Socio-ecological mechanisms for persistence of native Australian grasses under pressure from nitrogen runoff and invasive species

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ABSTRACT

Nitrogen runoff in certain southeastern Australian grasslands promotes the invasion of exotic grassland species at the expense of native species. Mitigation programs can reduce runoff and thus support native species, but their success may require the awareness and support of local populations. This situation represents a coupled socio-ecological system, since nitrogen runoff caused by local populations can enable the invasion of exotic grassland species, which can in turn stimulate a social response to restore the native species. Our objective is to use a mathematical model to identify potential socio-ecological mechanisms for the persistence of native grassland species, and the parameter regimes for which these mechanisms operate. We couple a model of southeastern Australian grassland dynamics with a model of human social dynamics concerning runoff mitigation. Nitrogen runoff can enter the ecosystem either through local sources under control of a human population, or through global sources not under their control. Humans learn mitigating behaviour socially, and respond to the prevalence of native and exotic grassland species. We find that socio-ecological dynamics introduce broad parameter regimes that are not present in the ecological system in isolation from the human system. We identify two mechanisms for native grassland persistence: one is associated with significant reductions in runoff rates and/or cost of runoff mitigation programs, resulting in a stable state where the native grassland species exists or dominates, with or without the support of socio-ecological feedback. A second mechanism associated with higher rates of nitrogen input supports persistence of the native species through oscillations in species abundance and mitigation behaviour in the human population. However, this state is less favourable to the native species because the oscillations may become extreme in amplitude. Finally, we find that increasing the cost of mitigation programs not only reduces mitigating behaviour in the population but also (more surprisingly) increases the tendency for the system to destabilize into a regime of oscillations in native species biomass. We conclude that multiple socio-ecological mechanisms could potentially support native species in grassland ecosystems under stress from nitrogen runoff and invasive species. Further research can refine such models to inform policy in the face of nonlinear socio-ecological responses.

Introduction

Numerous ecosystems around the world are negatively impacted by deposition processes that input excessive nutrients, pollutants, or sediments into the ecosystem through processes such as runoff[1]. For instance, lake ecosystems are adapted to natural background rates of nitrogen input, but excessive nitrogen loading due to runoff from industrial or agricultural sources can cause lakes to flip from a clear oligographic state to a eutrophic state where the lake is overgrown by algae, causing fish populations to suffer[2,3]. Similarly, excessive sedimentation impedes the growth and function of coral reefs[4]. Detrimental effects may lead to catastrophic shifts in ecosystem state, such as forest collapse due to acidification, or lake eutrophication[5,6]. Rehabilitating these degraded systems and restoring the ecological balance requires significant effort over long periods of time, depending on the severity of the degradation[7].

A further example of these effects has been observed in grasslands subject to excessive levels of nitrogen deposition. For instance, exotic grassland species primarily originating from Africa and Europe are capable of invading native southeastern Australian grasslands at sufficiently high rates of nitrogen deposition[8,9]. Exotic grasses and plants are often better competitors for sunlight and, with sufficient soil nitration, can out-compete native grassland species. This alters the biodiversity in these ecosystems and also causes a decline in grassland productivity[10,11], while also affecting neighbouring ecosystems[8]. Some of these exotic species are more flammable than native species[12], causing fire to encroach on nonflammable regions, and/or increasing the intensity of fires. In other cases, invasion can cause other changes to the local ecology, where once open water systems are subsequently colonized by the exotic grass species, creating wetlands in their place[12]. Although exotic grassland species are not without benefits, such as providing grazing[12], the touristic, agroeconomic, and cultural benefits of native grassland species are considerable and wide-ranging[8,13–15]. As such, many stakeholders wish to maintain and preserve grassland ecosystems based on native grassland species.

Programs such as Australia's Environmental Stewardship Program utilize incentive-based payments and promote a sense of stewardship to persuade landowners to protect and rehabilitate native ecosystems. These programs have shown successes in protecting Australian grasslands through landowner participation[16]. The development of this and other environmental protection programs in other countries are generally stimulated by the degradation of natural ecosystems, and require public support for environment protection, expressed either through grass roots efforts or through pressure for government interventions. Hence, many natural ecological systems and human systems can be conceptualized as a coupled socio-ecological system (equivalently, human-environment system or coupled human-and-natural system): human activities impact an ecological system, and the resulting changes in the ecological system in turn influence human opinion and behaviour, often to the point of altering the trajectory of these ecosystems toward restoration of their natural state[17–19]. This human response to human-caused changes in natural systems is widespread and has implications for ecological modeling[20–27]. Models of coupled socio-ecological systems capture how human system dynamics influence natural system dynamics and *vice versa*[17–19]. Coupled socio-ecological models typically consist of an ecological model coupled with a human model derived from economic, social or psychological assumptions. These socio-ecological models can be used to study how nonlinear ecological and social feedbacks modify the effectiveness of policy interventions, among other phenomena. Some examples of systems for which socio-ecological models have been developed include forest harvesting[28]; forest pests[29]; forest-grassland mosaics[14,20]; common pool resource problems[30,31]; water sharing[32]; vaccination preferences[33]; and coral reef ecosystems[25]. These models can be used to gain insights into socio-ecological dynamics; identify conditions for extinction or persistence of natural system states; and determine policies that are most likely to support persistence of natural states in the face of socio-ecological feedbacks.

Many of the natural systems subject to damage from deposition processes–including those that could be characterized as coupled socio-ecological systems–exhibit alternative stable states, where the ecosystem can persist in one state or in a dramatically different state depending on initial system conditions[3]. An implication of alternative stable states is that gradually changing environmental conditions may push the ecosystem past a threshold, beyond which the state of the system flips abruptly to a new and contrasting state[34]. These sudden regime shifts have been observed in the cases of lake eutrophication[2,3] and invasion of exotic grassland species in Australia[9], for example. As a result of these nontrivial dynamics, alternative stable states in ecological systems is a frequent subject of ecological modelling efforts[3,9,34,35]. However, socio-ecological models have identified conditions under which socio-ecological feedbacks can remove naturally-occurring alternative stable states[18,25] A coupled socio-ecological model of native and exotic grasses subject to human-caused nitrogen deposition has not been explored in the literature, to our knowledge. Therefore, the impact of socio-ecological feedback on species composition and alternative stable states in those ecosystems is an open question.

