation over a sufficiently long time period for a range of parameter combinations ( $\omega$ ,  $q_{\text{EF}}$ ).

The averaged density of forested land (calculated by sampling 100 time points after a sufficiently long simulation) was very low when  $\omega$  was small (Fig. 5a). It increased gradually with an increase in  $\omega$ , and finally approached 1 (Fig. 5a). This result implies that a long-term management perspective (i.e., large  $\omega$ ) is a critical factor in order to achieve a socially desirable land-use composition (Eq. 7). However even when  $\omega$  was large, the averaged density of forested land was low when the rate of forest regrowth was small (Fig. 5b). This illustrates the importance of management efforts that accelerate the speed of forest succession (i.e., large  $q_{\text{EF}}$ ) in addition to a long-term management perspective.

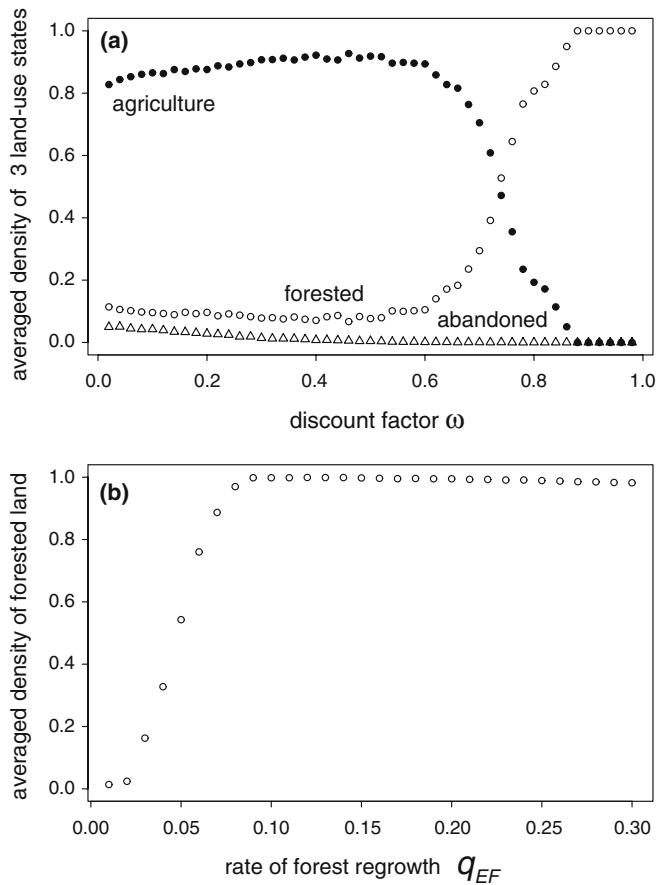
We also examined the situation in which agricultural land yields the largest utility (i.e.,  $u_{\text{A}} > u_{\text{F}} > u_{\text{E}}$ ). The land-use composition did not depend much on parameters—the system was always dominated by the agricultural state that generated the largest utility. There was no discrepancy between the outcome of the individual decision and the social optimum, as was expected from the analysis when  $\omega = 0$ .



**Fig. 4a–c** A diagram of a three-state cyclic model. Three land-use states (F, A, and E) are arranged along the vertical axes that represent the utility. Land-use states encircled with thick lines dominate the equilibrium land system.  $u_{\text{F}}$ ,  $u_{\text{A}}$ , and  $u_{\text{E}}$  are the utilities for the land parcels in a forested, agricultural, and abandoned state. **a** The case with  $u_{\text{A}} > u_{\text{F}} > u_{\text{E}}$ . **b** The case with  $u_{\text{F}} > u_{\text{A}} > u_{\text{E}}$  and the relative magnitude satisfies  $|u_{\text{F}} - u_{\text{A}}| > |u_{\text{A}} - u_{\text{E}}|$ . **c** The case with  $u_{\text{F}} > u_{\text{A}} > u_{\text{E}}$  and the relative magnitude satisfies  $|u_{\text{F}} - u_{\text{A}}| < |u_{\text{A}} - u_{\text{E}}|$ . For abbreviations, see Fig. 3

## Discussion

We have presented a Markov chain model for land-use dynamics that emphasizes the importance of the coupling of socioeconomic and ecological processes underlying landscape change. We were explicitly concerned with exploring how individual landowners make decisions about land conversion and how these decisions come to influence macroscopic patterns of land-use that could be different from the social optimum. Our model is too simplified for comprehensive forest management. However, we believe the simplified model provides key



**Fig. 5** **a** Plot of averaged density of F (open circles), A (solid circles), and E (triangles) versus the discount factor  $\omega$ .  $q_{EF}=0.15$ ,  $\beta=7$ . **b** Plot of averaged density of forested land versus rate of forest regrowth  $q_{EF}$ .  $\omega=0.9$ ,  $\beta=2$ . For both diagrams, other parameters are set as:  $u_F=1.0$ ,  $u_L=0.65$ ,  $u_A=0.0$ , and  $s=1$ . For abbreviations, see Fig. 3

insights into the mechanisms of land degradation and has important implications for forest management and policy.

