

Regime shifts in a socio-ecological model of farmland abandonment

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Abstract We developed a mathematical model with two-way linked socio-ecological dynamics to study farmland abandonment and to understand the regimes shifts of this socio-ecological system. The model considers that migration is a collective behavior socio-economically driven and that the ecosystem is dynamic. The model identifies equilibria that vary from mass migration, farmland abandonment, and forest regeneration, to no migration and forest eradication; partial migration and/or coexistence of farmland and forest also constitute possible equilibria. Overall, the model reflects farmland abandonment processes observed in the field and illustrates the importance of the complex interlinked mechanisms between the social and ecological systems determining farmland abandonment, that are not evident when approached independently. The model dynamics show that the hysteresis on the social

dynamics renders regimes shifts difficult to reverse, and that this difficulty is accentuated when considering the ecological system dynamic. Similar models could be applied to other socio-ecological systems to help their management.

Keywords Collective behavior · Deforestation · Forest regeneration · Human decision · Hysteresis · Linked social-ecological system · Migration · Threshold · Rural exodus · Utility

Introduction

Ecosystems are often resistant to naturally occurring changes and disturbances. However, occasionally they display large regime shifts and reach a new stable state, with a different community structure and inherent feedbacks (Folke et al. 2004). Regime shifts occur when gradual changes in the ecosystem, which generally have little impact (Scheffer et al. 2001), reach a threshold and the system undergoes a large shift that is often difficult to reverse (Scheffer and Carpenter 2003; Kinzig et al. 2006). Factors that may lead to regime shifts include disruption of species composition and trophic interactions, loss of connectivity, and long term climatic and abiotic changes (Suding et al. 2004). Examples of regime shifts include the Caribbean coral reefs which shifted from a coral to algal-dominated community after overfishing of herbivores (Hughes 1994; Mumby et al.

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2007); and a temperate lake shifting from oligotrophic to eutrophic due to increased agricultural nutrient input (Carpenter 2005).

Models help to understand and diagnose regime shift mechanisms (Scheffer and Carpenter 2003). Conceptual models have been developed for several ecosystems (see Hobbs and Suding 2009) and have been useful for exploring fundamental mechanisms of regime shifts such as spatial heterogeneity and environmental fluctuations (Scheffer and Carpenter 2003). Mathematical models can provide a more rigorous analysis than the qualitative reasoning used in many conceptual models by quantitatively predicting how certain mechanisms can lead to alternate states/regimes (Scheffer and Carpenter 2003). The effect of a driver of change on the ecosystem can often be described quantitatively using threshold models, as they embody an ecosystem's resistance to change until a certain threshold after which a sudden and considerable change occurs and the ecosystem establishes a new regime and stability point (Walker and Meyers 2004; Scheffer 2008; Suding and Hobbs 2009).

To enhance management and allow restoration of ecosystems and habitats, and to evaluate consequences of human activities, we must recognize human social dynamics associated with these ecosystems (Walker and Meyers 2004; King and Whisenant 2009). The development of socio-ecological models can help management and restoration. Most social ecological systems described in the literature are conceptual and exhibit thresholds in the ecological system driven by changes in the social system, but do not include feedbacks to produce reciprocal shifts in the social system (Walker and Meyers 2004; King and Whisenant 2009). According to the Resilience Alliance and SFI (2010), a small number of socio-ecological systems with reciprocity in the social system have been described, and only a few have been the subject of mathematical modeling (e.g., Bjørndal and Conrad 1987; Homans and Wilen 1997; Satake and Iwasa 2006; Iwasa et al. 2007; Satake et al. 2007a, b; Suzuki and Iwasa 2009a, b; Iwasa et al. 2010). Here we develop a mathematical model to describe farmland abandonment dynamics, considering the reciprocal feedbacks between the social and ecological dynamics of farmland abandonment.

In Europe, natural forest has long been cleared for agricultural purposes. However, in the last decades,

particularly in mountainous areas, we have been observing human migration to urbanized areas (rural exodus) and the abandonment of farmland (MacDonald et al. 2000), followed by forest regeneration (Poyatos et al. 2003; Bielsa et al. 2005; Nikodemus et al. 2005; Gellrich and Zimmermann 2006; Keenleyside and Tucker 2010). Migration and farmland abandonment are triggered by geo-physical and socio-economic aspects such as differences in income between farm and non-farm jobs, change in labor markets, relative prices of agricultural products, agriculture structures and policies, inability to modernize land-use (due to land steepness and/or inexistence of road access to more remote areas), and geographical and cultural isolation of settlements (MacDonald et al. 2000; Poyatos et al. 2003; Bielsa et al. 2005; Gellrich and Zimmermann 2006; Kanowski et al. 2009; Keenleyside and Tucker 2010). Migration to regions of greater wealth (Jokisch 2002) is often accentuated by the ongoing process of globalization which has increased the competition from other agricultural areas with lower production costs (Parés-Ramos et al. 2008; Keenleyside and Tucker 2010).

We use our socio-ecological model of farmland abandonment to examine the prevalence of regime shifts in these systems and their degree of irreversibility. We start by presenting and analyzing separate models for the ecological and social dynamics. Then, we link both components in an integrated socio-ecological model, and examine how the dynamics of the integrated model differs from the analysis of each component individually. We conclude by discussing how the socio-ecological model exhibits a higher degree of irreversibility than what would be expected by considering the social dynamics alone.

