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The impact of human-environment interactions on the stability of forest-grassland mosaic ecosystems

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Forest-grassland mosaic ecosystems can exhibit alternative stable states, whereby under the same environmental conditions, the ecosystem could equally well reside either in one state or another, depending on the initial conditions. We develop a mathematical model that couples a simplified forest-grassland mosaic model to a dynamic model of opinions about conservation priorities in a population, based on perceptions of ecosystem rarity. Weak human influence increases the region of parameter space where alternative stable states are possible. However, strong human influence precludes bistability, such that forest and grassland either co-exist at a single, stable equilibrium, or their relative abundance oscillates. Moreover, a perturbation can shift the system from a stable state to an oscillatory state. We conclude that human-environment interactions can qualitatively alter the composition of forest-grassland mosaic ecosystems. The human role in such systems should be viewed as dynamic, responsive element rather than as a fixed, unchanging entity.

Despite the tendency to refer to ecosystems as homogeneous (such as a “forest” or “grassland”), most ecosystems exist approximately as mosaics in which clusters of different landscape types scatter across a given partition of the environment^{1–6}. The distribution of these landscape types is governed by a variety of factors such as spatial inhomogeneities in landscape topology^{2,5} and random events like forest fires or hurricanes^{7–10}. Often these landscape types compete directly for resources^{8–13}. In such ecosystems, it is critical to consider these varying landscape types and their distributions individually in order to fully describe the ecosystem^{14–18}. A prime example of such a competitive mosaic ecosystem are forest-grassland mosaics, where grassland and forest compete directly for soil nutrients, sunlight and space^{10–12,19}.

Some ecosystems respond gradually (and thus predictably) to natural and human-induced influences. In other ecosystems, including certain types of lakes, coral reefs, oceans, forests and deserts, change can instead occur through a sudden shift to an alternative state^{20–25}. Such ecosystems can be formalized mathematically as bistable systems, which simultaneously exhibit two stable equilibrium states. Depending on the initial state of the system and magnitude of perturbations, the system could equally well be in either of the stable states, and under the right circumstances it could also shift from one stable state to the other^{20,21}.

Understanding the mechanisms governing the stability of these alternative stable states, and how transitions between states occur, has obvious significance for environmental management. These mechanisms have been modeled previously, for example in the case of forest-grassland mosaics such as savannas, which appear to be well-described by the bistability paradigm^{7,26}. Previous experimental and modeling research has explored how sufficiently frequent forest fires (and hurricanes, in some cases) can maintain savanna in a stable grassland state through deforestation^{7,26,27}. Conversely, below a certain fire frequency threshold, the system evolves toward a state where forest cover is very high; the resulting forested state is stable because dense stands of trees are resistant to forest fires^{7,26}.

For many ecosystems, human influence cannot be discounted in any reasonably valid model. It has been estimated that up to half of the earth’s land surface has been directly transformed by human action such as agriculture, and forest-grassland mosaics are no exception^{28,29}. However, human action does not always result in a mono-directional shift in mosaic ecosystem composition. For instance irrigation of farmland in arid regions leads to increased rainfall and hence reduced desertification. Alternatively, clearing pastures for grazing leads to



decreased rainfall and hence increased desertification²⁸. The same potential for dual influence exists in forested areas. For instance, grazing management, the planting of legumes and other means of carbon fixation leads to deforestation³⁰, whereas reducing silviculture and fire management leads to an increase in forest cover³¹. Hence, human activities have the potential to change the composition of a mosaic ecosystem in a variety of ways.

On the other hand, changes in ecosystem states can result in changes in human perceptions and thus changes in human activities³². For example, cross-sectional surveys that gauge public priorities for conservation consistently rank the rarity of a species and the severity of threats to its existence as a top determinant of a species' conservation value, along with taxonomic level, physical size, and ecological importance of the species^{33,34}. This suggests that as a species becomes more rare, its conservation value may increase in the eyes of the public, leading to efforts to protect and restore the species. Such a dynamic has been suggested as a possible driver behind the transformation of the North American wolf (*Canis lupus*) from being perceived as a pest species, in the era when they were very abundant, to a conservation priority in more recent years, after decades of extirpation by humans³⁵.

Because human activities influence ecosystems, and ecosystems can in turn influence human activities, they form a coupled human-environment system³². Mathematical models of natural systems for the most part have not accounted for the coupling between human actions and ecosystem dynamics, and this is particularly true for models of forest-grassland mosaics. However, given the sensitivity of forest-grassland mosaics to changing environmental conditions, it seems likely that human-environment system feedbacks could have a significant impact on the fate of these mosaics³⁶. Here, we develop a human-environment system model which couples a forest-grassland mosaic model to a dynamic model of rarity-driven perceptions of forest/grassland value, and how those perceptions influence the state of the mosaic. Our objective was to understand the impact of human-environment interactions on the stability properties of forest-grassland mosaics, with focus on the *Araucaria angustifolia* forest-grassland mosaic of southern Brazil.

Results

We first present a model of mosaic ecosystem dynamics in the absence of human effects, then we present a model of rarity-driven conservation values for forest versus grassland, and finally we present the coupled model that combines both of them.

Model of mosaic ecosystem dynamics. A simplified model of a forest-grassland mosaic is

$$\frac{dG}{dt} = \nu F - w(F)FG \quad (1)$$

$$\frac{dF}{dt} = w(F)FG - \nu F \quad (2)$$

where G and F represent the proportion of grassland and forest in the system, respectively, $w(F)$ modifies the rate of succession of grassland to forest and ν is the rate at which forest reverts to grassland through natural processes such as disturbance. These equations assume that new forest is created at a rate proportional to the product of the amount of existing forest F (from which new trees are created through dispersal) and the amount of existing grassland G (which is the amount of available space for newly forested lands), at a rate modified by $w(F)$. We assume $F + G = 1$ for the remainder of this paper, hence $w(F)FG$ becomes $w(F)F(1 - F)$, corresponding to density-dependent growth of forest, as modified by $w(F)$.

The function $w(F)$ represents the strong mediating role played by fire in many forest-grassland mosaics. In such mosaics, the most

common effect of fire is not to kill mature stands of trees ($F \rightarrow G$) but rather to kill saplings, or limit their growth ($G \rightarrow F$) while leaving adult trees relatively unharmed, hence decreasing the forest recruitment rate^{7,26}. Moreover, fire frequency is observed to decrease as forest cover F increases, because dense stands of trees are substantially more resistant to fire than sparsely forested plains of grassland^{7,26}. Hence, it is possible to express the effects of fire mediation implicitly in the $G \rightarrow F$ transition term, by modifying the tree recruitment FG with a factor $w(F)$ that depends on forest cover F . When forest cover F is low, we expect $w(F)$ to be low since recruitment is suppressed by fire, but when F is high, $w(F)$ is also higher because recruitment is not as affected by fire. Moreover, empirical studies indicate that the transition between low and high recruitment regimes is relatively sharp^{7,26}.