The analysis focused on the dynamics of three land-use states, namely forested, agricultural, and abandoned lands. We showed how slow ecological processes, such as forest succession, influenced the decisions of individual landowners and resultant land-use patterns. When the land-use transition is controlled solely by the decisions of landowners, individual decisions created the land-use pattern in which the land-use state with the highest utility occupied the entire system.

In contrast, while a number of years was required for abandoned land to develop community structure, biomass accumulation, and functioning similar to a mature forest (Aide et al. 2000), agricultural land needed to pass through an abandoned state that had very low utility until it underwent succession to become a secondary forest (Fig. 3c). The process of forest succession can be managed but cannot be perfectly controlled by the decision of landowners. In this case, the landscape which resulted from the decision of myopic landowners was

dominated by agriculture even when the forested state generated the highest utility. This result diverged from the socially optimal decision that attempts to let all the landowners achieve the land-use state that generates the highest utility. This deviation is not caused by a so-called “social dilemma,” but rather by the myopic decision of landowners to use land resources in such a manner that there is potential for slow renewal.

Several policy changes may help to overcome this discrepancy:

1. Creating institutionalized agreements that encourage landowners to take a long-term management view so as to anticipate the future value of land.
2. Investing in forest management that accelerates the rate of forest recovery.
3. Implementing economic incentives that enhance the utility of abandoned land (e.g., a subsidy), or decrease the utility of agricultural land (e.g., taxing of crops or timber products).

These propositions can facilitate a movement of the equilibrium composition toward a more socially desirable state.

After long and intensive use as agricultural land, abandoned land may not undergo transition to a forested state but may move toward becoming a grassland where no woody plants characterizing mature forest can establish. This would be an irreversible change because the reversal (i.e., the change from an abandoned to a forested state) would take several human generations. To avoid such disastrous shifts and to explore how to sustain land resources, further understanding of the contexts in which ecological changes are irreversible is necessary, as exemplified by resilience-based management approaches (Berkes and Folke 1998; Carpenter et al. 1999; Anderies et al. 2002; Walker et al. 2002).

The development of models of land conversion has been, at least partly, promoted by technological progress in acquiring time series of land-use data from remote-sensing (e.g., aerial photographs and satellite imagery of land-cover/use; Moran et al. 1996). Spatial factors, such as adjacency, accessibility to market, seed dispersal, and seed source availability, influence the patterns and underlying processes of land-use change. The increasing availability of spatio-temporal data will enable us to incorporate these factors into land-use modeling (Moran and Brondizio 1998).

Spatially explicit models are promising tools with which to analyze such data and have been intensively studied in theoretical ecology in the last few decades, leading to a subfield named “spatial ecology” (Wiens et al. 1993; Hastings 1994; Levin et al. 1997; Tilman and Kareiva 1997; summarized in Dieckmann et al. 2000). Lattice or cellular automaton models can be useful in simulating ecological dynamics in a spatially explicit fashion, e.g., population dynamics of terrestrial plants (Harada and Iwasa 1994), vegetation dynamics (Crawley



and May 1987; Silvertown et al. 1992; Sato and Iwasa 1993; Kubo et al. 1996; Satake et al. 1998, 2004), marine invertebrate communities (Caswell and Etter 1992; Etter and Caswell 1994), predator–prey, host–pathogen, and host–parasitoid dynamics (Hassell et al. 1991, 1994), as well as evolutionary games (Durrett and Levin 1994a, 1994b; Nakamaru et al. 1997; Iwasa et al. 1998). Cellular automata models have also been applied to study the social dynamics of urban growth (White and Engelen 1993; Clarke et al. 1997; White et al. 1997).

The integration of individual/social decisions and landscape dynamics in spatially explicit and more complex settings is necessary for further studies on land-use dynamics. We believe that, in addition to historical (Diamond 2005), experimental (Fehr and Fischbacher 2004), and neurological studies (McClure et al. 2004), theoretical studies can provide an in-depth understanding of human behavioral components needed for sustainable use of land resources (Levin 1999).

