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Decreases in Fire Spread Probability with Forest Age Promotes Alternative Community States, Reduced Resilience to Climate Variability and Large Fire Regime Shifts

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Abstract

The generalization that plant communities increase in flammability as they age and invariably lead to resilient self-organized landscape mosaics is being increasingly challenged. Plant communities often exhibit rapidly saturating or even hump-shaped age-flammability trajectories and landscapes often display strong non-linear behaviors, abrupt shifts, and self-reinforcing alternative community states. This plethora of fire-landscape interactions calls for a more general model that considers alternative age-flammability rules. We simulated landscape dynamics assuming communities that (1) increase in flammability with age and (2) gain flammability up to a certain age followed by a slight and moderate loss to a constant value. Simulations were run under combinations of ignition frequency and interannual climatic variability. Age-increasing fire probability promoted high resilience to changes in ignition frequency and climatic variability whereas humpbacked-shaped age-flammability led to strong non-linear behaviors. Moderate (20%) reductions in mature compared to peak flammability produced the least resilient behaviors. The relatively non-flammable mature forest matrix intersected by young flammable patches is prone to break up and disintegrate with slight increases in ignition/climate variability causing large-scale shifts in the fire regime because large fires were able to sweep through the more continuous young/flammable landscape. Contrary to the dominant perception, fire suppression in landscapes with positive feedbacks may effectively reduce fire occurrence by allowing less flammable later stage communities composed of longer lived, obligate seeders to replace earlier stages of light demanding, often more flammable resprouters. Conversely, increases

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in anthropogenic ignitions, a common global trend of many forested regions may, in synergism with increased climate variability, induce abrupt shifts, and large-scale forest degradation.

Key words: fire–landscape interactions; positive feedbacks; self-organized behavior; percolation; ignition frequency; fuel; fire suppression; forest degradation.

Introduction

The dominant view that plant communities steadily increase in flammability as they age is being challenged by a growing body of literature that is unveiling a wide array of more system-specific age-flammability trajectories. Despite these advances, however, we still poorly understand how changes in this important ecosystem property may impact long-term landscape resilience in the face of potential alterations of climate and fire regimes.

Fire science and fire management have long been dominated by the assumption that ecosystems steadily gain flammability as they age. These ideas originated mostly from extensive research in western north American open canopy surface fire/pine-dominated forests and woodlands where long fire-free intervals (for example, suppression) induce quantitative (fuel buildup) and qualitative changes in fuel structure and vertical canopy fuel connectivity that invariably lead to increasing stand flammability (for example, Covington and Moore 1994). Under this assumption, fires generate a mosaic of even-aged stands where young forests are relatively uncommon (compared to expectations of a random selection process) because young forests ''protect'' other forests from burning, thus lowering the rate of young forest production. Intermediate ages are relatively common because of the cumulative effects of young stands escaping fire whereas old stands are rare due to the overburning effect (Johnson and Van Wagner 1985). Under this model, fire spread and sizes are largely controlled (''self-organized'') by the existence of recently burned patches because these are assumed to have less fuel and be less flammable than mature patches (Cumming 2001). Moreover, because fire spread is largely controlled by fuel load/continuity, climatically induced changes in fuel moisture will possibly not lead to large increases in fire sizes as potentially burnable patches with large fuel loads may remain ''protected'' from fire spread by young forest fire breaks. This generates a system that remains relatively resilient to increases in fire ignitions or drought-induced changes in flammability.

Growing evidence from a range of biomes is, however, suggesting that the assumption of an age-dependent increase in forest flammability is not generalizable because structural or successional changes related to stand aging can lead to rapidly saturating or often even age-decreasing flammability trajectories (shrublands: Moritz and others 2004; boreal forest: Rupp and others 2000; Johnson and others 2001; tropical forests: Cochrane and others 1999; temperate forests-shrubland transitions: Odion and others 2010; forest-savanna transitions: Bowman 2000; Beckage and others 2009). Numerous mechanisms can be invoked by which a stand can reduce its probability to spread fire as it ages: (1) competitive exclusion of understory due to strong shading in mature phases may reduce fuel continuity (Azuma and others 2004), (2) less flammable vegetation may develop in darker/wetter microclimatic conditions of mature closed canopies (wetter fuels and/or higher lignin contents; Countryman 1955; Rebertus and others 1989; Uhl and Kauffman 1990; Pausas and others 2004), (3) abundant coarse woody debris in mature stages may act as heat sinks during fires thus reducing spread and severity, (4) vertical break up of understory-canopy fuel continuity may establish during mature stages of forest communities dominated by tall emergent trees (Azuma and others 2004), (5) larger quantities of flammable dead fuels during earlier self-thinning stages than during mature stages where the remains of the self-thinning stage are largely decomposed, and (6) later successional species may shed less flammable litter than early fire-adapted species (Peterson 2002b).

Moreover, it is clear that the prediction of an all aged, regularly shifting mosaic is not realistic for many landscapes, particularly highly degraded ones in which strong legacy effects of previous disturbances has locked the dynamics to create highly bi-modal age structures (or bi-phase compositions) composed of either very young (flammable and fire resistant) or old (less flammable and fire sensitive) forest phases (for example, Cochrane and others 1999). Furthermore, it is increasingly obvious that many forested landscapes are displaying non-linear regime shifts (Scheffer and others 2001) in response to changes in ignition frequency and climatic variability, such as the cases of large fire conflagrations in tropical (for example, Leighton and Wirawan 1986; Brown 1998; Laurance 1998) and temperate forests (for example, Veblen and others 2008) during ENSO-related events. Presumably, landscapes that during normal conditions of fire ignitions and climate develop apparently stable but highly intertwined edges between fire promoting and fire obstructing phases may, under increased anthropogenic ignition pressure and/or exogenous changes in flammability (for example, droughts), become highly susceptible to the spread of large fires with large reductions of normally fire resistant ''pristine'' forest (for example, Cochrane and others 1999; Mermoz and others 2005). These facts call for proposing new, more generalizable models that consider and evaluate the effects of alternative age-flammability rules on landscape configuration and their resilience to changes in fire ignitions and climatic variability.

Alternative stable states in ecological communities can occur when, under same site conditions, some components of the biota modify conditions in such a way that the effects of forces (for example, abiotic or biotic interactions, disturbances) will favor those same components, reducing the probabilities of shifting into other states and thus self-perpetuating their own state (Petraitis and Latham 1999). Such positive feedbacks can lead to the maintenance of spatially dichotomous landscapes composed of alternative states where sharp boundaries are relatively stable but do not correspond to any underlying environmental features. Also, when such a feedback gets established, landscapes may reflect historical legacies of previous disturbances that may trap portions of the system in self-maintaining domains. Understanding the causes of non-environmental switching (sensu Wilson and Agnew 1992) from shifting mosaics to highly dichotomized self-reinforcing landscapes is key in the context of climate change and increasing pressure from anthropogenic disturbances (for example, biomass burning, logging, Laurance 1998). Here, we propose that landscapes are highly sensitive to age-dependent flammability. We predict that slight changes in the way in which fire spread probability changes with age (time since last fire) will induce strong qualitative changes in landscape dynamics under scenarios of high disturbance frequency (for example, increased ignitions) or increased climatic variability (drought frequency).