Ecological model

Our ecological model has one state variable: the forest area, F . We assume that the total potential farmable area is a constant T , and therefore the farmland area A equals $T - F$. The forest system is subject to two processes of interest: growth and deforestation (logging). We assumed forest cover grows logistically (Tsukada 1981; Bennett 1983; MacDonald and Cwynar 1991) since after an initial

exponential increase (Bennett 1986), growth will be limited by the total area available; ε is the forest rate of increase and T is the maximum area available. We assume that deforestation depends on the following: each resident’s ability to deforest (remove native vegetation for agricultural purposes), λ , the number of residents, R , and the existing forest area, F , i.e., residents will tend to deforest more if there is a greater area available to deforest. This assumption relies on humans utility-maximizing behavior theory that states that, if possible, individuals are willing to maximize the utility they can obtain (Aleskerov et al. 2007), and that this determination will be greater the larger the utility (forest area) available to explore is; also, the probability of an individual to find land to deforest also increases with forest area. Therefore, the forest dynamics is given by:

$$\frac{dF}{dt} = \varepsilon F \left(1 - \frac{F}{T}\right) - \lambda RF \tag{1}$$

Equilibria and stability analysis

This equation has two equilibria, $\hat{F} = 0$ and $\hat{F} = \frac{T}{\varepsilon}(\varepsilon - R\lambda)$. Stability analysis reveals that if $R\lambda > \varepsilon$, $\hat{F} = 0$ is a stable equilibrium (and the other equilibrium is unstable), i.e., when the deforestation rate exceeds forest rate of increase, the forest disappears; if $R\lambda < \varepsilon$, $\hat{F} = \frac{T}{\varepsilon}(\varepsilon - R\lambda)$ is the stable equilibrium (and the other equilibrium becomes unstable), i.e., when the intrinsic forest growth rate exceeds the deforestation rate, forest area at equilibrium increases with the forest rate of increase, ε , and decreases with

residents’ increased deforestation ability, λ , or with increasing number of residents (Fig. 1).

Social model

Our social system has one state variable: the number of migrants, M . We assume that the population size is a constant, P , and therefore, the number of residents, R , is equal to $P - M$. Individuals migrate at rate given by

$$\frac{dM}{dt} = f\left(\frac{M}{P}\right) \tag{2}$$

where f is the function that describes how the rate of migration depends on the proportion of individuals that have already migrated, M/P . This reflects the reality of migration being a collective behavior (MacDonald et al. 2000; Jokisch 2002; Bielsa et al. 2005; Gellrich and Zimmermann 2006; Kanowski et al. 2009): an individual’s decision is frequently affected by the decision of others (Fischbacher et al. 2001).

Granovetter (1978) developed a threshold model to describe collective behaviors which can be applied to situations where actors have two alternatives and the costs and/or benefits of each depends on how many other actors choose each alternative (such as migrating, voting, abandoning a party, or joining a riot). The key concept of Granovetter’s model is the “threshold”, or the proportion of others who must make one decision before a given actor does so. In a population, each individual has a certain threshold, and only once this threshold is reached, this individual will change his/her decision (and choose the other alternative).

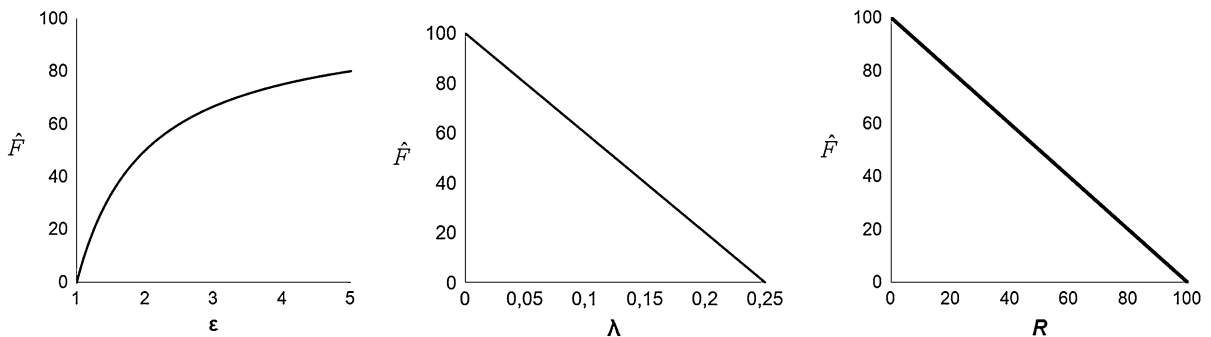


Fig. 1 Ecological model dynamics: effect of forest rate of increase, ε (with $T = 100$ ha, $R = 20$ individuals, $\lambda = 0.05$ resident⁻¹ year⁻¹), individual’s deforestation ability, λ (with

$T = 100$ ha, $R = 20$ individuals, $\varepsilon = 5$ year⁻¹), and number of residents, R (with $T = 100$ ha, $\lambda = 0.05$ resident⁻¹ year⁻¹, $\varepsilon = 5$ year⁻¹), on forest area (ha) in equilibrium

Therefore, we assume that, at any given time, an individual's probability of migrating depends on the proportion of individuals of the population that have already migrated, M/P i.e., an individual will only migrate if the proportion of migrants equals or exceeds its personal threshold. We assume that, in the population, thresholds have a bell-shaped distribution and follow the logistic distribution, which has been used to describe other human decision processes (Carpenter et al. 1999; Satake and Iwasa 2006; Satake et al. 2007a, b; Suzuki and Iwasa 2009a). Suppose that each individual has a probability per unit time, ω , of making a decision of whether to migrate. The proportion of individuals that will decide to migrate will be the proportion that has a threshold less than M/P , which is given by the cumulative distribution function of the logistic distribution, minus the proportion of individuals from the population that has already migrated (see a similar algorithm in Iwasa et al. 2010). The number of individuals that migrate is equal to this proportion multiplied by the population size, P . Therefore we have that

$$f\left(\frac{M}{P}\right) = \omega \cdot \left[\text{CDF}\left(\frac{M}{P}\right) - \frac{M}{P} \right] \cdot P \quad (3)$$

where

$$\text{CDF}\left(\frac{M}{P}\right) = \frac{1}{1 + e^{-\frac{(\mu - \frac{M}{P})}{s}}} \quad (4)$$