**Acknowledgements** This work was supported in part by a fellowship and a grant-in-aid from the Japan Society for the Promotion of Science to A. S. and another to Y. I. We thank the following for their helpful comments: K. Akao, N. Agetsuma, M. A. Janssen, K. Kitayama, H. M. Leslie, S. A. Levin, H. Ohtsuki, M. Potts, T. K. Rudel, M. Schlueter, J. Vincent, and H. Yokomizo.

## Appendix

The expected discounted utility  $\mathbf{V}$  and the transition matrix  $\mathbf{P}$  are dependent on each other (Fig. 1)—the transition rate  $r_{ij}$  is a function of  $V_i$  and  $V_j$  (Eq. 2 in the text);  $V_i$  and  $V_j$  in turn depend on  $\mathbf{P}$  (Eq. 3 in the text); but elements of  $\mathbf{P}$  includes  $r_{ij}$ . We explain a method of recursive calculation that is performed to cope with the interdependence between  $\mathbf{V}$  and  $\mathbf{P}$ . Let  $\mathbf{P}[\mathbf{V}]$  be the transition matrix given the expected discounted utility  $\mathbf{V}$ . We started with a simple set of the expected discounted utility, such as  $\mathbf{V}^{(0)} = \mathbf{u}$  in which there is no contribution of future utility. We then calculated the transition matrix  $\mathbf{P}^{(0)} = \mathbf{P}[\mathbf{V}^{(0)}]$ . Given  $\mathbf{P}^{(0)}$ , we obtained a set of the expected discounted utility  $\mathbf{V}^{(1)} = \sum_{n=0}^{\infty} \omega^n (\mathbf{P}^{(0)})^n \mathbf{u}$  (see Eq. 3 in the text). As a next step, using  $\mathbf{V}^{(1)}$ , we calculated  $\mathbf{P}^{(1)} = \mathbf{P}[\mathbf{V}^{(1)}]$ , and then obtained  $\mathbf{V}^{(2)} = \sum_{n=0}^{\infty} \omega^n (\mathbf{P}^{(1)})^n \mathbf{u}$ . We repeated this procedure, and when a series of  $\mathbf{V}^{(1)}, \mathbf{V}^{(2)}, \dots, \mathbf{V}^{(n)}$  converges (i.e.,  $\mathbf{V}^{(n)} = \mathbf{V}^{(n-1)}$ ),  $\mathbf{V}$  and  $\mathbf{P}$  satisfy both Eqs. 2 and 3 in the text.

## References

- Aide TM, Zimmerman JK, Pascarella JB, Rivera L, Marciano-Vega H (2000) Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restor Ecol* 8:328–338
- Anderies JM, Janssen MA, Walker BH (2002) Grazing management, resilience, and the dynamics of a fire-driven rangeland system. *Ecosystems* 5:23–44
- Armstrong PR, Roughgarden JE (2001) An invitation to ecological economics. *Trends Ecol Evol* 16:229–234
- Baker WL (1989) A review of models of landscape change. *Landsc Ecol* 2:111–133
- Batabyal AA (1996) The timing of land development: an invariance result. *Am J Agric Econ* 78:1092–1097
- Batabyal AA, Lee DM (2003) Aspects of land use in slash and burn agriculture. *Appl Econ Lett* 10:821–824
- Bell KP, Irwin EG (2002) Spatially explicit micro-level modelling of land use change at the rural–urban interface. *Am J Agric Econ* 27:217–232
- Berkes F, Folke C (eds) (1998) *Linking social and ecological systems*. Cambridge University Press, Cambridge
- Bockstael NE (1996) Modeling economics and ecology: the importance of a spatial perspective. *Am J Agric Econ* 78:1168–1180
- Boserup E (1965) *The condition of agricultural growth*. Allen & Unwin, London
- Boserup E (1981) *Population and technological change*. University of Chicago Press, Chicago, Ill.
- Carpenter S, Brock W, Hanson P (1999) Ecological and social dynamics in simple models in ecosystem management. *Conserv Ecol* 3:4. [Online] URL: <http://www.consecol.org/vol3/iss2/art4/>
- Caswell H, Etter RJ (1992) Ecological interactions in patchy environments: from patch-occupancy models to cellular automata. In: Levin SA, Powell TM, Steele JH (eds) *Patch dynamics*. Springer, Berlin Heidelberg New York, pp 93–109
- Chayanov AV (1966) Peasant farm organization. In: Thorner D, Kerblay B, Smith REF (eds) *The theory of peasant economy*. University of Wisconsin Press, Madison, Wis., pp 21–57
- Clarke KC, Hoppen S, Gaydos L (1997) A self-modifying cellular automaton model of historical urbanization in the San Francisco Bay area. *Environ Plan B Plan Des* 24:247–261
- Crawley MJ, May RM (1987) Population dynamics and plant community structure: competition between annuals and perennials. *J Theor Biol* 125:475–489
- Cuarón AD (2000) Effects of land-cover changes on mammals in a neotropical region: a modeling approach. *Conserv Biol* 14:1676–1692
- Diamond J (2005) *Collapse: how societies choose to fail or succeed*. Viking, New York
- Dieckmann U, Law R, Metz JAJ (2000) *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, Cambridge
- Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science* 263:185–190
- Durrett R, Levin S (1994a) *Stochastic spatial models: a user's guide to ecological applications*. *Philos Trans R Soc Lond B* 343:329–350
- Durrett R, Levin S (1994b) The importance of being discrete (and spatial). *Theor Popul Biol* 46:363–394
- Etter RJ, Caswell H (1994) The advantages of dispersal in a patch environment: effects of disturbance in a cellular automata model. In: Eckelbarger KJ, Young CM (eds) *Reproduction, larval biology and recruitment in the deep-sea benthos*. Columbia University Press, New York, pp 93–109
- Fehr E, Fischbacher U (2004) Third-party punishment and social norms. *Evol Human Behav* 25:63–87
- Feller W (1968) *An introduction to probability theory and its applications*, vol 1, 3rd edn. Wiley, New York
- Goulder LH, Kennedy D (1997) Valuing ecosystem services: philosophical bases and empirical methods. In: Daily G (ed) *Nature's services*. Island Press, Washington, D.C., pp 23–47
- Grau HR, Aide TM, Zimmerman JK, Thomlinson JR, Helmer E, Zou X (2003) The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *BioScience* 53:1159–1168
- Grünzweig JM, Sparrow SD, Yakir D, Chapin FS III (2004) Impact of agricultural land-use change on carbon storage in boreal Alaska. *Global Change Biol* 10:452–472
- Harada Y, Iwasa Y (1994) Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Res Popul Ecol* 36:237–249