Plants and fire are prone to develop self-reinforcing alternative states (Moritz and others 2005) because under the same environmental conditions alternative communities can differ in traits that confer differential flammability and/or resistance to fire. This is why in many parts of the globe potentially sustaining forests are dominated by self-promoting pyrogenic vegetation types (Bond and others 2005). At finer scales there is a growing awareness of fire-maintained pyrophylic/pyrophobic dichotomous landscapes (for example, Bowman 2000; Perry and Enright 2002a, b; Mermoz and others 2005; Warman and Moles 2009; Odion and others 2010). However, strikingly, this important fire dynamic of many parts of the world has been overlooked, and thus, has remained unexplained under the pine-oriented fire regime paradigm (Bond and others 2005) of space/time-shifting mosaic landscapes. In this article, we attempt to reconcile these apparently opposing views by proposing alternative ways in which forests can change their flammability as they age.

Several generic wildfire simulation models have been applied to test the effects of different shapes of relationships between time since fire and the probability of fire spread as indicators of succession changes or vegetation ecological memory of past fire on landscape patterns of persistence (Ratz 1995; Peterson 2002a). Motivated by the discovery of self-organized criticality (Bak 1990), in another set of models originated in statistical physics (Bak and others 1990; Drossel and Schwabl 1992), no explicit age-flammability assumptions are made but, instead, trees catch fire deterministically from neighboring cells only if trees regrow randomly into previously burned cells with a small probability p (that is, cell ignition is time-separated from sparking trials by a ''refractory'' state until trees are stochastically grown into the cell, Malamud and others 1998). Thus, instead of assuming a variable probability of catching fire they all share in a common regrowth-dependent flammability representing the ''ecological memory'' of the system (Zinck and Grimm 2009). Quite strikingly, however, none of these models have yet assumed an ''inverse ecological memory'' where older cells may become *less* likely to burn than younger cells.

Some models specifically developed for systems exhibiting known successional stages with declining flammability (for example, longleaf pine/oak: Peterson 2002b, maquis/*Araucaria* forest: Perry and Enright 2002a) have shown the development of alternative states or regimes, however, to our knowledge, no study has formally analyzed the effects of age-declining flammability nor the interactive effects of this property and changes in climatic variability and ignitions on landscape resilience and fire regime properties.

Here, we propose that landscapes dominated by forests with decreasing age-flammability relationships are more prone to develop alternative community states and non-linear threshold effects than landscapes dominated by age-increasing flammability. We examine and compare landscape models using two contrasting assumptions: one in which flammability steadily increases with age (that is, the traditional age-flammability assumption) and another in which communities gain flammability up to a certain age after which they start to lose flammability asymptotically to a constant value (that is, our alternative age-flammability assumption). We asked ourselves (1) to what degree are landscapes responding in terms of spatial persistence of patch age, boundaries and fire size distribution to changes in age–flammability relationships, (2) what is the role of ''landscape legacies'', this is, early historically contingent disturbance events, on future configuration and structure, in landscapes differing in age–flammability relationships, and (3) what is the relative sensitivity to changes in ignition frequency and climatic variability of landscapes differing in how flammability changes with age. We propose that the final outcome of the landscape structure and disturbance regime in terms of the distribution of forest-age classes and fire sizes will amply differ between these two contrasting assumptions. Although, the former may lead to classic patch age mosaics composed of young to intermediate-aged patches and a distribution of fire sizes highly skewed toward small fires (Moritz and others 2005), the latter lead to bi-phase mosaics composed of old ages and young ages and fire size distributions with less relative representation of small fires (Odion and others 2010).

Methods

To explore how the spatial dynamics of vegetation responded to different fire regimes with contrasting relationships between time since last fire and flammability, we developed a spatially explicit toy model implemented in SELES (SELES; Fall and Fall 1999; Online Appendix 1). SELES is a tool for constructing and running spatially explicit spatio-temporal landscape models that defines events and agents as the main modifiers of the conditions of specific cells of a given landscape (that is, variable). In this article, we define flammability as the probability that fire spreads from an adjacent burning cell to the focal cell in a single fire event. A simple model was conceived with the following assumptions: (1) only one vegetation type exists: forest, (2) regeneration always takes place 1 year after a cell is burned, so that vegetation age and time since fire are equivalent, (3) cells age every year and age is reset by fire, (4) abiotic conditions are homogeneous across the study area, and (5) only one coarse scale disturbance is present in the landscape: fire, and its only effect is to reset to 0 the age of the cells affected through fire ignition and spread.

The landscape model is represented as a square lattice of 200 × 200 cells, each cell representing a fraction of forest large enough (say 30 × 30 m) to potentially include more than one adult tree so that the structural changes in vegetation which might affect flammability could be accounted. The model is wrapped or toroidal (see Fall and Fall 1999) to avoid border effects: border right and left raster columns as well as upper and lower raster rows are functionally adjacent. In this way, borders are not barriers to the spreading process (for example, fire) because they can continue in the opposite side of the raster. We assume that every simulated year has a fire season when ignitions occur and fires can spread according to the rules described below. Burned cells are immediately set to age zero so that they cannot be burned more than once in a season. Once the fire season is over, all landscape cells age and their corresponding flammabilities are updated. The period of the simulation was set to 1000 years and replicated 10 times for each scenario. The initial state of the vegetation raster (age of vegetation or time since last fire—TSF) was set to 200 years for every cell. TSF increased 1 year every year unless it was affected by fire which reset TSF to 0.

We set our simulations to produce a fixed number of ignitions per year during the fire season. Under different scenarios, fire ignitions were set to 1, 5, and 10 fires per year. Fire events start from cells that are ignited at random and may propagate or not depending on the characteristics of the neighboring cells and the weather conditions for the year. Fires can only spread to the four adjacent cardinal cells (that is, no diagonal spread) with probability P. The probability of fire spreading to an adjacent cell located at x during year t ($P_{x,t}$) is a function of time since last fire (TSF) of that focal cell but modified by the current year fuel desiccation weather factor (w).

$$P_{x,t} = P_{\text{base}}(\text{TSF}_x) \times w_t \quad (1)$$

The baseline probability P_{base} of fire spread is given by an increase in flammability with time since fire using the logistic model, as described by Li and others (1997), combined with a reduction in flammability triggered at a specific age:

$$P_{\text{base}}(\text{TSF}) = \frac{k_1}{1 + \exp(a_1 - b_1 \times \text{TSF})} \times \frac{1 - k_2}{1 + \exp(a_2 - b_2 \times \text{TSF})} \quad (2)$$

The first factor in this product is related to the rise in flammability with TSF and the second to the reduction in fire spread probability after a certain age. In the first, the parameter a_1 is indicative of the age at which the slope change accelerates, b_1 controls the speed of the slope increase, and k_1 defines the asymptote of the function. In the second, k_2 defines the level of reduction in flammability with age. When $k_2 = 0$, the right product becomes zero and forest maintains its maximum flammability as it ages. Increasing values of k_2 produce stronger reductions in flammability with age. The parameter a_2 regulates the age at which the slope starts to decrease and b_2 controls the speed of the decrease. Using similar values to those used by Li and others (1997) the parameters a_1 and k_1 were maintained constant ($a_1 = 4$, $k_1 = 0.5$) in all simulations to fix some properties that govern the increasing portion of the TSF-flammability function, whereas the parameter a_2 was held constant ($a_2 = 16$) to obtain forest types that eventually reduce flammability at the same time since fire. Parameters b_1, b_2, and k_2 were changed for each forest type according to Table 1.

