Ecosystems
DOI: 10.1007/s10021-014-9773-5

ECOSYSTEMS

Abrupt Climate-Independent Fire Regime Changes

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Abstract

Wildfires have played a determining role in distribution, composition and structure of many ecosystems worldwide and climatic changes are widely considered to be a major driver of future fire regime changes. However, forecasting future climatic change induced impacts on fire regimes will require a clearer understanding of other drivers of abrupt fire regime changes. Here, we focus on evidence from different environmental and temporal settings of fire regimes changes that are not directly attributed to climatic changes. We review key cases of these abrupt fire regime changes at different spatial and temporal scales, including those directly driven (i) by fauna, (ii) by invasive plant species, and (iii) by socio-economic and policy changes. All these drivers might generate non-linear effects of landscape changes in fuel structure; that is, they generate fuel changes that can cross thresholds of landscape continuity, and thus drastically change fire activity. Although climatic changes might contribute to some of these changes, there are also many instances that are not primarily linked to climatic shifts. Understanding the mechanism driving fire regime changes should contribute to our ability to better assess future fire regimes.

Key words: fire regime changes; abrupt changes; land-use changes; fire-grazing; invasive-fire cycle; socio-economic changes.

Introduction

Wildfires are a key ecosystem process in many biomes around the world. They have played a determining role in the distribution and composition of many ecosystems (Bond and others 2005; Bond and Keeley 2005; Pausas and Ribeiro 2013) and in global biogeochemical cycles (Bowman and others 2009). Because fire is a recurring disturbance, many plant species have acquired traits to cope with them, and thus fire has acted as an evolutionary pressure shaping plant traits (Pausas and Keeley 2009; Keeley and others 2011). Although we have made major strides over the last few decades in understanding fire regimes (Box 1), their role in global change is still poorly understood.

Climatic changes may result in fire regime changes (for example, Westerling and others 2006; Marlon and others 2009; Daniau and others 2013), but the relationship between climate and fires is not straightforward, due to interactions with factors such as vegetation structure and productivity (Pausas and Bradstock 2007; Westerling and others 2011; Pausas and Paula 2012; Pausas and Ribeiro 2013). When fire regime changes are observed in association with changes in climate, a causal relationship is often assumed. Certainly there is an evidence of rapid fire regime changes associated with shifts in climate, and this process is expected

Received 1 October 2013; accepted 10 April 2014

Author contributions: JGP conceived the idea and sketched out the first rough draft, JGP and JEK contributed to subsequent drafts.

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Published online: 15 May 2014

Table 1. Examples of Abrupt Climate-Independent Fire Regime Changes (+/−, Increase/Decrease)

Initial fuel consumers	Driver of change	Fire driver (fuel/ignitions)	Wildfire activity change	References*
(a) Fauna				
Megaherbivores	Extinction of megafauna (by climate changes and/or human arrival)	+ Woody	+	1
Megaherbivores	Rinderpest virus eradication; wildebeest population explosion	− Grass	−	2
Understory fires	Bark beetle outbreaks	Fuel redistribution	− Intensity	8
(b) Invasive plants				
Rare or no fire	Invasion of flammable perennial plants	+ Grass	+ Frequency + Intensity	9, 10
Low frequency of intense fires	Anthropogenic ignitions and invasion of flammable annuals	+ Grass − Woody	+ Frequency − Intensity	11, 12, 13
(c) Socioeconomic changes				
Controlled fires	Demise of Native American cultures (by Europeans); reduced ignitions	− Ignitions	−	3
Farming	Collapse of a rural lifestyle	+ Woody	+	4, 5
Understory fires	Change in fire policy: fire exclusion	+ Woody	− Frequency + Intensity	6, 7
No fires	Arrival of human populations	+ Ignitions	+	14
Wildfires + controlled fires	Demise of Native American cultures, fragmentation, and fire suppression	− Ignitions	−	15

** References: 1: Burney and Flannery (2005); 2: Holdo and others (2009); 3: Nevle and Bird (2008); 4: Pausas (2004) and Pausas and Fernández-Muñoz (2012); 5: Dubinin and others (2011); 6: Covington and Moore (1994); 7: Taylor (2007); 8: Simard and others (2011); 9: Coffman and others (2010); 10: Hiremath and Sundaram (2005); 11: Keeley and others (2005); 12: Gómez-González and others (2011); 13 Keeley and Brennan (2012); 14: McWethy and others (2010); 15: Nowacki and Abrams (2008)*

to play an increasing role in the future (for example, Westerling and others 2006, 2011; Marlon and others 2009; Pausas and Paula 2012; Moritz and others 2012). However, there are other rapid changes that cannot be linked directly to climatic oscillations (Table 1) and may provide important lessons for interpreting future fire regime changes. The focus of this paper is to consider the diverse ways in which abrupt changes in fire regimes have occurred due to non-climatic factors, although we recognize that climate cannot be totally excluded from the story. Although changes in fire regime may sometimes be temporary, more often they alter community composition in ways that set the community on a trajectory of more lasting changes. These changes can greatly alter ecosystem functioning (''ecological surprises'' *sensu* Paine and others 1998; Scheffer and others 2001), and have cascading effects on different trophic levels (producers, consumer, and decomposers).

