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Alternative community states maintained by fire in the Klamath Mountains, USA

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Summary

1. The earliest examples of alternative community states in the literature appear to be descriptions of natural vegetation said to both depend on and promote fire. Nonetheless, alternative community states determined by fire have rarely been documented at landscape scales and in natural vegetation. This is because spatial autocorrelation may confound analyses, experimental manipulations are difficult and a long-term perspective is needed to demonstrate that alternative community states can persist for multiple generations.

2. We hypothesized that alternative community states occur in a largely forested landscape in the Klamath Mountains, north-western California, USA, where shrub-dominated sclerophyllous vegetation establishes after fire that is lethal to forests. Forests redevelop if succession is not arrested by fire. Our hypothesis would require that sclerophyll and forest vegetation states each be maintained by different self-reinforcing relationships with fire.

3. To test this hypothesis, we examined pyrogenicity of forest and sclerophyll vegetation as a function of time since the previous fire, accounting for spatial autocorrelation. Fire exclusion served as a *de facto* experimental treatment. Areas where fire had proceeded to occur served as controls.

4. Our findings are consistent with the occurrence of alternative community states established and maintained by different self-reinforcing feedbacks with fire. Sclerophyll vegetation was more pyrogenic, especially where time-since-fire (TSF) was relatively short, a favourable relationship for this fire-dependent vegetation. Forests were much less pyrogenic, especially where TSF was long, favouring their maintenance. Fire exclusion therefore has led to afforestation and rapid retreat of fire-dependent vegetation.

5. *Synthesis*: We have documented how different self-reinforcing combustion properties of forest and sclerophyll vegetation can naturally produce alternative states coexisting side-by-side in the same environment. Such fire-mediated alternative states may be underappreciated, in part, because they are difficult to demonstrate definitively. In addition, the dynamics they exhibit contrast with common perceptions that fire hazard increases deterministically with TSF in forests and shrublands. Addressing the impacts of fire exclusion will probably require a management shift to better allow fire to perform its ecological role in shaping landscape diversity and maintaining fire-dependent biota.

Key-words: alternative states, chaparral, conifers, fire regime, fire severity, hardwoods, pyrogenic, spatial autocorrelation, succession, vegetation switch

Introduction

Different assemblages of species can exist in the same environments or occupy the same site and disturbance is a key mechanism that allows this to occur (Petraitis & Latham 1999). There has been a resurgence of interest in the occurrence of alternative community states, and the concept has been broadened to include ecosystem degradation (van de Koppel, Rietkerk & Weissing 1997; Beisner, Haydon & Cuddington 2003; Suding, Gross & Houseman 2004; Suding & Hobbs 2009). However, examples that show that the same site conditions can support different natural communities are rare

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(Petraitis & Latham 1999; Jasinski & Asselin 2004; Schröder, Persson & De Roos 2005). A particular difficulty in demonstrating alternative states is proving the ability of the community to maintain itself through more than one generation (Connell & Sousa 1983; Sousa & Connell 1985).

Most examples of naturally occurring alternative states persisting in the same environment are from marine communities (Sutherland 1974; Peterson 1984; Knowlton 1992; Law & Morton 1993; Petraitis & Dudgeon 2004), lakes (Scheffer *et al.* 2001), or rangelands (Noy-Meir 1975; Westoby 1979; van de Koppel, Rietkerk & Weissing 1997). Alternative states at landscape scales and in natural vegetation have only been demonstrated in a handful of cases (Bowman 2000; Jasinski & Payette 2005; Schröder, Persson & De Roos 2005; Warman & Moles 2009). Here, at the landscape scale, we focus on the disturbance-mediated establishment and persistence of different natural vegetation in the same environment for more than one generation (Petraitis & Latham 1999; Scheffer *et al.* 2001).