- Hassell M, Comins HN, May RM (1991) Spatial structure and chaos in insect population dynamics. *Nature* 353:255–258
- Hassell M, Comins HN, May RM (1994) Species coexistence and self-organizing spatial dynamics. *Nature* 370:290–292
- Hastings A (1994) Conservation and spatial structure: theoretical approaches. In: Levin SA (ed) *Frontiers in mathematical biology*. Springer, Berlin Heidelberg New York, pp 494–503
- Heal G (2000) Valuing ecosystem services. *Ecosystems* 3:24–30
- Hofbauer J, Sigmund K (2003) *Evolutionary game dynamics*. *Bull Am Math Soc* 40:479–519
- Houghton RA, Skole DL, Nobre CA, Hackler JL, Lawrence KT, Chomentowski WH (2000) Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature* 403:301–304
- Irwin EG, Bockstael NE (2002) Interacting agents, spatial externalities and the evolution of residential land use patterns. *J Econ Geogr* 2:31–54
- Irwin EG, Geoghegan J (2001) Theory, data, methods: developing spatially explicit models of land use change. *Agric Ecosyst Environ* 85:7–23
- Iwasa Y, Nakamaru M, Levin S (1998) Allelopathy of bacteria in a lattice population: competition between colicin-sensitive and colicin-producing strains. *Evol Ecol* 12:785–802
- Kubo T, Iwasa Y, Furumoto N (1996) Forest spatial dynamics with gap expansion: total gap area and gap size distribution. *J Theor Biol* 180:229–246
- Lambin EF, Rounsevell MDA, Geist HJ (2000) Are agricultural land-use models able to predict changes in land-use intensity? *Agric Ecosyst Environ* 82:321–331
- Lerner AP (1944) *The economics of control: principles of welfares*. Macmillan, New York
- Levin SA (1999) *Fragile dominion: complexity and commons*. Perseus, Reading
- Levin SA, Grenfell B, Hastings A, Perelson AS (1997) Mathematical and computational challenges in population biology and ecosystems science. *Science* 275:334–343
- Lewis SL, Malhi Y, Phillips OL (2004) Fingerprinting the impacts of global change on tropical forests. *Philos Trans R Soc Lond B* 359:437–462
- Lugo AE, Brown S (1993) Management of tropical soils as sinks on sources of atmospheric carbon. *Plant Soil* 149:27–41
- Matson PA, Parton WJ, Power AG, Swift MJ (1997) Agricultural intensification and ecosystem properties. *Science* 277:504–509
- Matsui A, Matsuyama K (1995) An approach to equilibrium selection. *J Econ Theory* 65:415–434
- McClure SM, Laibson DI, Loewenstein G, Cohen JD (2004) Separate neural systems value immediate and delayed monetary rewards. *Science* 306:503–507
- McKelvey RD, Palfrey RD (1995) Quantal response equilibrium for normal-form games. *Games Econ Behav* 10:6–38
- Mertens B, Lambin EF (1997) Spatial modelling of deforestation in southern Cameroon—spatial disaggregation of diverse deforestation processes. *Appl Geogr* 17:143–162
- Millennium Ecosystem Assessment (2005) *Millennium ecosystem assessment synthesis report*. Island Press, Washington, D.C. <http://www.maweb.org>
- Moran EF, Brondizio ES (1998) Land-use change after deforestation in Amazonia. In: Liverman D, Moran EF, Rindfuss RR, Stern PC (eds) *People and pixels*. National Academic, Washington, D.C., pp 94–119
- Moran EF, Packer A, Brondizio E, Tucker J (1996) Restoration of vegetation cover in the eastern Amazon. *Ecol Econ* 18:41–54