Climate-driven changes in fire regimes primarily work through altering spatial patterns in fuel structure and temporal patterns of fuel moisture. However, as discussed in this paper, there are other factors that can generate changes in fuels and induce novel fire behavior and fire regime properties; especially relevant are those factors that change the relative importance of grass and woody fuels (Table 1). A particular case of abrupt fire regime changes is switching fire regime type (Box 1); for example, switching from surface to crown fires, which involves marked changes in fuel and fire behavior (from grass-fueled to woody-fueled fires). Another source of past fire regime changes is linked to changes in ignitions driven by human social changes. Here, we review key cases of fire regime changes that are largely independent of climate, with an emphasis on abrupt changes. We include changes that can occur at different spatial and temporal scales and are detected with contemporary observations or with palaeological records. We have aggregated these fire regime changes by those directly driven by (1) fauna, (2) invasive plant species, and (3) socio-economic and policy changes (Table 1). Faunal impacts, as well as invasive plants directly affect fuel quantity and structure, whereas socioeconomic changes modify both fuels and ignition frequency and timing. These categories might not be fully independent of each other, but are useful for descriptive purposes. However, all of these processes have in common the fact that they strongly affect the structure of the vegetation and can cause landscapes to cross thresholds of fuel continuity that change fire

Box 1. Key Concepts

Fire regime: the characteristic of wildfire activity that prevails in a given area; it is typically determined by its frequency, intensity, seasonality, and type of fuels consumed. Two common fire regimes are surface fire regimes and crown fire regimes

Fire regime changes: changes in the frequency, intensity, seasonality, and type of fires beyond the historical variability. An example of a strong fire regime change is switching from surface to crown fires

Surface fires: fires that affect surface fuels only; they spread through the herbaceous and litter layer. In forest ecosystems, surface fires are often called understory fires, and there is a vertical discontinuity of the fuels in such a way that tree crowns are not affected by the fire

Crown fires: fires in woody-dominated vegetation that affect most of the crown of the dominant plants; fire might spread through the crowns, through the surface (and torching to the crowns), or through both crowns and surface simultaneously

Ladder fuels: fuels (both living and dead) that facilitate the capacity for surface fires to spread into the tree canopies. Common fuel ladders include tall grasses, shrubs, vines, tree saplings, and lower tree branches