Here we extend an existing ecological model that captures the effects of excessive nitrogen deposition on southeastern Australian grasslands[9]. The model predicts that these grasslands can exhibit bistability, with grasslands being dominated either by the native grassland species, or an alternative state dominated by the exotic grassland species due to higher nitrogen input. Nitrogen pollution in such systems may be broken down into contributions from global sources not under the control of local populations (such as atmospheric deposition from distant industrial sources) versus contributions from local sources that can be controlled by local populations (such as runoff from local fertilizer usage in agricultural lands or local industries)[36,37]. Hence, we create a socio-ecological model of this system by coupling a model of a human social subsystem that can control the contribution of local (but not global) nitrogen sources with the existing grassland model[9]. The prevalence of mitigating behaviour in the human population depends on mitigation costs, social learning, social norms, and the current ecosystem state. Unlike most previous socio-ecological models, this allows us to model a human population where only a certain proportion of environmental impact can be controlled by the local population. We formulate the model using known features of the southeastern Australian grasslands socio-ecological system and other similar systems (vaccination dynamics, ecosystem dynamics, etc.[25,33]). We analyze it numerically to identify asymptotic dynamical states and their dependence on model parameters. Our objective is to identify potential socio-ecological mechanisms for the persistence of native grassland species, and the parameter regimes for which these mechanisms operate. This allows us to understand: what are the impacts of changing the cost of nitrogen runoff mitigation, and what kind of dynamical regimes are observed in the socio-ecological model that would not be observed in an ecological model assuming a fixed human influence? Our approach is to explore the model's parameter space in order to gain qualitative insights into possible dynamical regimes and their dependence on parameter trends, rather than fitting the model to empirical data in order to obtain quantitative predictions for a specific population and time.

Methods

Model overview

The socio-ecological model divides the human population into a proportion x who support conservation of natural grasslands by reducing nitrogen runoff ("mitigators") and a proportion $1-x$ who do not ("non-mitigators"). Support may be through individual actions to reduce runoff, or through supporting the implementation of local mitigation programs or bylaws. Individuals switch between these two strategies according to a social learning process determined by the cost of conserving native grasslands, the prevalence of native grasslands, and social norms. Grassland dynamics are determined by an existing model[9], wherein native and exotic species of grass compete, and nitrogen input may cause a critical transition from native-dominated to exotic-dominated grassland states. In our socio-ecological model, the input rate of nitrogen from local sources is reduced according to the current proportion of mitigators in the population. Additional details about the model structure and assumptions appear in *Model Construction* where we first explain the existing grassland model, and then build on this first model by introducing the coupled socio-ecological model. Following that, we explain our parameterization and approach to model analysis.

Model Construction

A previous model[9] was extended to a coupled socio-ecological system. We built on this model because it is relatively simple, exhibits alternative stable states according to nitrogen runoff rates, and was developed for the southeastern Australian grassland ecosystem. The previous model is represented by the system of differential equations:

$$\frac{dB_n}{dt} = B_n(\omega_n \nu_n A - \mu_n - m_n f_n(B_n, B_e)) \tag{1}$$

$$\frac{dB_e}{dt} = B_e(\omega_e \nu_e A - \mu_e - m_e f_e(B_n, B_e)) \tag{2}$$

$$\frac{dA}{dt} = I - kA - B_n\left(\nu_n A - (\mu_n + m_n f_n(B_n, B_e))\frac{1-\delta_n}{\omega_n}\right) - B_e\left(\nu_e A - (\mu_e + m_e f_e(B_n, B_e))\frac{1-\delta_e}{\omega_e}\right) \tag{3}$$

Here, B_n and B_e represent the biomass of native and exotic species respectively, and A represents the environmental nitrogen level. The model assumes a fixed nitrogen input rate I. In addition, the model assumes interspecific light competition between the native and exotic species, governed by the functions $f_n(B_n, B_e)$ and $f_e(B_n, B_e)$ (see Ref.[9] for details). The environmental nitrogen level is determined by the nutrient deposition constant I. Parameters are defined along with their baseline values in Table 1.

This model represents human impact through a fixed parameter I representing the rate of nitrogen input. However, social behaviour is dynamic and varies based on perceptions of ecological conditions. Hence we write down a dynamic equation for x, the proportion of the population that supports nitrogen runoff mitigation to preserve native grasslands ('mitigators'). Conversely, the remaining proportion $1-x$ are assumed to adopt a 'non-mitigator' strategy. We use utility functions to quantify the incentive to adopt 'mitigator' or 'non-mitigator' strategies. We let U_M (U_{NM}) represent the utility for mitigators (non-mitigators). Utility functions are used in game theory to quantify the motivation–whether economic, psychological, social or otherwise–to adopt a strategy[18,38,39]. U_M is given by:

$$U_M = -z + \eta\left(\frac{B_e}{B_n + B_e}\right) + \phi x, \tag{4}$$

where z represents the cost to protect native grassland species by reducing personal contributions to nitrogen runoff or personal efforts to support bylaws and mitigation programs that reduce runoff; η is a proportionality constant that controls the sensitivity of the mitigator utility to the amount of native grassland cover; and ϕ controls the strength of social norms[25,29,33]. This utility function captures how the utility for mitigation increases as the native grassland cover B_n becomes rare. Similarly, U_{NM} is given by:

$$U_{NM} = w + \phi(1-x). \tag{5}$$

where w is the cost associated with producing nitrogen runoff, such as fines paid for bylaw violations.

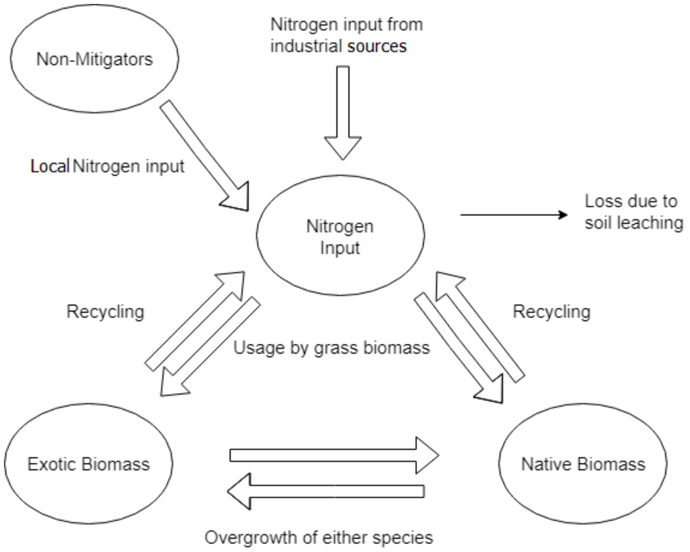

Figure 1. Schematic diagram of the socio-ecological model, combining an existing model of exotic and native grassland species under nitrogen loading[9] to a model of human social learning dynamics.Non-mitigators do not contribute to nitrogen runoff and hence do not appear in the diagram.

