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LETTER

A minimal model of fire-vegetation feedbacks and disturbance stochasticity generates alternative stable states in grassland–shrubland–woodland systems

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Abstract

Altered disturbance regimes in the context of global change are likely to have profound consequences for ecosystems. Interactions between fire and vegetation are of particular interest, as fire is a major driver of vegetation change, and vegetation properties (e.g., amount, flammability) alter fire regimes. Mediterranean-type ecosystems (MTEs) constitute a paradigmatic example of temperate fire-prone vegetation. Although these ecosystems may be heavily impacted by global change, disturbance regime shifts and the implications of fire-vegetation feedbacks in the dynamics of such biomes are still poorly characterized. We developed a minimal modeling framework incorporating key aspects of fire ecology and successional processes to evaluate the relative influence of extrinsic and intrinsic factors on disturbance and vegetation dynamics in systems composed of grassland, shrubland, and woodland mosaics, which characterize many MTEs. In this theoretical investigation, we performed extensive simulations representing different background rates of vegetation succession and disturbance regime (fire frequency and severity) processes that reflect a broad range of MTE environmental conditions. Varying fire-vegetation feedbacks can lead to different critical points in underlying processes of disturbance and sudden shifts in the vegetation state of grassland–shrubland–woodland systems, despite gradual changes in ecosystem drivers as defined by the environment. Vegetation flammability and disturbance stochasticity effectively modify system behavior, determining its heterogeneity and the existence of alternative stable states in MTEs. Small variations in system flammability and fire recurrence induced by climate or vegetation changes may trigger sudden shifts in the state of such ecosystems. The existence of threshold dynamics, alternative stable states, and contrasting system responses to environmental change has broad implications for MTE management.

Introduction

Understanding and predicting ecological responses to environmental change, which can be modulated by stochastic processes such as disturbances, are key challenges in environmental research. Mediterranean-type ecosystems (MTEs) are a prime example of temperate vegetation where climate and the regular occurrence of fire as a natural disturbance have influenced plant traits and the structure, composition,

and diversity of vegetation (Callaway and Davis 1993, Keeley *et al* 2012). Nevertheless, climates of MTEs may change dramatically over the century (Klausmeyer and Shaw 2009), and it is unclear how alterations in fire activity (e.g., Batllori *et al* 2013) will affect their composition and function.

Models of varying complexity have been developed for prediction of MTE vegetation dynamics, many of which include fire as a key process. Except for a few physiological process-based and dynamic

vegetation models (e.g., Mouillot *et al* 2002, Kelley *et al* 2014), most recent approaches use landscape fire-succession models (e.g., Syphard *et al* 2007, Millington *et al* 2009, Loepfe *et al* 2011, Brotons *et al* 2013). Landscape models emphasize spatially explicit dynamics and allow for simulation of realistic landscape patterns induced from past fire regimes (i.e., area burned and fire recurrence). However, such detailed and highly parameterized approaches are not designed to identify general fire ecology principles and predictions related to environmental change (Zinck and Grimm 2009).

Simple and generalized fire models capture key processes that explain properties and patterns observed in real ecosystems on large spatial and temporal scales (e.g., Zinck and Grimm 2009, Pueyo *et al* 2010). In semi-arid, fire-prone ecosystems such as savannas, minimal models have been used to examine the stability of tree/grass dominance as a result of stochastic fire–vegetation interactions (D'Odorico *et al* 2006) or associated with percolation dynamics and fire spread (Staver and Levin 2012); fire has been suggested to promote alternative stable states and ecosystem shifts due to crossing of critical thresholds or altered system feedbacks (Hoffmann *et al* 2012). Although fire can strongly influence the distribution of grass and woody cover in MTEs (e.g., Callaway and Davis 1993, Vilà *et al* 2001, Koniak and Noy-Meir 2009), the study of regime shifts and system feedbacks and their implications in these ecosystems is still very limited. Characterizing ecosystem behavior to identify sensitive thresholds and their causes in MTEs is an indispensable first step towards the specification of management and conservation scenarios.

Conceptual models such as state-and-transition modeling frameworks (STMs) reflect our understanding of ecosystem dynamics and can be easily adjusted to include new knowledge and/or specific landscape and climate conditions (Westoby *et al* 1989, Bestelmeyer *et al* 2004). Such approaches have been widely used to analyze restoration actions and management benchmarks. Our objective was to develop a minimal STM incorporating key aspects of fire ecology to evaluate the relative influence of environment, disturbance stochasticity, and plant traits on the dynamics of ecosystem types dominated by grassland–shrubland–woodland (G–S–W) mosaics, characteristic of many MTEs. The model incorporates: (i) the rate of vegetation succession in the absence of disturbance; (ii) the probability of fire and the severity of fire, including feedback effects of vegetation on flammability; and (iii) stochasticity in fire return intervals. The influence of both environment and vegetation on fire and the inclusion of disturbance stochasticity make our STM framework a novel approach towards better understanding basic ecological mechanisms constraining G–S–W dynamics in fire-prone vegetation such as MTEs, and lays the groundwork for investigations of global change influences.

We used coastal California ecosystems dominated by three vegetation types (mosaics of woodlands, shrublands, and grasslands) as an example of MTE vegetation and as a reference system for model development and to define the parameter space used in this theoretical study. We assess: (a) whether gradual variation in succession rates, disturbance frequency or disturbance severity (e.g., due to external ecosystem drivers such as climate) can promote threshold changes in MTE vegetation composition; (b) whether alternative stable states exist, and what factors drive system bifurcations; and (c) how disturbance stochasticity and fire-vegetation feedbacks influence system responses.
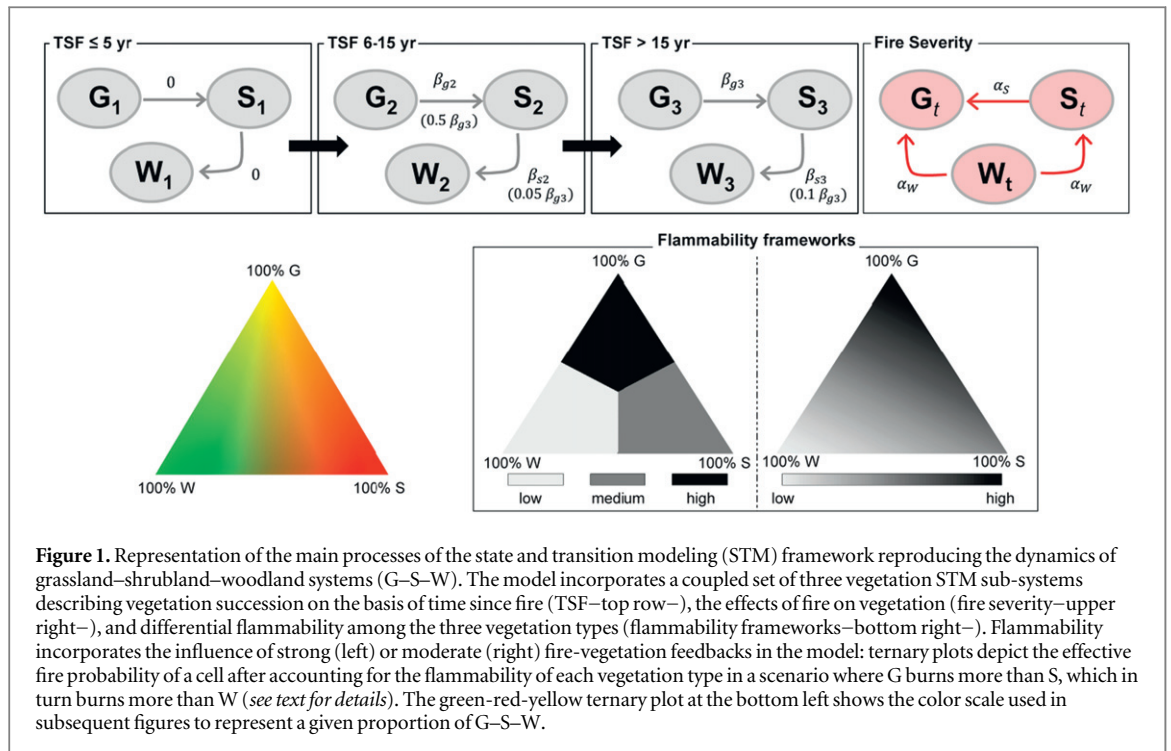
Material and methods

Model and simulation runs overview

Our STM framework (figure 1) corresponds to a semi-Markov model based on discrete-time theory (Scanlan 1994). The system moves from one vegetation state to another in a successional sequence and fire sets back vegetation to earlier succession stages as defined by fire severity. Fire is incorporated as a stochastic process influenced by vegetation flammability, and the succession rate of vegetation is temporally constrained on the basis of time since disturbance (Hobbs 1994; figure 1). The rate of succession among vegetation types and the strength of fire-vegetation feedbacks capture the importance of productivity and fuel structure, respectively, for fire activity in fire-prone ecosystems (e.g., Krawchuk and Moritz 2011, Pausas and Paula 2012), whereas altered fire probabilities and fire severities across changing conditions reflect climate–fire interactions (e.g., Marlon *et al* 2008, van Mantgem *et al* 2013).