Forest type 1 represents a community that gradually increases in flammability reaching its maximum P_{base} value of 0.5 after 187 years. Although, specific parameters do not mimic any forest type in particular, this pattern is intended to generally reproduce the typical behavior of many xeric pine open woodland and forests where gradual accretion of fuel ladders determines that longer fire-free intervals (for example, suppression) generate larger fuel buildup and therefore higher fire spread probability. Forest type 2 represents a community that rapidly gains flammability with age to reach a peak flammability value P_{base} of 0.5 at 40 years after which it starts loosing flammability to reach a constant P_{base} value of 0.4 at ages of at least 80 years, and Forest type 3 represents a community similar to Forest 2 but loosing flammability to reach a lower constant P(base) value of 0.3 at ages of at least 80 years (Figure 1; Table 1). Again, although we do not intend to reproduce a particular ecosystem, change in flammability of

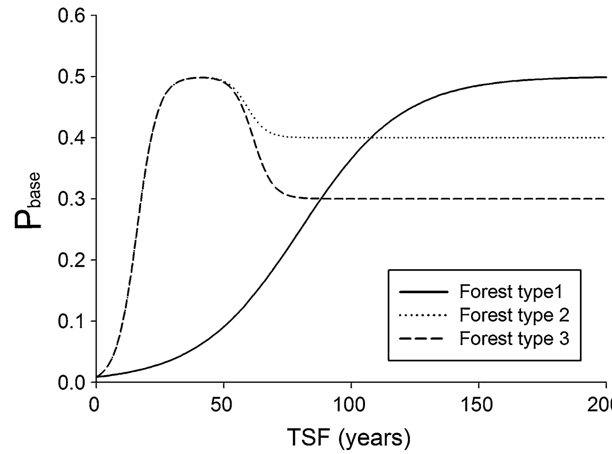

Figure 1. Baseline probability of fire spread as a function of time since fire for the three forest types tested. Forest type 1: slow increment in fire spread probability, Forest type 2: rapid increase in fire spread probability with a 20% reduction after reaching maximum fire spread probability, and Forest type 3: rapid increase in fire spread probability with a 40% reduction after reaching maximum fire spread probability.

Forest type 2 could be representing mesic temperate forest communities that, after fire, rapidly resprout or are restocked from seeds but which eventually stop accumulating fuels due to competition and undergo structural and/or successional changes that slightly reduce intrinsic flammability (wetter microenvironments or less flammable understory species) or dissociate the previous vertical continuity of fuels (for example, generating an emergent canopy and/or thinning the understory). Finally, Forest type 3 is similar to 2 but with a more pronounced (40%) reduction in flammability in old growth stages. This reduction is similar to that used by Perry and Enright (2002a, b) to model base flammability reductions between the maquis and the forest successional/transitional states (46% reduction). Similarly, Baeza and others (2011) measured along a chronosequence in Mediterranean shrublands a 40% reduction in flammability using standing dead biomass retention and accumulation as a community flammability trait. Two

Table 1. Parameters and Characteristics of Fire Spread Probability for the Three Forest Types Tested, Age to Reach the Maximum Fire Spread Probability, Age at which Reduction in Fire Spread is Completed, Maximum Fire Spread Probability, and Fire Spread Probability at Mature Stages (>187 years)

Forest type	Parameters	Age of $P(\text{base})_{max}$ (years)	Age P(base) reduction (years)	$P(\text{base})_{max}$	P(base) mature
1	$b_1 = 0.05$, $k_2 = 0$	187	–	0.5	0.5
2	$b_1 = 0.25$, $k_2 = 0.2$, $b_2 = 0.27$	40	80	0.5	0.4
3	$b_1 = 0.25$, $k_2 = 0.4$, $b_2 = 0.26$	40	80	0.5	0.3

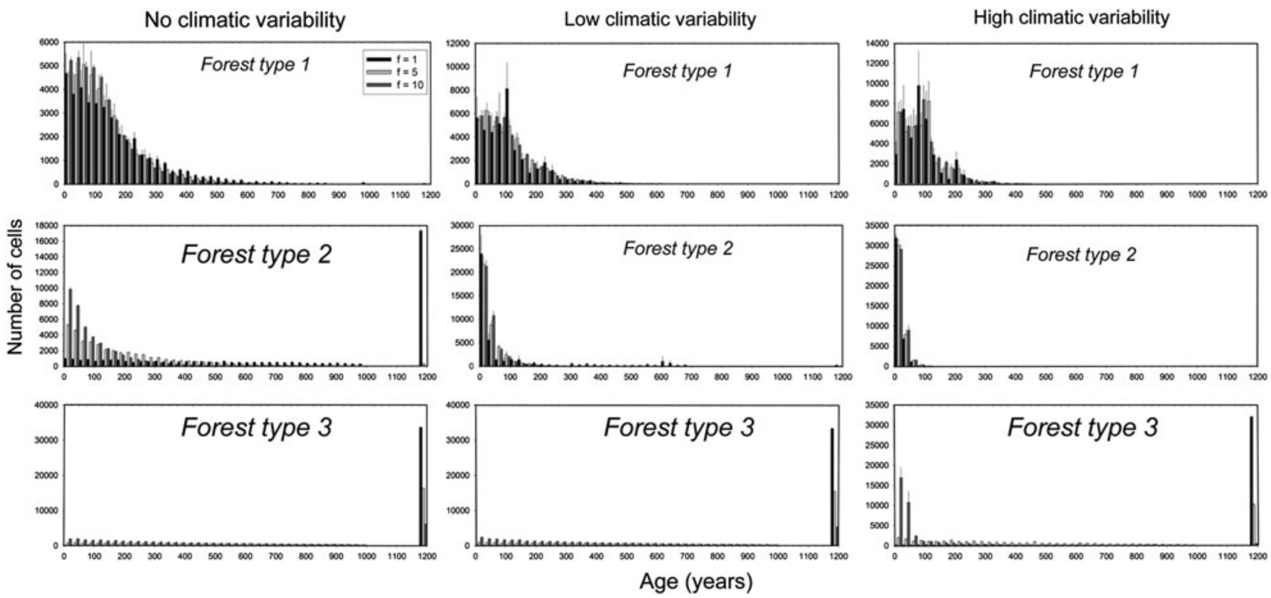

Figure 2. Final age distribution (25 year classes) attained by landscapes by year 1000 of simulation for increasing ignition frequencies ($f = 1$, $f = 5$ and $f = 10$, respectively). *Bars' height* and *whiskers* represent mean and SE of ten simulations.

ignition assumptions were tested: (1) sparks deterministically ignite cells (main results of the manuscript) and (2) sparks ignite cells with probability $2{*}P_{x,t}$ (Online Appendices 2 and 3).

A weather condition factor w_t, representing the average desiccation of fuels in a given fire season (year), was simulated as a random event that follows a normal probability distribution. In the base model, with a stable climate scenario, the mean value was set to 1 with no variance (SD = 0), so w_t was 1 for every year (no interannual climatic variability). Climatic variability was simulated with two additional scenarios, low interannual climatic variability (SD = 0.08) and high interannual climatic variability (SD = 0.15). Results were evaluated by analyzing age frequency distributions, fire size distributions, mature forest persistence, and spatial patterns of autocorrelation in fire recurrence. In all cases our combinations of parameters for P_{base} and w_t resulted in fire spread probability values between 0 and 1.