The full dynamics of the number of migrants is:

$$\frac{dM}{dt} = \omega \left[\frac{1}{1 + e^{-\frac{(\mu - \frac{M}{P})}{s}}} - \frac{M}{P} \right] P \quad (5)$$

The parameters of the logistic distribution μ and s determine the probability of migration. The parameter μ represents the average threshold in the population, i.e., the average proportion of migrants that triggers the others to migrate too. We develop below an economic sub-model to determine this parameter and link it to the ecological component of the system. The parameter s is proportional to the variance of the thresholds in the population, and therefore we will use it to characterize the strength of personal connections (social bonding that leads to higher levels of conformity) in the population (i.e., a smaller s represents a population where individuals have similar thresholds, and therefore, a greater synchronism of migration).

Equilibria and stability analysis

Since the equilibria of this equation cannot be analytically determined, we estimated it numerically. Depending on the combination of μ and s , the number of migrants can have different equilibria. For high values of s (i.e., individuals of the population have dissimilar thresholds), the number of migrants in equilibrium, \hat{M} , decreases with increasing μ (Fig. 2a). For small values of s (i.e., individuals have similar thresholds), the social system can have one or three equilibria: when μ is small, there is one stable equilibrium, $\hat{M} \approx P$ and all or most individuals will abandon farmland; when μ is high, there is one stable equilibrium, $\hat{M} \approx 0$ which will trigger a return of all or most of the migrants to the farmland; when μ has an intermediate value, there are three equilibria, one of the equilibria is unstable and the other two are stable ($\hat{M} \approx 0$ and $\hat{M} \approx P$) (Fig. 2b). In the latter case, the social dynamics is partially irreversible because it exhibits a hysteresis. For example, a population of 100 individuals with a similar threshold (small s corresponding to high social bonding, e.g., $s = 0.1$) will initiate a process of migration if the mean threshold (μ) is smaller than 0.3, however in order for those individuals to return, it would not suffice to increase μ to 0.3, instead μ would have to increase to 0.7 (Fig. 2b).

The economics of migration

Migration is triggered by socio-economic conditions (MacDonald et al. 2000; Jokisch 2002; Bielsa et al. 2005; Gellrich and Zimmermann 2006; Kanowski et al. 2009). Hence, we will use μ (average threshold in the population) to characterize the socio-economic dynamics. Let the farmland utility (this is the satisfaction that one individual derives from being a farmer) including income and other non-financial benefits, be the product of the farmland area, A , and the utility per agricultural area unit per year, h . The farmland utility per resident is given by $Ah/(P-M)$, where P is the total population. Let the city utility per capita be γ . When the farmland utility equals the city utility, the economics reasons to migrate are irrelevant; in this case, the reasons to migrate would be strictly social and motivated by social-bonding. Studies in diverse research fields, such as social

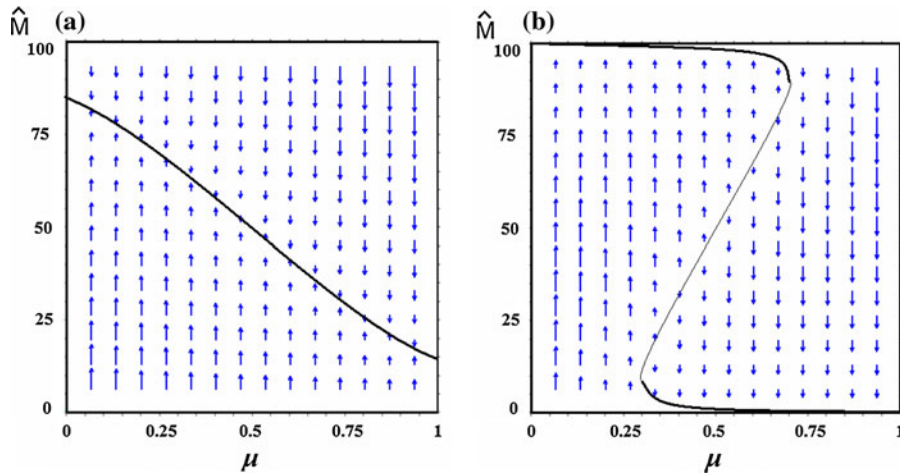


Fig. 2 Phase portrait of social model dynamics: effect of μ on the number of migrants in equilibrium (\hat{M}) and stability analysis with $P = 100$ individuals, $\omega = 1 \text{ year}^{-1}$, and **a** $s = 0.5$ (\hat{M} decreases with increasing μ ; stable equilibrium),

and **b** $s = 0.1$ (two stable equilibria: $\hat{M} \approx P$ and $\hat{M} \approx 0$, and an unstable equilibrium in the diagonal). *Thick and thin lines* represent stable and unstable equilibria, respectively; *arrows* represent vectors of change

psychology, politics, and economy, reveal that humans tend to “follow the crowd/majority”. For instance, voters will tend to be influenced by election polls and vote for the party to which the polls attributed the majority (Callander 2007). The social scientists name it conformity behavior (Nemeth and Wachtler 1983). Hence, we assume that, in this situation, individuals only migrate if more than half of the population already did so. Hence, when $Ah/(P - M) = \gamma$, the average threshold should be $\mu = 0.5$, and therefore the mean threshold in the population is given by

$$\mu = \frac{Ah}{P - M} \tag{6}$$

Therefore, the final equation of the social model, representing the migrants dynamics, is:

$$\frac{dM}{dt} = \omega \cdot \left[\frac{P}{1 + e^{\frac{\left(\frac{Ah}{P-M} - \frac{M}{P}\right)}{s}}} - M \right] \tag{7}$$