When $U_M - U_{NM} > 0$ the preservation of native grassland species becomes a more valuable strategy, whereas when $U_{NM} - U_M > 0$, the population starts to abandon conservation. We assume that each individual 'samples' other individuals at rate κ_0 (social learning) and that, upon encountering someone with a different strategy, the individual switches strategies with a probability proportional to the difference in utility (with proportionality constant p_0). Hence, after re-scaling, the differential equation governing x is given by

$$\frac{dx}{dt} = \kappa x(1-x)(-W + \left(\frac{B_e}{B_n + B_e}\right) + \varepsilon(2x-1)). \tag{6}$$

where $\kappa \equiv \kappa_0 p_0 \eta$ is the rescaled rate of social learning; $W \equiv (z+w)/\eta$ is the rescaled net cost of mitigation; and $\varepsilon \equiv \phi/\eta$ is the effect of social norms. Despite this rescaling, changes in rescaled parameters have a clear interpretation in terms of the original parameter definitions. For instance, an increase in W without a change in other parameters corresponds to an increase in the cost of mitigation, hence we will continue to refer to this as the (rescaled net) mitigation cost. Similar interpretations apply to κ and ε, although changes in η correspond to simultaneous changes in W, κ and ε. We note that these equations are identical to the replicator dynamics used in evolutionary game theory[40,41]. Further examples and full derivation of this differential equation can be found elsewhere[18,20,39,42].

Only a proportion of nitrogen runoff is under the control of local human populations such as municipalities, while the remainder can be due to upstream sources or atmospheric deposition. Hence, we assume that total nitrogen is flowing into the grasslands comes from global sources that are not under the control of the local population at a rate J, as well as from local sources at a rate ρ that is reduced by a factor $1-x$ in proportion to the prevalence of mitigators, x. The socio-ecological model for the southeastern Australian grasslands is therefore:

$$\begin{aligned}
\frac{dB_n}{dt} &= B_n(\omega_n \nu_n A - \mu_n - m_n f_n(B_n, B_e)) && (7)\\
\frac{dB_e}{dt} &= B_e(\omega_e \nu_e A - \mu_e - m_e f_e(B_n, B_e)) && (8)\\
\frac{dA}{dt} &= J + \rho(1-x) - kA - B_n\left(\nu_n A - (\mu_n + m_n f_n(B_n, B_e))\frac{1-\delta_n}{\omega_n}\right) - B_e\left(\nu_e A - (\mu_e + m_e f_e(B_n, B_e))\frac{1-\delta_e}{\omega_e}\right) && (9)\\
\frac{dx}{dt} &= \kappa x(1-x)[-W + \left(\frac{B_e}{B_n + B_e}\right) + \varepsilon(2x-1)] && (10)
\end{aligned}$$

where all parameters and variables are as defined previously in this subsection and in Table 1. A model diagram appears in Figure 1. In equation (3), nitrogen input occurs at a fixed rate I, whereas in equation (9), nitrogen input is the sum of a fixed input rate J and a local nitrogen input term $\rho(1-x)$ that depends upon x. We note that this model assumes the effects of the human population on nitrogen runoff to unfold continuously in time through the $\rho(1-x)$ term. Hence, this approach could capture situations where existing bylaws, recommendations or guidelines can wax or wane smoothly depending on factors such as individual participation in programs and public support for enforcement of existing bylaws, or based on the current state or level of economic development. However, it would not capture discrete events, such as a sudden drop in nitrogen runoff after introducing a new bylaw. (We note that the cases $x = 0$ and $x = 1$ reduce the model to that of Chisholm *et al.* [9] where nitrogen input is fixed.)

Parameterization

Model parameters concerning the grassland subsystem were taken from the previous grassland model[9]. The additional model parameters govern human social dynamics and the coupling between the human and grassland subsystems. These additional parameters were calibrated to satisfy two conditions that met our objective of obtaining qualitative insights into dynamics. Firstly, we required that application of human effort to curb nitrogen input should cause a decline in exotic grassland species and an increase in the native species, and *vice versa*, in order for the model to be consistent with experience from Australia's Environmental Stewardship Program. Secondly, we chose a region of parameter space in which native and exotic species could co-exist and the proportion of mitigators and non-mitigators were nonzero. These two conditions ensured that parameter variation away from the baseline values produced a meaningful change in model dynamics that could be explored through time series and parameter planes. The resulting baseline parameter values appear in Table 1.

Baseline Simulation

The model was numerically simulated in Matlab using the ode23 solver. A time series of the model simulation at the baseline parameter values provides insight into how the model assumptions translate into the observed dyanamics and especially the interactions between natural and human variables (Figure 2). The time series shows damped oscillations leading to an interior equilibrium where native and exotic grass co-exist (with the native species being most prevalent); mitigators constitute 10% of the population; and nitrogen input is nonzero. As the proportion of mitigators increases and decreases, nitrogen input evolves accordingly, which in turn forces changes in the grassland composition. A sufficient increase in the native grassland species increases causes the proportion of mitigators to decrease, which in turn eventually causes a resurgence of the exotic species. However, the overall free nutrient availability is relatively constant through these cycles, since free nitrogen is rapidly assimilated into plants and thus cycles in nitrogen input are translated directly into cycles in species abundance.

Time Series and Parameter Planes

Simulations of parameter regimes away from the baseline parameter values indicate the potential for a wide range of outcomes with respect to both natural and human dynamics. We illustrate these regimes through time series and parameter planes. For time series, we note that the scale of the left vertical axis pertains to simulated trajectories of native and exotic biomasses, whereas the scale of the right vertical axis pertains to plant available N-pool and the proportion of mitigators.

Parameter planes describing the model's dynamical regimes as a function of two model parameters were also generated in order to understand how model dynamics depend on parameter values. The parameter planes illustrate the impact of changes in parameter values on asymptotic states of the model. We generated parameter planes for J, ρ, W and κ. We studied the effects of J and ρ because the contrast between nitrogen inputs under local versus global control is one the main distinguishing features of this socio-ecological system, as discussed in the Introduction. We also studied the effects of W and κ because both the rate of social uptake of a mitigation program and the cost for individuals to adopt it can be strongly influential in program success, and can be influenced through program subsidies or information campaigns, for instance.

To construct the parameter planes, two parameters were selected to be varied around baseline values, while all other parameters were held constant at baseline values. Initial conditions for B_n, B_e, A, and x far from equilibrium values were randomly chosen and the model was run long enough for transient dynamics to disappear, allowing the system to converge to its asymptotic state (this "burn-in" period of 3,000 years was not used in model analysis). Exploring a large number of random initial conditions allowed us to detect alternative stables states and thereby completely characterize the asymptotic states of the model at any given set of parameter values. Approximately 30,000 time series were thereby generated over 256 different initial conditions and the asymptotic state(s) of the system at each parameter pair on the plane were determined from the numerical results. These results were then compiled into an $11x11$ grid to form the parameter plane. All figures were generated using Matlab 2016.