Results

Effects of Alternative Flammability Stand Trajectories

Without climatic variability, simulated landscapes showed highly contrasting forest age distributions depending on how fire spread probabilities changed with time since fire. Landscapes composed of Forest type 1 (that is, age-increasing flammability) developed the classic ''pine forest'' patch age distribution in which the modal patch age is between 50 and 100 years and the frequency of older forest falls gradually with few forests older than 500 years. This behavior is relatively unaffected by increases in the number of ignitions, the only effect being an increment in the frequency of intermediate-aged (50–100 years) forest cells (Figure 2A, B, C). By year 1000 of simulations without climatic variability, the mean size of the largest patch of mature forest (>200 years) decreased about one order of magnitude with an increase of an order of magnitude in ignitions (Table 2) whereas the number of mature forest patches was relatively insensitive to changes in ignition frequency (Table 2).

Simulations on landscapes composed by Forest type 2 behaved radically differently. Landscapes were highly sensitive to changes in ignition frequency. Low ignitions generated a landscape dominated by unburned forest and a wide array of forest ages. Higher ignition frequency drastically changed this structure leaving few unburned forests and sharply increasing young forest dominance. The mean patch size of mature forest (>200 years) left by year 1000 of the simulation decreased one order of magnitude when ignition frequency increased from low (1 per year) to medium (5) and another order of magnitude with high (10) ignition frequency (Table 2). With increasing ignition frequency, the large matrix of mature forest fragmented into approximately 6 and 7 times more (smaller) patches with changes from low, to medium and low to high ignition frequency, respectively (Table 2).

Landscapes composed of Forest type 3 were highly resistant to changes in ignition frequency, with large percentages of forest cells remaining unburned during at least 1000 years of simulation. Only high ignition frequency (10 per year) generated a dichotomous landscape composed of unburned persistent mature forest and frequently burned young patches (Figure 4). Mean patch size of the largest mature forest was relatively insensitive to changes in ignition frequency (Table 2), yet intense mature forest fragmentation is evident given the 7- and 25-fold increase in the number of mature forest patches with changes from low, to medium and low to high ignition frequency, respectively (Table 2).

Low ignition frequency generated fire regimes dominated by large fires only in Forest type 1 landscapes. Forest types 2 and particularly 3 were dominated by small fires (Figure 3A). Medium ignition frequency reduced fire sizes in Forest type 1 landscapes and largely increased fire sizes in Forest type 2 landscapes (Figure 3B), whereas a high ignition scenario reduced fire sizes in that landscape. Fire size in Forest type 3 was relatively insensitive to changes in ignition frequency (Figure 3A, B, C).

In Forest type 1, although, mature forests are present in the landscapes (Figure 2A), their persistence in space is low (Figure 4). Increasing fire ignition frequency erases mature forests faster than the maturation time of the forest and few places have a persistence of mature forests longer than 500 years (Figure 4A). In contrast, under low fire ignition frequencies Forest type 2 as well as Forest type 3 under low and medium fire frequencies, landscapes are dominated by a matrix-forming mature unburned forests interspersed by small patches of young forest. The density of these

Table 2. Mature Forest (MF, >200 Years) Patch Characteristics by Year 1000 of Ten Replicated Simulations for Three Forest Types under Variable Ignition Frequency and Climatic Variability

Climatic variability	Low ignition	Medium ignition	High ignition
Largest MF patch size (cells)			
Forest type 1			
No	1392.6 (219.8)	470.5 (46.1)	196.6 (27.6)
Low	581.4 (97.7)	319.8 (41.0)	172.2 (15.9)
High	271.6 (82.4)	153.0 (27.7)	86.1 (8.8)
Forest type 2			
No	33127.2 (219.5)	3169.4 (587.7)	289.7 (39.7)
Low	3085.8 (2611.7)	69.4 (33.9)	19.0 (4.0)
High	0.7 (0.3)	0.6 (0.3)	0.6 (0.3)
Forest type 3			
No	32118.2 (4379.4)	33203.7 (78.0)	26692.8 (131.0)
Low	38517.1 (36.6)	32907.4 (63.6)	24966.5 (366.1)
High	38333.0 (64.9)	25668.9 (2951.1)	2670.3 (1243.5)
Number of MF patches			
Forest type 1			
No	956 (33)	1099 (12)	1179 (13)
Low	995 (55)	1044 (12)	1100 (15)
High	883 (83)	739 (66)	773 (46)
Forest type 2			
No	106 (6)	610 (10)	751 (9)
Low	198 (70)	105 (23)	100 (18)
High	1 (0)	1 (0)	2 (1)
Forest type 3			
No	6 (1)	43 (2)	151 (6)
Low	8 (1)	47 (2)	175 (5)
High	10 (1)	127 (18)	241 (38)

Mean (SE) size of the largest mature forest patch (in cells) (top) and mean (SE) number of individual mature forest patches (diagonal cell connections included) in the landscape (bottom). Low ignition frequency: f = 1, medium ignition frequency: f = 5, and high ignition frequency: f = 10.