Because fire frequency drops off sharply at a specific threshold in forest cover^{7,26}, we will assume $w(F)$ to be sigmoidal. For numerical analysis we will assume the functional form

$$w(F) = \frac{c}{1 + e^{-k(F/(1-F)) + b}} \quad (3)$$

where c , b and k are parameters, and k controls how sharp the transition is. An example of $w(F)$ is visualized in Supplementary Figure S1.

This model is similar to previous models for savanna ecosystems^{7,26} but makes the simplifying assumption of ignoring intermediate successional states between grassland and forest. This assumption may be reasonable when considering certain forest-grassland mosaics such as the naturally occurring *Araucaria angustifolia* mosaic in southern Brazil³⁷ and other mosaics that lack a savanna state. Here we will focus on such forest-grassland mosaics.

Because $F + G = 1$, the single equation

$$\frac{dF}{dt} = w(F)F(1 - F) - \nu F \quad (4)$$

is sufficient to describe the system. As in previous mosaic ecosystem models²⁶, the system exhibits two equilibria that can be simultaneously stable: (i) $F^* = 0$ (all grassland equilibrium) and (ii) $F^* > 0$ such that $w(F)(1 - F) = \nu$ (an "interior" equilibrium).

Model of human perception of conservation priorities. Natural grassland ecosystems can be highly biodiverse and hence have significant conservation value³⁷. We assume that the human population can be stratified into individuals who value forest over grassland (at their present relative abundance), versus individuals who value grassland over forest. The proportion of the population consisting of forest-preferrers is x , hence the proportion consisting of grassland-preferrers is $1 - x$. The value of forest versus grassland is determined by their relative scarcity (details below), and individuals change between these two states through a social learning (imitation) process³⁸⁻⁴⁰.

According to this social learning process, a forest-preferrer samples individuals at a constant rate d . If they sample another forest-preferrer, nothing happens. If they sample a grassland-preferrer (which happens with probability $1 - x$), and if the current value of grassland exceeds the current value of forest ($U_G(F) > 0$), they switch to being a grassland-preferrer with a probability proportional to the current difference in value, $L \cdot U_G(F)$. Finally, there are x forest-preferrers at any given time going through this process, so the total rate at which forest-preferrers become grassland-preferrers is

$$x \cdot d(1 - x)LU_G(F) \quad (5)$$

The function $U_G(F)$ equals the perceived value of grassland minus the perceived value of forest. Because the public often appears to prefer the conservation of rare or endangered species to those that are more common³³⁻³⁵, we assume that $U_G(F)$ depends on the relative abundance F of forest and grassland. For numerical analysis, we will assume the functional form



$$U_G(F) = q_0F - r_0(1 - F) \quad (6)$$

where the first term represents value of grassland and the second term represents the value of forest. The parameter q_0 controls the conservation value of grassland whereas r_0 controls the conservation value of forest. We note that the value of grassland $U_G(F)$ is highest when grassland is rare but forest is abundant ($F = 1$) and $U_G(F)$ is lowest when the reverse is true ($F = 0$).

Following similar steps, the rate at which grassland-preferrers become forest-preferrers is

$$(1 - x) \cdot dxLQU_F(F) \quad (7)$$

where $U_F(F)$ is the same as $U_G(F)$ except it equals the perceived value of forest minus the perceived value of grassland, and where Q is scaling constant which represents an innate tendency to value conversion of forest to grassland differently than conversion of grassland to forest. For numerical analysis, we will assume the functional form

$$U_F(F) = r_0(1 - F) - q_0F \quad (8)$$

where we note that $U_F(F) = -U_G(F)$.

Combining the two processes governing conversion between forest- and grassland-preferrers yields:

$$\frac{dx}{dt} = -x(1 - x)QLdU_G(F) + (1 - x)xLdU_F(F) \quad (9)$$

where the first term is negative because it corresponds to individuals leaving the forest-preferring state. Without loss of generality let $s \equiv Ld$ and $U(F) \equiv U_F(F) - U_G(F)$. For simplicity let $Q = 1$, yielding

$$\frac{dx}{dt} = sx(1 - x)U(F) \quad (10)$$

where s can be thought of as a social learning rate (a product of the rate of sampling and the probability of switching opinions). For numerical analysis, from equations (8) and (6) we obtain

$$U(F) = r(1 - F) - qF \quad (11)$$

where $r \equiv r_0/2$ and $q \equiv q_0/2$. Note that $U(F) = 0$ only once, due to monotonicity. A nonlinear version of equation (11) can be obtained by exponentiating the two terms of the equation, and appears in Methods (equation (24)). In sensitivity analysis we explored the impact of using the nonlinear version.

In the next subsection, we define how the dynamics of x are coupled to the dynamics of F .

Model of coupled human-environment interactions. Since our aim is to establish the effect of a wide range of potential human activities on mosaic bistability, we model human impacts on the mosaic

ecosystem in a simple, phenomenological way. The mosaic ecosystem equations are modified by a transition function $J(x)$, which governs the net conversion of forest into grassland or *vice versa*. The resulting system of equations formed by coupling equations (4) and (10) is

$$\frac{dF}{dt} = w(F)F(1 - F) - vF - J(x) \quad (12)$$

$$\frac{dx}{dt} = sx(1 - x)U(F) \quad (13)$$

where $J(x)$ represents only human-driven transitions, in contrast to v which represents only natural-driven transitions. When $J(x) > 0$, the abundance of forest-preferrers x in the population is sufficiently low that deforestation dominates reforestation, causing a net reduction in forested lands, whereas when $J(x) < 0$, x is sufficiently high that reforestation dominates deforestation, causing a net expansion in forested lands.

For numerical analysis, $J(x)$ will use the functional form

$$J(x) = h(1 - 2x) \quad (14)$$

where h governs the potential magnitude of human influence on the ecosystem. A nonlinear version of equation (14) appears in Methods (equation 25)). In sensitivity analysis we explored the impact of using the nonlinear version. The model parameters and variables are summarized in Table 1.