Parameter	Definition	Value(s)	Units
ω	nitrogen use efficiency of each species	(n) = 39.6, (e) = 27.1	$\frac{kgC}{kgN}$
ν	nitrogen uptake rate of each species	(n) = 0.0211, (e) = 0.0877	$\frac{ha}{kgCyr}$
μ	biomass turnover rate of each species in the absence of light competition	(n) = 0.14, (e) = 0.81	yr^{-1}
m	the maximum increase in biomass turnover rate for each species due to interspecific light competition	(n) = 0.17, (e) = 0.32	yr^{-1}
k	soil leaching rate of plant-available nitrogen	0.4	yr^{-1}
δ	proportion of nitrogen in literfall lost from the system in plant-unavailable forms	(n) = 0.06, (e) = 0.06	–
α*	light competition coefficients	(n) $\rightarrow$ (e) 19, (e) $\rightarrow$ (n) 0.05	–
h*	half-saturation constant for the Hill function for coexistence equilibria	3890	$\frac{kgC}{ha}$
p*	parameter controlling sharpness of transitioning from low to high cover of the Hill function	3	–
J	global nitrogen input rate	2	$\frac{kgN}{hayr}$
ρ	maximal local nitrogen input rate	3	$\frac{kgN}{hayr}$
z	cost to protect native grassland species via reduction in personal contributions to nitrogen runoff	–	–
η	proportionality constant	–	–
w	cost associated with producing nitrogen runoff	–	–
κ	(rescaled) social learning rate	1.5	yr^{-1}
W	(rescaled) net cost of supporting runoff mitigation programs	0.1	–
ε	(rescaled) strength of injunctive social norms	0.001	–

Table 1. Parameters and their definitions and baseline values. (n) denotes a parameter value specific to the native grassland species, while (e) denotes a parameter value specific to the exotic species. Parameters were obtained from the previous grassland model[9] except for ρ, J, w,η,z κ, W and ε which were calibrated as described in the Methods section. *These parameters govern competition between the native and exotic species via $f_e(B_n,B_e)$ and $f_n(B_n,B_e)$ in Equation 3 (see Ref.[9] for details.)

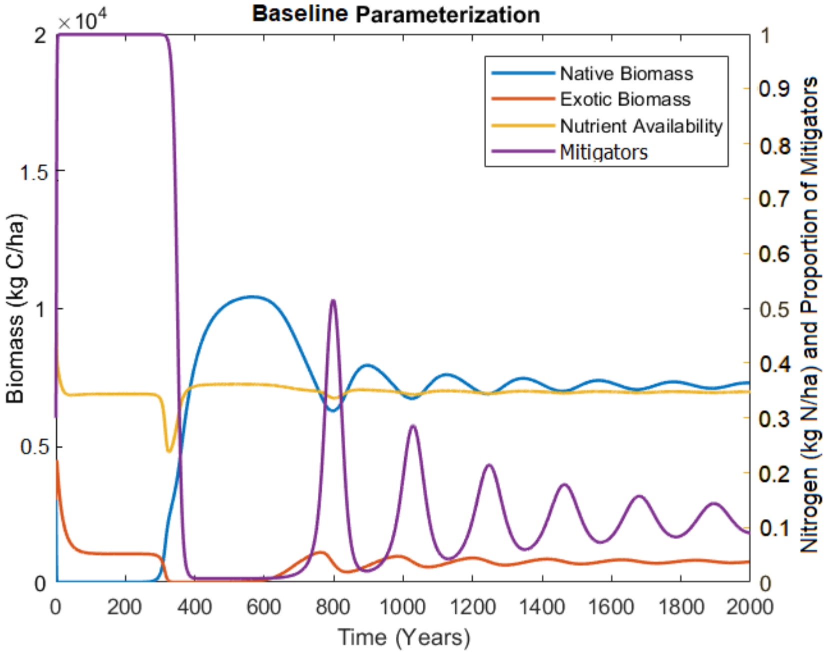

Figure 2. Dynamics of the model at baseline parameter values, showing damped oscillations converging to an interior equilibrium where native and exotic species co-exist and where the proportion of mitigators is nonzero. Parameter values come from Table 1. Left vertical scale pertains to simulated trajectories of native and exotic biomasses and right vertical axis pertains to plant available N-pool and the proportion of mitigators.

Results

We organize the results into subsections according to the most important findings emerging from the model. Results appear as time series (Figures 3, 4, 5) and parameter planes (Figure 6). A detailed legend describing the numbered regions in the parameter planes appears in Table 2.

The results show that nonlinear interactions between social and natural dynamics exemplify a broad range of parameter values. A sufficiently small cost of mitigation W not only promotes persistence of the native species but can also stabilize socio-ecological dynamics. We also observe that even when nitrogen runoff from local sources is very high, a decline in biomass of the native species can stimulate a mitigation response in humans and thus prevent eradication of the native species, resulting in oscillatory coexistence of native and exotic species. Finally, oscillations are pervasive, suggesting that stable equilibrium persistence of the native species is only possible for very favourable environmental and social conditions. We discuss these findings in more detail in the following subsections.