- Müller D, Zeller M (2002) Land use dynamics in the central highlands of Vietnam: a spatial model combining village survey data with satellite imagery interpretation. *Agric Econ* 27:333–354
- Nakamaru M, Matsuda H, Iwasa Y (1997) The evolution of cooperation in lattice-structure population. *J Theor Biol* 184:65–81
- Oyama D (2002)  $\rho$ -dominance and equilibrium selection under perfect foresight dynamics. *J Econ Theory* 107:288–310
- Pascarella JB, Aide TM, Serrano MI, Zimmerman JK (2000) Land-use history and forest regeneration in the Cayey mountains, Puerto Rico. *Ecosystems* 3:217–228
- Priess JA, de Koning GHJ, Veldkamp A (2001) Assessment of interactions between land use change and carbon and nutrient fluxes in Ecuador. *Agric Ecosyst Environ* 85:269–279
- Rudel TK, Coomes OT, Moran E, Achard F, Angelsen A, Xu J, Lambin E (2005) Forest transitions: towards a global understanding of land use change. *Global Environ Change* 15:23–31
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity—global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Satake A, Kubo T, Iwasa Y (1998) Noise-induced regularity of spatial wave patterns in subalpine *P. abies* forests. *J Theor Biol* 195:465–479
- Satake A, Iwasa Y, Hakoyama H, Hubbell SP (2004) Estimating local interaction from spatiotemporal forest data, and Monte Carlo bias correction. *J Theor Biol* 226:225–235
- Sato K, Iwasa Y (1993) Modeling of wage regeneration (shimagare) in subalpine *P. abies* forests: population dynamics with spatial structure. *Ecology* 74:1538–1550
- Silvertown J, Holtier S, Johnson J, Dale P (1992) Cellular automaton models of interspecific competition of space—the effect of pattern on process. *J Ecol* 80:527–534
- Thornton PK, Jones PG (1998) A conceptual approach to dynamic agricultural land-use modeling. *Agric Syst* 57:505–521
- von Thünen JH (1966) *Der isolierte Staat in Beziehung auf Landwirtschaft und Nationalökonomie*. Neudruck nach der Ausgabe letzter Hand (1842/1850). Fischer, Stuttgart
- Tilman D, Kareiva P (1997) *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, N.J.
- Vance C, Geoghegan J (2002) Temporal and spatial modeling of tropical deforestation: a survival analysis linking satellite and household survey data. *Agric Econ* 27:317–332
- Waldhardt R, Simmering D, Otte A (2004) Estimation and prediction of plant species richness in a mosaic landscape. *Landsc Ecol* 19:211–226
- Walker BH, Carpenter S, Anderies J, Abel N, Cumming G, Janssen M, Lebel L, Norberg J, Peterson GD, Pritchard R (2002) Resilience management in social-ecological systems: a working hypothesis for participatory approach. *Conserv Ecol* 6:14. [Online] URL: <http://www.consecol.org/vol6/iss1/art14>
- White R, Engelen G (1993) Cellular automata and fractal urban form: a cellular modeling approach to the evolution of urban land-use patterns. *Environ Plan A* 25:1175–1199
- White R, Engelen G, Uljee I (1997) The use of constrained cellular automata for high-resolution modelling of urban land-use dynamics. *Environ Plan B Plan Des* 24:323–343
- Wiens JA, Stenseth NC, van Horne B, Ims RA (1993) Ecological mechanisms and landscape ecology. *Oikos* 66:369–380