Scenarios evaluated. We evaluated three cases: no human influence, corresponding to the original mosaic ecosystem model on its own (equation (4)); weak human influence (equations (12), (13)); and strong human influence (equations (12), (13)). We conducted both stability analysis of model equilibria as well as numerical analysis to establish dynamical regimes of the model.

The differences between these three scenarios can be understood in terms of the overall magnitude of human influence $J(x)$ on land states. In particular, the number and type of equilibria are controlled by the intersection of the curves $w(F)F(1 - F) - J(0)$ and $w(F)$, where $dF/dt = 0$ in equation (12). Figure 1 depicts these intersections for the functional forms used in our numerical analysis (equations (4), (11), and (14)). In the absence of human influence, we have $J(0) = 0$ and there are three points of intersection and thus three equilibria (Figure 1a). As human influence increases and the $w(F)F(1 - F) - J(0)$ curve moves downward due to larger values of $J(0)$, the $F^* = 0$ equilibrium disappears, leaving only two equilibria remaining (this is the weak human influence case, Figure 1b). Finally, as $J(0)$ becomes very large, the $w(F)F(1 - F) - J(0)$ curve moves downward far enough that all equilibria are lost (this is the strong human influence case, Figure 1c). It is possible to show that the strong human case is

Table 1 | Parameters and variables used in the model

| Symbol | Definition | Baseline value |
|--------|--|---------------------|
| v | rate at which forest becomes grassland due to natural processes | years ⁻¹ |
| s | social learning rate | years ⁻¹ |
| h | proportionality constant, harvesting function $J(x)$ | years ⁻¹ |
| r | proportionality constant, conservation value function $U(F)$ (forest component) | unitless |
| q | proportionality constant, conservation value function $U(F)$ (grassland component) | unitless |
| k | scaling factor controlling abruptness, recruitment function $w(F)$ | unitless |
| b | constant controlling minimum, recruitment function $w(F)$ | unitless |
| c | proportionality constant, recruitment function $w(F)$ | years ⁻¹ |
| $J(x)$ | rate at which forest is harvested | years ⁻¹ |
| $U(F)$ | conservation value of forest versus grassland | unitless |
| $w(F)$ | recruitment function governing conversion of grassland to forest | years ⁻¹ |
| F | percentage of total land area covered by forest | unitless |
| G | percentage of total land area covered by grassland ($G = 1 - F$) | unitless |
| x | percentage of the population that prefers forest over grassland | unitless |

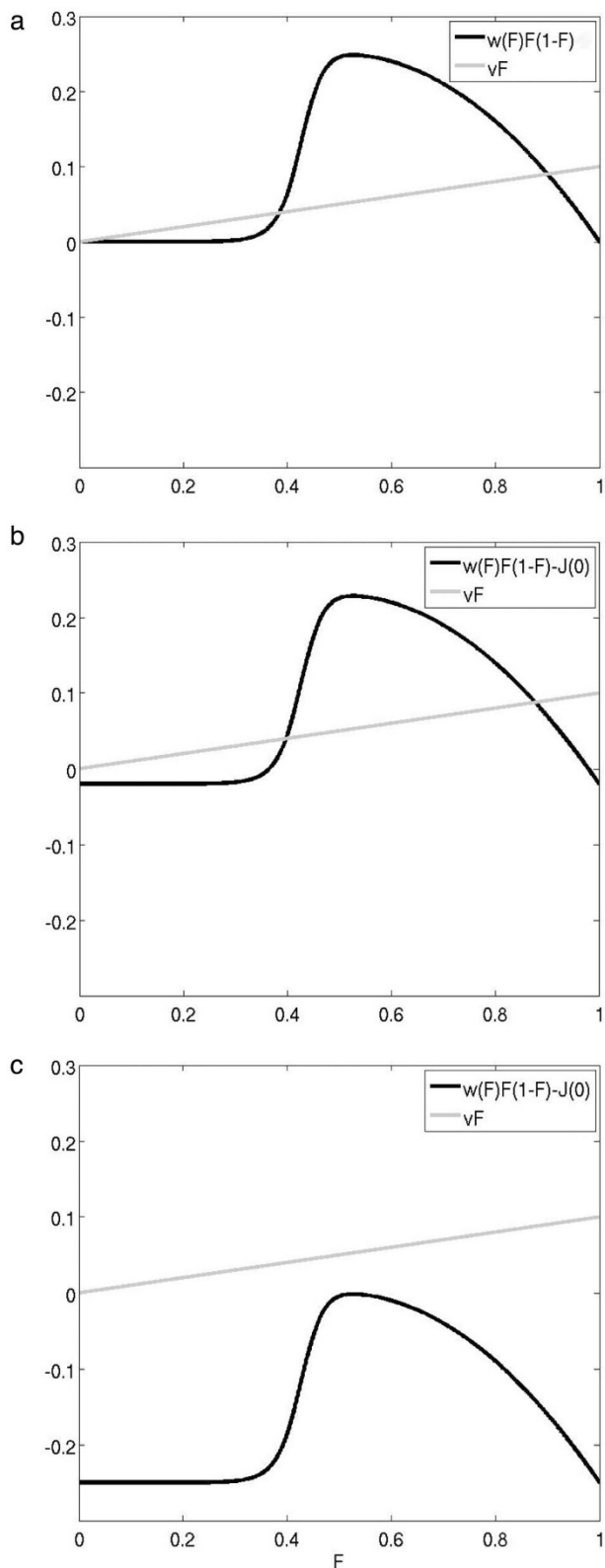


Figure 1 | Intersections of $w(F)F(1 - F) - J(0)$ and $w(F)$ in equation (12), indicating model equilibria, for the (a) no human influence, (b) weak human influence, and (c) strong human influence cases.

obtained when $J(0) > w(F)/4$ and $J(1) < -v$, and otherwise we remain in the domain of weak human influence as long as $J(0) > 0$ (see Methods for details).

We provide more details about the properties of equilibria under these three scenarios in the following subsections, and note that most

of the stability properties do not depend on the details of the functional forms chosen for $J(x)$ and $U(F)$.

Stability properties: no human influence. When human-environment feedbacks are ignored and the mosaic ecosystem dynamics are described only by equation (4), only two stable equilibria are possible. The first consists entirely of grassland ($F^* = 0$). It always exists and is stable whenever

$$v > w(0) \tag{15}$$

Equation (15) means that forest is removed by natural processes, v , faster than it can be created through the recruitment rates at low forest cover, $w(0)$. Hence, the system remains in a state of complete grassland, $F^* = 0$.