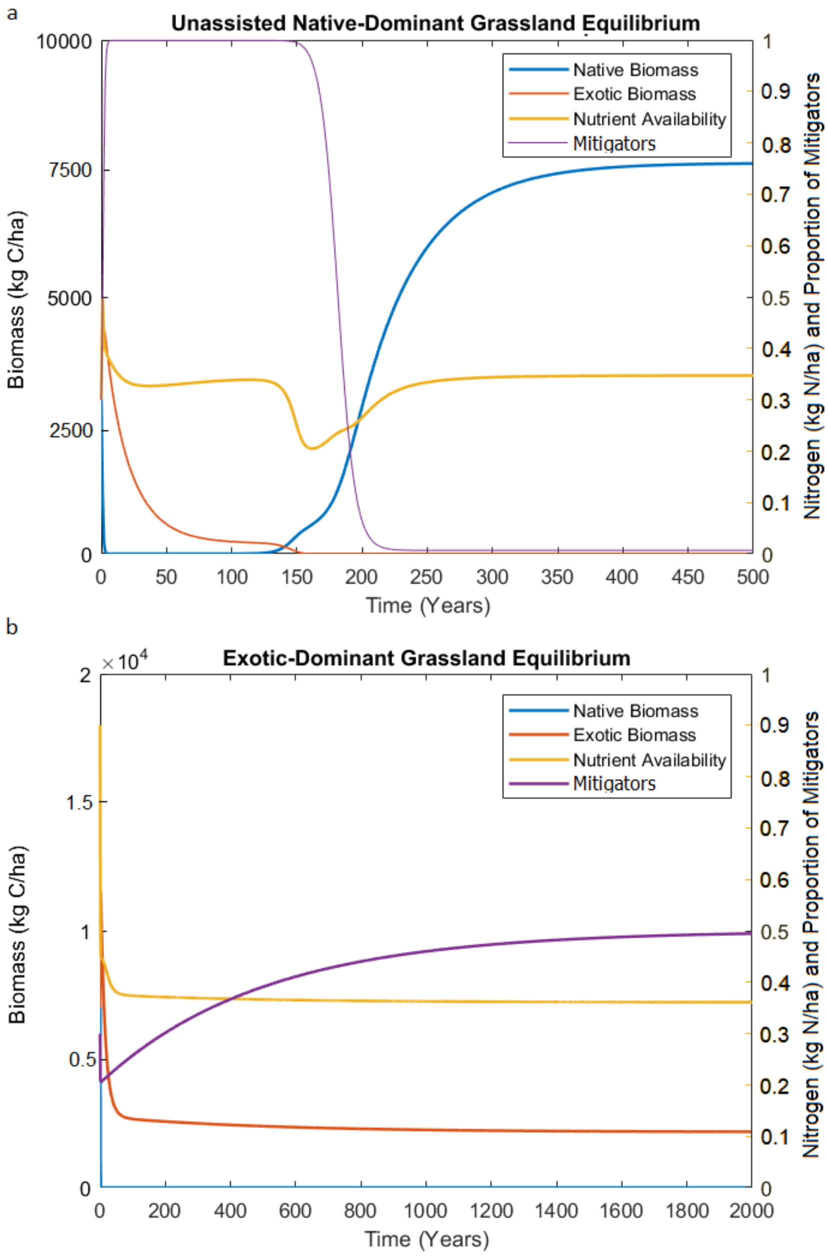

Figure 3. Time series representing the (a) native grassland dominance without human assistance, assuming global nitrogen input $J = 0.5$, and the cost of supporting runoff mitigation programs $W = 0.1$ and all other parameters held at baseline, and (b) representing the exotic grassland domination under the assumption that local nitrogen input $\rho = 4.5$, and $W = 1$ and all other parameters held at baseline values. Left vertical scale pertains to simulated trajectories of native and exotic biomasses and right vertical axis pertains to plant available N-pool and the proportion of mitigators.

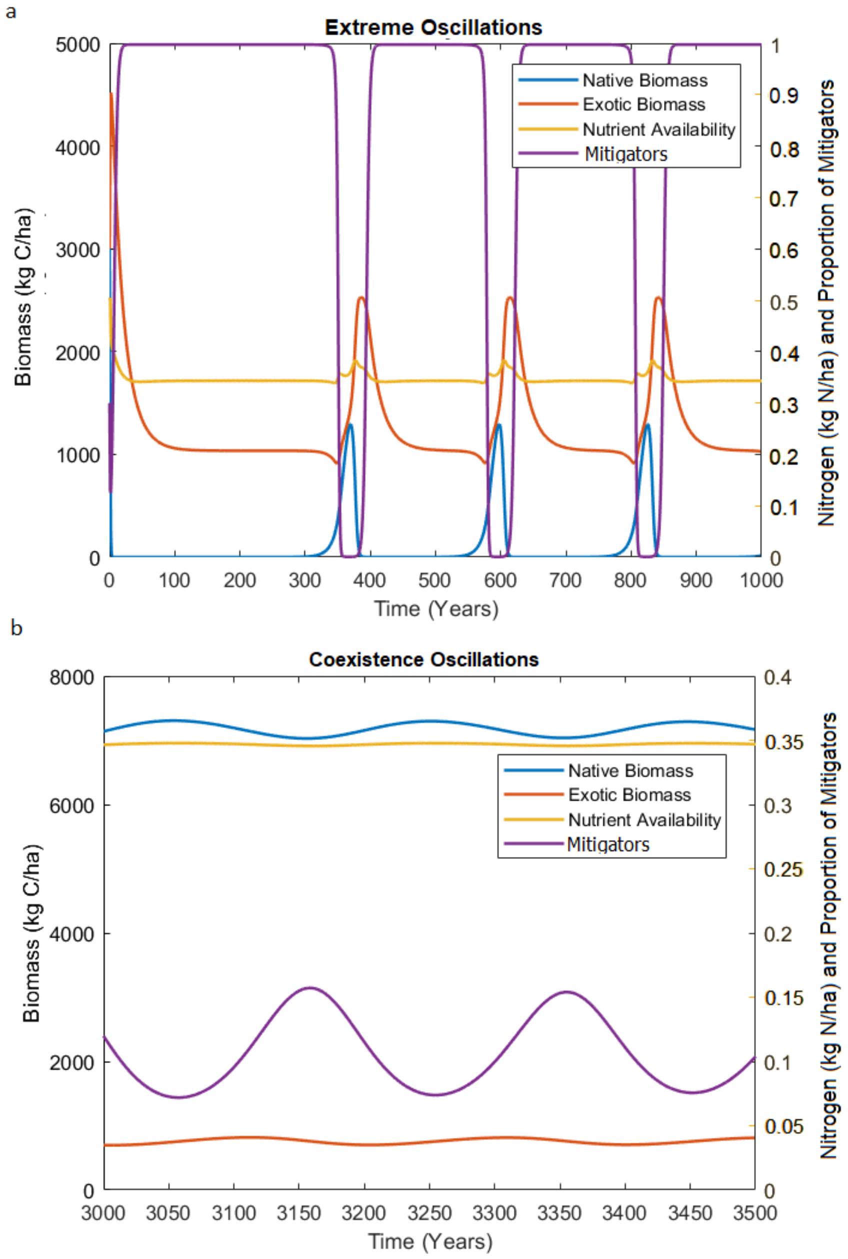

Figure 4. Time series representing oscillations (stable limit cycles) predicted by the model, either (a) extreme oscillations that support species eradication in the troughs (where social learning $\kappa = 4$, and the cost of supporting runoff mitigation programs $W = 0.9$) or (b), more moderate oscillations that support coexistence of the two species (local nitrogen input $\rho = 3$, and $\kappa = 2$). All other parameters were held at baseline values. Left vertical scale pertains to simulated trajectories of native and exotic biomasses and right vertical axis pertains to plant available N-pool and the proportion of mitigators.