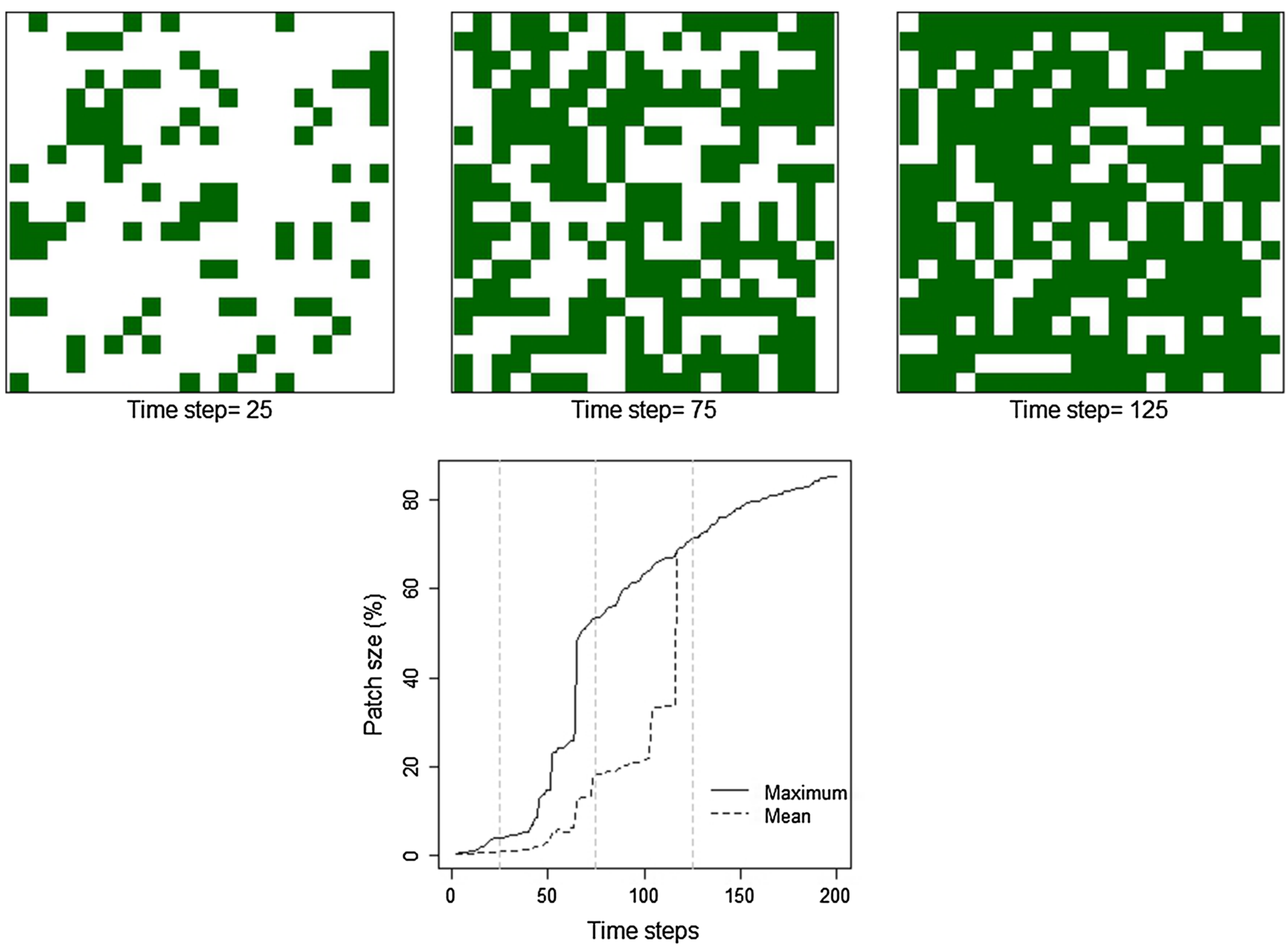

Figure 1. Schematic representation of how a gradual change in a driver (for example, a constant colonization/invasion of a flammable plant) can produce an abrupt change in landscape structure (for example, continuity of the flammable vegetation). The *bottom panel* represents the changes through time in mean and maximum patch size in an idealized landscape that is invaded by plants (*dark cells*) with a constant probability ($P = 0.01$ in each time step). The *upper panel* shows three snapshots of these dynamics (time steps = 25, 75, and 125, also represented by *vertical lines* in the *bottom panel*).

regimes abruptly (Figure 1). Past fire regime changes have implications for the way we interpret contemporary landscapes and understanding these processes should contribute to our ability to assess factors most critical for predicting future fire regime changes.

Fauna and Fire Regimes

Vegetation is not only a necessary resource for wildfires but also for herbivores and consequently they both interact and 'compete' for this resource (Bond and Keeley 2005; Fuhlendorf and others 2008). A diverse array of animals, from insects to megaherbivores, has the potential to significantly alter fuel loads and structure and alter fire regimes. This can potentially occur through natural population cycles or, more often, to changes in animal populations driven by human interventions. Although natural cycles may be coupled with climate fluctuations, there is evidence of fire changes not directly related to the climate but to the fuel modification by animal activities.

Insects

Natural insect cycles can play havoc with fire regimes by increasing dead fuels and modifying fuel structure. However, the role of insects in modifying fire regimes has been little studied, with the exception of the role of bark beetles (*Dendroctonus* species, Coleoptera: Scolytidae) that cause tree mortality in the western US coniferous forests (Jenkins and others 2008; Hicke and others 2012; Donato and others 2013). Both positive and negative fire feedback processes have been reported after bark beetle outbreaks. Infestation by bark beetles increased dead and ladder fuels in the short-term, with the consequence of increasing the probability of surface fires to develop into crown fires (Jenkins and others 2008; Donato and others 2013). However, bark beetles often reduce crowning probability, especially with the increasing time-since-outbreak, because by killing trees bark beetles reduce tree density and overstory fuel continuity (Simard and others 2011; Donato and others 2013). The increased coarse fuels on the forest floor can also increase fire resident time, and thus the severity of surface fires (Donato and others 2013). A fire after a large and intense infestation may kill regenerating trees and generate a type conversion to non-forest ecosystems (Billings and others 2004).

Another example of insects that have a large-scale impact on fuels are *Aroga* moths in the sage scrublands of the Great Basin of North America. Although not well studied, there are reports that this moth infested thousands of hectares of sage stands in the 1960s, the early 1970s and more recently during the 2004–2006 period (Gates 1964; Chambers and others 2008). The dead fuels generated by these outbreaks contributed to a marked change in fuel continuity such that fires spread more evenly across the landscape leaving fewer patches of unburned vegetation. Because the dominant shrubs in this system neither resprout nor store dormant seed banks, recolonization is jeopardized when fires fail to leave patches of unburned vegetation as seed sources for recolonization. In such cases, the system might reach a tipping point where the native shrubland is replaced by alien annual grasses that encourage further fire (Keeley and others 2009).

Overall there is evidence that insect epidemics might generate anomalous fuel loads and continuity so that the ecosystem becomes vulnerable to changes in fires regimes, but the type and magnitude of this shift may vary depending on the community structure and the time-since-outbreak. Although potentially affected by past land use practices and climate changes, insect cycles may also operate independently of these factors (for example, Speer and others 2001; Haynes and others 2014).