The second stable equilibrium is an interior equilibrium (meaning that $F^* > 0$) where the ecosystem consists of a stable mixture of grassland and forest. The interior equilibrium occurs whenever the curve $w(F)$ intersects the curve $v/(1 - F)$ (because when $w(F) = v/(1 - F)$, from equation (4) we have that the forest cover does not change since $dF/dt = 0$; biologically, this means that forest cover can be maintained if recruitment, as mediated by fire, exactly balances removal through natural processes, v). The curve $w(F)$ increases with F , whereas the curve $v/(1 - F)$ decreases with F , hence, there will usually exist at least one such interior equilibrium where the curves intersect. It can furthermore be shown²⁶ that this interior equilibrium is stable when

$$\frac{dw(F^*)}{dF} < \frac{v}{(1 - F^*)^2}. \tag{16}$$

The slope of the recruitment curve, $dw(F^*)/dF$, is part of the stability condition because the slope determines how the systems reacts when it is pushed slightly above or below the equilibrium state F^* . When $F > F^*$, equation (16) means that removal through natural processes v will outpace the recruitment $w(F)$, and F will go down to F^* . However, when $F < F^*$, equation (16) means that recruitment $w(F)$ will instead outpace removal v , meaning F will go up to F^* . Details of the stability analysis appear in the Supplementary Text S1.

If equations (15) and (16) are satisfied at the same time, then both the grassland only equilibrium $F^* = 0$ and the mixed grassland-forest equilibrium $F^* > 0$ are stable. When such bistability occurs, the system could equally well be in a state of pure grassland, or a state of mixed grassland and forest: the landscape is a mosaic of two possible states²⁶. Bistability is possible when the recruitment function $w(F)$ is sigmoidal²⁶.

Stability properties: weak human influence. Introducing human behaviour through the coupled human-environment system model (equations (12) and (13)) can change the bistability properties of the forest-grassland mosaic. When human influence is sufficiently weak, the effects can be subtle, for instance by making multiple interior equilibria possible, even when everyone prefers grassland ($x^* = 0$) or when everyone prefers forest ($x^* = 1$).

If everyone prefers grassland at the equilibrium ($x^* = 0$), then from equation (12) we see that an equilibrium where $dF/dt = 0$ is possible for forest cover F^* such that

$$w(F^*)F^*(1 - F^*) - vF^* = J(0) \tag{17}$$

Likewise, when everyone prefers forest ($x^* = 1$), an equilibrium is possible for forest cover F^* such that

$$w(F^*)F^*(1 - F^*) - vF^* = J(1) \tag{18}$$

Hence, the equilibria take on the form (F^*, x^*) where $x^* = 0$ or $x^* = 1$, and $F^* > 0$ in general. Because there can be multiple values of F^* that satisfy either equations (17) or (18), there can be multiple possible equilibria, unlike the case where human influence is absent (equation (4)).



We show in the Supplementary Text S1 that the stability conditions for these equilibria are

$$\frac{dJ(x)}{dx} \left(x(1-x) \frac{dU(F)}{dF} \right) + U(F) \left(\frac{dw(F)}{dF} - v \right) (s(1-2x)) \quad (19)$$

$$((1-2F)w(F) + (F-F^2)) > 0$$

and

$$(1-2F)w(F) + (F-F^2) \frac{dw(F)}{dF} - v + s(1-2x)U(F) < 0 \quad (20)$$

It can be shown that there are at most two equilibria that satisfy both equations (19) and (20), hence bistability can also occur for the case of weak influence. Equations (19) and (20) are more complicated than equations (15) and (16), which means the requirements for bistability in the weak human influence case can be either stronger or weaker than the conditions for bistability in the no human influence case, depending on the specific parameter values and functional forms used. Hence, weak human influence can either broaden or restrict the parameter regimes under which bistability is possible. The details of this analysis are included in Supplementary Text S1.

However, there is one important qualitative difference in the nature of bistability under weak human influence versus no human influence. Because only a very narrow range of functions $J(x)$ can satisfy equations (17) and (18) when $F^* = 0$, we expect that $F^* > 0$ in general, so there will be no equilibria consisting of pure grassland except under very specific assumptions. This is very different from the case of no human influence, where the $F^* = 0$ equilibrium is always present, and is stable under a relatively wide range of conditions (equation (15)). Hence, even weak human influence has a significant qualitative impact on ecosystem composition, in this case by precluding a grassland-only equilibrium.

Stability properties: strong human influence. When human influence is sufficiently strong, then it is no longer possible to obtain stable equilibria in the cases where everyone prefers forest ($x^* = 1$) or everyone prefers grassland ($x^* = 0$). (Mathematically, the harvesting term $J(x)$ is sufficiently large that equations (17) and (18) cannot be satisfied for any choice of F .) Because humans can easily transform ecosystem landscapes, we expect this to be the most common scenario in real populations.

However, an equilibrium is still possible if there is a level of forest cover F^* at which there is no net preference of forest over grassland or *vice versa*; mathematically, there is a value of F^* such that $U(F^*) = 0$ in equation (13), in which case $dx/dt = 0$ and so x does not change over time. Then, if we can also find x^* such that $dF/dt = 0$, or equivalently from equation (12),

$$w(F^*)F^*(1-F^*) - vF^* = J(x^*) \quad (21)$$

an equilibrium (F^*, x^*) is possible, usually with $0 < F^* < 1$ and $0 < x^* < 1$. However, because we expect $U(F)$ to be a monotonically decreasing function of F (meaning that it always goes down as F increases), $U(F)$ can equal zero at most once, meaning that only one equilibrium is possible. As a result bistability is no longer possible because there is only one equilibrium.

This sole remaining equilibrium is stable when

$$\frac{dw(F^*)}{dF} < \frac{v}{(1-F^*)^2} \quad (22)$$

and

$$\frac{dJ(x^*)}{dx} \left(x^*(1-x^*) \frac{dU(F^*)}{dF} \right) > 0 \quad (23)$$

(see Supporting Text S1). Equation (22) is identical to the stability condition on the interior equilibrium $F^* > 0$ in the mosaic ecosystem on its own, Equation (16). However, equation (23) represents an

additional condition that the interior equilibrium (F^*, x^*) of the coupled system must satisfy. Hence, not only does strong human influence remove bistability, it also tends to destabilize the remaining equilibrium.