The model was built in R (R Development Core Team 2013) and implemented as a bi-dimensional lattice. Each cell in the lattice presents a state defined by the proportion of three vegetation types: grassland (G), shrubland (S), and woodland (W), and by a time since fire (TSF). By defining the cells' vegetation as G–S–W fractions, flammability effects and different levels of fire severity (e.g., proportion of W and S set back to G) can be easily implemented. Fire spread is implicitly captured by assuming that cells burn entirely when ignition occurs, impacting all vegetation types, but among-cell connectivity is not incorporated in the model. Therefore, each cell in this implementation is assumed to experience independent fire probability, successional dynamics, and state transitions. This simplified framework allows us to keep the number of model parameters and associated uncertainty at a minimum, while also retaining the capacity for simulating underlying spatial gradients in a STM framework (Bestelmeyer *et al* 2011).

For this theoretical study, we defined a simulation domain of 300 vegetated cells (i.e., no empty spaces). Geographic cell size is not fixed, but following

Figure 1. Representation of the main processes of the state and transition modeling (STM) framework reproducing the dynamics of grassland–shrubland–woodland systems (G–S–W). The model incorporates a coupled set of three vegetation STM sub-systems describing vegetation succession on the basis of time since fire (TSF−top row−), the effects of fire on vegetation (fire severity−upper right−), and differential flammability among the three vegetation types (flammability frameworks−bottom right−). Flammability incorporates the influence of strong (left) or moderate (right) fire-vegetation feedbacks in the model: ternary plots depict the effective fire probability of a cell after accounting for the flammability of each vegetation type in a scenario where G burns more than S, which in turn burns more than W (*see text for details*). The green-red-yellow ternary plot at the bottom left shows the color scale used in subsequent figures to represent a given proportion of G–S–W.

ecological site descriptions (ESDs; Brown 2010), corresponds to an area of homogeneous climatic and edaphic conditions large enough (e.g., $2 \times 2\,\text{km}^2$) to encompass patches of multiple vegetation types (e.g., G–S–W) with shared capabilities to respond to management or disturbance. Coastal California ecological and fire literature (table S1 in the supplementary data, available at stacks.iop.org/ERL/10/034018/mmedia), descriptions of ecosystem processes in ESDs, and LANDFIRE National Vegetation Dynamics Models (LANDFIRE 2010) were used to infer parameter ranges for succession rate, fire probability, and fire severity. The parameters required for the simulations presented here, however, are not available from any one site and we thus used general rates representative of ecosystem types where fire defines the extent of G–S–W (e.g., California blue oak or coastal live oak woodlands and savannas; Brown 2010, Landfire 2010, Keeley *et al* 2012). Consequently, model results cannot be directly compared to specific historical dynamics or landscape patterns but to general ecosystem features and trends.

In this initial investigation, the environment was set as spatially homogeneous and initial model parameters were thus the same across the system. The lattice of 300 cells thus provided multiple realizations of the model's processes at the same time, allowing us to determine whether all cells follow similar dynamics for a given set of model parameters, or whether divergent vegetation trajectories occur due to stochastic dynamics or local feedbacks.

We performed a set of simulations representative of ecosystem processes in Mediterranean-climate California; grasslands are primarily annual grasses, which

are highly flammable in the summer dry season of the Mediterranean-type climate. Dense and continuous shrub cover characterizes the shrublands, which are comprised of fire-resilient, chaparral dominated species that both resprout after fire and have fire-stimulated seed germination. Woodlands are primarily oak woodlands dominated by fire resistant species that present a thick bark and ability for basal and epicormic resprouting. Throughout the simulations, the broad range of parameter' values evaluated reflect different environmental conditions. Higher fire probabilities would correspond to climatic conditions associated with higher fire risk (e.g., warmer-drier conditions), and/or could be regarded as a function of ignition probability (e.g., reflecting human-induced fires, or conversely, fire suppression). Low and high succession rates of vegetation would represent productivity gradients (e.g., linked to precipitation or soil fertility) translating into slow or fast successional changes towards woodlands, respectively, and higher fire severities would reflect more extreme climatic conditions (e.g., extended periods of drought) which increase fire intensity and the probability that burned vegetation is unable to regenerate, or alternatively can represent plant communities composed of less resilient taxa. Variation of vegetation flammability and persistence following fire incorporates the varying importance of feedbacks from vegetation in driving system dynamics.

Model processes

The state of each cell is modified in discrete time steps (i.e., one year) following a probability β of changing state due to succession (change from G–S and S–W) and a probability F for a cell to be struck by an ignition

source. When fire occurs, the entire cell is considered effective fuel (i.e., it burns when ignited), but fire severity α defines state transitions to earlier successional states (proportion changing from W to S or G, or from S to G). Parameters β, F, and α are jointly determined by the environmental conditions and cell vegetation characteristics and thus the model incorporates fire-vegetation feedbacks.

The successional process at the cell-level is expressed as $C_{i(t+1)} = \beta_I \cdot C_{i(t)}$, where $C_{i(t+1)}$ and $C_{i(t)}$ are vectors whose elements are proportions of G–S–W within cells, which are also characterized by a state i of 3 possible TSF: TSF $\leqslant$ 5 years, TSF from 6 to $\leqslant$ 15 years, and TSF > 15 years (figure 1; Landfire 2010). Sensitivity analyses of the model using accelerated or delayed TSF intervals exhibit qualitatively similar results (see supplementary data). Parameter β_i corresponds to a square matrix composed of probabilities representing the proportion of vegetation in one state (e.g., G) changing to another (e.g., S) at a given time step; values of such succession probabilities depend on TSF. Therefore, β_i incorporates time lags and different rates of vegetation change after disturbance. Cell-level successional dynamics are thus described by

$$
\begin{aligned}
C_{i\,(t+1)} &= \begin{pmatrix} W \\ S \\ G \end{pmatrix}_{i\,(t+1)} \\
&= \begin{pmatrix} 1 & \beta_{s,i} & 0 \\ 0 & 1-\beta_{s,i} & \beta_{g,i} \\ 0 & 0 & 1-\beta_{g,i} \end{pmatrix} \begin{pmatrix} W \\ S \\ G \end{pmatrix}_{i\,(t)}, \quad (1)
\end{aligned}
$$

where $\beta_{g,i}$ and $\beta_{s,i}$ define the rate of succession from G to S and from S to W, respectively, contingent on cells' TSF state i (figure 1). Direct succession of G to W and additional factors (e.g., shallow soils) constraining succession from S to W are not considered in this study; S are thus a transient state between G and W (table S1, Landfire 2010), though they could persist for many years prior to succession to W (e.g., Keeley 1992).

Changes in vegetation are also influenced by fire. At each time step it is determined whether each cell burns or not on the basis of its fire probability F, which is defined by both baseline fire probability f (capturing environmental or human influence) and vegetation flammability v (*see below*). Because in this parameterization the fire season peaks in late summer and early fall (Davis and Borchert 2006), fire was computationally implemented after the successional change of vegetation at each time step. Cells cannot burn more than once in a given time step.

Cells burn entirely but this does not cause state transitions of all the vegetation. Fire severity α, which is jointly modulated by environmental conditions and vegetation type, determines the proportion of a cell's vegetation to be set back to earlier successional states by burning (figure 1). Vegetation remaining in the same state captures the capacity of many

Mediterranean-climate plant species of California to regenerate and persist through fire events (Keeley *et al* 2012).