Wild Megafauna

Megaherbivores (that is, herbivores larger than a human) can be keystone species that are capable of massive vegetation disturbance that contributes to landscape heterogeneity and potentially to rapid alterations in fuel structure that can have profound impacts on fire regimes. This is because megaherbivores maintain grass-dominated ecosystems, which have very different fire regimes compared to forests and shrublands. For instance, most grass-fueled fires are frequent and of low intensity, but fires in woody vegetation with similar climatic conditions are less frequent and, although they can be of low intensity in some forest types, often they can reach very high intensity and consume large amounts of biomass (Knapp and others 2005). In contrast to insect epidemics that exert a pulse-like (sensus Bender and others 1984) effect on fire regimes, megaherbivores exert a press-like sustained effect that maintain grass-dominated ecosystems.

These contemporary patterns provide insights into potential historical effects of megaherbivores on fire regimes. For example, in North America during a brief 500 year period toward the end of the Pleistocene, four genera of megaherbivores went extinct (Barnosky and others 2004; Faith and Surovell 2009). The mass disappearance of megafauna at this time has been hypothesized to have led to a rapid change in landscape fuel patterns, from grass-dominated to woody-dominated systems. Coupled with the landscape change in fuel structure was an increase in ignition frequency due to the impact of humans on lower elevations and foothill environments that were originally ignition-limited due to low lightning activity (Pinter and others 2011). This increase in human ignitions could facilitate burning the fuel built up by the megafauna extinction, thus generating a sudden shift in the dominant disturbance regime, from low-intensity surface fires to high intensity crown fires. Such rapid changes have been detected through an increase in soil-borne charcoal (grass-fires do not leave as much charcoal as woody fuels) and a decrease in the density of spores of *Sporormiella*, a fungus that resides in the dung of large herbivores. The increased fire activity is believed to be a consequence of fuel changes driven mainly by the faunal extinction, independent of the driver of the extinction (climate, humans or both; Barnosky and others 2004). In many palynological sites in North America there is a temporal sequence in which *Sporormiella* declined rapidly at the same time that pollen of early successional species (for example, *Picea*) increased, followed after several centuries by a charcoal spike (Robinson and others 2005; Gill and others 2009). The timing of events at each site suggests a regionally consistent sequence driven by the abrupt faunal extinctions. This process in which the reduction of megaherbivores changed fuel properties and generated abrupt fire regime changes is likely to have happened in many parts of the world and at different times, despite the fact that the relative role of humans and climate in the megafauna extinction might vary cross continents (for example, Barnosky and others 2004; Burney and Flannery 2005).

Livestock

Although natural grazing by megaherbivores maintains grass-dominated ecosystems, intense grazing by livestock may produce the opposite effect of reducing grass fuel loads. Illustrative of this process is the policy changes in Texas, USA, during the 2009 wildfire catastrophe. With the anomalous drought conditions, grassland fires were seemingly unstoppable and in response, some nature reserves changed their policy of livestock exclusion to bringing livestock in for the purpose of controlling fuels. On a global scale, an overall decline in fire over the past 150 years has been ascribed to a global expansion of intensive livestock grazing and expansion of agriculture, both of which have reduced landscape fuel connectivity (Marlon and others 2008, 2013) and resulted in rather abrupt fire regime changes.

Intensive livestock grazing in forest ecosystems may have even stronger consequences, as it prevents grass fires and allows woody species to recruit due to reduced fire frequency. These woody species create ladder fuels capable of carrying fires into the canopy (van Wagner 1977). Such an effect is to be expected in open forest types where fire spread is dependent on herbaceous surface fuels, as in some parts of the southwestern USA (Savage and Swetnam 1990). A similar model has been used to explain the apparent shrub encroachment into many grasslands around the world (for example, Van Auken 2000). Disease outbreaks in herbivores can also lead to complex trophic cascades regulating fire activity. For instance, the wildebeest population explosion in Serengeti was due to the eradication of rinderpest in the 1960s and in turn was responsible for an abrupt reduction of fire activity, with a consequent increase in tree density and carbon fixation (Holdo and others 2009).

Invasive Plants Changing Fire Regimes

Invasive plant species have a strong impact on local biodiversity, however, they may also change fuel structure, and thus fire regimes. For instance, fire frequency might be abruptly altered by a rapid climate-independent change in the species composition driven by invasion of a plant species that modifies the intrinsic flammability properties of the fuels (Brooks and others 2004; Mandle and others 2011). The flammability of the invader might determine a strong change in the flammability of the community, and thus fire ignition and spread behavior. There are many examples of invasive species that increase fire frequency because of their high surface-to-volume ratio (alien grass invasion) or because of the high content of flammable compounds (for example, *Laurus*, *Eucalyptus*). There are also examples of low-flammability species invading highly flammable ecosystems (for example, outcompeting flammable grasses), such as the case of alien species with high moisture contents (invasion by succulent species) or with low surface-to-volume ratio and high moisture retention (for example, *Triadica sebifera* invasion of North America prairies). Other species are able to switch from surface to crown-fire regimes (some shrubs and vines; for examples of all these types of invasion see Brooks and others 2004; Mandle and others 2011; and Table 1). However, many invasive grasses are very flammable and resilient to fire and thus they have fire-promoting capacity. Invasive grasses can create a grass-fire cycle where initial invasion promotes further success of fire-promoting grasses