Wilson & Agnew (1992) introduced the concept of vegetation switches to describe positive feedback processes in which vegetation modifies the environment to favour its maintenance. This process leads to sharp vegetation boundaries where there are no corresponding changes in the underlying environment. Such self-organizing dynamics may be expected to arise through interactions between vegetation and fire disturbances (Moritz *et al.* 2005). Plants have interacted with fire for millions of years and can influence their own fire regimes, potentially affecting their own fitness (Mutch 1970; Bond & van Wilgen 1996; Schwilk 2003). Bond & Keeley (2005) point out how plant traits that promote fire contribute to a large mismatch between climate and potential vegetation. At a global scale, Bond, Woodward & Midgley (2005) found that half the area that could be occupied by forest is instead occupied by pyrogenic vegetation like savanna or shrublands maintained by fire. In fact, the earliest examples of alternative states in the literature appear to be descriptions of natural vegetation said to both depend on and promote fire [e.g. P.E. Müller 1896 (cited in Handley 1954); Leiberg 1902; Show & Kotok 1924; Jackson 1968]. A number of additional examples of alternative states from many parts of the world have been attributed to the effects of fire (Bond & van Wilgen 1996, table 7.1; Latham *et al.* 1996; Bowman, Boggs & Prior 2007; Warman & Moles 2009; Hoffmann *et al.* 2009). Yet, these fire dynamics remain unappreciated, especially in the northern hemisphere (Bond, Woodward & Midgley 2005). Thus, ecosystems in which different vegetation states can be maintained by fire may be especially suitable for testing overlooked hypotheses about alternative states at landscape scales (Petraitis & Latham 1999; Warman & Moles 2009).

Documenting alternative states at landscape scales is, however, problematic. Fire in particular can exhibit strong spatial autocorrelation, making inferences about the causes of variation in its behaviour difficult (Bigler, Kulakowski & Veblen 2005; Bataineh *et al.* 2006). In addition, although alternative vegetation states maintained by fire have been demonstrated by relatively fine-scale experimentation (e.g. Gabriel *et al.* 1998; Valone *et al.* 2002; Wright & Chambers 2002), replicated experiments are rarely possible at landscape scales. However, fire exclusion can be considered a *de facto*, long-term, landscape experiment, as long as comparable areas that have continued to experience regular fire are available to act as controls. Lastly, data covering a long period will often be needed to demonstrate that an alternate state is maintained through time (Connell & Sousa 1983; Jasinski & Payette 2005; Schröder, Persson & De Roos 2005).

In a recent study, we investigated spatial patterns of wildfire severity in relation to management in a landscape in northwestern California and hypothesized that coexisting forest and sclerophyll vegetation are naturally occurring alternative states maintained by fire (Odion *et al.* 2004). Our goal here is to test this hypothesis systematically taking into account spatial autocorrelation, time-since-fire (TSF) as affected by fire exclusion and the potential for vegetation to persist for multiple generations. Our hypothesis would require that co-occurring vegetation states be maintained by different, self-reinforcing relationships with fire. Therefore, sclerophyll vegetation where TSF is relatively short should be especially pyrogenic, and forests where TSF is long should be especially non-pyrogenic. These dynamics are consistent with the observations of Jackson (1968) in Tasmania. Another possibility is that pyrogenicity remains unchanged with TSF because available fuel reaches equilibrium, as occurs in high latitude or high elevation forests (Johnson, Miyanishi & Bridge 2001). An alternative hypothesis is that vegetation pyrogenicity increases deterministically with TSF, leading to high susceptibility of vegetation to severe fire after long fire intervals. This dynamic is assumed for most low- and mid-elevation western US forest ecosystems such as those in the study area (reviewed by Jensen & McPherson 2008) and for sclerophyllous shrub vegetation (reviewed by Moritz *et al.* 2004).

To test for alternative states, we analysed fire severity patterns. Fire severity is not a physical measure of fire intensity (heat released per unit area), but an indirect measure of lethal fire effects (Gutsell & Johnson 2007). However, it is from these lethal effects that the potential for fire to maintain alternative states arises. We examined how fire severity was affected by the occurrence of forest and sclerophyll vegetation, TSF and their interaction at independent locations in the landscape. We also analysed patch size of severe fire and how it is affected by TSF. Lastly, we analysed fire severity and rates of establishment of a third vegetation type, conifer plantations. To illustrate the patterns and processes operating in contemporary vegetation, we quantified transition rates since 1950 among vegetation types and synthesized these dynamics into a state and transition model.