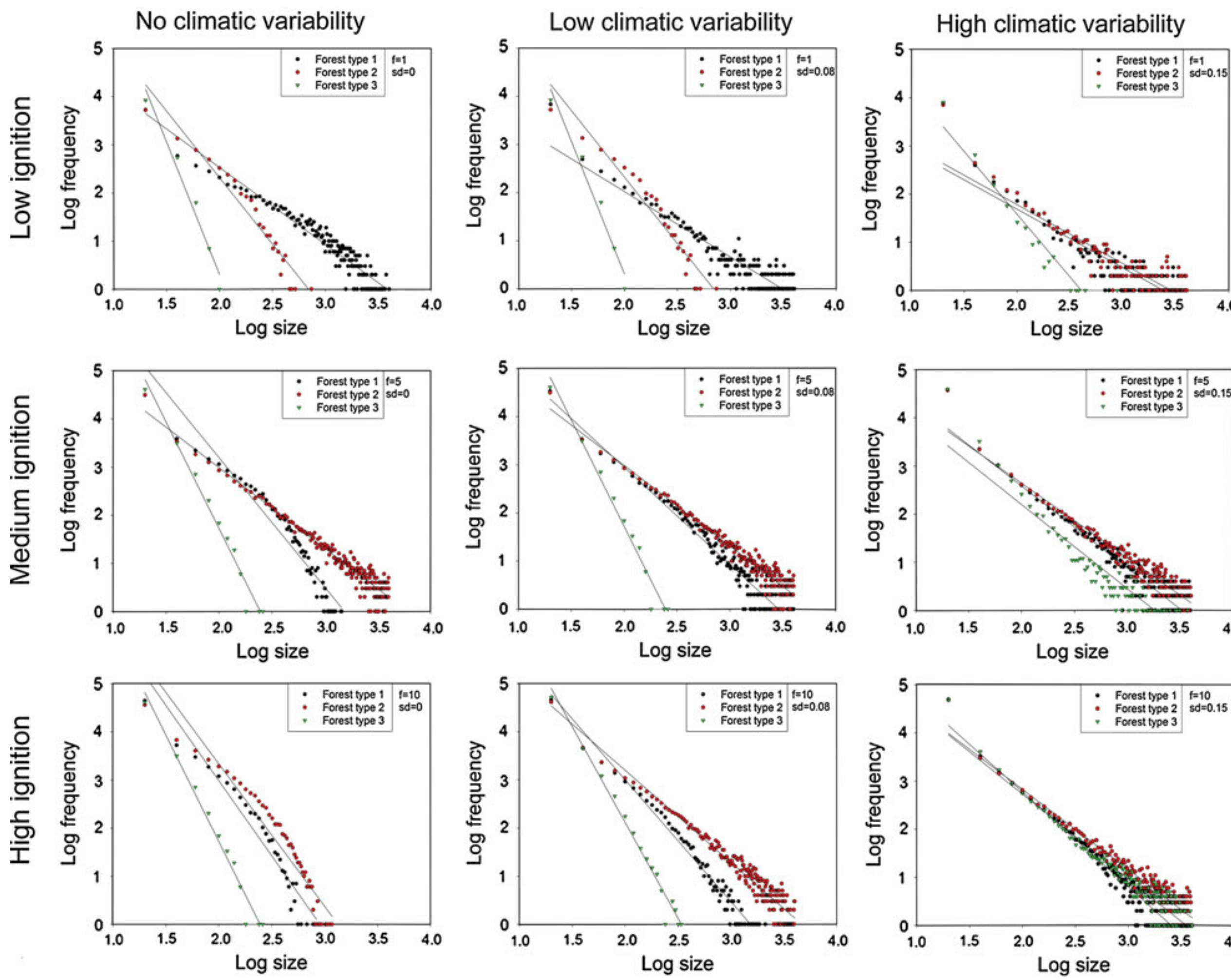

Figure 3. Fire size distributions (log-transformed) and fit to power law distributions. Steep slopes indicate fire regimes dominated by many small fires and flatter slopes more dominance of large fires. (Fires size data for replicate 1).

patches is directly related to the frequency of ignitions (Figure 4B, C). In the landscape dominated by Forest type 2, an increase from low to medium levels of ignitions leads to a change in the matrix from mature forest to young forest, concomitant with an increment in fire size. Higher ignition frequencies virtually erase the mature forest islands that under lower frequencies of ignition remain unburned (Figure 4B). Stable states with coexisting phases of persistent mature and young forest are observable in landscapes dominated by Forest type 2 under low and medium ignition frequencies and in Forest type 3 under high ignition regime (Figure 4B, C).

At low fire ignition frequency spatial autocorrelation patterns of the cumulative number of fires per cell were similar among landscapes composed of different forest types. Fires tend to be spatially autocorrelated due to the nature of individual fires themselves which spread from an ignition point. No additional levels of autocorrelation due to a recurrent pattern of burning on specific points in the landscapes are detectable, thus suggesting that the recurrence of fires is distributed at random in the landscape. Only Forest type 2 was sensitive to increasing levels of ignition frequency displaying a pattern of spatially recurrent smaller fires (distances < 10 cells) with f equal to 5 and intermediate sized fires (distances < 20 cells) with f equal to 10 (Figure 5). When ignited more frequently, fires spreading on landscapes composed of Forest type 2 tend to recur at certain locations and tend to be less frequent at others thus suggesting that the presence (absence) of previous fires (legacies) tends to increase (decrease) the probabilities of later fires.

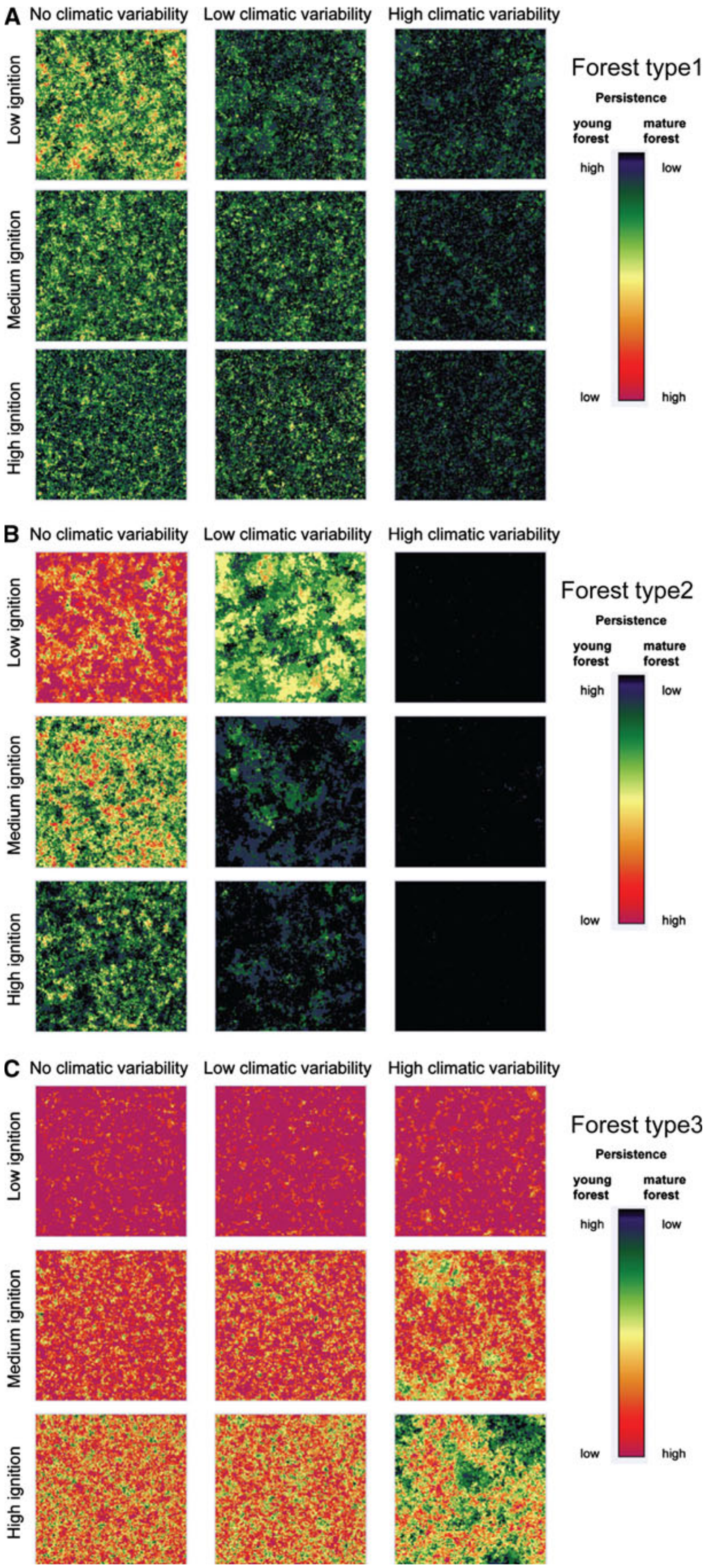

Figure 4. Mature forest (>200 years) and young forest (<200 years) persistence in the landscapes during the 1000 years of simulation for **A** Forest type 1, **B** Forest type 2, and **C** Forest type 3 (simulation 1). High: more than 8 centuries of forest persistence. Low: less than 2 centuries of forest persistence.