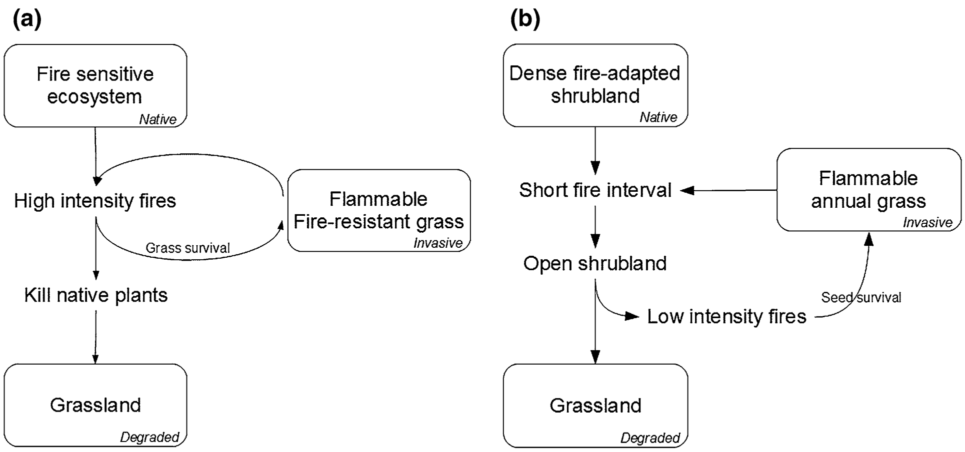

Figure 2. Two types of positive feedback fire cycles in which the invasion of a flammable plant (*right box*) can generate a type conversion from native vegetation (*upper box*) to invasive dominated (*degraded*) ecosystem (*lower box*): the herbaceous perennial plant-fire cycle (**A**) and annual plant-fire cycle (**B**).

(D'Antonio and Vitousek 1992), driving the system to an abrupt fire regime change. Although this cycle is common in invasive grasses, it is not exclusive to this life form. We can distinguish two very different fire-promoting invasion processes that are functionally quite different (Keeley and others 2012), one is the *perennial plant-fire* cycle and another is the *annual plant-fire cycle* (Figure 2).

The *perennial plant-fire cycle* occurs in fire-sensitive ecosystems and is dependent on the invading species elevating fire intensity, thus killing native woody species, which regenerate poorly after fire (Figure 2a). Such invasions usually involve perennial plants with highly flammable biomass (for example, large grasses) that generate sufficient fire intensity to promote canopy gaps, and the underground vegetative structures and buds of these invasives are protected during high intensity fires. Consequently, there is an abrupt fire regime change from mesic forests comprising fire-sensitive tree species to grasslands with highly flammable and fire resistant grasses. Examples of this invasion process are the fire-driven C_4 grass invasion of tropical woodlands (Mack and D'Antonio 1998; Silvério and others 2013), the invasion of the C_3 bamboo-like grass *Arundo donax* in temperate ecosystems (Coffman and others 2010) and the invasion of the resprouting shrub *Lantana camara* into some Asian and Australian forests (Hiremath and Sundaram 2005).

This perennial plant-fire cycle is less effective in fire-adapted shrublands because the native vegetation is very resilient to high fire intensities. Nonetheless, some of these shrublands are vulnerable to fires fueled by annual grasses, the *annual plant-fire cycle* (Figure 2b). Mediterranean shrublands are sensitive to short fire intervals as many postfire seeder species are dependent on a sufficient number of years (5–15 years) between fires to reach maturity and replenish seed banks. Under a frequent fire regime, annual grass invasion is promoted because these grasses can invade rapidly and produce new flammable fuels that promote reburning. If a repeat fire occurs before shrub canopy closure, the lower shrub biomass leads to lower fire intensity, which promotes survival of annual grass seeds that are typically exposed on the soil surface. Type conversion of shrublands to grasslands in turn decreases water-holding capacity of the soils (Williamson and others 2004), further adding to persistence of annuals. With each succeeding short-interval fire the shrub canopy becomes sparser and annual grasses and forbs spread and these highly combustible fuels promote repeated fires. Consequently there is a type-conversion with an abrupt fire regime change from high-intensity fires in the native shrubland to very frequent low-intensity fires in the invaded grassland. Examples of this annual plant-fire cycle can be found in the mediterranean shrublands of California (Keeley and others 2005) and Chile (Gómez-González and others 2011). The invasion of *Bromus tectorum* and *B. rubens* across vast landscapes of interior western North America has also increased fire frequency (for example, Balch and others 2013) to the point that native shrub-steppe species cannot recover, leading to other cascading effects (Knick and others 2003).

Although invasive success and community susceptibility to invasion are difficult to predict (Kolar and Lodge 2001), it is clear that once an ecosystem is invaded, alien species tend to modify many ecosystem properties, including fuel properties. Depending on the flammability of the alien plants, relative to the flammability of the original ecosystems, the invaded ecosystem would be more or less susceptible to carry a fire and thus to change fire regime in one or the other direction. However, most examples suggest that invasion increases fire activity (Brooks and others 2004). This is because highly flammable species that are able to support a new fire regime are going to be successful invaders through one of the plant-fire feedback cycles (Figure 2). This is especially true in fuel-limited ecosystems, however, it is not exclusive to these ecosystems, as very flammable invasive species may significantly increase flammability in dense nonflammable forests (Coffman and others 2010).