The flammability v of each vegetation type influences fire occurrence which, together with the differing capacity of each vegetation type to persist through fire, defines fire-vegetation feedbacks in the model. This is implemented by modifying the baseline fire probability (f) and fire severity (α) factors of each cell on the basis of its G–S–W abundance. The dynamic role of vegetation in fire-vegetation feedbacks was incorporated through two alternative flammability frameworks (figure 1): a) the dominant vegetation rule where the cell's baseline fire probability is modulated by the flammability of the dominant vegetation type (strong or nonlinear feedbacks) and b) the weighted average rule where the baseline fire probability is weighted in accordance to the relative abundance of each vegetation type (moderate or linear feedbacks).

The dominant vegetation rule represents a scenario in which changes in the abundance of the non-dominant vegetation types may have little impact on the resulting fire probability until a threshold is reached (i.e., change in vegetation dominance), when fire probability changes abruptly (e.g., Staver and Levin 2012). On the other hand, the weighted average rule represents a scenario where small changes in the abundance of vegetation types have a proportional impact on the resulting fire probability (e.g., D'Antonio and Vitousek 1992). We considered G the most flammable vegetation type and expressed S and W flammability as a percentage of G flammability and independent from each other.

Implementation of the STM framework

The simulation loop forming the core of the model consists of the following rules:

Rule 1—successional process

The TSF in all cells within the system (lattice of 300 cells) is increased by one year. Vegetation dynamics due to succession at the system-level is described as:

$$
L_{(t+1)} = \frac{1}{N} \sum_{j=1}^{N} \beta_i \, C_{ij(t)}, \quad (2)
$$

where $C_{ij(t)}$ corresponds to cell j (of $N = 300$) in TSF state i (of three possible TSF states) at a given time t, and β_i is the succession matrix as defined by each TSF state (see equation (1)). L is thus a vector whose elements are system-level proportions of G–S–W; the parameter $1/N$ is introduced so that vegetation proportions in L sum to one.

Rule 2—vegetation flammability feedbacks

Selection of the flammability framework (i.e., strong or moderate feedbacks) and modification of cells' baseline fire probability. Feedbacks are implemented at the cell-level as:

$$F = \sum_{k=1}^{N} p_k \, f \, \nu_k, \qquad (3)$$

where F is the effective fire probability of a cell, f corresponds to the baseline fire probability defined by the environment, and p_k and ν_k are the proportion and flammability of vegetation type k (of $N = 3$; G, S, and W), respectively. When strong feedbacks operate, ν_k of the non-dominant vegetation types is set to 0. Note that ν is a unitless modifier of f that is always smaller than or equal to 1.

Rule 3—ignition
Random ignitions based on each cell's effective fire probability (F) at each time step; TSF for burned cells is reset to 0. Ignitions are implemented at the cell-level using the beta and Bernoulli probability distributions:

$$r_{j,t} \sim \text{Beta}\,(2, \ F)$$
$$\text{Ignition}_{j,t} \sim \text{Bernoulli}\,(r_{j,t}). \qquad (4)$$

In temperate fire-prone vegetation, many tree and shrub species have the ability to resprout and grass biomass approaches pre-burn levels quickly following fire. Additionally, much of the area burned in this California implementation exhibits minimal influence of vegetation age on fire probabilities (e.g., Moritz 2003). Therefore, for our initial investigation we approximate fire as a stochastic process in which the probability of burning is independent of the time since last burn. This is a simplifying assumption that can be explored in more detail in future versions of the model. Note, however, that due to the influence of vegetation types on F, the observed time elapsed between fires will vary among cells for a given f (e.g., cells dominated by grasslands will experience more frequent fire under either flammability feedback rule).

Rule 4—fire severity effects
In cells that burn, fire severity determines vegetation transitions to earlier successional states. Severity effects at the system-level are described as:

$$\alpha = \sum_{j,\,k=1}^{N} p_{jk} \alpha_k, \qquad (5)$$

where α is the amount of vegetation set back to earlier states due to burning, p_{jk} corresponds to the proportion of vegetation type k (of $N = 2$; W and S) of cell j (see equation (2)), and α_k is the severity of fire on vegetation type k; α_k can vary from 0 (no change in W and S proportion due to fire) to 1 (all W and S experiencing state type-conversion as a result of burning). In this study, G is not type-converted by fire and, for simplification to avoid the inclusion of another model parameter, type-conversion for W is equally split to S and G; this has no qualitative impact on the model, though it may influence the quantitative behavior of the system under some parameterizations.

The complete functioning of the model (figure 1) is formalized as:

$$G_{t+1} = G_t - \beta_{g2} G_2 \left(1 - \frac{1}{F} \right)$$
$$- \beta_{g3} G_3 \left(1 - \frac{1}{F} \right) + \frac{\alpha_w W_t \dfrac{1}{F}}{2} + \alpha_s S_t \frac{1}{F},$$
$$S_{t+1} = S_t - \beta_{s2} S_2 \left(1 - \frac{1}{F} \right) - \beta_{s3} S_3 \left(1 - \frac{1}{F} \right)$$
$$+ \beta_{g2} G_2 \left(1 - \frac{1}{F} \right) + \beta_{g3} G_3 \left(1 - \frac{1}{F} \right)$$
$$+ \frac{\alpha_w W_t \dfrac{1}{F}}{2} - \alpha_s S_t \frac{1}{F},$$
$$W_{t+1} = W_t - \alpha_w W_t \frac{1}{F}$$
$$+ \beta_{s2} S_2 \left(1 - \frac{1}{F} \right) + \beta_{s3} S_3 \left(1 - \frac{1}{F} \right),$$

where G, S, W corresponds to frequency distribution of grasslands, shrublands, and woodlands across the simulation domain at each time step (t), respectively. The coefficients β, which define succession rates from one vegetation type to another, are contingent on vegetation type (βg and βs) and TSF (subscripts 2 and 3 —from 6 to $\leqslant$ 15 years, and > 15 years, respectively; equation (1)). Vegetation type does not change due to succession during the first 5 years following fire (all $\beta = 0$). Effective fire probability (the likelihood of burning at each time step; equation (3)) is defined by F, and α defines fire severity (the amount of type-conversion to earlier successional states when burning; equation (5)). Fire-vegetation feedbacks are incorporated through the influence of vegetation on both F and α. All model parameters are independent among cells and thus there can be spatial heterogeneity at the system-level. Each cell is characterized by a TSF and a G–S–W proportion, so full characterization of the system's vegetation state is represented by a 9-cell matrix including proportions of G–S–W in three age classes (defined by TSF).

Simulation experiments
We conducted a comprehensive set of simulation experiments (parameter scenarios) to evaluate how the coupled effects of environmental conditions (influencing β, α, and F) and fire-vegetation feedbacks (influencing α and F) determine the dynamics of G–S–W systems (table 1). In each simulation run, we assumed homogeneous and constant (i.e., no temporal change) conditions over the simulation domain: there were no spatial differences in succession rate, fire probability, fire severity, and vegetation flammability across the system. These background model parameters were therefore reduced to a common set of initial values for all cells, though their effective values could change in time and space due to within-cells fire-vegetation feedbacks. Through the simulation experiments, model processes were systematically modified two at a time while setting the rest at baseline levels to evaluate system behavior and the implications of such processes in G–S–W dynamics. The parameter

Table 1. Parameter settings of the model (see figure 1) for the simulation experiments (parameter scenarios) conducted to evaluate the effects of succession rate of vegetation (β), fire probability (f), vegetation flammability (v), and fire severity (α) on the dynamics of grassland–shrubland–woodland systems. Each scenario consisted in the modification of two of the model processes at a time (highlighted in bold) while fixing the others at baseline values: scenario 1—variation of fire probability and succession rate (number of simulations $N = 2240$); scenario 2—variation of fire probability and fire severity (number of simulations $N = 2240$); scenario 3—variation of fire severity on woodlands and shrublands (number of simulations $N = 1092$); scenario 4—variation of vegetation flammability (number of simulations $N = 14\,112$). In each scenario, model parameterization was homogeneous among cells, and an initial random time since fire between 1 and 100 years, fixed across all simulations, was used for each cell.