Most functional forms and parameter regimes will correspond to the strong human influence case, rather than the weak human influence case which has highly specific restrictions. Thus, in general, we predict that human influence precludes bistability and leads to unstable dynamics. Biologically, this means that human influence, if motivated by rarity-based perception of the relative value of different land states, will tend to create landscapes of relatively homogeneously nature as opposed to a distinct mosaic patchwork of forest and grassland. Moreover, the relative composition of grassland versus forest may vary over time according to current preferences.

Phase diagram: no human influence. How human influence alters bistability properties can be further understood by exploring how dynamical behaviour of the mosaic-only model and coupled human-mosaic models vary with parameter values. Numerical analysis was conducted using the functional forms for $J(x)$, $U(F)$ and $w(F)$ (equations (14), (11) and (3)).

We constructed phase diagrams showing the number and type of equilibria as a function of k (the parameter governing how abruptly forest recruitment increases as forest cover is increased in equation (3)) and v (the rate at which forest becomes grassland, due to natural disturbances). By varying these two parameters, we can describe a relatively broad range of dynamics of the mosaic ecosystem. For the mosaic model on its own, equation (4), there are two distinct domains of stability (Figure 2a). The first is a regime where only the pure grassland equilibrium is stable ($F^* = 0$). It occurs when conditions strongly favour grassland: forest reverts rapidly to grassland (high v) or tree recruitment remains low unless forest cover is very high (low k). However, as v decreases or k decreases, conferring more advantage to trees, the phase diagram enters a second domain of bistability, where both the pure grassland equilibrium ($F^* = 0$) and the interior equilibrium consisting of trees and grassland ($F^* > 0$) are stable. The bistability region comprises the majority of the parameter plane. When the system is in the bistable regime, the system can converge either to the pure grassland state or to the mixed forest/grassland state depending on the initial conditions; when forest cover is sufficiently high initially, the system will converge to the interior equilibrium, but when forest cover is sufficiently low initially, it will converge to the grassland-only equilibrium (Figure 3a, b).

The choice of b (equation (3)) significantly affects the domain of bistability. When b is large, the recruitment rate $w(F)$ is vanishingly low at small values of F , meaning that fire is very effective in suppressing recruitment of saplings at low tree density. In contrast, when b is small, $w(F)$ can be significantly nonzero even at small values of F , meaning that fire retards but does not prevent sapling recruitment at low tree density. A smaller value of b is justified when considering savanna-forest mosaics where saplings can resprout after topkills caused by fire^{26,41}. In contrast, a larger value of b is justified when considering grassland-forest mosaics such as those including *Araucaria angustifolia*, whose seedlings and saplings are killed by fire^{42,43}.

In our analysis we assume a value of b that is large enough to prevent recruitment at low tree density (hence capturing the effects of fire in the *Araucaria angustifolia* forest-grassland mosaic). However, in our sensitivity analysis we explored the “savanna” scenario where b is small, finding that the region of bistability shrinks and much of the phase plane contains only a single equilibrium point, either grassland-only or forest-only (Supplementary Figure S2).

Phase diagram: weak human influence. Bistability persists under the weak human influence case. It is qualitatively different in that both stable equilibria are interior, rather than one being interior and one

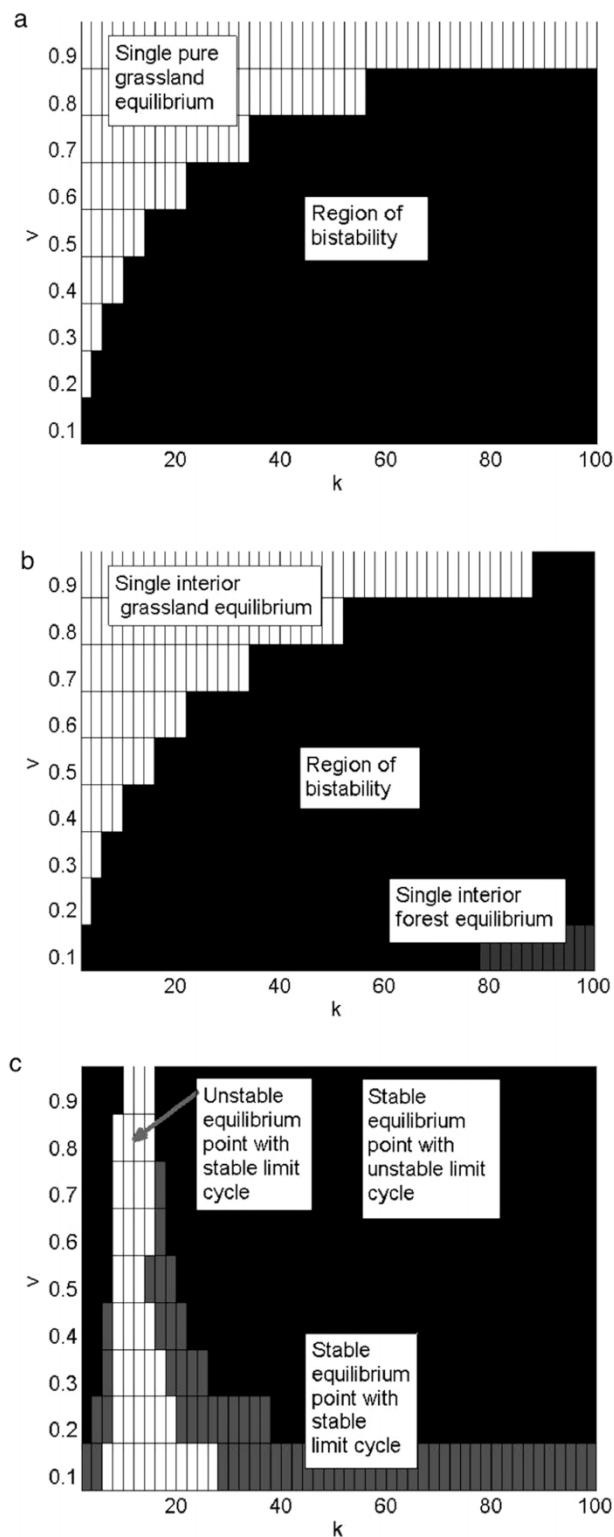


Figure 2 | Parameter plane showing dynamical regimes for (a) no human influence, (b) weak human influence, and (c) strong human influence cases. In the region of bistability there exist two stable equilibria for a given set of parameter values, either interior and grassland-only or forest-only and grassland-only. Other parameters are $c = 1$, $b = 11$. “Grassland only” equilibrium means an interior equilibrium consisting almost entirely of grassland.

corresponding to pure grassland (Figure 2b). However, the new interior equilibrium is dominated by grassland and so it approximates $F^* = 0$. Compared to the case of no human influence, there is little change in the region of parameter space for which bistability

exists, except that a region with a single stable equilibrium dominated by forest is introduced in the lower right-hand corner, where the natural disturbance rate v is low and the abruptness factor k is high (hence, conditions favouring forests) (Figure 2b). The size of the basins of attraction for the two equilibria in the region of bistability are also similar in the pure mosaic case versus the moderate human influence case. The results for the “savanna” scenario are qualitatively similar.