Socio-ecological model

The equations of the socio-ecological model for the farmland-forest ecosystem result from the combination of the equations of the ecological and social models (Eqs. 1 and 7, respectively). Since the

number of residents, R , used in the ecological model, is equal to $P - M$, and the farmland area, A , is given by $T - F$, the equations of the socio-ecological model are:

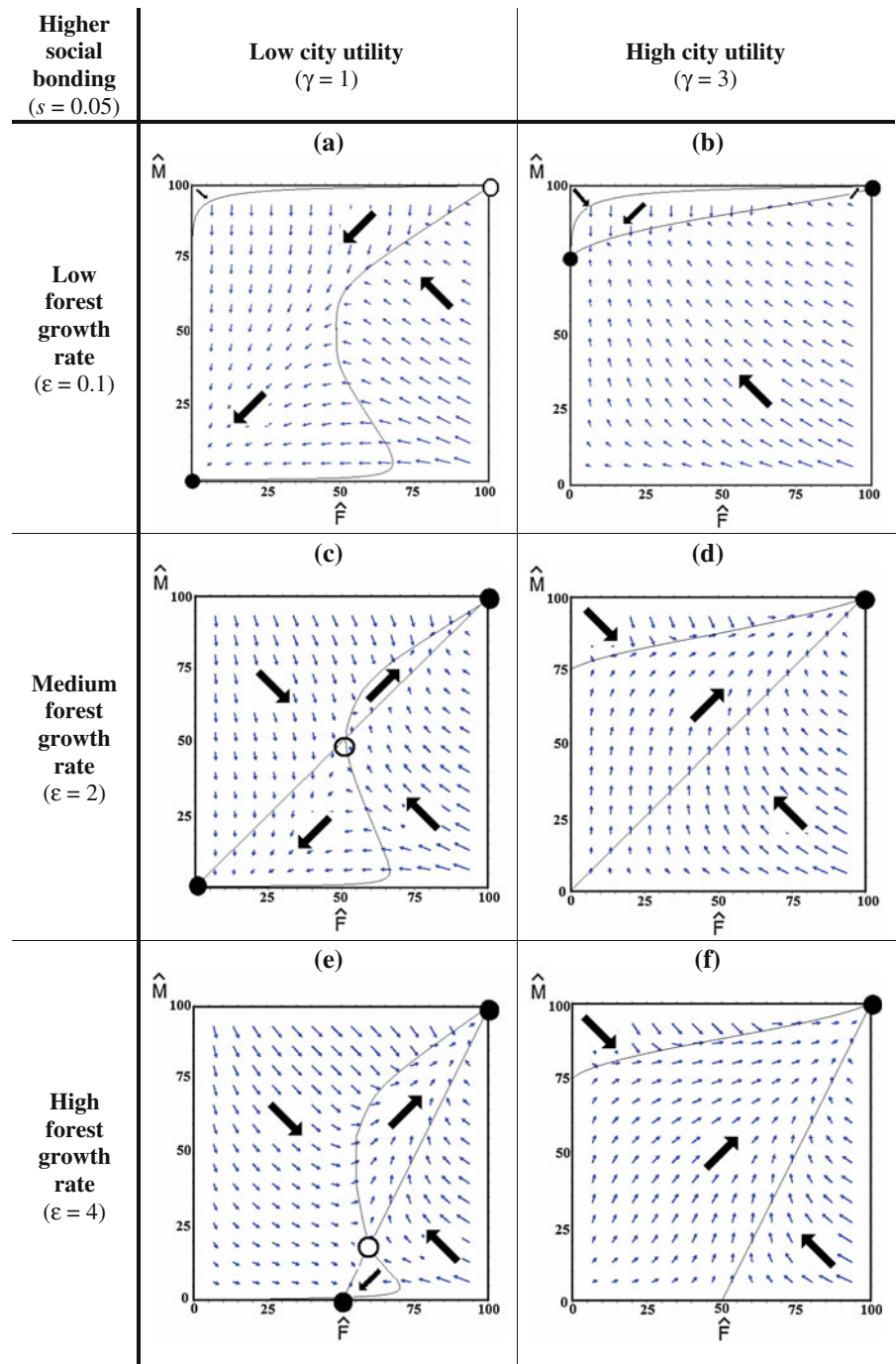
$$\begin{aligned} \frac{dF}{dt} &= \varepsilon F \left(1 - \frac{F}{T} \right) - \lambda(P - M)F \\ \frac{dM}{dt} &= \omega \cdot \left[\frac{P}{1 + e^{\frac{\left(\frac{(T-F)A}{P-M} - \frac{M}{P}\right)}{s}}} - M \right] \end{aligned} \tag{8}$$

Note that in the integrated socio-ecological model (Eq. 8), the number of residents, R , of the ecological model equation (Eq. 1) and the farmland area, A (or $T - F$), of the social equation (Eq. 7) are no longer parameters, but state variables. The two variables may now change over time and affect both social and ecological dynamics, generating reciprocal influence between the ecological and social systems.