	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Succession rate (β) (proportion/year)				
β_{g2} (Grass → shrub 6–15 yr after fire)	$0.5\,\beta_{g3}$	$0.5\,\beta_{g3}$	$0.5\,\beta_{g3}$	$0.5\,\beta_{g3}$
β_{s2} (Shrub → wood 6–15 yr after fire)	$0.05\,\beta_{g3}$	$0.05\,\beta_{g3}$	$0.05\,\beta_{g3}$	$0.05\,\beta_{g3}$
β_{g3} (Grass → shrub >15 yr after fire)	**0.01–0.2** (by +0.01; $n = 20$)	0.05	0.05	0.05
β_{s3} (Shrub → wood >15 yr after fire)	$0.1\,\beta_{g3}$	$0.1\,\beta_{g3}$	$0.1\,\beta_{g3}$	$0.1\,\beta_{g3}$
Baseline fire probability (f) (1/fire frequency)	**0.01–0.685** (by + 0.025; $n = 28$)	**0.01–0.685** (by + 0.025; $n = 28$)	0.1	**0.05, 0.1, 0.2, 0.3** ($n = 4$)
Vegetation flammability (v) (unitless modifier of fire probability)				
v_g (Grassland flammability)	1	1	1	1
v_s (Shrubland flammability)	$1^{\star}v_g$	$1^{\star}v_g$	$1^{\star}v_g$	**0.01$^{\star}v_g$–1$^{\star}v_g$** (by + 0.05; $n = 21$)
v_w (Woodland flammability)	$1^{\star}v_g$	$1^{\star}v_g$	$1^{\star}v_g$	**0.01$^{\star}v_g$–1$^{\star}v_g$** (by + 0.05; $n = 21$)
Fire severity (α) (proportion set back to earlier vegetation stages)				
α_S (Fire severity on shrubland)	0.25	**0.05–0.5** (by + 0.05; $n = 20$)	**0.05–0.55** (by + 0.02; $n = 21$)	0.25
α_W (Fire severity on woodland)	$0.1\,\alpha_S$	$0.1\,\alpha_S$	**0.005–0.125** (by + 0.02; $n = 13$)	$0.1\,\alpha_S$
Initial cells composition	100% W, 100% S, 100% G, mixed	100% W, 100% S, 100% G, mixed	100% W, 100% S, 100% G, mixed	100% W, 100% S, 100% G, mixed
Flammability rule	—	—	—	Weighted/ dominant
Total number of parameter combinations	2240	2240	1092	14 112

space evaluated in this theoretical study encompasses a wide range of empirical observations (table S1) and reference conditions (e.g., ESDs) on vegetation succession and fire occurrence in Mediterranean-climate California; within this range, a total of 19684 different combinations of model parameters were evaluated (table 1).

Model runs

Simulation runs on each background set of parameters were performed on four initial, spatially homogeneous vegetation conditions: 100% dominance of each vegetation type in all cells (i.e., G, S, W), plus a system where all cells were initiated with equal proportion of G–S–W. Cells were assigned an initial random TSF between 1 and 100 years fixed through all model runs. Each individual simulation comprised 10 000 model steps to ensure the system reached a stable state or equilibrium, which was defined as a de-trended proportion of G–S–W over time. That is, even if the system is dynamic because the proportion of each vegetation type may fluctuate through time, at equilibrium such fluctuations are centered on a certain level and the long-term proportions of G–S–W do not increase or decrease.

During the simulations, the proportion covered by each vegetation type and the age (i.e., TSF) of each cell were reported at each time step and integrated across the entire system (i.e., frequency distribution of G, S, and W across all cells). System-level stability (proportion of area not exhibiting vegetation transitions due to fire or succession) and heterogeneity (Shannon diversity index on the proportion of G–S–W) were computed at each time step. Results for each simulation were then expressed as 1000-year averages (under equilibrium conditions). Variation in the frequency distribution of vegetation types at the cell-level was also examined to test for internal bifurcations into alternative states that would be masked by considering only system-level statistics.

Results

Vegetation dynamics across parameter space

When different vegetation types have the same probability of burning (i.e., no vegetation feedbacks that alter fire probabilities; parameter scenarios 1–3), the system exhibits a single stable state for a given set of model parameters irrespective of its initial vegetation state (figure 2 and S1). As expected, fire probability exerts a strong influence on vegetation composition, determining major patterns of G, S, and W abundance at the system-level. Regardless of the succession rate of vegetation or fire severity, W dominates at low levels of fire (static system), whereas G dominate under high fire occurrence (dynamic system). At intermediate fire frequencies S are most abundant, and they are
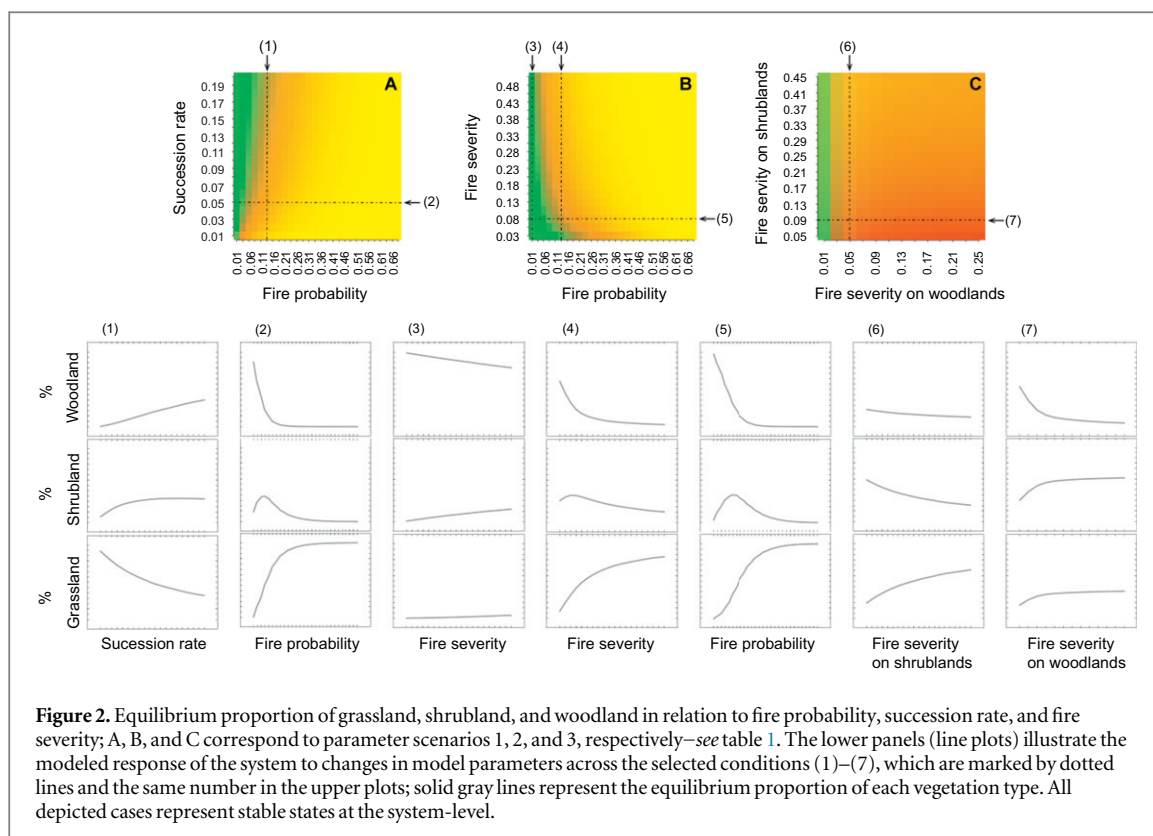
associated with higher system-level vegetation heterogeneity (figure 2 and S2).

Drastic changes in G–S–W dominance can occur over narrow ranges of the parameter space (figure 2), especially with changes in fire probability. Similarly, over a limited range of fire probability values, the succession rate of vegetation and fire severity strongly influence the abundance of W, S, and G at equilibrium: faster succession rates and lower fire severity lead to increased W dominance. Given the transient nature of S in this study, shrublands only become dominant when fire severity is higher on W than on S (figure 2). The dominance or relatively high presence of S is generally associated with higher temporal variation in within-cell vegetation proportions that result in larger system-level fluctuations of G–S–W abundance when equilibrium is reached (figure S3).