Depending on initial conditions, in the region of bistability, the system can evolve either toward a state of high forest cover F and low numbers of forest-preferrers x , or a state of low F and high x (Figure 3c, d): because perception of value is rarity-based, at equilibrium the preferred landscape type is the one which is most rare.

Phase diagram: strong human influence. Strong human influence completely precludes bistability, in place of which three dynamic regimes emerge: a single stable interior equilibrium accompanied by an unstable limit cycle; a single stable interior equilibrium accompanied by a stable limit cycle (with an unstable limit cycle in-between); or a single unstable interior equilibrium accompanied by a stable limit cycle (Figure 2c). A stable limit cycle corresponds to oscillations in the amount of forest cover and the proportion of forest-preferrers. This oscillation is driven by rarity-based perception of land state value: as forest becomes rare, the number of individuals preferring forest over grassland increases, and eventually the result is net conversion of grassland to forest. The opposite process occurs when grassland becomes rare, completing the cycle and sustaining the oscillations.

When a stable equilibrium coexists with a stable limit cycle, the system can either converge to an equilibrium or it can oscillate over time, depending on initial conditions (Figure 3e, f). This sensitivity also has implications for how the system response to perturbations. For instance, a small perturbation from the stable equilibrium will simply cause the system to return to the equilibrium state via damped oscillations (Figure 3g), but a sufficiently large perturbation will move the system onto the limit cycle, causing sustained oscillations in land states and population opinions (Figure 3h).

Results are qualitatively similar in the “savanna” scenario, except that the region of instability is markedly smaller and shifted to the left in the parameter plane (Supplementary Figure S2).

As the impact of harvesting practices increases (the h parameter in equation (14), the region of bistability initially expands but then declines (Figure 4). The increase occurs because rarity-based preferences initially stabilize the interior equilibrium, since it consists of a mixed land state that is favoured over monolithic land states. However, as human influence increases further, the pure grassland equilibrium loses stability, and thus bistability is lost. Hence, human influence can either increase or decrease the regime of bistability depending on which effect dominates, but sufficiently strong human influence precludes bistability.

Sensitivity analysis. Our baseline scenario assumed that the conservation value function $U(F)$ and the harvesting function $J(x)$ are linear in F and x . In sensitivity analysis we explored nonlinear functional forms: equation (24) for $U(F)$ with $m = n = 2/3$ and $m = n = 3$ cases; equation (25) for $J(x)$ with $p = 7$ and $p = 2/3$ cases). Results were qualitatively unchanged (Supplementary Figure S3, S4).

We also explored the impact of varying the social learning rate s . We found that increasing s had minimal impact on the weak human influence case, but reduced the parameter range for which the model showed oscillatory behaviour in the strong human influence case (Supplementary Figure S5). This occurs because a higher learning rate allows the population to adjust its opinions more rapidly to changes in land states, which prevents extreme amplitude oscillations due to delayed feedbacks.