Equilibria and stability analysis

The equilibria of the socio-ecological model can be determined by plotting on the same graph (with the variables of interest, F and M , in the axis) the zero isoclines of the ecological and social models. The points of intersection of the zero isoclines of the social and ecological models constitute the equilibria

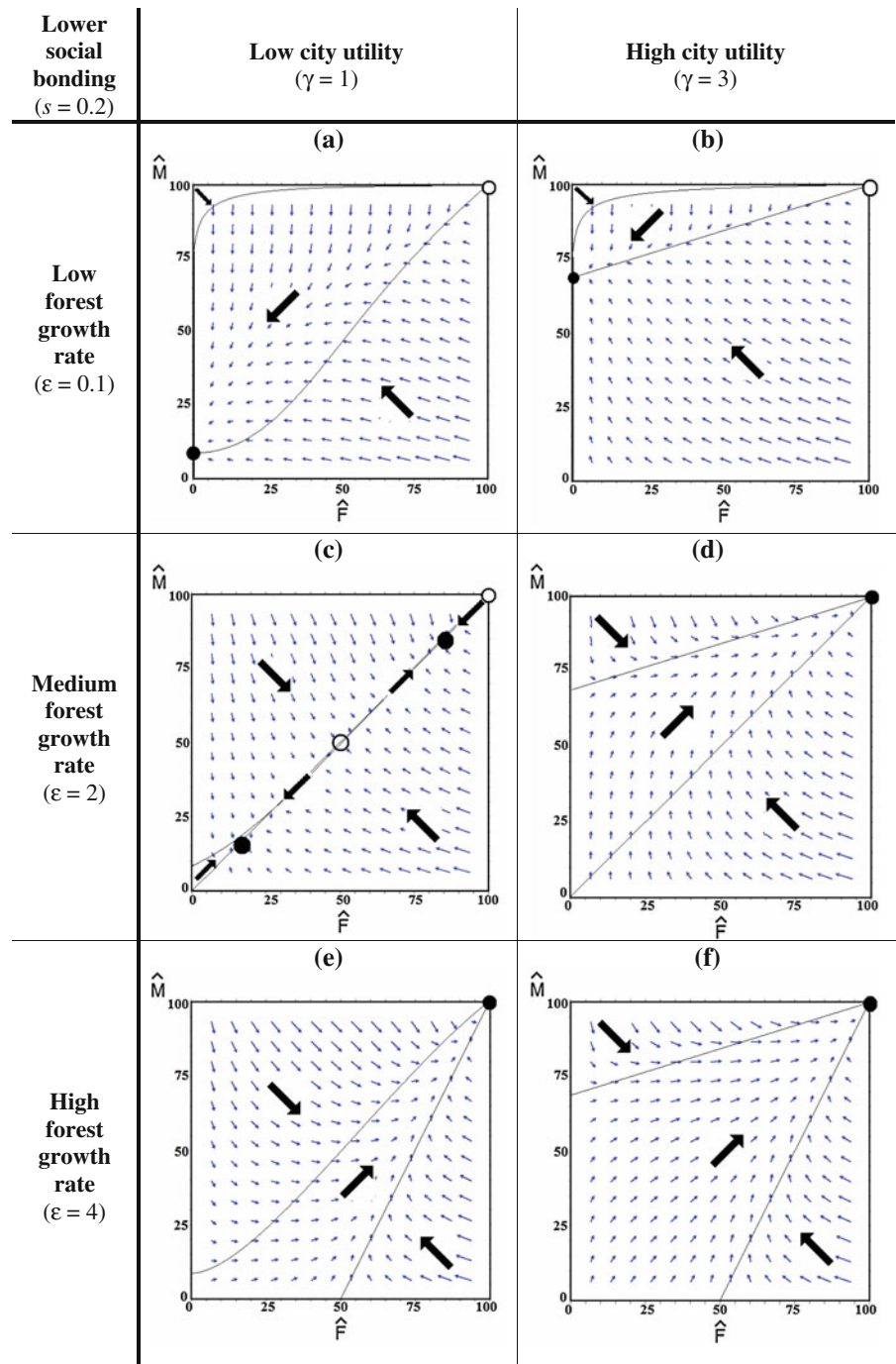
Fig. 3 Phase portrait of socio-ecological dynamics with higher social bonding ($s = 0.05$): equilibria and stability with low to high forest growth rate ($\varepsilon = 0.1, 2$ or 4 year^{-1}), and low and high city utility ($\gamma = 1$ or 3 utility $\text{year}^{-1} \text{ individual}^{-1}$) with $\lambda = 0.02 \text{ individual}^{-1} \text{ year}^{-1}$, $h = 1 \text{ utility year}^{-1} \text{ ha}^{-1}$, $P = 100$ individuals, and $T = 100$ ha (*lines* represent the social and ecological model zero isoclines, *full circles* indicate the socio-ecological model's stable equilibria, *empty circles* indicate the socio-ecological model's unstable equilibria, and *arrows* indicate the trend to achieve the equilibrium)



of the socio-ecological model. The stability of these equilibria is determined by the sum of the vectors of change of the social and ecological models: if the sum vectors point to the equilibrium, this will be stable; if they point in opposite directions, the equilibrium will be unstable (Figs. 3, 4). For a given

combination of parameters, the socio-ecological model can have one to four equilibria. Not only the number but also the position of the equilibria varies with the parameters. Overall, the SES has five types of stable equilibria: (1) $\hat{M} \approx P$ and $\hat{F} \approx T$, i.e., all individuals migrate and forest area grows to occupy