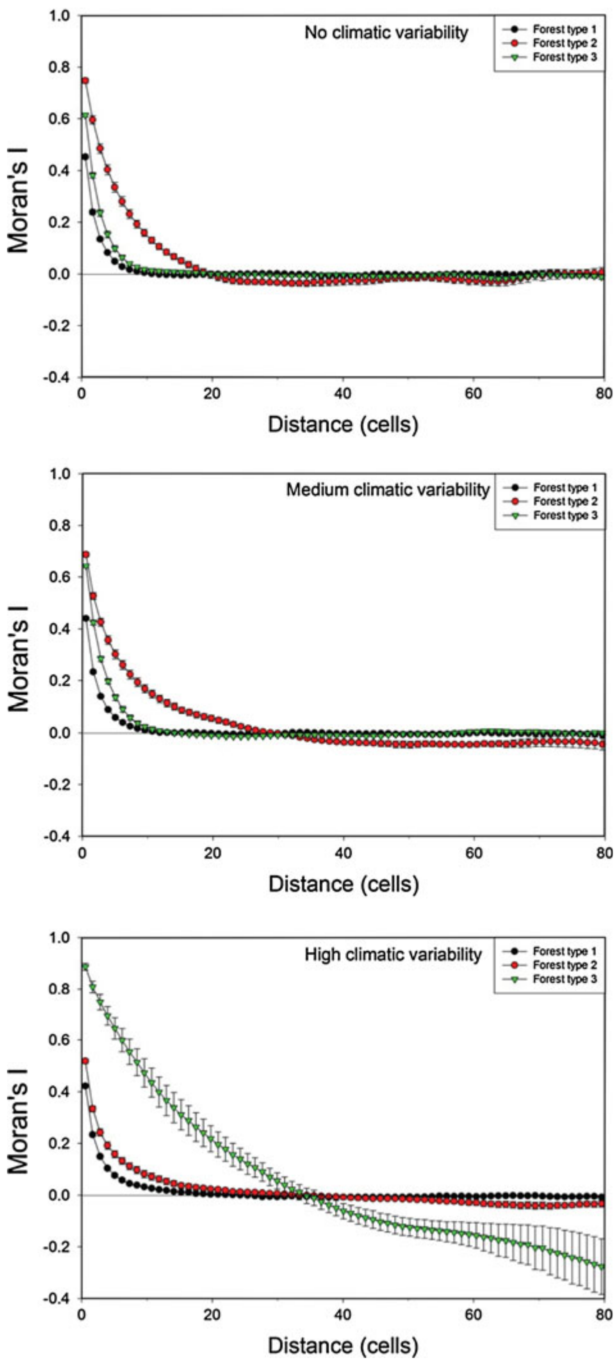

Figure 5. Moran's I spatial autocorrelograms of the integrated number of fire events that occurred during the 1000 years of simulations in each pixel (with high fire frequency; $f = 10$). *Dots* represent means of Moran's I and *whiskers* SE of ten replicate simulations. Due to computational limitations, spatial autocorrelation was calculated only for the upper left 80 × 80 cell window of each simulated landscape.

Interactions with Climatic Variability

Changes in climatic variability induced contrasting responses of landscapes that differed in flammability-stand age trajectories. Landscapes composed of Forest type 1 show a decrease in the number of old forest patches with increasing climatic variability as well as a 3 to 4-fold reduction in the mean size of the largest mature forest patch (Table 2). However, the general dynamics of the landscape is not largely modified. Landscapes behave as shifting mosaics where old patches, despite occurring at lower frequency, still persist in the landscape at medium ignition frequencies or climate variability. Fire sizes increase only slightly with increasing climatic variability but are relatively unaffected by changes in ignition frequency (Figure 3).

In contrast, landscapes composed of Forest type 2 where fire spread probability decreases slightly after reaching a maximum, show qualitative changes in fire regimes and vegetation responses under contrasting climatic variability regimes. Irrespective of fire frequency, even at the lower levels of disturbance, forests with a slight reduction in intrinsic flammability with age (20%) were highly sensitive to changes in climatic variability. Under these parameters landscapes displayed a sudden shift in behavior. Landscapes that under a fixed climate are composed of a dominant matrix of unburned forest (Figures 2, 4B; Table 2) suffer the virtual elimination of that component, even under low levels of climatic variability. This effect is particularly evident under low ignition frequency scenarios where about half of the landscape represented by mature forest is burned and converted into younger forests. Increases from no climatic variability to high climatic variability produced a reduction of the mean size of the largest patch of mature forest of 4 orders of magnitude suggesting that the system shifts from a persistent matrix-forming mature forest (few very large mature forest patches) to a persistent matrix-forming young forest (few and small mature forest patches) (Figures 2, 4B; Table 2). Concomitantly with the elimination of the mature forest matrix, fire size distributions change abruptly. Under low ignitions an abrupt change toward large fires is evident between low and high climatic variability scenarios. Under high ignitions, a similar abrupt shift in fire sizes takes place between the no variability to the low climatic variability scenarios (Figure 3).

Landscapes with forests having a more pronounced dip in the hump-shaped age fire spread function (40% reduction; Forest type 3) seem to be more resilient to increased levels of climatic variability at least at low fire frequencies ($f = 1$). With one fire ignition per year and high climatic variability a very structured landscape is generated

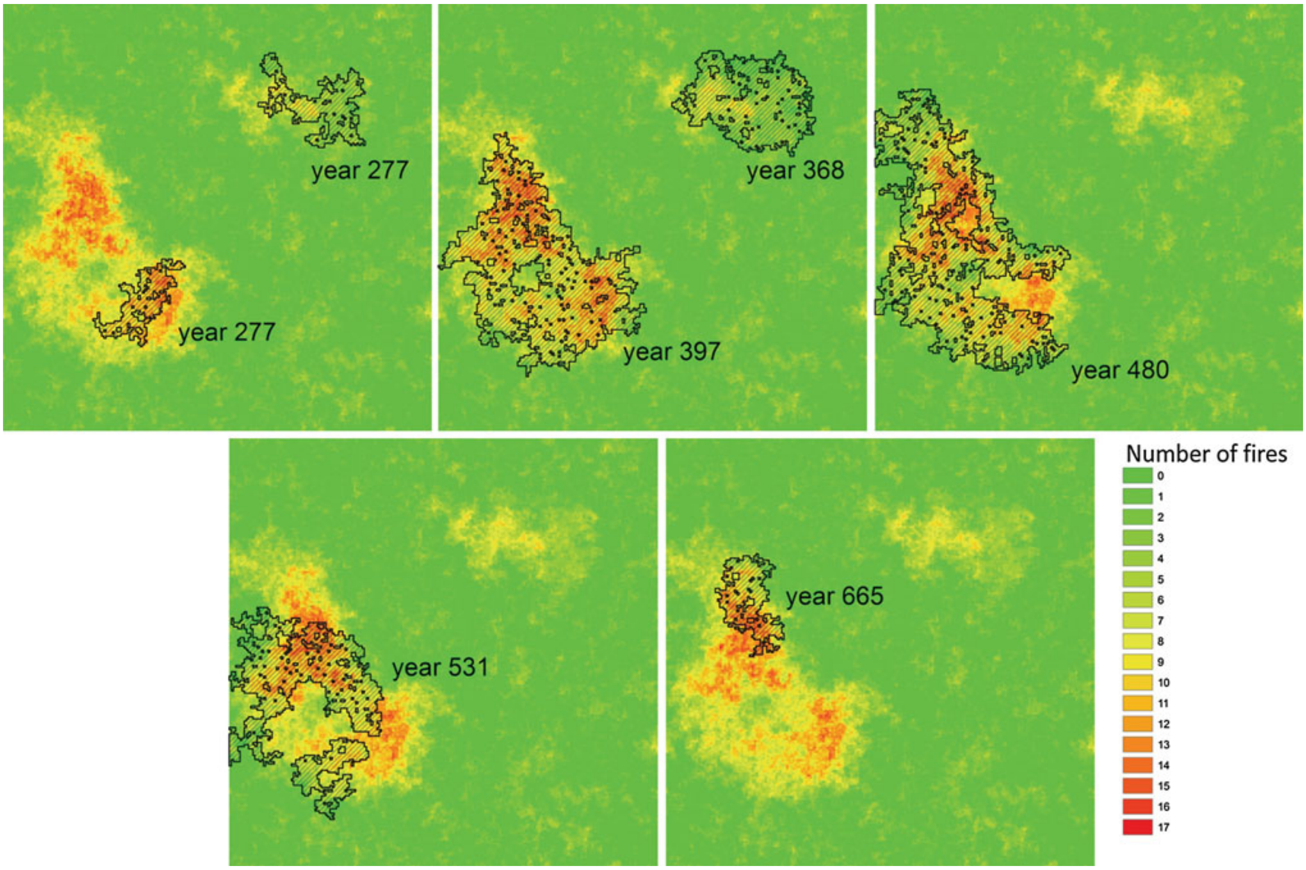

Figure 6. Boundaries of the ten largest fires (labeled with dates of occurrence) during simulation replicate 8 of Forest type 3 under medium ignition and high climatic variability. In the background are represented the integrated number of fires over the entire 1000 years of simulation. Notice the clustering of large fires on previous large fires suggesting the existence of strong legacy effects characteristic of Forest types 2 and 3.