Materials and methods

The vegetation and fire severity data used in this analysis are the same as those in Odion *et al.* (2004), where a location map and an analysis of management influences on fire can be found. For this article, we overlaid the vegetation and fire severity data we previously used with fire history maps available from the state of California (http://frap.cdf.ca.gov/) to derive data for hypothesis testing. We also used these fire history data to evaluate the annual area burned from 1950 to 2007.

STUDY AREA

The topography in the 514 000-ha study landscape (Fig. 1, 41°00′00″–42°00′00″ N, 122°53′00″–123°30′00″ W) is steep and mountainous with elevation ranging from 300 to 2000 m a.s.l., but with most of the area below 1000 m a.s.l. Soils are highly diverse and generally shallow (Coleman & Kruckeberg 1999). Soils derived from ultra-mafic substrata, which are limiting to most plant growth, occur in select portions of the study area, mainly towards the north. The climate is moist Mediterranean, characterized by generally wet and relatively mild conditions except for summers, which are mostly quite hot and dry. Annual precipitation ranges from about 1100 mm in the driest low-elevation settings, to more than double that on the mountain crests, based on the few stations with long-term data (Taylor & Skinner 1998). About 85–90% of precipitation falls between October and May. Summer thunderstorms are a common source of wildfire ignitions. A complex of lightning ignitions following severe drought caused fires that burned an extensive portion of the landscape in 1987.

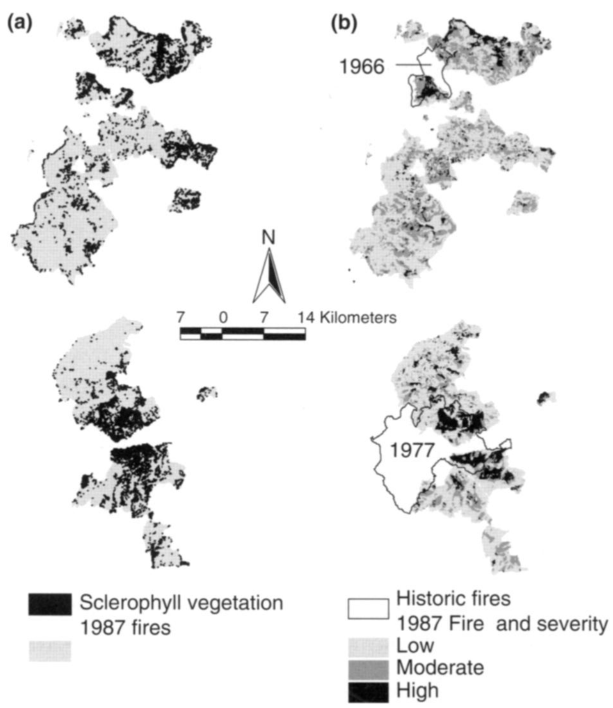

Fig. 1. Map of the study area in the Klamath Mountains, northern California, USA, showing (a) distribution of sclerophyll vegetation at the time of the 1987 fires and (b) severity of the 1987 wild fires and the 1966 and 1977 fire perimeters.

Substantial palaeoecological evidence over the Holocene indicates that fire has long been a consistent force in shaping the vegetation in the study region (Whitlock *et al.* 2004, 2008). The natural fire regime has included burns ranging from local surface fires to large stand-replacing events (Whitlock *et al.* 2004, 2008). Fire episodes have generally been increasing in the last 2000 years, albeit inconsistently among sites; at no site in the region for which palaeoecological data exist is the fire-episode frequency constant over this period (Whitlock *et al.* 2008). Aboriginal people of the Klamath Mountains are credited with managing fire (Lewis 1993); however, the spatial extent of fires associated with their ignitions is unknown (Whitlock *et al.* 2004). In the century prior to Euro-American settlement, fires burned at intervals of 5–75 years in the study area and nearby, with longer fire-free periods reported in some Douglas-fir (*Pseudotsuga menziesii*) stands (Agee 1991) and higher elevation white fir (*Abies concolor*) forests (Stuart & Salazar 2000). Fires appear to have become more common and widespread during the late 19th and early 20th centuries as a result of burning by miners and settlers and shifts in climate at the end of the Little Ice Age (Whitlock *et al.* 2004). This was followed by the current period of much-reduced burning as a result of effective fire exclusion, particularly since World War II (Taylor & Skinner 1998, 2003).