Fig. 4 Phase portrait of socio-ecological dynamics with lower social bonding ($s = 0.2$): equilibria and stability with low to high forest growth rate ($\varepsilon = 0.1, 2$ or 4 year^{-1}), and low and high city utility ($\gamma = 1$ or 3 utility $\text{year}^{-1} \text{ individual}^{-1}$) with $\lambda = 0.02 \text{ individual}^{-1} \text{ year}^{-1}$, $h = 1 \text{ utility year}^{-1} \text{ ha}^{-1}$, $P = 100$ individuals, and $T = 100 \text{ ha}$ (*lines* represent the social and ecological model zero isoclines, *full circles* indicate the socio-ecological model's stable equilibria, *empty circles* indicate the socio-ecological model's unstable equilibria, and *arrows* indicate the trend to achieve the equilibrium)



all the area previously occupied by farmland (e.g., situations with high city utility and medium–high forest growth rate, Figs. 3d, f, 4d–f); (2) $\hat{M} \approx 0$ and $\hat{F} \approx 0$, i. e., individuals do not migrate and all farmable area is farmed (forest is decimated) (e.g., situation with high social bonding, slow forest growth

rate and low city utility, Fig. 3a); (3) $\hat{M} \approx 0$ and $\hat{F} = \frac{T}{\varepsilon}(\varepsilon - P\lambda)$, i.e., individuals do not migrate but do not have the ability to deforest all farmable area, letting some area be occupied by forest (e.g., situation with high social bonding, elevated forest growth rate, and low city utility, Fig. 3e); (4) $\hat{M} \in]0, 100[$ and $\hat{F} \approx 0$,

i.e., part of the population migrates, all farmable area is occupied by farmland activities (e.g., situations with low social bonding and low forest growth rate, Figs. 4a and b), (5) $\dot{M} \in]0, 100[$ and $\dot{F} \in]0, 100[$, i.e., part of the population migrates and part of the farmable area is occupied by forest (e.g., situation with low social bonding, low city utility, and medium forest growth rate, Fig. 4c). Hence, the system can display an intermediate stable equilibrium, i.e., cases when only part of the population migrates and farmable area is divided by farmland and forest, as well as the extreme cases (no migration or mass migration in the social system and decimation of the forest or complete forest regeneration in the ecological system).

A broad range of parameter combinations were explored, with forest growth rate (ε) ranging from 0.1 to 5, resident's ability to deforest (λ) ranging from 0 to 0.25, annual farmland ha utility (h) ranging from 0.1 to 3, annual city utility (γ) ranging from 1 to 5, and social bonding (s) ranging from 0.01 to 0.5. The parameter exploration (e.g., Figs. 3, 4) reveals that: (i) a decrease in social bonding contributes to an increase in the frequency of the equilibria with partial migration; (ii) the increase in social bonding potentiates the extreme situations of no migration at all or mass migration events; (iii) the increase of forest growth rate, increases the frequency of equilibria

where forest cover is larger; (iv) mass migration (and consequent farmland abandonment) processes are more frequent with increasing city : farmland utility ratio; (v) the equilibria of no migration or mass migration in the social system and decimation of the forest or complete forest regeneration in the ecological system, respectively, are more frequent than the other equilibria; (vi) when city and farmland utilities are similar, two stable equilibria are possible (e.g., Figs. 3b, c, e, 4c), particularly when social bonding is strong.

Socio-ecological model linked dynamics and (ir)reversibility of regime shifts

The socio-ecological model dynamics and mechanisms of (ir)reversibility were evaluated through manipulation of city utility, γ . In the scenario presented in Fig. 5a, initially, residents and forest area are in equilibrium: there are no migrants and farmland occupies 99% of the farmable area (forest occupies only 1%). The relative increase of the city utility at time $t = 10$ (from $\gamma = 2$ to 2.7) leads to migration, farmland abandonment, and forest regeneration. A posterior decrease in city utility to a level equal to the initial state ($\gamma = 2$) does not suffice to trigger the return of the individuals to the farmland

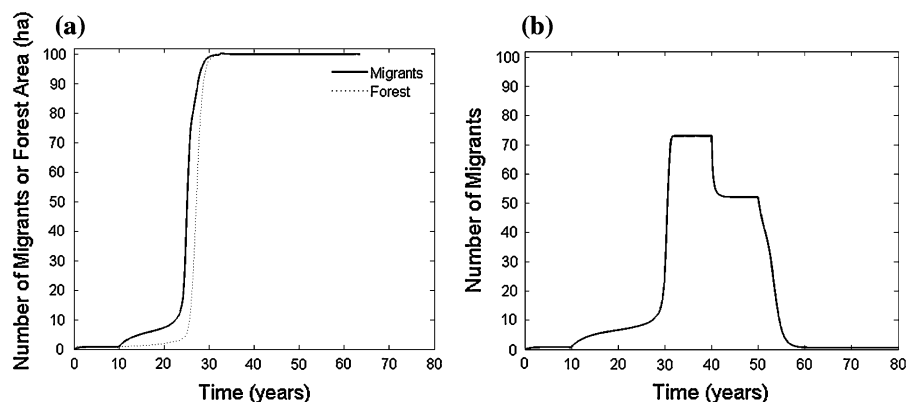


Fig. 5 Social dynamics (number of migrants over time) with city utility, γ , changing over time ($\gamma = 2, 2.7, 2$, and 1.9 utility individual⁻¹ year⁻¹, respectively for $t \in [0, 10[$, $[10, 40[$, $[40, 50[$, and $[50, 80[$ years), when considering that the **a** the social dynamics are linked to a dynamic ecological system (SES) ($M_{t=0} = 0$ individuals, $T = 100$ ha, $P = 100$ individuals, $h = 1$ utility ha⁻¹ year⁻¹, $s = 0.05$, $\varepsilon = 2$ year⁻¹,