which consists of aggregated persistent old forests and aggregated young unstable forests. However, at higher fire frequency ($f = 5, 10$) and high climatic variability (SD = 0.15) abrupt shifts in fire sizes are evident, leading to salt and pepper-like bi-phase mosaics similar to those found in Forest type 2 landscapes and uniform climate. Only at the highest levels of fire frequency and climate variability do these landscapes shift from old-dominated forests to young dominated forests (Figures 2, 4C; Table 2). The mean size of the largest mature forest patch decreased by one order of magnitude under high ignition and high climatic variability compared to lower levels of ignition frequency and/or variability (Table 2). This change is also concomitant with an abrupt shift in fire sizes (Figure 3).

Climatic variability did not alter patterns of autocorrelation in the spatial recurrence of fire in landscapes dominated by Forest type 1 even at high ignition frequencies (Figure 5). In sharp contrast, spatial patterning of fire recurrence in landscapes composed of Forest types 2 and 3 were highly sensitive to increased climatic variability. Even low levels of inter annual climatic variability and low ignition frequency were sufficient to induce a large degree of clustering of recurrent fires at scales of about 30 cells in landscapes composed of Forest type 2. Medium to high levels of ignition and high climatic variability were needed to generate large-scale clumping of fires in landscapes dominated by Forest type 3 (Figure 5).

Figure 6 exemplifies how climatic variability may enhance these positive feedbacks in landscapes composed of forests with hump-shaped functions relating time since last fire (age) to fire spread probability. In a landscape composed of a normally less flammable mature forest, random extreme climatic events may generate uncommon larger fires (for example, in simulation year 277 of replicate 8, Forest type 3, $f = 5$; Figure 6). These fires in synergy with climatic variability and high or moderate-high ignitions may generate other opportunities for reburning so that previous large fires generate a legacy effect for subsequent fires which may somewhat trace earlier events. Eventually, under extreme climate conditions, later fires may spill over earlier fire boundaries ''eating up'' normally less flammable forest and creating megafire events (for example, year 397, Figure 6). Provided there are sufficient ignitions, larger fires tend to recur on previously burned areas (Figure 6). However, in the case of Forest type 2 where the mature forest matrix has an intrinsic higher flammability than Forest type 3, high climate variability and/or ignition frequency may induce qualitative changes in the matrix in which mature forest may become ''eaten up'' by fire and replaced by young more flammable forest. In this case fires stop recurring in a spatially clumped fashion (Figure 6) as Forest type 2 is driven by the same dynamics of Forest type 1.

Discussion

Our simulations illustrate that slightly different assumptions of how communities change in flammability with age can induce non-linear shifts in both fire dynamics and landscape structure. Furthermore, we show that these qualitative changes may be triggered both by ignition frequency and inter annual climatic variability.

We show that systems in which plant communities steadily increase their capacity for spreading fire across the landscape as they age are highly resilient to changes in ignition frequency and inter annual variability in climate-induced fuel desiccation. With increasing ignition frequency and climatic variability mean age of patches, abundance of old grown forest, and size of mature forest patches decreased. Fire size decreased with increasing ignition frequencies but increased with increasing climatic variability. The number of old growth patches and fire recurrence autocorrelation, however, remained remarkably constant. This is consistent with the idea of self-organization of forest fires which proposes that present (and past) fire events can influence the occurrence and behavior of future fires (Cui and Perera 2008). Specifically, past fires can act as fire breaks for the spread of subsequent fires, a phenomenon largely documented by empirical studies and conceptualized in simulation studies as an emergent property influencing, for example, fire size distributions (Malamud and others 1998). In concordance with other modeling exercises (Drossel and Schwabl 1992; Ratz 1995), we propose that the age-increasing capacity of spreading fire is a key aspect that confers the self-organizing property (and consequent resilience) to these systems.

More importantly, we demonstrate that a qualitative change in behavior emerges when we modified the assumption of how plant communities change their probabilities to spread fire as they age. Landscapes dominated by communities with hump-shaped age–flammability relationships (a peak in their capacity to spread fire at some time in their postfire succession followed by a reduction in this capacity as stands enter mature stages) produced behaviors that display strong non-linearities in relation to ignition frequency and climate variability, alternative states, self-reinforcing positive feedbacks and time-enduring legacy effects. Specifically, plant communities in which the probability of fire spread is only slightly reduced during mature stages (Forest type 2) were the most sensitive and fragile systems. Our simulations show that even moderate increases in ignition frequency and/or climatic variability induced large-scale landscape and fire regime shifts. In this system older (as opposed to younger in Forest type 1) patches act as firebreaks. Fire recurrence rapidly leads to a bi-phase system of young communities prone to high fire recurrence and older stages that constrain fire sizes. As long as ignition frequency remains low the bi-phase system is stable. This system with alternative stable states is similar to those produced by similar models that assigned lower fire spread probabilities to later successional stages (Peterson 2002b; Perry and Enright 2002a, b).

However, once fire frequency is increased the less flammable matrix breaks up generating a large-scale shift in fire regime and landscape structure because large fires are able to sweep through the more continuous young and flammable landscape (Figure 4B, C). Similarly, if increased climatic variability renders the matrix more flammable (Turner and Romme 1994; Mermoz and others 2005) more frequently (that is, droughts), more and larger fires break up the normally less flammable matrix, or fires sweeping from the young flammable patches are able to reach thanks to large edge effects larger portions of the normally less flammable forest eventually reaching a threshold state of the matrix beyond which new fires are able to freely percolate through the landscape (Turner and others 1989). Landscapes initially composed of relatively unflammable mature stages are rapidly converted into homogeneous young and highly flammable landscapes supporting large frequent fires which cannot surpass the peak of maximum flammability at 40 years of time since fire staying trapped in the ''young stage''.

Therefore, contrary to communities with age-increasing fire spread, a self-de-organizing system behavior is evident under altered fire ignitions or climate variability in communities with slight hump-shaped age-flammability relationships.

When the mature forest is substantially less flammable than younger forests, as in the case of our Forest type 3, it acquires higher resilience than Forest type 2. Landscapes composed by these kinds of communities are generally less fire prone and thus the unflammable matrix requires higher levels of ignition and climatic variability to break up and produce large shifts in disturbance regimes and landscape composition. Even in our simulated highest levels of ignition and climate variability landscapes retained some percentage of mature patches. Based on these results, we propose that communities with moderate reductions in flammability with age but also those which are intrinsically unflammable as mature forests will display non-linear behaviors at least in the range of fire ignition frequency, initial time since fire, and climatic variability we have explored.

These results suggest that it will be critical to assess (or eventually reassess) whether a given community displays age-decreasing fire spread probabilities, and if so, the magnitude of this reduction.