Another example of increased landscape flammability that very often drives abrupt fire regime changes is the plantation of exotic trees in fire-prone ecosystems. There has been a tendency to plant flammable fast-growing exotic trees in many Mediterranean and subtropical landscapes over the world. The prominent examples are the extensive pine plantations in the southern hemisphere (Richardson and others 1994, Simberloff and others 2010) and the eucalypt plantations worldwide out of Australia (Paquette and Messier 2009).

Socioeconomic Changes Driving Abrupt Fire Regime Changes

The influence of humans on fire activity is overwhelming and has been reviewed elsewhere (for example, Marlon and others 2008; Bowman and others 2011; Archibald and others 2012; Bird and others 2013; McWethy and others 2013). Here, we review cases in which socio-economic changes led to strong changes in ignitions or in fuel structure, both of which may lead to abrupt fire regime shifts. These anthropogenic changes in fuel may be driven by the direct effect on the fuel (for example, logging, and land abandonment) or by indirect effects through changes in ignition patterns (for example, loss of ignitions increase fuels in the landscape). Social and economic changes often occur in parallel with some shifts in climate, but the examples selected are those in which most variability in fire regime changes are better attributed to drivers other than climate.

Changes in Native Societies

Early human populations had relatively few land management tools other than the use of fire. Burning was used for a wide range of purposes, including clearing ground for human habitats, facilitating travel, killing pests, hunting, regenerating plant food resources for both humans and livestock, warfare among tribes, and even for stimulating precipitation. Contemporary indigenous populations of America, Africa and Australia still depend on fire as an important land management tool. The massive reduction of Native Americans by the European invasion (sixteenth to eighteenth centuries), drastically reduced fire ignitions and thus fire activity as indicated by the decrease in charcoal accumulation in soils and lacustrine sediments of the Neotropics (Carcaillet and others 2002; Nevle and Bird 2008). The magnitude of this change was so strong that the resulting buildup of fuel was depicted by variations in atmospheric CO_2 concentration and $\delta^{13}C$ in Antarctica ice cores and tropical sponges, and apparently contributed to the approximately 2% global reduction in atmospheric CO_2 (Nevle and Bird 2008). Another indicator of the changes in land use is the divergence between observed and climate-based predictions of charcoal influx curves after 1800 CE in America (Marlon and others 2012).

Humans impact fire regimes by affecting fuels, ignitions, and fire season. As discussed above, early human populations sometimes altered landscape fuel patterns by depressing large herbivore populations, but another common impact was adding additional ignitions. This would have had minimal impact on landscapes saturated with natural lightning ignitions, but profound impacts on fire regimes on landscapes where lightning ignitions were limited. For instance, African savannas have a very high lightning density (Christian and others 2003), and thus human ignitions would likely have played little role in changing natural (climate-driven) fire activity (Daniau and others 2013). In higher elevation mountainous landscapes in the western USA natural ignitions are plentiful, but are more limiting at lower elevations. When Native Americans moved into the region at the end of the Pleistocene, the increased ignitions caused rapid changes in fire regimes at low elevations both by increasing frequency of fire and also changing the seasonal distribution of fire (Pinter and others 2011). However, the most striking example of adding ignitions is in the Polynesian islands like New Zealand. New Zealand was one of the last major landmasses settled by humans and previous to their arrival, fires were very rare due to the wet climate. There is evidence of an abrupt increase in charcoal abundance in lake sediments of the South Island shortly after the Maori settlement in the thirteenth century (McWethy and others 2010, 2013). This charcoal increase reflects the introduction of fire in New Zealand's ecosystems with catastrophic effects on forest communities that were not adapted to fire. A similar process may have occurred in other moments in history and in other non-fire prone regions (Rolett and Diamond 2004).

The European Experience

Socio-economic and political change in rural societies have a strong impact on land-cover patterns and population densities, and thus on fire regimes; the nature of these changes (for example, favoring or limiting rural lifestyle) would determine the direction of the fire regime change. For instance, the unprecedented high population of farmers around the Mediterranean Sea during recent history (nineteenth and early twentieth century), strongly controlled landscape fuel patterns. The extensive agricultural areas, large herds of livestock in the surrounding landscapes, and the intensive use of forest products (firewood, wood for house and boat building, fuel for pottery and food ovens, and so on) depleted fuels and limited fire activity, as can be currently observed in many North African countries. In contrast, industrialization of the European Mediterranean region resulted in a depopulation of landscapes with consequent reduction of agriculture, grazing, controlled fires, and wood collection, with the associated sudden buildup of fuels on these abandoned landscapes. This fuel buildup in association with the increased ignitions at the wildland-urban interface, has resulted in an increase of large high-intensity fires (Pausas 2004; Figure 3). Similarly, the collapse of the Soviet Union induced a depopulation of rural areas, a reduction in grazing pressure and a subsequent abrupt increase in area burned (Dubinin and others 2011). In the Mediterranean basin and the former Soviet Union, fire activity is also related to climatic characteristics (that is, more fires in dry years), but the intensity and impacts of such fires were substantially higher after the rural collapse than in previous eras. In short, fire activity was previously fuel-limited and then became more susceptible to drought and climatic changes (drought-driven fire regimes, Pausas and Fernández-Muñoz 2012). A consequence of this process is the recent large fire activity associated with especially severe drought years and heat waves; as observed in Spain (1994, 2012), Portugal (2003), Greece (2007), and Russia (2010). The increased fire activity due to the collapse of the rural lifestyle is well documented in the Mediterranean basin and the former Soviet Union, but may be currently occurring in other Old World regions such as Africa and Asia.