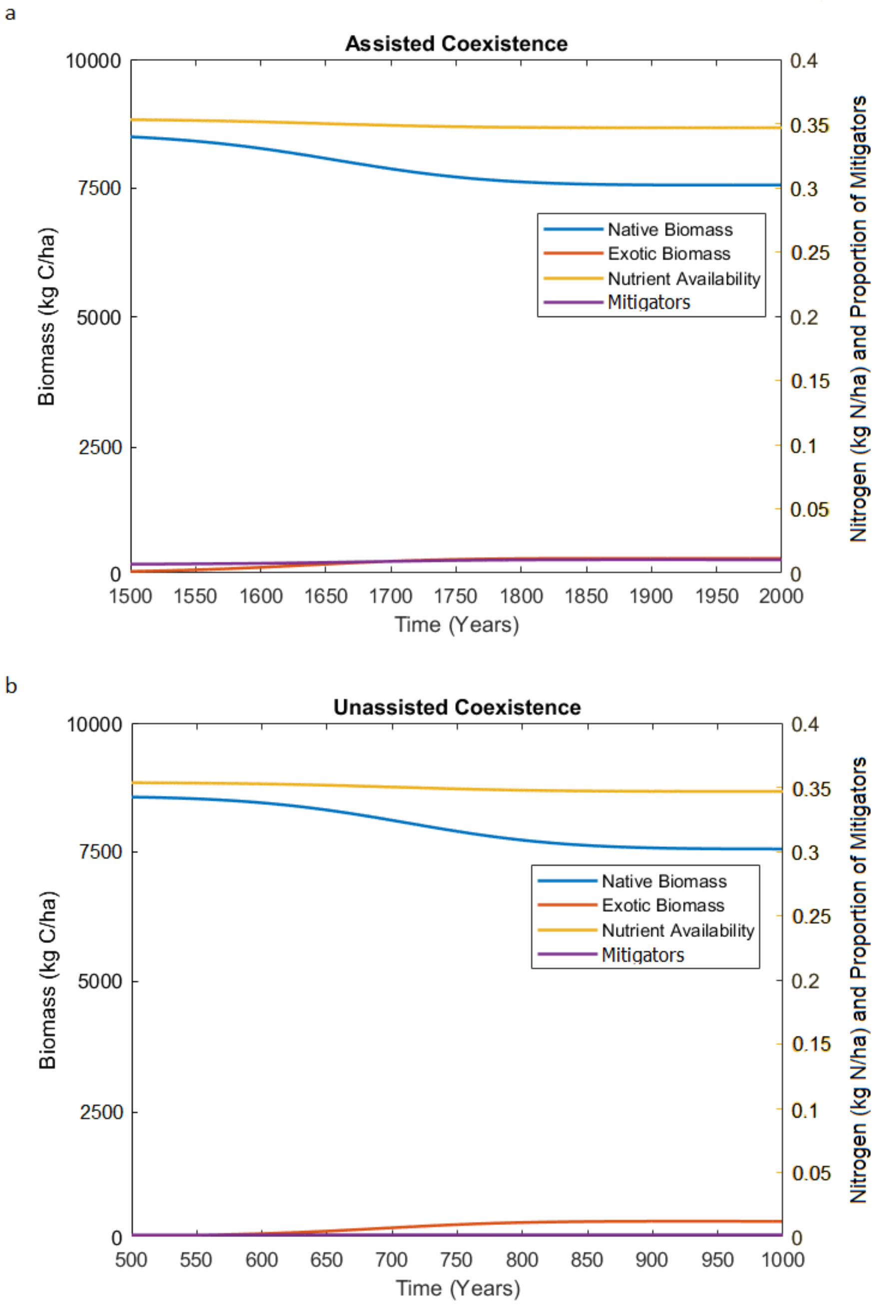

Figure 5. Time series representing stable coexistence. The results were generated under the assumption that for assisted coexistence (a) global nitrogen input $J = 1$, and the cost of supporting runoff mitigation programs $W = 0.1$ with other parameters at baseline values. For the unassisted coexistence scenario (b) - $J = 1$, and $W = 0.5$ and all other parameters were held at baseline values. Left vertical scale pertains to simulated trajectories of native and exotic biomasses and right vertical axis pertains to plant available N-pool and the proportion of mitigators.

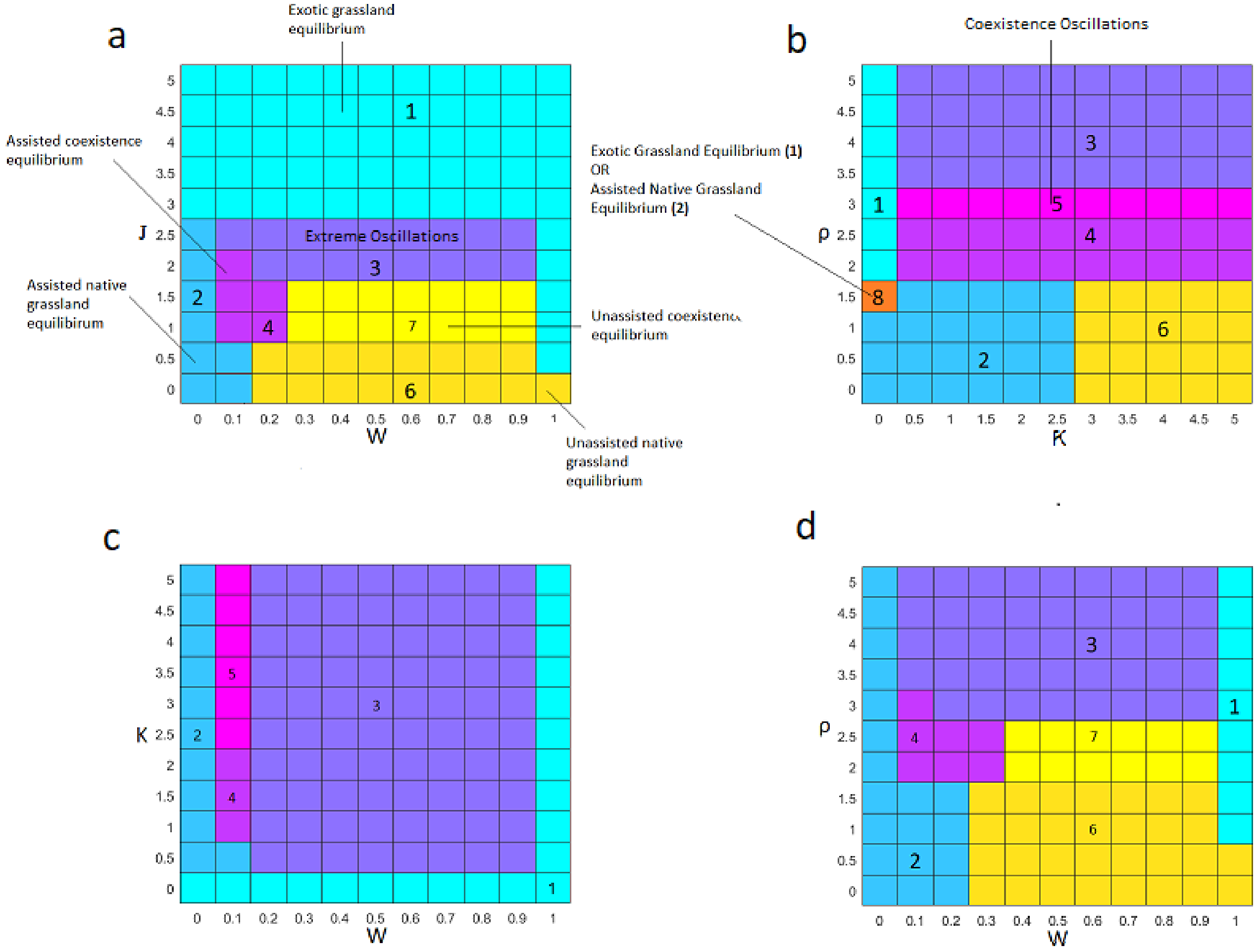

Figure 6. Parameter planes indicating model dynamical regimes with respect to variation in parameter pairs: **(a)** J-W, **(b)** κ-ρ, **(c)** κ-W, **(d)** ρ-W. All parameter values are at baseline values except the two being varied. Further details on the dynamics of the numbered regions are provided in Table 2.