$\lambda = 0.02$ individual⁻¹ year⁻¹, $\omega = 1$ year⁻¹, and $F_{t=0} = 1$ ha), and when considering that **b** ecological system is static, i.e., not dynamic ($M_{t=0} = 0$ individuals, $T = 100$ ha, $P = 100$ individuals, $h = 1$ utility ha⁻¹ year⁻¹, $\tau = 0$ utility year⁻¹, $s = 0.05$, $\omega = 1$ year⁻¹ and $F = 1$ ha for $t \in [0, 80[$ years)

due to the hysteresis of the social dynamics (Fig. 5a). The return of the residents would only be possible if the city utility reduced significantly (e.g., decrease to $\gamma = 0.6$, not represented on Fig. 5). This example (Fig. 5a) illustrates the characteristic resistance of each stable state/regime and the high chances of irreversibility of regime shifts of this socio-ecological system. In order to investigate if this irreversibility is due to the hysteresis in the social dynamics (Fig. 2b) and/or to the interaction between the social and ecological dynamics, we compared the social dynamics linked to a dynamic ecological system, (socio-ecological model here developed, Eq. 8, Fig. 5a) with the social dynamics linked to a static ecological system (Fig. 5b). The comparison of the two shows that not only the social equilibria are different between the two cases, but also that the consideration of a dynamic ecological system increases the irreversibility of the regime shift on the social system; without the link to a dynamic ecological system, the social system would revert to the initial state if city utility was reduced to 1.9. (Note that the change in the threshold might not be universal, this is just an example where we show that this is likely to occur for some parameter combinations). On the other hand, whether considering the ecological system static or dynamic, we show that a reduction to the initial city utility, $\gamma = 2$, would not suffice to reverse the regime shift. Therefore, we can conclude that the irreversibility is caused by the social dynamics, but its effect can be enhanced by its link to a dynamic ecological system. In other words, once the individuals abandon the farmland to migrate to the city, it is very difficult to make them return. This is not only due to the hysteresis in the social system (caused by individual's decision being influenced by the other members of the community), but also due to the fact that farmland area is gradually overtaken by the forest, and thus its utility (and farmland utility: city utility ratio) is also gradually reduced. Therefore, chances to revert the regime shift diminish progressively.

Discussion

One of the most interesting novelties of this model is the ability to reproduce the two-way coupling of the social and ecological dynamics. We present one of the few socio-ecological models which explores the

effect of the ecological dynamics on the social system (Carpenter et al. 2009; Resilience Alliance and SFI 2010). The socio-ecological model for farmland abandonment mathematically expresses human migration as a collective behavior which is socio-economically driven (Satake et al. 2007a, b; Kuemmerle et al. 2008; Parés-Ramos et al. 2008; Lakes et al. 2009) and forest as a dynamic system (Gellrich and Zimmermann 2006; Verburg and Overmars 2009). To our knowledge, this is the first model of farmland abandonment exploring both of these key aspects simultaneously. The model provides a framework to better understand how these processes interact and why (and when) do they lead to regime shifts within the system. In the farmland abandonment model, the ecological dynamics can be vital in reinforcing the irreversibility of the regime shift generated by the social dynamics.

Overall, the socio-ecological model for farmland abandonment is able to describe the dynamics observed in previous field studies, such as: rapid socio-economic changes lead to general farmland abandonment (Poyatos et al. 2003; Parés-Ramos et al. 2008); farmland abandonment is more common in regions where land has low profitability (Gellrich et al. 2007 and forest re-growth); trees and shrubs occupy the abandoned land, which hampers its re-occupation (Bielsa et al. 2005). The model equilibria range from mass migration and forest regeneration to no migration and complete deforestation (with intermediate cases of partial migration and/or partial farmland abandonment). In addition, the model reproduces the (ir)reversibility mechanisms of the regime shifts we often find in the field.

In the model, the area occupied by farmland depends on the balance between forest growth and deforestation, the latter being a result from the number of residents and their ability to deforest. In average, individuals decide to migrate when they can attain a greater utility in the city than in the farmland; the greater the difference between the city and farmland utility, the more likely they are to migrate. However, migration can be more or less synchronous depending on the strength of social bonds within the population.

The parameter exploration identified situations where, for the same set of parameters, there are two possible stable equilibria (Figs. 3b, c, e, 4c). These represent conditions where a regime shift can occur

and in which reversibility is likely difficult. When we are in a region of parameters with multiple stable equilibria, dynamics do not respond linearly to external parameters (such as utility ratio, e.g. Fig. 5a). When the system is at one of its two stable equilibria and is perturbed by a change in the external parameter, it is attracted to the other stable equilibrium. Then, even when the external parameter is restored, the internal dynamics have already changed and thus, reversing to the initial equilibrium can only be possible if the system is again significantly perturbed. Under these conditions (combination of parameters that leads to multiple stable equilibria), in the farmland model, when the social system shifts, a regime shift will also be triggered in the ecosystem, i.e., once population migrates to new areas and abandons the farmland, forest gradually regenerates. The regime shift created by the social system exhibits a clear hysteresis which explains the difficulty to reverse it. Furthermore, the resilience of the new steady state in the social system can be amplified by the ecological dynamics; allowing the ecological system to be dynamic not only may increase the amplitude of the regime shift as it may enlarge its irreversibility (Fig. 5). Therefore, one can categorize this system as a linked socio-ecological system with regime shifts in both systems and reciprocal influences (Walker and Meyers 2004; Resilience Alliance and SFI 2010). In our model, when city and farmland utility are similar, a situation where two stable equilibria are possible is common. When city has high utility, but forest grows slowly (e.g. Fig. 3b), farmland area tends to remain stable and therefore its utility remains high. In this case, the system can alternate between total migration with forest regeneration and forest eradicated and significant migration. When city utility is low, but forest grows very fast (e.g., Figs. 3c, e, 4c) and takes over farmland area, the residents need to deforest very often which reduces farmland utility. In this case, the system can alternate between very significant migration with significant forest regeneration, and reduced migration with complete (or partial) forest regeneration. The greater the social bonding, the less similar the farmland and city utility need to be to still have two stable equilibria.