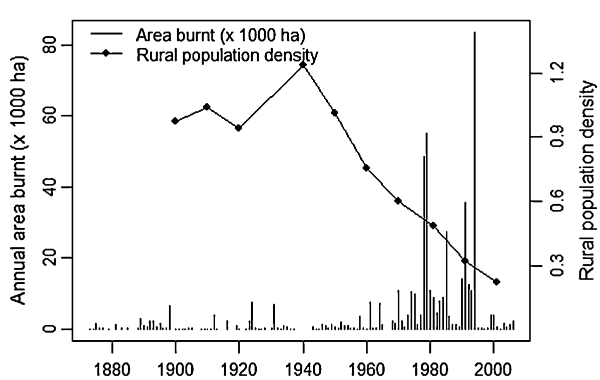

Figure 3. Evidence of the collapse of the rural lifestyles in eastern Spain. *Line* with *black symbols* refers to the changes of the rural population density (inhabitants/ha) during the twentieth century; *vertical lines* are the annual area burned (in thousands of ha). Data from Pausas and Fernández-Muñoz (2012) where the role of climate changes during the study period is also described (see also Pausas 2004).

The North American Experience

Fire was widespread in many ecosystems throughout western USA before European settlement. The loss of Native Americans (and thus ignitions), the fragmentation of native vegetation by farming, and later the fire suppression policy, all contributed to drastically changing fire regimes during the last several decades. An abrupt decline in fire activity, uncoupled from the climatic conditions, is depicted in sedimentary charcoal and tree-ring scars (Covington and Moore 1994; Taylor 2007; Marlon and others 2012; Figure 4) and might show a magnitude similar to the climatic-driven fire decline during the Little Ice Age (Marlon and others 2012). This demise of fire had different consequences in different ecosystems. For instance, many western coniferous forests (for example, dry ponderosa pine forests, Covington and Moore 1994) have suffered dramatic increases in understory fuels and a switch from frequent low-intensity surface fire regimes to a susceptibility to high-intensity crown fires (Allen and others 2002; Keeley and others 2009).

In contrast, the decline of fires in the eastern USA, once dominated by fire-dependent open communities (oak-pine and tallgrass prairies-savanna formations), has favored the invasion of shade-tolerant hardwoods (Peterson and Reich 2001). These species reduce understory light conditions further promoting shade-tolerant over fire-adapted species and generating a positive feedback that drives the system to non-flammable closed-canopy forests (mesophication *sensu* Nowacki and Abrams 2008). This phenomenon is not confined to

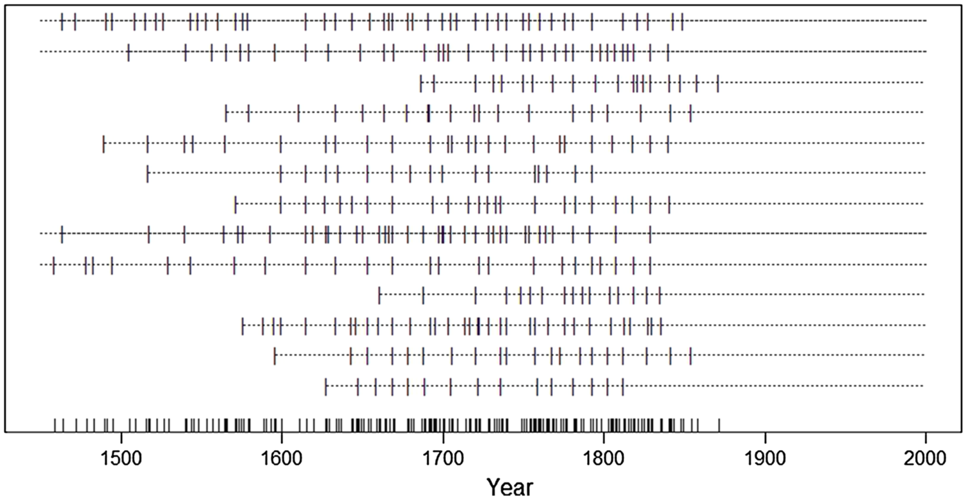

Figure 4. Fire chronology for Jeffrey pine-white fir forests for the period 1450–2000 for 13 sample sites (*horizontal lines*) and overall (in the *x*-axis) on the east shore of Lake Tahoe, Carson Range, Nevada. Fire dates are indicated by *short vertical lines*; the *bottom line* indicates the aggregation of fires for all 13 trees. The last fire occurred in 1871; MFI (1450–1850) = 2.9–11.4. Elaborated from Taylor (2007).

this region as it also happens in tropical savannas when fires are excluded (Bond and others 2005; Dantas and others 2013). The large magnitude of this process in eastern USA might be due to the fast and widespread socio-economics changes during the last decades in this region.