Socio-ecological dynamics emerge as global nitrogen input becomes small

In the parameter plane for J (global nitrogen input) and W (cost of mitigation program), we observe that high values of J favour dominance of the exotic species and low values of J favour dominance of the native species, as expected, but there is also an intermediate regime in J where the two species coexist either in an equilibrium state or through oscillations (Figure 6a). These dynamics are illustrated in timeseries that contrast the coexistence equilibria (Figure 5) and coexistence through extreme oscillations (Figure 4a). In this parameter regime, a coexistence equilibrium can occur either with (Figure 5a) or without (Figure 5b) assistance from the human population. The case of extreme oscillations can be considered as nominal coexistence, since the species abundance is extremely small in the trough of the oscillations and stochastic effects can easily cause species extinction in this regime.

Dynamics for dominance of the native (sufficiently low J) and exotic species (sufficiently high J) observed in the parameter plane (Figure 6a) are also exemplified in time series (Figure 3). In the time series for native dominance (Figure 3a), the proportion of mitigators is initially high but eventually declines to zero during a time period when the native grassland species are still recovering. Despite the collapse in support for the native species, the native grasses are still able to recover and establish dominance. In this case, the net cost of mitigation make it unattractive to the population, but the native species can re-invade anyway because J is sufficiently low. In contrast, higher J values allow dominance of the exotic species. Figure 3b illustrates a case where the exotic species invades rapidly in the first few years, stimulating a rapid shift to an equilibrium proportion of 50 % mitigators. This surge of interest in mitigation is inadequate to allow the native species to re-invade, however, and the population eventually converges to an equilibrium where the exotic species is dominant.

Region	Behaviour
1	Stable equilibrium where exotic grassland species dominate, with a human population fully dominated by mitigators.
2	Stable equilibrium where native grassland species dominate, with a human population fully dominated by mitigators.
3	Extreme oscillations: A state governed by oscillations where native and exotic grassland biomass can vary drastically between levels of near extinction and of high density. One can thrive if the other approaches ≈ 0 kh C/ha biomass.
4	Stable equilibrium where both native and exotic grassland species coexist, with minor assistance from mitigators.
5	Coexistence oscillations: a state where the model predicts cyclic coexistence of both native and exotic grassland species, with fluctuating proportion of mitigators. In contrast to region **[3]**, both exotic grass and native grass biomass are always $\gg 0$ kg C/ha and thus not in danger of elimination during troughs of oscillations.
6	Stable equilibrium where native grassland species dominate in a human population without mitigators.
7	Stable equilibrium where both native and exotic grassland species coexist, with no assistance from mitigators.
8	A bistable region, where system dynamics predict convergence to either the exotic grassland equilibrium **(1)** or the assisted native grassland equilibrium **(2)**.

Table 2. Legend for dynamical regimes exhibited by the model and illustrated in the parameter planes.

The dynamics are generally less variable along changes in W in the parameter plane (Figure 6a). When J is very large, the exotic species dominates regardless of W–in this regime, global nitrogen input overwhelms any attempts to restrict local input. However, when J is small, reducing the cost of runoff mitigation programs sufficiently ($W \lesssim 0.05$) replaces three regimes (oscillatory coexistence, equilibrium coexistence, and unassisted native dominance equilibrium) with the assisted native dominance equilibrium (Figure 3).

Socio-ecological dynamics can protect the native species even for high rates of local nitrogen input

In the parameter plane for ρ (local nitrogen runoff rate) and κ (social learning rate, Figure 6b) we observe that a low value of ρ supports dominance of the native species, yielding a stable native species equilibrium that excludes the exotic species. However, unlike the case for larger values of the global nitrogen input J, larger values of ρ continue to permit the existence of the native species through coexistence regimes of both equilibria and oscillations between native and exotic species abundance due to mediation by the human response. Hence, even at very high values for local nitrogen input to the grasslands, feedback from the human social system is sufficiently strong to prevent eradication of the native species, although it is also not strong enough to eradicate the exotic species. In comparison, changing the social learning rate κ has relatively little impact on dynamics, except when κ is very low and ρ is relatively large, where increasing the social learning rate can shift the system from a regime of exotic species dominance to coexistence. This occurs because if κ is too small and the initial proportion of mitigators is also very small, mitigating behaviour does not spread fast enough. Whereas, for higher κ, individuals are more likely to adopt new strategies, converting non-mitigators into mitigators and thereby supporting the native species.

We also note in this parameter plane a small regime corresponding to coexistence through moderate oscillations (Figure 6). These oscillations are a cycling between the abundance of native and exotic grassland species, and reflect the same underlying dynamic as observed in the damped oscillations of the baseline scenario (Figure 2b, ‘coexistence oscillations’), where support for mitigation becomes widespread in time periods when the exotic species is dominant, which eventually causes a return of the native species and, in turn, a decline in support for mitigation. This regime also appears in Figure 6c.

Social learning can support coexistence, but increasing mitigation costs destabilize the ecosystem

The parameter plane for the social learning rate κ and the cost of supporting mitigation W illustrates the pervasiveness of extreme oscillations in the system at these parameter values (Figure 6c). The effect of increasing W is immediately apparent: unless κ is extremely low in which case mitigator behaviour cannot spread, an increase in W shifts the system from a dynamical regime where the native species dominates with the assistance of humans, to a regime of oscillatory behaviour, where both exotic and native species are present. Hence, increasing the mitigation cost not only allows the exotic species to establish, but also destabilizes the ecosystem through large-amplitude oscillations. Increasing W still further (thus making mitigation too expensive) predicts native species eradication and convergence to a regime dominated by the exotic species. Increasing the social learning rate has little effect on qualitative dynamics, except when κ is very low in which case an increase in κ will allow mitigating behaviour to spread. Oscillations dominate the dynamics for almost all of the κ-W parameter combinations. Hence, the model predicts that an important mechanism for persistence of the native grassland species is a social dynamic that responds to the prevalence of native versus exotic species in the ecosystem and adjusts local nitrogen input accordingly. We note that extreme oscillations are driven by the high social learning rate, which has also been observed to destabilize equilibria in other socio-ecological models[18,20,39].