Closed, mixed evergreen forests as described by Whittaker (1960) and Barbour, Keeler-Wolf & Schoenherr (2007) are the predominant vegetation of the study region, occurring in all topographic settings (Table 1). At low and medium elevations, these forests are characterized by a mix of conifers, especially Douglas-fir. These conifers do not resprout after fire; they are replaced by new cohorts after fire (Thornburgh 1982) that germinate from seed that disperses from

Table 1. Pre-burn vegetation formations for the Klamath Mountains, northern California, USA, as identified by unsupervised classification of a 1986 Landsat image. Total area and area burned for each type in 1987 are shown for the three time-since-fire (TSF) classes analysed. The study area supports a small amount of woodland vegetation, as well as water

Vegetation class	Area (ha)	Area burned (ha) in 1987	Structure
Closed forest			
All	338 981	77 888	Medium to tall forest with high leaf area, typically with an evergreen conifer overstorey and an intermediate layer with shade-tolerant, evergreen hardwoods. Understorey vegetation generally sparse or with shade-tolerant herbs, ferns or deciduous shrubs.
TSF, 10–32 years	22 033	4648	
TSF, 33–75 years	46 549	13 846	
Sclerophyll vegetation			
All	82 660	12 033	Medium to tall shrubs or small trees. Evergreen, xeromorphic, with tough, leathery, waxy leaves with high energy content and possessing compounds that are volatile at low temperatures. Generally dense with touching or interlocking crowns.
TSF, 10–32 years	7728	3482	
TSF, 33–75 years	14 386	1801	
Plantations	27 231	3965	Dense, even-aged and evenly spaced plantings of evergreen conifers, usually monospecific, Douglas-fir (*Pseudotsuga menziesii*). With age, developing vertically and horizontally continuous foliage. Hardwoods generally absent or unimportant. Shrubs and especially grasses often present in the understorey.

surviving trees. An exception is knobcone pine (*Pinus attenuata*), whose seeds survive in serotinous cones despite adult mortality. However, this tree is less relevant in mixed forests as it is an early-successional tree more associated with sclerophyll vegetation. Hardwoods, especially tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), chinquipin (*Chrysolepis chrysophylla*) and California black oak (*Quercus kelloggii*) are abundant in forests. They resprout after fire and sexual reproduction is not associated with fire. From west to east, and with increasing elevation, Douglas-fir is replaced by white fir and tanoak by chinquipin. Ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*) and several other conifers also are common in many of these forest types. Most of the forests in our study area had not burned in > 75 years at the time of the fires in 1987 (Table 1).

Throughout the elevation range of the study area in all non-riparian environments, shrubby sclerophyll vegetation (Table 1) can be found in patches in the landscape where high-severity fires have occurred. This vegetation occupied a greater proportion of the landscape where TSF was relatively short (Table 1). Xeromorphic, evergreen shrubs generally dominate sclerophyll vegetation, especially species of *Arctostaphylos* and *Ceanothus*. These are examples of plants well suited to combustion, which survive fire as specialized resprouting lignotubers and in soil-stored seed banks. Palaeoecological data show an increase in fire-dependent *Ceanothus* and a scrub oak (*Quercus vaccinifolia*) during the mid-Holocene when temperatures were estimated to be 1.5 °C warmer and fire episodes correspondingly more frequent (Briles *et al.* 2008). Young conifers, including knobcone pine, which remains small-statured, are also common in the sclerophyll vegetation. Sclerophyll vegetation can most effectively persist on drier south-facing exposures and in areas of low soil fertility or on rocky substrata where forests take longer to grow. Fire severity also tends to be greater on southern exposures regardless of vegetation (Weatherspoon & Skinner 1995; Alexander *et al.* 2006).