Alternative stable states

When G, S, and W experience a different probability of burning because of their flammability, the system exhibits two alternative stable states (bistability) under certain parameter combinations (figure 3). The nature of fire-vegetation feedbacks induced by vegetation flammability determines whether alternative stable states exist or not. Bistability in system behavior arises when the flammability of G > S > W and the effective fire probability of a cell is determined by strong feedbacks (figure 1). In this case, given a baseline fire probability, fire severity, and flammability of G and W, increasing the flammability of S leads to high G dominance when the initial cell vegetation is not dominated by W (figure 4(A)). However, increased S flammability does not result in G dominance when the flammability of W is low and cells are initially dominated by W. When moderate fire-vegetation feedbacks operate (figure 1) the system still shows nonlinear changes in G–S–W dominance, but only one stable equilibrium exists for any given condition, irrespective of initial vegetation composition (figure S4).

Regardless of the existence of one or two stable states, the abundance of G, S, and W vegetation states can respond in different ways to changing conditions and thus to altered levels of system processes (succession rate, flammability, fire probability, and fire severity; figures 2, 3, and S1). Changes in the abundance of G and W are coupled (with opposite trends) and exhibit both gradual and threshold-type responses depending on the process that is governing such changes. However, S shows in some cases a differential response from W and G, and it displays hump-shaped relationships with fire probability and severity (figures 2 and 3). The high sensitivity of G–S–W dominance to changes in fire probability is related to threshold-type responses of G and W abundance to this process. In addition, for a limited range of conditions and when strong fire-vegetation feedbacks occur,

Figure 2. Equilibrium proportion of grassland, shrubland, and woodland in relation to fire probability, succession rate, and fire severity; A, B, and C correspond to parameter scenarios 1, 2, and 3, respectively–*see* table 1. The lower panels (line plots) illustrate the modeled response of the system to changes in model parameters across the selected conditions (1)–(7), which are marked by dotted lines and the same number in the upper plots; solid gray lines represent the equilibrium proportion of each vegetation type. All depicted cases represent stable states at the system-level.

vegetation proportions can be insensitive to parameter change (figure 3).

Divergent vegetation trajectories

To better characterize alternative stable states in the dynamics of the system, we performed additional simulations to evaluate whether the entire system (i.e., all 300 cells) settles eventually to the same vegetation state irrespective of the initial vegetation composition. We tested different model parameterizations (homogeneous among cells) defined by different combinations of G–S–W flammability and strong fire-vegetation feedbacks; in each case 441 initial conditions defined by cells' G–S–W proportion were evaluated ($N = 7056$ simulations). Results corroborate the existence of two major basins of attraction at the system-level where vegetation in all cells is either dominated by W or G, but also the presence of intermediate stability attractors between them (figures 4(B) and S6). Such intermediate attractors are determined by high levels of among-cell vegetation heterogeneity (figure 4(C)): combinations of contrasting vegetation states among individual cells average out to define the stable vegetation state at the system-level.

The mechanisms that determine the dynamics of G–S–W vegetation and which basin of attraction the system will follow depend both on factors extrinsic and intrinsic to the system (figure 5). System-level transitions to different stable states can be driven by extrinsic factors such as the environment (e.g., different fire probability; figure 5(A)), but also by intrinsic

fire-vegetation feedbacks under a given environment (e.g., different vegetation composition; figures 5(B) and (C)). On the other hand, under some parameter combinations, stochastically driven transitions in the vegetation state of some cells, together with the effects of post-disturbance dynamics, result in contrasting stable states at the cell-level and thus increased system heterogeneity (figures 5(D)–(F)).

Discussion

High rates of vegetation succession, low flammability, and low severity (or high capacity of vegetation to persist through fire) promote rather static systems dominated by woodlands. However, because of the relatively slow dynamics of vegetation successional change (years to decades), high fire frequencies inevitably lead to a single stable state dominated by grasslands. The interplay of factors extrinsic and intrinsic to the system determines the nature of transitions between vegetation states. As evidenced by the dynamics of ecosystems representative of Mediterranean-climate California, transitions between grasslands and woodlands in G–S–W systems can encompass a continuum of possible behavior, including continuous responses (gradual or threshold-like) and catastrophic shifts (alternative stable states).