High rates of local nitrogen input generate heterogeneous human populations

The parameter plane for ρ (local nitrogen input) and W cost of mitigation program yields similar insights to the other parameter planes: higher values of ρ stimulate oscillations, except when W is very small or very large, in which case the population is characterized by an equilibrium of native or exotic species dominance (Figure 6d). As before, coexistence is possible in broad intermediate parameter regime, often through oscillations. When ρ is small, dynamics are at equilibrium and may be characterized by presence or absence of assistance from humans. Of note is the fact that here (as in other parameter planes), ρ influences social dynamics very strongly. In particular, when ρ is small (which we can conceptualize as representing human populations with low industrial capacity), the mitigation cost W determines whether a population is characterized by complete dominance by mitigators or complete dominance by non-mitigators. Moreover, the boundary between these two regions is sharp: on one side of the boundary exists a homogeneous population of mitigators and on the other side is a homogeneous population of non-mitigators. But when ρ is larger (such as in industrialized populations), the strategy composition swings back and forth in conjunction with grassland dynamics and populations always consist of a heterogeneous mix of mitigators and non-mitigators. This effect is observed in

Discussion

A model of southeastern Australian grassland dynamics was coupled with a model of human behaviour to explore potential dynamics that could arise in the resulting socio-ecological system. In particular, we wished to explore conditions that supported the persistence of the native grassland species in the face of an invasive grassland species assisted by nitrogen deposition. The model predicted two mechanisms corresponding to native species persistence. The first mechanism was an equilibrium of native species dominance achieved by a combination of reducing the cost of nitrogen runoff mitigation programs (thus making uptake of the program more desirable to the population) and decreasing global sources of nitrogen pollution and/or the maximal capacity for local sources of pollution. These conditions created an environmental regime that supports convergence to an asymptotic regime dominated by native grasslands species, either with or without human assistance. (We note that the case of achieving native species persistence in the absence of human assistance recovers one scenario of the uncoupled model in Ref.[9]). In the second mechanism, for somewhat less favourable environmental conditions where nitrogen input is higher, persistence of the native species was still possible but it occurred through oscillations in the biomass of the native species, exotic species, and mitigation support in the human population. These oscillations were driven by our assumption that the prevalence of mitigating behaviour in the population depended on the current state of the grasslands (mitigation behaviour is reinforced when the native species is rare, but are relaxed when the native species is common).

Under the second mechanism for support of the native grassland species, persistence of the native species is gained at the cost of admitting dynamics where the prevalence of both native and exotic species oscillate. The danger of such oscillations is the possibility of extinction of other native species (plant or animal) that depend on the native grasslands, at times when native grassland biomass is at a low point in the cycle. Although some parameter regimes corresponded to coexistence oscillations through relatively gentle oscillations, most of the dynamics we observed in the parameter planes corresponded to extreme oscillations where the native species are almost eradicated in the troughs of the cycles (Figure 4a versus Figure 4b)[43]. We also found that decreasing the cost of a runoff mitigation program not only increases the prevalence of mitigators in the population (as expected), but more surprisingly is also predicted to stabilize both social dynamics and grassland dynamics. Hence, the benefits of subsidizing runoff mitigation programs could be twofold.

These results are relevant to concepts of ecological[44] and socio-ecological resilience[45]. The traditional conception of resilience in ecology is the ability of an ecosystem to return to its original, pre-disturbed state[44,46,47]. Mathematically, this is connected to the asymptotic stability of a model's steady state solution[44]. However, subsequent conceptual development has emphasized that dynamical systems can exhibit a wide variety of attractors besides steady states, such as complicated cycles or chaotic dynamics, suggesting a need to nuance definitions of socio-ecological resilience[45,48]. Other research has noted how instability in real socio-ecological systems, such as elk-human interactions in Yellowstone National Park, could manifest as oscillations but may also appear as other irregular patterns[26]. Accordingly, our model could be argued to manifest two forms of resilience: the oscillations generated by socio-ecological feedback in our model represent resilience in a looser sense, since they allow persistence of the native grassland species. However, on account of generating oscillations with sometimes dramatic swings in species abundances, this resilience is arguably less desirable than the conventional resilience associated with a stable, high cover of native grasses that occurs in favourable environmental conditions in a different parameter regime. Real populations may not exhibit such smooth oscillations on account of stochasticity, population structure, and other heterogeneities, but the precise form of instability is secondary to the prediction that a socio-ecological equilibrium will destabilize into a less resilient dynamical regime.

Our model assumed that incentives can increase the proportion of the population engaging in mitigating behaviour that reduces local sources of nitrogen runoff. This pattern appears to be consistent with field data from Australia's Environmental Stewardship Program[16]. In particular, native plant species richness is significantly higher in grasslands under the Environmental Stewardship Program, while exotic plants species richness does not differ significantly between site (although it does vary regionally)[49]. This regime corresponds to a region of coexistence where native species are supported by mitigation efforts, as exemplified in Figure 5 for instance.

Other model assumptions were simplifying assumptions that could be relaxed in future research. For instance, we note that introducing institutions might dampen the observed oscillations. Laws and bylaws have the effect of institutionalizing behaviours and norms and thus can make behaviours conform to a norm of mitigation, thereby removing the possibility of oscillations or at least dampening them. These effects could be particularly significant in dampening the extreme oscillations observed at many parameter values. We assumed that all mitigators in the population mitigate runoff to the same degree. However, efforts to mitigate can vary between individuals in real populations. In experimental settings, this has led to the observation of a trade-off whereby some interventions can increase individual effort to mitigate at the expense of decreasing population participation in mitigation programs[50]. A worthwhile approach for future research would be to allow mitigation effort to vary between individuals in the model.

A previous ecological model of southeastern Australian grassland dynamics illustrated the effect of pulsing the system with significantly higher rates of nutrient input for a specific period of time, causing dominance of the exotic species[9]. Nutrient spikes such as these in lake systems are associated with a regime shift to an undesirable state of eutrophication[51] although in grasslands these nutrient spikes can play a beneficial role in abandoned lands[52]. We did not explore the effect of exogenous nutrient spikes in our model, although extreme oscillations in the proportion of mitigators in the local population has a similar effect. Future research could explore the impact of spikes in the globally sourced nitrogen deposition (model parameter J). We expect this extension to have nontrivial effects, given the tendency of equilibria in our socio-ecological model to destabilize into oscillations. The timing of spikes could interact with the oscillations to produce very different outcomes depending on the timing of the spike (e.g., very long transient dynamics[53]).

Other simplifying assumptions that we used to facilitate gaining insights include the assumption of a constant global source of nitrogen availability. In fact, it can vary over time and this can influence dynamics. If authorities implement policies to penalize excessive nitrogen runoff from industrial sources, this can cause a decline in global nitrogen deposition over time. An extended model with multiple populations representing both local and global sources of nitrogen could be developed to explore this scenario. We also note that we restrict our attention to a limited portion of a high-dimensional parameter space and rely upon analyzing two-dimensional cross-sections of that parameter space. Hence, there might be other relevant dynamical regimes that our analysis does not reveal. However, finding more dynamical regimes that correspond to persistence of the native species would not qualitatively alter our conclusion (although it could expand our findings).

In summary, there exist many opportunities to pursue research in the mathematical modelling of socio-ecological dynamics. In this case, the incorporation of human social dynamics into the model has revealed more than one mechanism to support persistence of a native grassland species, although the mechanisms relying upon socio-ecological oscillations result in non-equilibrium dynamics in native species biomass. Reducing the cost of mitigation not only increases the proportion of individuals who participate in mitigation but can also stabilize socio-ecological dynamics. Further research on coupled socio-ecological systems could provide a deeper understanding of socio-ecological mechanisms for reducing nitrogen pollution and restoring human-affected grassland ecosystems.

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Author contributions statement

MA and CTB conceived the study, all authors developed the model, VAT conducted model simulations and drafted the manuscript, all authors revised the manuscript.

Competing Interests

There are no competing interests.