Conifers may be only 1.5 m tall after 15–30 years, but on favourable sites they may reach 15 m after 30 years (Wills & Stuart 1994; Shatford, Hibbs & Puettmann 2007). Their growth rate increases after shrubs are overtopped (Thornburgh 1982). It is difficult to identify exactly when trees are dominant enough to be considered forest vegetation and this also depends on site conditions. However, based on our observations and published descriptions of conifer growth (e.g. Thornburgh 1982; Wills & Stuart 1994; Shatford, Hibbs & Puettmann 2007) forests typically redevelop after *c.* 35–100 years or, on average, in *c.* 60 years.

Dense, even-aged conifer plantations, as described by Weatherspoon & Skinner (1995), are scattered in the study area (Table 1), where they often displace the sclerophyll vegetation that develops after fire. The first tree plantations were established in 1936, but before 1955 less than 100 ha were planted. After 1955, plantation establishment became a regular management practice. In recent years, it has been mostly limited to burned areas. Plantations are mainly dominated by relatively young Douglas-fir, a valuable commercial species, and have a fuel array of conifer foliage that is closer to the ground and much more uniform than mixed evergreen forests of the region.

VEGETATION AND FIRE SEVERITY

Vegetation structure at the time of the 1987 fires was determined by analysis of satellite (Landsat) data (see Odion *et al.* 2004) and is summarized in Table 1. The fire-severity mapping was done by Jay Perkins of the Klamath National Forest (retired) using aerial photos as a regional assessment in the months following fire to identify areas of high tree mortality for logging and planting (see Odion *et al.* 2004). High-severity fire was defined as complete canopy scorch or consumption. Low- and moderate-severity fire was defined based on 0–49% and 50–99% canopy scorch, respectively. Fire severity effects vary by vegetation strata. All fire is generally lethal to herbaceous vegetation and non-sprouting shrubs. Hardwoods and resprouting shrubs are generally top-killed by most fire, but resprout vigorously. Crown fire is lethal to all conifers, whereas complete crown scorch is lethal to small conifers and most medium and large conifers, but not all (Odion & Hanson 2006; Miller *et al.* 2009).

DATA ANALYSES

Spatial autocorrelation can inflate significance test statistics considerably beyond what the data justify (Haining 2003). There are several ways to deal with this problem (reviewed by Fortin & Dale 2005). One approach is to reduce the sample size used in statistical tests to account for the effects of the spatial autocorrelation. To determine the appropriate effective sample size a semi-variogram can be used to identify the distances over which samples should be excluded as a result of spatial dependence (Haining 2003; Griffith 2005). We employ this approach, which has been used with contingency table data such as we analyse here (e.g. Cerioli 1997). We assessed separate vegetation and fire severity semi-variograms, both of which were based on grids at a 30-m resolution. The vegetation semi-variogram was based on 5000 random points within the 514 000-ha image and the burn severity semi-variogram was based on 1000 random points within the 98 814-ha of vegetation that burned.

We used the effective sample size of independent pixel data, as determined from the semi-variograms, to prepare a multidimensional contingency table of observation data. The three variables were vegetation (forest or sclerophyll), fire and TSF obtained from fire history maps (http://frap.cdf.ca.gov/) and divided into three categories, 10–32, 33–75 and > 75 years. We used log-likelihood chi-square analyses and log-linear modelling to test null hypotheses of no dependence of fire severity on vegetation, TSF and their interaction. We also evaluated patch size of high-severity fire and tested the hypothesis that it did not differ as a function of TSF.

We computed the fire rotation intervals (FRI, amount of time required for an area to burn, on average, once) under current management based on rates of burning from 1950 to 2007 obtained from fire history maps. To estimate the rotation interval for lethal fire (high severity in forest, high- and moderate-severity fire in sclerophyll vegetation), we divided the FRIs for all fire by the proportions of high and moderate severity reported here for the extensive 1987 fires, which are representative of all cumulative area burned from 1950 to 2007 (Odion *et al.* 2004). We also present a variance term with fire rotation and calculations derived from it to characterize the variability inherent in the estimates of rates of burning from 57 years of data. This term is the standard error of the mean decadal area burned from 1950 to 2000.