Dynamics of california ecosystems

Although a direct quantitative model validation was not possible, the modeling framework presented here
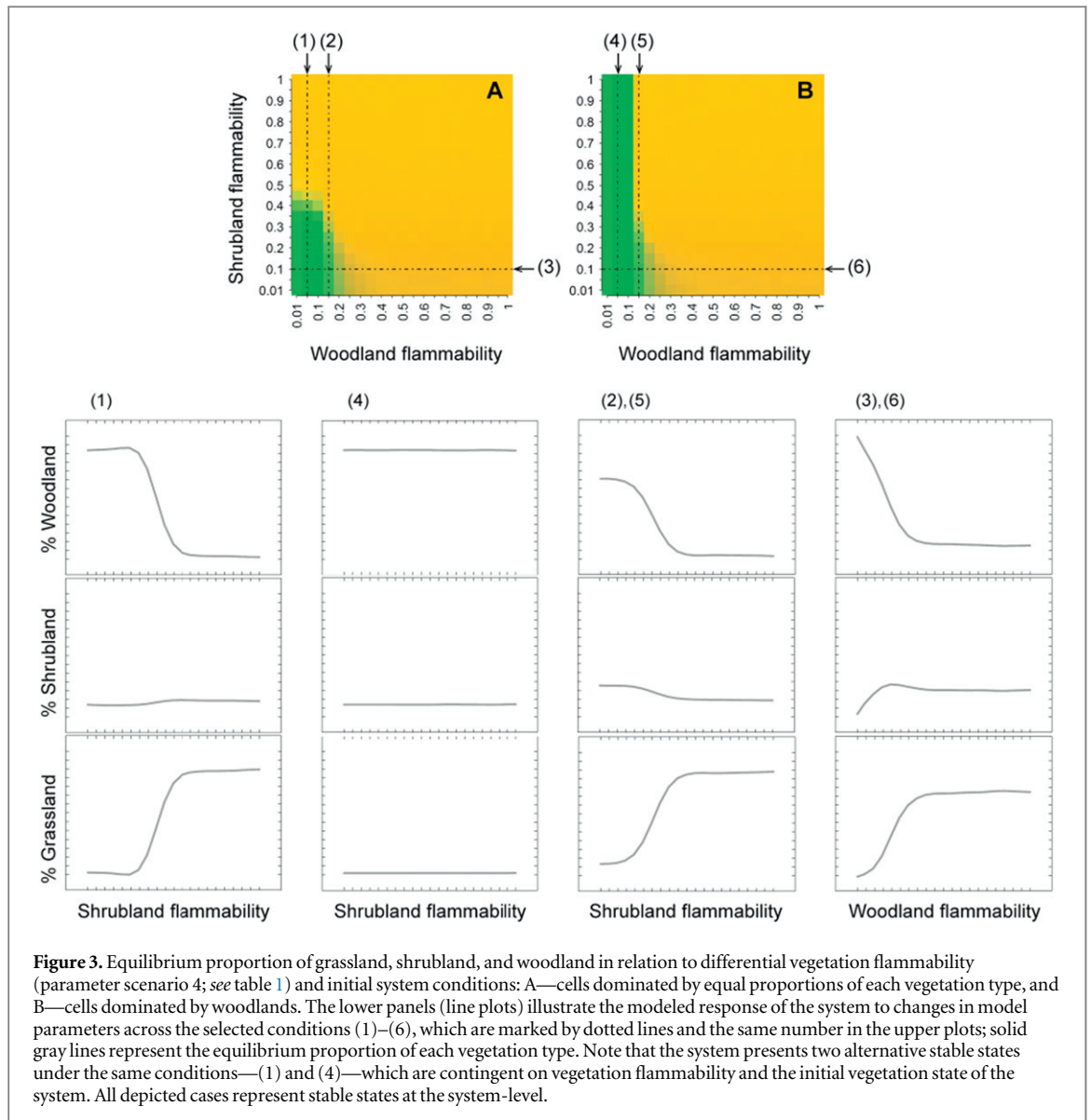
Figure 3. Equilibrium proportion of grassland, shrubland, and woodland in relation to differential vegetation flammability (parameter scenario 4; *see* table 1) and initial system conditions: A—cells dominated by equal proportions of each vegetation type, and B—cells dominated by woodlands. The lower panels (line plots) illustrate the modeled response of the system to changes in model parameters across the selected conditions (1)–(6), which are marked by dotted lines and the same number in the upper plots; solid gray lines represent the equilibrium proportion of each vegetation type. Note that the system presents two alternative stable states under the same conditions—(1) and (4)—which are contingent on vegetation flammability and the initial vegetation state of the system. All depicted cases represent stable states at the system-level.
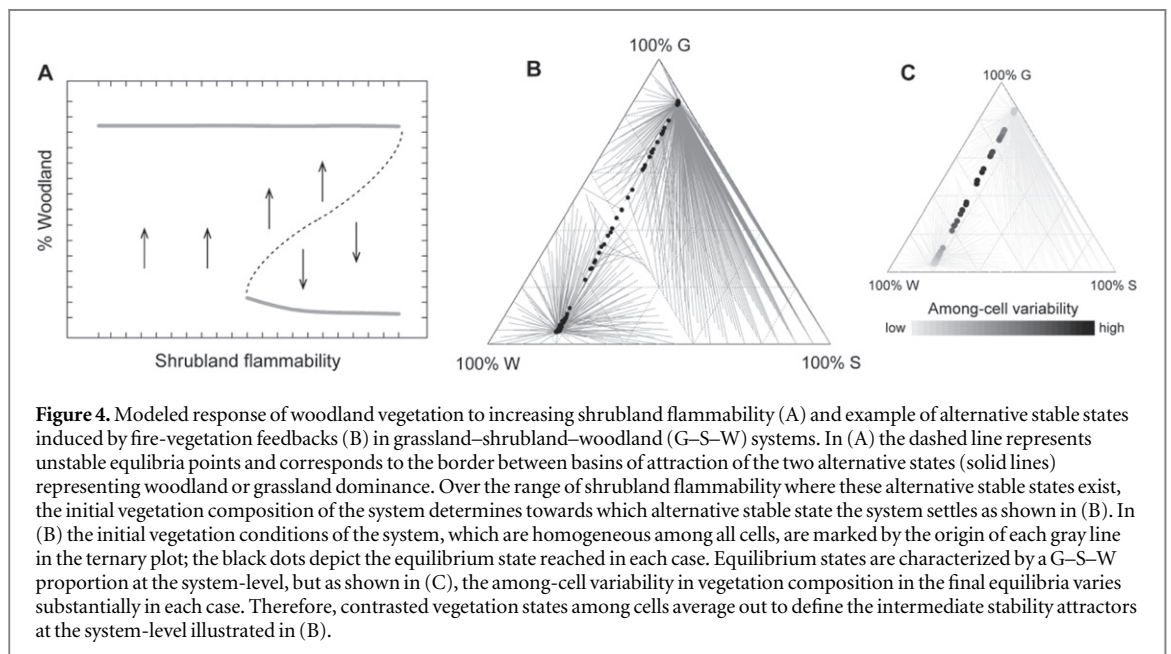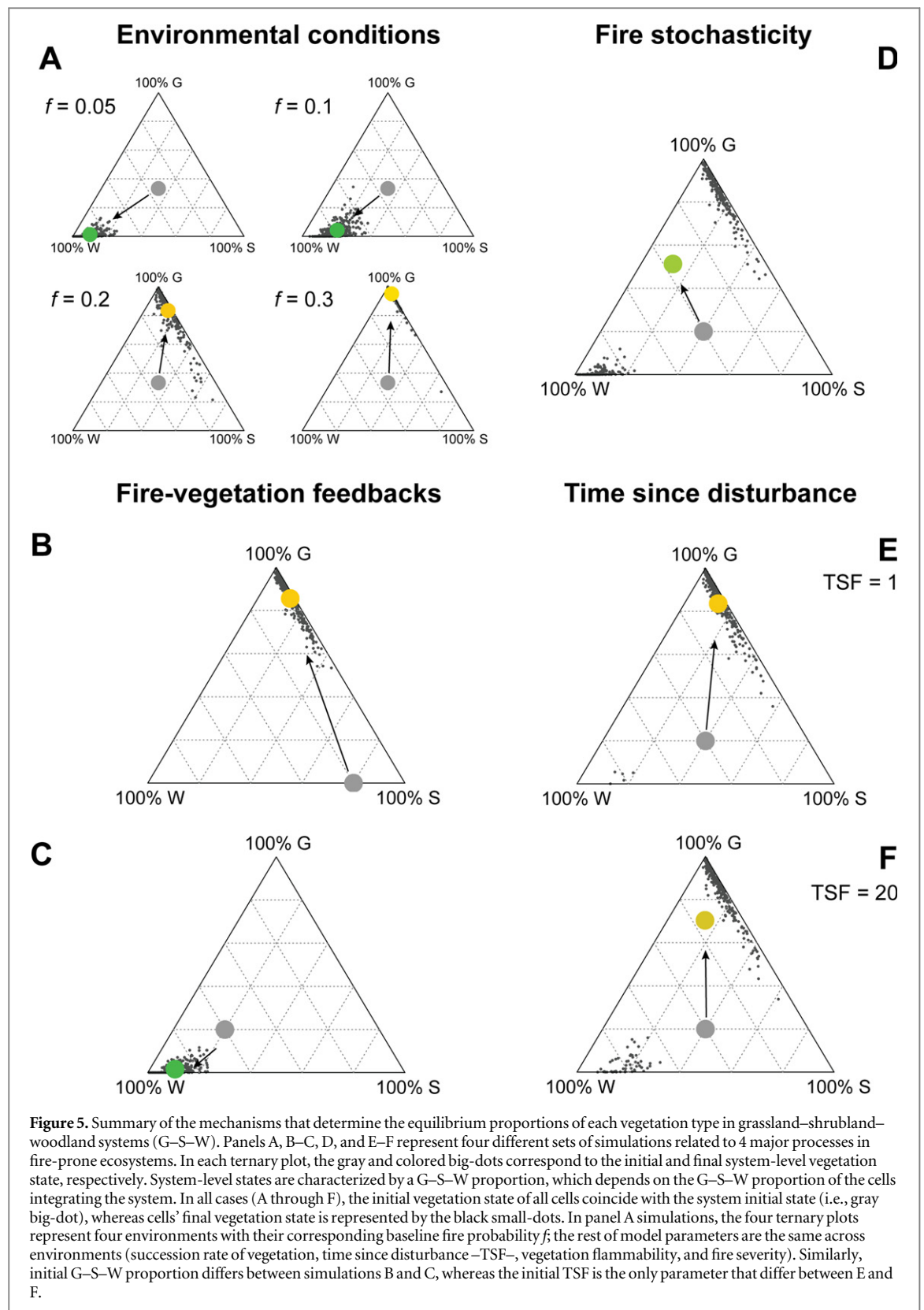

Figure 4. Modeled response of woodland vegetation to increasing shrubland flammability (A) and example of alternative stable states induced by fire-vegetation feedbacks (B) in grassland–shrubland–woodland (G–S–W) systems. In (A) the dashed line represents unstable equilibria points and corresponds to the border between basins of attraction of the two alternative states (solid lines) representing woodland or grassland dominance. Over the range of shrubland flammability where these alternative stable states exist, the initial vegetation composition of the system determines towards which alternative stable state the system settles as shown in (B). In (B) the initial vegetation conditions of the system, which are homogeneous among all cells, are marked by the origin of each gray line in the ternary plot; the black dots depict the equilibrium state reached in each case. Equilibrium states are characterized by a G–S–W proportion at the system-level, but as shown in (C), the among-cell variability in vegetation composition in the final equilibria varies substantially in each case. Therefore, contrasted vegetation states among cells average out to define the intermediate stability attractors at the system-level illustrated in (B).