In mountainous areas, agriculture productivity and profitability is usually low due to geographical constraints. Therefore, farmland is rarely sold after

being abandoned (Keenleyside and Tucker 2010). The individuals that do not abandon their parcel of farmland generally do not have physical conditions to explore an extra parcel. Still, the model developed allows for some change in the farmland utility that could alter the migration dynamics. Despite not presented in the results section, there are parameters in this model, such as the resident's ability to deforest (λ) and annual farmland profit per ha (h), which, if changed over time, can alter the model outcomes. The access to machinery to help deforestation and plantation would boost λ and h , which would increase farmland profit and reduce abandonment. In addition, the change of crop to achieve higher profit (h) could also contribute to it.

Understanding the dynamics of the socio-ecological system allows us to identify the tipping point that leads to a rapid change in the system. A better understanding of the mechanisms generating farmland abandonment will hopefully help to better manage this socio-ecological system (both to avoid change or to restore forest ecosystems). Farmland abandonment can be considered desirable or undesirable since, on one hand, it may increase connectivity between forest patches and restore the natural ecosystems, but on the other hand, it may lead to declines or local extinctions of several flora and fauna species associated with farmland, and increase frequency of fires (Bielsa et al. 2005; Proença and Pereira 2010). Since the tipping point of ecological system is mainly dependent on the farmland: city utility ratio, migration could be avoided by increasing subsidies to agricultural production. If the objective is to restore the forest ecosystem, one could instead decrease existing agricultural subsidies in these regions, although the negative social impacts of such measure would have to be considered beforehand.

The model here developed focused on rural exodus and was inspired by small rural communities, particularly in mountainous regions away from major economic centers, in which each individual or small group of individuals (e.g. family) owns a relatively small land parcel that they personally explore. The conditions assumed by the model are currently observed, in several mountainous regions in Europe (Poyatos et al. 2003; Bielsa et al. 2005; Gellrich et al. 2007; Kuemmerle et al. 2008; Parés-Ramos et al. 2008). In addition, this trend is expected to intensify

over the century and spread to other parts of the world such as USA, China, and Australia (van Vuuren et al. 2006; Proença and Pereira 2010). However, this model might not be so suitable to explain other farmland systems, particularly systems where individuals commute daily or weekly to their place of work and behave as weekend farmers, or in systems where the possibility of aggregation of land parcels allows for increased economic viability of farming and a different socio-ecological dynamics.

We used a simple mean-field model, i.e., a coupled differential equation model, to describe the behavior of two variables: resident population and farmland area. More complexity and realism can be added by using other approaches. For instance, one can make the model spatially explicit by simulating the land use transitions in each grid cell using a set of rules related to the location suitability for farming and the local spatial neighborhood context (Verburg and Overmars 2009). Variation in individual decision-making can be explored by developing an individual-based model (Tilman and Kareiva 1997). These more complex models require more parameters and the full range of dynamics can be, as a result, difficult to explore. Our analysis of the mean-field model dynamics can be used to set parameter boundaries of interest and guide the future exploration of more complex models.

Models constitute simplifications of the real world and therefore they can always be improved to attain higher realism. Future developments of the model presented could include more realistic population dynamics, namely, considering an age-structured population. This configuration would allow the incorporation of a specific farmland:city utility ratio for each generation (as this is expected to vary, Pereira et al. 2005). In addition, it would be interesting to develop a study of social decision-making in farmland abandonment to test the ideas presented in this model.

In coupled socio-ecological systems, humans and nature interact reciprocally and form complex feedback loops (Liu et al. 2007). Most studies of socio-ecological systems do not explore the human component of the system, considering only the ecological dynamics (Resilience Alliance and SFI 2010). Others address the impact of humans on the ecosystem, but fail to address the impact of ecological dynamics on the social system (Resilience Alliance and SFI 2010,

a few exceptions include fisheries (e.g. Bjørndal and Conrad 1987; Homans and Wilen 1997) and lake models (Iwasa et al. 2010). The management of a socio-ecological system with lack of understanding of the complexity of its socio-ecological dynamics might lead to unexpected outcomes (Liu et al. 2007). For instance, conservation policies which intended to protect the panda habitat through the establishment of a reserve and attribution of subsidies to local residents (to reduce logging) failed. Managers overlooked the fact that when residents' income increases, the number of households increases and the number of persons per household decreases. This policy led to an increased need for fuelwood and land for house construction, and consequently further destruction of the panda habitat (Liu et al. 2007). The socio-ecological model of farmland abandonment is also a good example of how social and ecological dynamics have to be explored concurrently when studying a socio-ecological system in order to illustrate their complex interactions that are not evident when studied independently. Figure 5 illustrates that ignoring the fact that both social and ecological systems are dynamic, may lead to inconsequent management efforts. For instance, if the ecological system dynamics are not considered, managers interested in maintaining farmland may attribute a certain value in agricultural subsidies to farmland residents in order to reduce farmland:city utility ratio to a particular target that would reverse farmland abandonment. However, since they are not considering the ecosystem to be dynamic, the value of subsidies attributed will likely be insufficient to reverse farmland abandonment. We believe models with a similar framework to the one here presented (coupled socio-ecological dynamics two-way linked, in opposition to models focusing solely on the ecological dynamics or on the humans' impacts on the ecosystem) could be applied to other interlinked socio-ecological systems, such as lakes and wetlands (Gunderson et al. 2006), marine reserves (Pollnac et al. 2010), fisheries (Peterson 2000; Cinner et al. 2009), and ecological conservation and community-based ecotourism (Walker et al. 2004). Mathematical models of linked social-ecological systems are fundamental as they may contribute to implement an appropriate management and effective restoration policies (Bielsa et al. 2005; Liu et al. 2007; Carpenter et al. 2009).

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