We synthesized our findings into a state and transition model. This model is adapted from one presented by Petraitis & Latham (1999), to illustrate possible alternative states of forest and fire-dependent, xeromorphic shrub vegetation. The annual rate of transition from forest to sclerophyll vegetation was calculated as: 1/Forest FRI, where Forest FRI equals the estimated high-severity FRI for forests described before. The annual rate of transition from forests to plantations was based on the total amount of plantations in the study area divided by the number of years since the plantings commenced (71). To obtain an estimate of the average transition rate from sclerophyll to forest vegetation under the current fire regime, the proportion of sclerophyll vegetation not burned by moderate or severe fire over the last 60 years (the average time for forests to develop) was divided by the high and moderate FRI for sclerophyll vegetation. The transition rates are presented to illustrate, for general comparison only, the relative rates of change that are expected based on the fire regime since 1950.

Results

Overall fire severity and vegetation patterns exhibited almost identical trends in spatial autocorrelation. In both cases, semi-variances increased steeply and levelled off distinctly at lags of about 2 km. Therefore, locations less than this distance apart exhibited spatial dependency, and the effective sample size was reduced to pixel locations separated by 2 km. This resulted in an effective sample size of 218 pixels for the landscape where forest and sclerophyll vegetation burned and 10 pixels where plantations burned. This was only about 0.02% of the total number of pixels in this landscape.

Sclerophyll vegetation was much more pyrogenic than forests (Fig. 2a) and the null hypothesis of no association between fire severity and natural vegetation was rejected ($\chi^2_2 = 10.1$, $P = 0.006$). Plantations experienced more high-severity fire than natural forests (Fig. 2a). However, with only 10 independent locations, effective sample sizes were too small for statistical analysis. The hypothesis that fire severity in natural vegetation was not associated with TSF was also rejected as a result of a significant inverse relationship ($\chi^2_4 = 10.5$, $P = 0.033$; Fig. 2b,c). The presence of a greater proportion of sclerophyll vegetation where TSF was 10–32 years (Table 1 and Fig. 2b,c) partially explained the greater fire severity in this TSF category. A significant interaction between vegetation and TSF was found by testing the effects of removing the interactive term between them from a log-linear model ($\chi^2_2 = 15.2$, $P < 0.001$). The full model with the interactive term and main effects also was marginally significant ($\chi^2_{10} = 18$, $P = 0.056$). Combining the intermediate TSF category (33–75 years) with the > 75-year category, which had similar fire severity (Fig. 2b,c), produced a full model that was more significant ($\chi^2_6 = 17.2$, $P = 0.009$). Thus, as a result of both significant main and interactive effects, the highest severity, as well as highest relative abundance of sclerophyll vegetation, occurred where TSF was shortest. Conversely, the lowest fire severity and greatest abundance of forests occurred where TSF was longer (Fig. 2b,c). Therefore, we can reject the hypothesis that vegetation pyrogenicity increases deterministically with TSF. Our results are consistent with the hypothesis that co-occurring vegetation states can be maintained by different fire regimes caused by different combustion properties of the vegetation.

Much of the high-severity fire within the 1987 perimeter occurred in areas that had previously burned in 1966 and particularly in 1977 (Fig. 1). Roughly 60% of the area that burned at high severity in the 1977 fire and also burned in the 1987 fires burned again at high severity in 1987, and many of the patch boundaries were identical. Much of this area was forested at the time of the 1977 fires (Odion *et al.* 2004) and has been sclerophyll vegetation since.