Figure 5. Summary of the mechanisms that determine the equilibrium proportions of each vegetation type in grassland–shrubland–woodland systems (G–S–W). Panels A, B–C, D, and E–F represent four different sets of simulations related to 4 major processes in fire-prone ecosystems. In each ternary plot, the gray and colored big-dots correspond to the initial and final system-level vegetation state, respectively. System-level states are characterized by a G–S–W proportion, which depends on the G–S–W proportion of the cells integrating the system. In all cases (A through F), the initial vegetation state of all cells coincide with the system initial state (i.e., gray big-dot), whereas cells' final vegetation state is represented by the black small-dots. In panel A simulations, the four ternary plots represent four environments with their corresponding baseline fire probability *f*; the rest of model parameters are the same across environments (succession rate of vegetation, time since disturbance –TSF–, vegetation flammability, and fire severity). Similarly, initial G–S–W proportion differs between simulations B and C, whereas the initial TSF is the only parameter that differ between E and F.

successfully captures major ecosystem features and trends observed in recent decades over California landscapes. For instance, the model can reproduce the dominance of oak woodlands reported under fire frequencies of ∼10 years associated with ground fires before the implementation of fire suppression policies in the 1930s (Sugihara *et al* 2006). This can be modeled by implementing low fire severities thus reducing the rate of vegetation conversion driven by fire. In contrast, the dynamics of forests of fire-sensitive species (e.g., Douglas-fir, Lazzeri-Aerts and Russell 2014) are captured over a range of fire frequencies when high fire severities are implemented. On the other hand, landscapes dominated by shrublands

under a fire return interval of ∼30–40 years, characteristic of chaparral (Sugihara *et al* 2006, table S1), were observed under relatively high fire severity consistent with the crown-fire regime of such communities.

Despite the often assumed high fire resilience of MTE vegetation, our approach reinforces that such ecosystems can be very sensitive to altered fire frequency and severity. Our results show that fire return intervals under five years result in grass-dominated systems irrespective of the succession rate of vegetation. This is consistent with trends observed in recent decades over Mediterranean-climate California (e.g., Minnich and Dezzani 1998, Sugihara *et al* 2006) and with anthropological knowledge regarding Native American burning practices over central coastal California (e.g., Lightfoot *et al* 2013). On the other hand, reduced ignition rates allow buildup of fuels and succession from grassland to shrubland or from shrubland to woodland, as observed over California after implementation of fire suppression policies (e.g., Russell and McBride 2003, Meentemeyer *et al* 2008). Our model does not have fuel buildup effects on severity, so we do not address the question of whether suppression will contribute to extreme or uncharacteristic fires (see Keeley *et al* 1999), nor do we model extreme fire weather effects that can overwhelm inherent vegetation flammability characteristics (Moritz 2003).

Feedbacks, bistability and disturbance stochasticity

Switches between contrasting stable vegetation states in G–S–W systems may occur as a result of small variations in extrinsic ecosystem drivers of disturbance (climate) or in fire-vegetation feedbacks (e.g., invasive species). Such switches are triggered by the existence of critical points in underlying processes of disturbance linked to external drivers (Beisner *et al* 2003). Phase transitions may also result, however, from variation in processes that are not dependent on or induced by disturbance such as succession rate of vegetation. In these cases, system behavior is not determined by feedbacks, and state dynamics are governed by gradual or threshold changes (Suding and Hobbs 2009).

In our model, the inclusion of moderate fire-vegetation feedbacks successfully reproduce the observed self-reinforcing grass-fire cycle (D'Antonio and Vitousek 1992), whereas alternative stable states (bistability) and hysteresis emerge when strong fire-vegetation feedbacks operate (Scheffer *et al* 2001). In both cases, feedbacks induced by differential vegetation flammability drive the behavior of the system by effectively modifying environmental drivers (e.g., fire probability). Plant traits that modulate fire-vegetation feedbacks are thus key in determining the nature and location of critical thresholds in the dynamics of fire-prone G–S–W systems. Other studies point to the importance of plant life history strategies (e.g., Saura-Mas *et al* 2010), self-reinforcing combustion

properties (e.g., Odion *et al* 2010), and vegetation traits related to flammability (e.g., Hoffmann *et al* 2012) in generating feedbacks and conditions that allow long-term persistence of vegetation states.

The analysis presented in this theoretical study indicates that threshold responses in the probability of fire (induced by fire-vegetation feedbacks) and disturbance stochasticity may be strong enough mechanisms to generate system bistability in fire-prone G–S–W systems such as MTEs. Such mechanisms have been associated with alternative stable states in other fire-prone ecosystems (D'Odorico *et al* 2006). Our framework, however, emphasizes that these mechanisms operate at different scales; disturbance stochasticity can generate spatial heterogeneity (i.e., state change only at local scales) as opposed to system-wide shifts modulated by strong fire-vegetation feedbacks. When strong feedbacks operate, system-level alteration in the abundance of one ecosystem component (e.g., grass) can be expected to permanently change the nature of system interactions and the dynamics of vegetation towards a different stable state (Suding and Hobbs 2009, Staver and Levin 2012). However, if such changes occur when the state of the system is close to bifurcation points (Scheffer 2009), then disturbance stochasticity can effectively modulate shifts across the bifurcation threshold. For instance, locally delayed (or expedited) fire occurrence may allow (or prevent) vegetation successional changes that can override system-level feedback switches and thus determine trajectory towards one state or the other at the local scale. Overall, our findings suggest that, under some conditions, disturbance stochasticity may translate into more gradual responses of the system as a whole to altered conditions even when strong feedbacks operate.

Framework limitations and implications

Clearly, extrinsic ecosystem drivers such as climate are not spatially homogeneous, and extreme events and climate fluctuations can be particularly important in modulating system dynamics and stability through time. Similarly, additional spatially heterogeneous drivers (e.g., herbivory, nutrient cycling, hydrology, edaphic factors or humans) might prevent some sites from vegetation succession during disturbance-free intervals (e.g., Callaway and Davis 1993, Landfire 2010). Even though our model can incorporate environmental gradients and other spatially explicit ecosystem drivers (figure S7), these factors are not implemented in the simulations presented here, which aim to evaluate basic fire-vegetation mechanisms underlying the behavior of G–S–W systems. The future inclusion of climate fluctuations into a spatially informed STM (e.g., incorporating patterns of soil typology and climate gradients; Bestelmeyer *et al* 2011) will allow a more sophisticated predictive approach for characterizing dynamics and

understanding general pattern-process relationships across scales in fire-prone communities.

It is encouraging that a simple STM model like the one presented here can approximate some of the human and environmental influences in the dynamics of MTE fire regimes. Refined models representing specific ecosystems are needed to be able to assess if, when, and where drastic shifts may occur in reality. The possibility of abrupt and non-reversible state changes in such ecosystems, however, evidences the uncertainty and unpredictability that can be associated with their management. Comprehensive understanding of system behavior is needed to infer feedback mechanisms, identify system thresholds, and determine biotic and abiotic factors that affect the resilience of ecosystems (e.g., van de Koppel *et al* 2002, Suding and Hobbs 2009). Identifying thresholds related to collapse and recovery is a first step that can help prioritize adaptive management efforts to sustain desired states and associated ecosystem services (Folke *et al* 2004, Bestelmeyer 2006). We believe our conceptual framework could thus represent a useful starting point for specifying management scenarios based on refined predictive local models and assessing threshold responses and disequilibrium dynamics derived from ongoing land-use and climate changes. This may help resolve under which fire modeling or scales of analysis the inclusion of feedback effects is critical to capture MTEs dynamics, and to assess when and where drastic ecosystem shifts may occur under future MTE climates so that conditions resulting in state changes can be attenuated via resilience-based management.

Conclusion

Our minimal dynamic framework provides deeper mechanistic understanding of how certain aspects of a disturbance regime (fire recurrence, severity, and stochasticity), vegetation characteristics (succession rate and flammability), and fire-vegetation feedbacks determine system composition and dynamics in G–S–W systems, which characterize many temperate fire-prone vegetation. Our findings strongly suggest that vegetation alteration in MTEs may not only occur after extreme fire events (e.g., Rodrigo *et al* 2004), contrasting states in such ecosystems may be driven by small variation in ecosystem processes such as fire recurrence and system flammability. Plant traits that modulate system feedbacks effectively modify the behavior of MTEs and determine the nature and location of critical thresholds in their dynamics. The existence of alternative stable states and of contrasted MTEs response to environmental change has broad implications for their management.