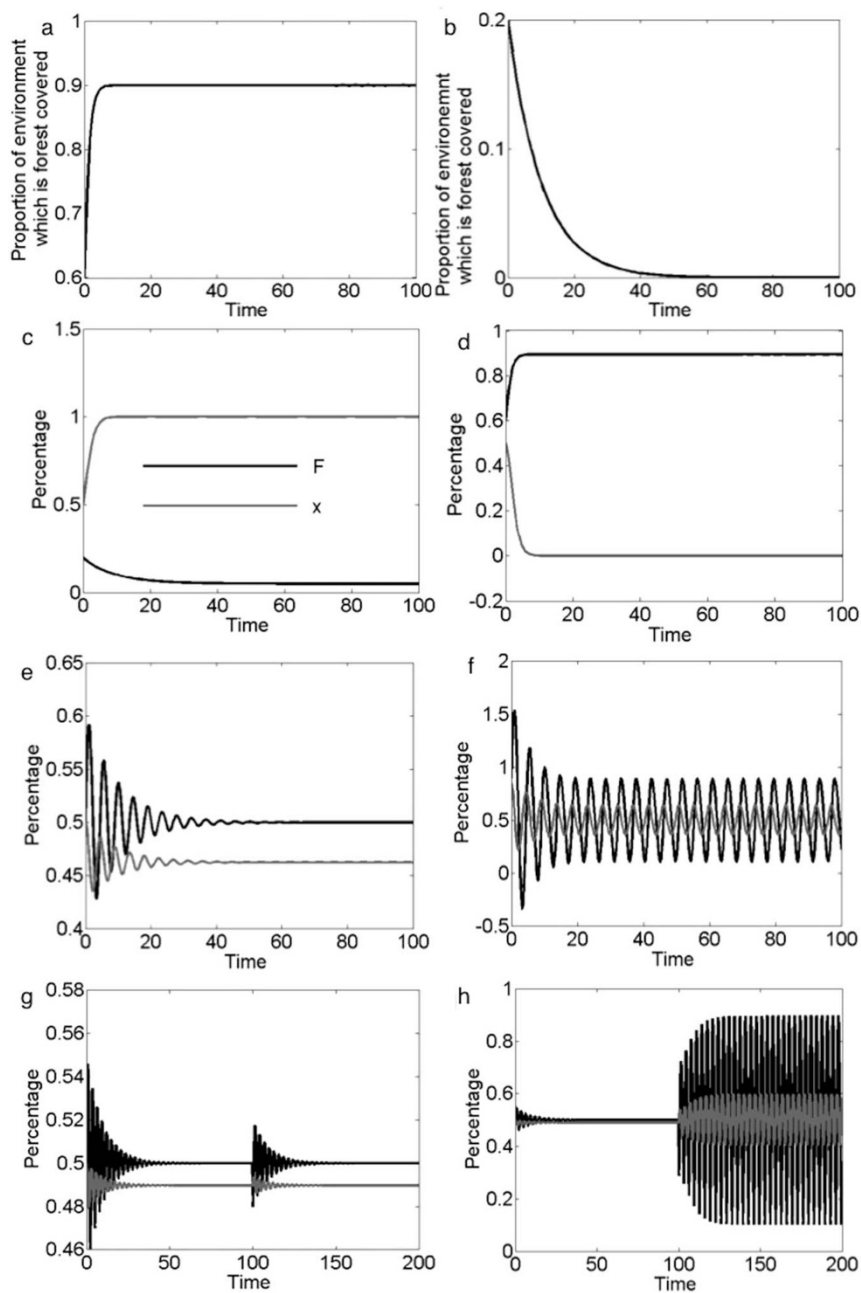


Figure 3 | Time series trials: proportion of landscape which is forested (F , black line) and proportion of individuals who prefer forest to grassland (x , grey line) versus time, (a) $k = 15$, $b = 11$, $\nu = 0.1$ uncoupled, (b) $k = 15$, $b = 11$, $\nu = 0.1$, uncoupled, (c) $k = 15$, $b = 11$, $\nu = 0.1$, $J(x) = 0.005(0.5 - x)$, $U(F) = (1 - 2F)$, (d) $k = 15$, $b = 11$, $\nu = 0.1$, $J(x) = 0.005(0.5 - x)$, $U(F) = (1 - 2F)$, (e) $k = 23$, $b = 11$, $\nu = 0.2$, $J(x) = 2(0.5 - x)$, $U(F) = (1 - 2F)$, (f) $k = 23$, $b = 11$, $\nu = 0.2$, $J(x) = 2(0.5 - x)$, $U(F) = (1 - 2F)$, (g) $k = 23$, $\nu = 0.2$, $J(x) = 2(1 - 2x)$, $U(F) = (1 - 2F)$. A perturbation of $F \rightarrow F + 0.02$ was applied at $t = 100$, (h) $k = 23$, $\nu = 0.2$, $J(x) = 2(1 - 2x)$, $U(F) = (1 - 2F)$. A perturbation of $F \rightarrow F + 0.2$ was applied at $t = 100$.

We explored a model variant with multiple social groups exhibiting intrinsically varying landscape preferences (Supplementary Text S1). This resulted in few changes in the weak human influence case, but significant changes under the strong human influence case: the parameter regime giving rise to a simultaneously existing stable equilibrium and stable limit cycle was significantly reduced, meaning that dynamics were less sensitive to initial conditions (Supplementary Figure S6). This means that dynamics tend to be stabilized, at least under the form of social heterogeneity we introduced. However, overall, strong human influence continues to preclude bistability and cause unstable dynamics for certain parameter values, when social heterogeneity is included in this way.

We also explored a model variant where the value function $U(F)$ incorporates memory of past land states. The instantaneous forest cover F used in the value function $U(F)$ was replaced by an exponentially weighted average of the forest cover F in the past z time units. A second variant introduced a time delay by replacing instantaneous forest cover F in the value function $U(F)$ by forest cover at z time units ago. Both variants caused few changes to the weak human influence scenario, but resulted in more parameter sets giving rise to oscillations in the strong human influence scenario (Supplementary Figure S7, S8). Moreover, many of these oscillations were sufficiently large to correspond to complete removal of either forest or grassland in the extremes of the cycle (Supplementary Figure S9). Hence,

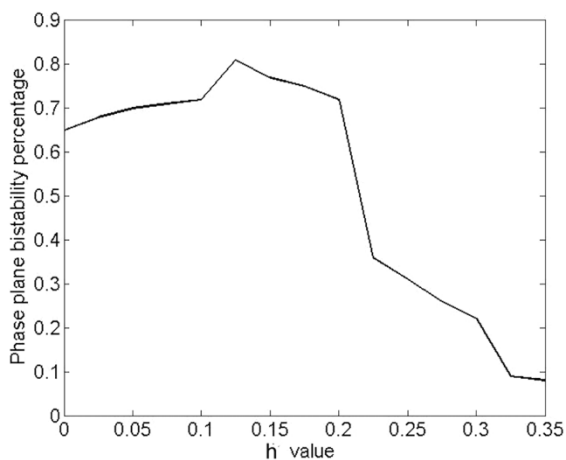


Figure 4 | Proportion of parameter plane exhibiting bistability, versus h , when $J(x) = h(1 - 2x)$: $c = 1$, $b = 11$, $U(F) = (1 - 2F)$. Curve interpolated via spline.

overharvesting and local extirpation may occur in populations where rarity-based perception of value does not keep up with changes in land state frequencies.

Additionally we investigated the case where the harvesting function is dependent on both forest cover F and human preferences x . This allows us to extend our conclusions regarding the effect of human influence to regimes where the potential for land conversion is also dependent on the availability of land for conversion. This also avoids potential discontinuities at $F = 0$ and $F = 1$ which may occur under equation (14). Results were qualitatively similar (Supplementary Text S1, Figure S10).

Discussion

Here we analyzed a human-environment system that couples a model of forest-grassland mosaic land state dynamics to a model of how rarity-based human perceptions of land state value translate into human-driven conversion between land states. We focused on how human behavioural feedbacks alter the stability properties of a forest-grassland mosaic ecosystem such as the *Araucaria angustifolia* mosaic of southern Brazil³⁷.

We found that rarity-driven human feedbacks on environmental states can alter the nature of mosaic ecosystems. Sufficiently strong human influence removes bistability entirely, making the outcome either a single equilibrium consisting of a mixed state of trees and grassland, or an oscillatory state where tree cover and human opinions about which land state has most value oscillate over time due to “boom-bust” cycles reminiscent of cyclical partisan voter patterns⁴⁴. Sensitivity analysis indicated that increasing the social learning rate at which individuals sample others and adopt their opinions, or decreasing the lag between changes in land states and changes in opinions, can stabilize dynamics and make oscillations less likely: this highlights a role for environmental education efforts and for forums allowing individuals to exchange ideas on the environment. Even when human influence is relatively weak and bistability persists, the mosaic is qualitatively changed since monolithic land states (such as pure grassland) become impossible, with both alternative stable states consisting of a mixture of forest and grassland.

We also found that sufficiently strong human influence can result in multiple basins of attraction, such that initial conditions can determine whether the system converges to a stable equilibrium of mixed forest and grassland, or a stable limit cycle where forest cover and opinions about relative land state values cycle over time. As a result, a perturbation can move the system from the stable equilibrium to the stable limit cycle, or *vice versa*. This suggests that institutional interventions to increase forest cover rapidly over a short period of time

could potentially result in longer-term instabilities, in these parameter regimes. Efforts to increase forest cover could be partially mitigated if the resulting increase in forest cover causes the public to perceive decreased forest value, relative to other possible alternative land states such as natural grassland. This demonstrates how the success of an environmental policy is highly dependent on the environmental and social context under which it is being implemented.