Long debates about the role of fire suppression in temperate northern hemisphere forests have revitalized the debate about whether all aging communities inevitably progress toward increased likelihood of fire (Keeley and others 1999; Johnson and others 2001; Moritz and others 2004; Plucinski and others 2009). This paradigm, originated from studies of open canopy communities dominated by low intensity fires such as southwestern North American Ponderosa pine forests, proposes the buildup of intermediate-height ladder fuels which connect the litter with the canopies and increase canopy density and fuel continuity as the main mechanism of age related increases in fire hazard (Covington and Moore 1994).

The universality of this mechanism has come under scrutiny in closed canopy ecosystems where crown fires are the norm (for example, shrublands, boreal forests, Keeley and others 1999; Johnson and others 2001). In systems that are strongly limited by light, the stand development patterns do not necessarily conform to the idea of ladder fuels increasing fuel continuity. On the contrary, many closed canopy communities display strong self-thinning processes which produce large quantities of flammable dead fuel during intermediate stages but that result in the long term in a separation between understory and forest litter. This is the case of mesic *Nothofagus* forests of northern Patagonia where young post fire forests are highly flammable due to the coexistence with flammable resprouting shrubs and bamboo in the main canopy (Raffaele and others 2011; Veblen and others, in press). Later stages during the process of self-thinning are also highly flammable, when most heliophyllous shrubs and suppressed individuals of *Nothofagus* accumulate high volumes of flammable dead stems. However, these forests turn less flammable when the main canopy separates physically from the understory layer, often composed of shade-tolerant species (Veblen and others, in press). Many recent forest fires in northern Patagonia trace the boundaries of historical fires and generally stop when reaching mature *Nothofagus* forest except during extreme droughts or massive bamboo die-off (Mermoz and others 2005; Veblen and others 2008). The consequences of this repeated burning on the same site has been the elimination of obligate seeding trees and the conversion to communities dominated by resprouting shrubs commonly found in mid slope positions in northern Patagonia which feed back into a regime of more frequent fires, generating alternative (shrubland/forest) stable states self-maintained by fire (Veblen and others 2003; Kitzberger and Veblen 1999; Mermoz and others 2005).

Similar landscape–fire interactions have been documented and modeled by Perry and Enright (2002a, b) in a New Caledonian landscape composed of *Nothofagus* forest, *Araucaria* woodland and sclerophyllous maquis heath-like vegetation. Similar to our study, these authors, by assigning decreasing base flammability probabilities to maquis, maquis-*Araucaria* and *Nohofagus* forests in a fire percolation model were able to reproduce the structure and dynamics of this highly dichotomous landscape and demonstrate its anthropogenic-related origin, mediated by strong positive feedbacks between vegetation flammability and fire. In our study, although, documenting the same landscape behavior, we additionally were able to assess the influences of changes in ignition and climate on communities prone to these self-reinforcing properties. In an empirical study in northwestern Californian forests, Odion and others (2010) also found self-reinforcing feedbacks of vegetation with fire. Pyrogenicity of sclerophyllous vegetation was higher than that of forests, especially after long times since fire, producing self-reinforcing structuring of the landscape. In tropical forests this same phenomenon may be operating as an important driver of deforestation. Cochrane and others (1999) found that fires were far more likely to occur and spread in previously burned forest than in unburned Amazonian rainforests. Once fires have penetrated in the normally unflammable forest (for example, during droughts) positive feedback mechanisms establish for these areas to carry more fire because previously burned areas are less dense favoring higher fine fuel loads, higher evapotranspiration and fuel desiccation rates, higher intensity fires, higher fire induced tree mortality rates and thus recurrent fires have the potential to eradicate trees from the landscape (Cochrane and others 1999).

Contrary to the dominant perception, fire suppression in landscapes that exhibit such positive feedbacks may effectively reduce fire occurrence by allowing less flammable later stage communities composed of longer lived, obligate seeders to replace earlier stages of light-demanding flammable resprouters. Conversely, increases in anthropogenic ignitions, a common trend in modern tropical regions stimulated by forest land conversion in synergistic interaction with increased climate variability (for example, stronger, more frequent ENSO-related drought) may induce abrupt shifts mediated by fire percolation and rupture of the less flammable forest matrix (Pueyo and others 2010).

Criticality in disturbed systems may attain low resilience resulting in sudden state shifts triggered by small parameters when the susceptibility to disturbances is increased as a function of the local neighborhood (edge effects) to a previous disturbance and where the mobility of the disturbance agent (for example, wind throw in forests, waves in intertidal mussel beds) is fast or large scale compared with the recovery process [well mixed disturbance (Pascual and Guichard 2005)]. In our hump-shaped age-flammability landscape, highly intricate boundaries that divide the alternative states of young flammable (pyrophilic) and the less flammable (pyrophobic or ''ombrophytic'', Warman and Moles 2009) communities are formed (Figure 4B, C) and fire is highly mobile and easily percolates along these edges. Thus, stochastic (for example, climate driven) changes in the normally unflammable forest may be responsible for sudden shifts of the system, in this case the virtual elimination of the unflammable phase and the shift to regimes dominated by large fires. These state/regime shifts may be largely irreversible (Folke and others 2004) or at least highly hysteretic in their return to the previous condition of unflammable communities or the balanced coexistence of flammable and flammable communities. Present day and historical examples of human (that is, ignition)-driven large-scale irreversible shifts can be found in tropical, subtropical, and temperate rainforests worldwide (reviewed by Whitlock and others 2010). Continental-scale forest to grassland conversion (or savanna to desert scrub) occurred in New Zealand (Ogden and others 1998; McWethy and others 2009), the Pacific Basin Islands (Kirch 1996) and Australia (Miller and others 2005; Haberle and others 2001) and central Africa (Taylor and others 2000), following major immigration fluxes of humans. At present, globalization of biomass burning practices in large areas of tropical forests (Amazon, Indonesia, Madagascar) are producing irreversible phase and regime shifts where population is sufficiently large or concentrated (Lawrence 2004; Nepstad and others 2001) and where repeated burning of the forest enhances the impact of subsequent fires (Cochrane and others 1999; Uhl and Kauffman 1990), particularly in the context of climate change-related droughts that increase forest flammability (Malhi and others 2008). These examples of large-scale shifts share various components with our simulation results: (1) systems are more prone to sustain fire when young than when they reach old growth stages thus producing positive fire vegetation feedbacks, (2) systems develop alternative states or stages lacking clear underlying environmental controls, (3) systems display very pronounced edges between relatively flammable and unflammable phases, (4) regime shifts occur when climatic variability is high, turning normally unflammable vegetation flammable, and (5) regime shifts occur whenever or wherever ignitions increase, temporally due to immigrations, increases in human population or land-use changes and spatially as with increasing probability as a function of distance to human settlements, roads, rivers, agricultural frontiers, and wildland–urban interfaces.

The strong modifying action of humans and climate interactions mediated by the deliberate alteration of ignitions is largely documented as a worldwide phenomenon (Marlon and others 2008), but particularly in systems were fire opportunities are weather limited but fuel availability is non-limiting. Here, we propose that the way systems modify their flammability as they age is an underlying natural property that unifies apparently opposing views of the spatial–temporal dynamics of fire disturbed forest landscapes, and that largely governs the ecosystem's proneness to display alternative states, ecological legacy effects or even undergo large regime shifts, and irreversible collapses in the face of modern and future anthropogenic and climatic scenarios (Gunderson and Holling 2002).

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