References

Batllori E, Parisien M, Krawchuk M A and Moritz M A 2013 Climate change-induced shifts in fire for Mediterranean ecosystems *Glob. Ecol. Biogeogr.* **22** 1118–29

Beisner B E, Haydon D T and Cuddington K 2003 Alternative stable states in ecology *Frontiers Ecol. Environ.* **1** 376–82

Bestelmeyer B T 2006 Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious *Restor. Ecol.* **14** 325–29

Bestelmeyer B T, Goolsby D P and Archer S R 2011 Spatial perspectives in state-and-transition models: a missing link to land management? *J. Appl. Ecol.* **48** 746–57

Bestelmeyer B T, Herrick J E, Brown J R, Trujillo D A and Havstad K M 2004 Land management in the american southwest: a state-and-transition approach to ecosystem complexity *Environ. Manage.* **34** 38–51

Brotons L, Aquilué N, de Cáceres M, Fortin M-J and Fall A 2013 How fire history, fire suppression practices and climate change affect wildfire regimes in Mediterranean landscapes *PLoS ONE* **8** e62392

Brown J R 2010 Ecological sites: their history, status, and future *Rangelands* **32** 5–8

Callaway R M and Davis F W 1993 Vegetation dynamics, fire, and the physical environment in coastal Central California *Ecology* **74** 1567–78

D'Antonio C M and Vitousek P M 1992 Biological invasions by exotic grasses, the grass/fire cycle, and global change *Annu. Rev. Ecol. Systematics* **23** 63–87

Davis F W and Borchert M I 2006 Central coast bioregion *Fire in California's Ecosystems* ed ed N G Sugihara *et al* (Berkeley, CA, USA: University of California Press) pp 321–49

D'Odorico P, Laio F and Ridolfi L 2006 A probabilistic analysis of fire-induced tree-grass coexistence in savannas *Am. Nat.* **167** E79–87

Folke C *et al* 2004 Regime shifts, resilience, and biodiversity in ecosystem management *Annu. Rev. Ecol. Evol. Systematics* **35** 557–81

Hobbs R J 1994 Dynamics of vegetation mosaics: can we predict responses to global change? *Écoscience* **1** 346–56

Hoffmann W A *et al* 2012 Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes *Ecol. Lett.* **15** 759–68

Keeley J E 1992 Recruitment of seedlings and vegetative sprouts in unburned chaparral *Ecology* **73** 1194–208

Keeley J E, Fotheringham C J and Morais M 1999 Reexamining fire suppression impacts on brushland fire regimes *Science* **284** 1829–32

Keeley J E, Bond W J, Bradstock R A, Pausas J G and Rundel P W 2012 *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management* (Cambridge: Cambridge University Press)

Kelley D I, Harrison S P and Prentice I C 2014 Improved simulation of fire–vegetation interactions in the land surface processes and exchanges dynamic global vegetation model (LPX-Mv1) *Geosci. Model. Dev. Discuss.* **7** 931–1000

Klausmeyer K R and Shaw M R 2009 Climate change, habitat loss, protected areas and the climate adaptation potential of species in the Mediterranean ecosystems worldwide *PLoS ONE* **4** e639

Koniak G and Noy-Meir I 2009 A hierarchical, multi-scale, management-responsive model of Mediterranean vegetation dynamics *Ecol. Model.* **220** 1148–58

Krawchuk M A and Moritz M A 2011 Constraints on global fire activity vary across a resource gradient *Ecology* **92** 121–32

LANDFIRE 2010 LANDFIRE National Vegetation Dynamics Models, LF2010 (LF_1.2.0) (www.landfire.gov) (www.landfire.gov/national_veg_models_op2.php)

Lazzeri-Aerts R and Russell W 2014 Survival and recovery following wildfire in the sourthern range of the coast redwood forest *Fire Ecol.* **10** 43–55

Lightfoot K G *et al* 2013 Anthropogenic burning on the Central California coast in Late Holocene and early historical times: findings, implications, and future directions *Calif. Archaeol.* **5** 371–90

Loepfe L, Martinez-Vilalta J and Piñol J 2011 An integrative model of human-influenced fire regimes and landscape dynamics *Environ. Model. Softw.* **26** 1028–40

Marlon J R *et al* 2008 Climate and human influences on global biomass burning over the past two millennia *Nat. Geosci.* **1** 697–702

Meentemeyer R K, Rank N E, Anacker B L, Rizzo D M and Cushman J H 2008 Influence of land-cover change on the spread of an invasive forest pathogen *Ecol. Appl.* **18** 159–71

Millington J D A, Wainwright J, Perry G L W, Romero-Calcerrada R and Malamud B D 2009 Modelling Mediterranean landscape succession-disturbance dynamics: a landscape fire-succession model *Environ. Model. Softw.* **24** 1196–208

Minnich R A and Dezzani R J 1998 Historical decline of coastal sage scrub in the Riverside-Perris plain, California *West. Birds* **29** 366–91

Moritz M 2003 Spatiotemporal analysis of controls on shrubland fire regimes: age dependency and fire hazard *Ecology* **84** 351–61

Mouillot F, Rambal S and Joffre R 2002 Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem *Glob. Change Biol.* **8** 423–37

Odion D C, Moritz M A and DellaSala D A 2010 Alternative community states maintained by fire in the Klamath Mountains, USA *J. Ecol.* **98** 96–105

Pausas J G and Paula S 2012 Fuel shapes the fire-climate relationship: evidence from Mediterranean ecosystems *Glob. Ecol. Biogeogr.* **21** 1074–82

Pueyo S, De Alencastro Graça P M L, Barbosa R I, Cots R, Cardona E and Fearnside P M 2010 Testing for criticality in ecosystem dynamics: the case of Amazonian rainforest and savanna fire *Ecol. Lett.* **13** 793–802

R Development Core Team 2013 R: a language and environment for statistical computing (Vienna, Austria: R Foundation for Statistical Computing) ISBN 3-900051-07-0

Rodrigo A, Retana J and Picó F X 2004 Direc regeneration is not the only response of Mediterranean forests to large fires *Ecology* **85** 716–29

Russell W H and McBride J R 2003 Landscape scale vegetation-type conversion and fire hazard in the San Francisco bay area open spaces *Landscape Urban Plan.* **64** 201–08

Saura-Mas S, Paula S, Pausas J G and Lloret F 2010 Fuel loading and flammability in the Mediterranean basin woody species with different post-fire regenerative strategies *Int. J. Wildland Fire* **19** 783–94

Scanlan J C 1994 State and transition models for rangelands. 5. The use of state and transition models for predicting vegetation change in rangelands *Tropical Grasslands* **28** 229–40

Scheffer M 2009 *Critical Transitions in Nature and Society* (New Jersey, UK: Princeton University Press)

Scheffer M, Carpenter S, Foley J A, Folke C and Walker B 2001 Catastrophic shifts in ecosystems *Nature* **413** 591–96

Staver A C and Levin S A 2012 Integrating theoretical climate and fire effects on savanna and forest systems *Am. Naturalist* **180** 211–24

Suding K N and Hobbs R J 2009 Threshold in restoration and conservation: a developing framework *Trends Ecol. Evol.* **24** 271–9

Sugihara N G, Van Wagtendonk J W and Shaffer K E 2006 *Fire in California's Ecosystems* (Ewing, NJ, USA: University of California Press)

Syphard A D, Yang J, Franklin J, He H S and Keeley J E 2007 Calibrating a forest landscape model to simulate frequent fire in Mediterranean-type shrublands *Environ. Model. Softw.* **22** 1641–53

van de Koppel J *et al* 2002 Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems *Am. Naturalist* **159** 209–18

van Mantgem P J, Nesmith J C B, Keifer M, Knapp E E, Flint A and Flint L 2013 Climatic stress increases forest fire severity across the western United States *Ecol. Lett.* **16** 1151–56

Vilà M, Lloret F, Ogheri E and Terradas J 2001 Positive fire–grass feedback in Mediterranean basin woodlands *Forest Ecol. Manage.* **147** 3–14

Westoby M, Walker B and Noy-Meir I 1989 Opportunistic management for rangelands not at equilibrium *J. Range Manage.* **42** 266–74

Zinck R D and Grimm V 2009 Unifying wildfire models from ecology and statistical physics *Am. Naturalist* **174** E170–85