At least one previous coupled human-environment system model of forest harvesting practices has also identified a similar tendency toward oscillations in forest cover⁴⁵. As in our model, the oscillations in this model were sensitive to natural history parameters, in particular the rate of forest recovery from natural disturbance (as opposed to the rate of forest loss due to natural disturbance (v) and the rate of fire-mediated recruitment ($w(F)$) as in our model)⁴⁵. The oscillations in this previous model were also driven by forest scarcity. However, the mechanism was different, because forest scarcity increased the economic value of forested land parcels, thus influencing the landowners’ decisions on purely economic grounds, whereas in our model, forest scarcity created broader social concern which led to forest conservation and/or restoration for its own sake. In other human-environment system models, strong human influence appears not to remove bistability, as for example in a model of human-environment interactions in lake systems, where decisions regarding how much phosphorus to allow in runoff are dictated not only by social concern as in our model, but also by economic costs and conformist tendencies (the latter being crucial in generating bistability)⁴⁶.

Designers of ecosystem interventions may need to consider how long-term population behavioural or land state feedbacks could modify and possibly mitigate the objectives of the intervention. The history of environmental policy in the United States contains many examples of “policy resistance” where socio-environmental responses to government interventions have defeated the intent of the intervention^{47,48}. The response to perturbations observed in this model also has implications for long-term human-environment system responses to rapid economic development, wherein human populations can go from having a relatively limited impact on the environment to having an enormous impact, over time scales that are short relative to time scales of natural changes in land states^{49,50}.

Our land state model is well supported by empirical data, since structurally similar models have been developed to describe specific ecosystems elsewhere^{26,37}. However, our model of human perception and behaviour was relatively simple, and only supported qualitatively by empirical data on perception of land state values indicating that relatively rare species are considered to be of higher conservation priority by the general public^{32–34}. We relaxed a number of these simplifying assumptions in our sensitivity analysis. For example, we introduced memory for past land states, social heterogeneity, and variable social learning rates. We found that these extensions often caused dynamics that differed from those of our baseline model. However, in every case, sufficiently strong human influence continued to preclude bistability. There are many other ways in which simplifying assumptions could be relaxed, such as through introducing the presence of institutions or opinion leaders, or introducing mosaics as a distinct land state in and of themselves. It is possible that relaxing other simplifying assumptions would result in unanticipated predictions, and this is a topic for further research.

Our model indicates that sufficiently strong human influence precludes bistability, suggesting that mosaic ecosystems are particularly fragile in the face of human activities. This is ironic because the collapse of bistability is caused by conservation values that are sensitive to ecosystem rarity. It also suggests that conservation efforts may be partly misdirected. For example, in the restoration of the Sudbury, Ontario region after its devastation due to mining activities, convenient but non-native species were used, fundamentally altering the ecosystem composition⁵¹. Strong human influence without intervention



from institutions, in the context of well-intentioned human-environment feedbacks, could mean that it will only ever be possible to restore or preserve ecosystems to pseudo-natural “garden” states, due to the relative fragility of ecosystem mosaics in the face of anthropogenic effects. To better understand the long-term implications of human-environment feedbacks, the next step is constructing empirically supported human-environment mosaic models. This will require collaborations between ecologists, psychologists, sociologists and economists.

Methods

Nonlinear functional response for $U(F)$. The nonlinear version of equation (11) is given by

$$U(F) = r(1 - F)^m - qF^n \quad (24)$$

where m and n control the shape of the curve relating F to $U(F)$. When m and n are close to 1, conservation value $U(F)$ responds in linear proportion to changes in F , but when m and n are significantly smaller or larger than 1, changes in conservation value can depend nonlinearly on changes in F .

Nonlinear functional form for $J(x)$. The nonlinear version of equation (14) is given by

$$J(x) = \begin{cases} h(1 - 2x)^p & \text{if } x < 0.5, \\ -h(2x - 1)^p & \text{if } x \geq 0.5. \end{cases} \quad (25)$$

where $p > 0$ controls how strongly nonlinear the relationship between x and J is. When p is close to zero, a slight majority of forest-preferrers over grassland-preferrers or *vice versa* will result in a large impact on the conversion of one land state to the other, whereas when p is large, a slight majority results in little net conversion of one land state to the other. Both Equation (25) and (14) permit the possibility that $dF/dt < 0$ when $F = 0$, hence we constrained $0 \leq F \leq 1$ for both equations (thus introducing discontinuities at $F = 0$ and $F = 1$). However, negative values of forest cover never occurred at parameter values we used for our baseline analysis. In sensitivity analysis, we explored a version of the model which avoids this possibility, and we found that results were qualitatively unchanged (Supplementary Text S1).

Quantifying weak and strong human influence. If we begin from the basic premise that $J(0) > 0$ and $J(1) < 0$ i.e. when all humans prefer grassland, they convert forest to grassland and *vice versa*, we can arrive at the following definition of strong human influence:

$$w(F)F(1 - F) - vF < J(0) \quad (26)$$

$$w(F)F(1 - F) - vF > J(1) \quad (27)$$

for all $F \in [0, 1]$. The above comes from the fact that the weak human influence domain corresponds to when the $x = 0$ and $x = 1$ equilibria are possible. When human influence becomes too large in magnitude, the natural portion of the land use model, $w(F)F(1 - F) - vF$, fails to cancel out the effects of the large $J(0)$ and $J(1)$ terms and hence, the $x = 0$ and $x = 1$ equilibria cease to exist. Additionally the above two bounds can be relaxed for the sake of simplicity, by noting that both $w(F)$ and v are greater than or equal to zero by definition. This implies that:

$$w(F)F(1 - F) - vF \leq w(F)F(1 - F) \leq w(F)/4 \quad (28)$$

$$w(F)F(1 - F) - vF \leq -vF \leq -v \quad (29)$$

for all $F \in [0, 1]$. Hence, the sufficiency condition for strong human influence is

$$w(F)/4 < J(0) \quad (30)$$

$$-v > J(1) \quad (31)$$

for all $F \in [0, 1]$.

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Author contributions

C.T.B. and M.A. conceived of the study. C.I. analyzed the model. All authors developed the model and wrote the manuscript.

Additional information

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