However, much of Western North America is dominated by non-forested landscapes where humans have caused a very different type of changes in fire regimes. Although management policy has been mainly to suppress fires, fire exclusion has rarely been reached on these non-forested landscapes. The high human populations and consequent increase in anthropogenic ignitions and alien grasses, and the change in seasonal distribution of fires, have limited the ability of fire suppression policy to exclude fire; in fact, fires are more frequent now than in the pre-EuroAmerican period (Keeley and others 2009). On many non-forested landscapes in western North America, increased fire frequency has disturbed ecosystems by pushing them beyond the threshold tolerance of many native species (Keeley and Brennan 2012). Indeed in the Great Basin and California many shrubland ecosystems have been converted from woody vegetation to herbaceous alien-dominated vegetation that encourages even higher fire frequency (Billings 1994; Keeley 2006). In fact, much of the fire activity on these non-forested landscapes is driven by the annual fire-cycle of introduced invasive plants described above (Figure 2). In southern California, this type conversion has accelerated due to large portions of the landscape having recently reburned at short intervals (Keeley and others 2009). There are multiple causes, some related to climate, but a major factor is increased human ignitions and seasonal change in ignitions, primarily during the autumn Santa Ana wind season. Santa Ana winds are katabatic foehn winds with easterly offshore flow arising from high-pressure systems in the Great Basin and generate extreme fire weather conditions (Keeley and others 2012). Exacerbating the situation too is the increased urban sprawl into more eastern portions of the region, thus placing ignitions further from the coast and placing larger portions of the landscape at risk from fires driven by these high velocity off shore winds.

Concluding Remarks

Climatic changes are widely considered to be a major driver of future fire regime changes. However climatic changes alone cannot explain many observed abrupt fire regime changes (Table 1). The examples presented here illustrate the need for a wider perspective on global change drivers in making forecasts of future fire regimes. Our examination of past abrupt changes in fire regimes shows that these can arise from a diversity of causes. Beyond climatic changes, shifts in fuel structure caused by changes in both domestic and wild grazing animals and by the increasing alien plants can lead to abrupt changes in fuel structure and fire behavior. Humans often play a role in these processes, but in addition they directly alter fuel structure in ways that can lead to fire regime changes. Also, humans profoundly affect fire regimes through changes in ignitions, both by diminishing the potential for natural ignitions to play an ecosystem role (fire suppression), and by adding to the natural ignition frequency and altering the seasonal distribution of fires. As human populations expand on many fire-prone landscapes it is to be expected that they will play a major role in determining future fire regimes. In addition, there are indirect effects from human activities that can also contribute to fire regime changes. For example, anthropogenic CO_2 and N_2 fertilization of the atmosphere can alter fuel levels, as well as fuel moisture. Although there are still many uncertainties regarding direct effects of CO_2 on ecosystems, where water or nutrients are not limiting, increased CO_2 might enhance rates of net photosynthesis and biomass production, and thus biomass accumulation. In addition, increased CO_2 enhances water-use efficiency, that is, the amount of carbon gained per unit of water lost, in a wide range of plants (for example, Conley and others 2001), and thus it should also favor growth and biomass accumulation in water-limited ecosystems as well (Bond and Midgley 2012). A more subtle effect, however, is in the effect on fuel availability for burning. Although global warming is widely interpreted as producing more drought-prone, and thus more fire-prone vegetation, increased water-use efficiency may have the opposite effect. In some Mediterranean climate ecosystems, this increase in water-use efficiency has been predicted to be more than 30% (Cheng 2003), with potential impacts on fuel moisture and subsequent fire activity.

The importance of climate-independent factors in abrupt fire regime changes can be viewed positively: whereas climate is very difficult to modify in the short term, fuels can potentially be managed to shape fire regimes and to mitigate the effects of global warming (Stephens and others 2013). However, the success of these actions may be diverse, depending on the historical fire regimes and the adaptive traits of the species in the community. Overall we have shown that many abrupt fire regime changes may not be a direct effect of climate change and that changes in other drivers affecting fuel dynamics and ignitions may be as relevant or even more than changes in climate, and this should be considered when predicting future fire regimes.

ACKNOWLEDGMENTS

This work has been performed under the framework of the VIRRA and TREVOL projects (CGL2009-12048/BOS, CGL2012-39938-C02-01) from the Spanish government. CIDE (*Centro de Investigaciones sobre Desertificación*; Desertification Research Center) is a joint institute of the Spanish National Research Council (CSIC), the University of Valencia and *Generalitat Valenciana*. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government

CONFLICT OF INTEREST

The authors declare no conflict of interest

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