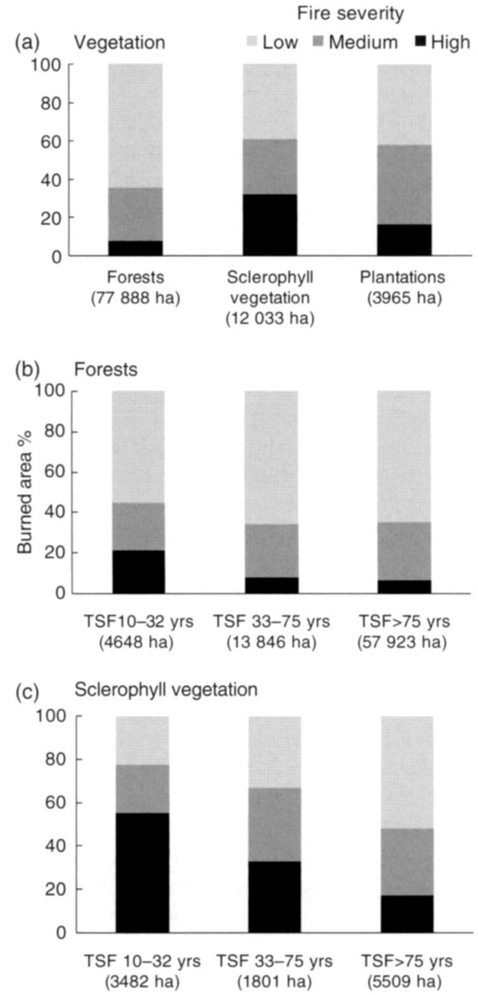

Fig. 2. Proportion of area burned in the Klamath Mountains, northern California, USA, at low, moderate and high severity in 1987 in (a) closed forests, sclerophyll vegetation and plantations, (b) forests in three time-since-fire (TSF) catogories and (c) sclerophyll vegetation in three TSF categories.

Although concentrated primarily in the 1966 and 1977 burn areas, patches of high-severity fire were also widely dispersed across the landscape (Fig. 1). The largest high-severity patch was 1125 ha. The median size of high-severity patches was 3.8 ha, whereas the average size of high-severity patches (18.7 ha) was much bigger than the median as a result of the effects of a few large patches. The nine largest high-severity patches, out of 643, accounted for almost half of all high-severity fire. Four out of the six largest high-severity patches were in areas that burned in 1977 or 1966 (Fig. 1). High-severity patches were significantly smaller ($P = 0.036$, *t*-test) where TSF was > 75 years (12.3 ha, SD 41.7, $n = 587$) than where it was 10–32 years (68.5 ha, SD = 219, $n = 121$; Table 2). High-severity patch shapes were complex, with a perimeter-to-area ratio of 58. Patch size probability functions suggest different relationships governing fire behaviour among the TSF categories (Fig. 3). Where TSF was > 75 years, there was a higher frequency of relatively small patches than where TSF was shorter. Patch frequency also decreased much more rapidly as a function of patch size where TSF was > 75 years, even though patch size was constrained most where TSF was shorter as a result of much smaller contiguous burned area.

The FRI for the study area since fire suppression became clearly effective (in *c.* 1950) was 136 years. The standard error associated with temporal variability in fire over this period was 62.1. The amount of high-severity fire was 7.8% in forests, excluding plantations, yielding a rotation interval of 1740 years (decadal SE = 762.5). In sclerophyll vegetation, fire severities of 32% and 29% for high and moderate, respectively, yielded FRIs of 424 and 468 years, respectively, or a combined interval of 223 years (SE = 101.6) for lethal fire, much longer than the 35–100 years required for forests to develop.

With current rates of moderate- and high-severity fire since 1950 in sclerophyll vegetation, about 1.2% per year will transition to forest (Fig. 4). This rate is 21 times the current rate of transition from forest to sclerophyll vegetation. With current rates of burning, sclerophyll vegetation maintained by fire would eventually decrease to about 750 ha in the entire study area. This would take about 80 years. However, the amount of sclerophyll vegetation has decreased faster because some burned forests have been replaced with plantations, which occurred at a rate of about 0.2% per year over the whole landscape. This affects only the half of the landscape that is managed (Odion *et al.* 2004); so, loss of sclerophyll vegetation is more pronounced there.

Table 2. Characteristics of 1987 high-severity burn patches in the three different time-since-fire (TSF) categories in forest and sclerophyll vegetation combined of the Klamath Mountains, northern California, USA. Numbers with different letters indicate a statistically significant difference

	High-severity patches		
	TSF, 10–32 years	TSF, 33–75 years	TSF, > 75 years
Number	59	147	587
Total area	3957	2100	7220
Maximum size (ha)	1125.3	302.5	595.6
Median size (ha)	4.1	3.3	3.7
Mean size (ha)	68.5[a]	14.3	12.3[b]
Standard deviation	218.9	35.4	41.7

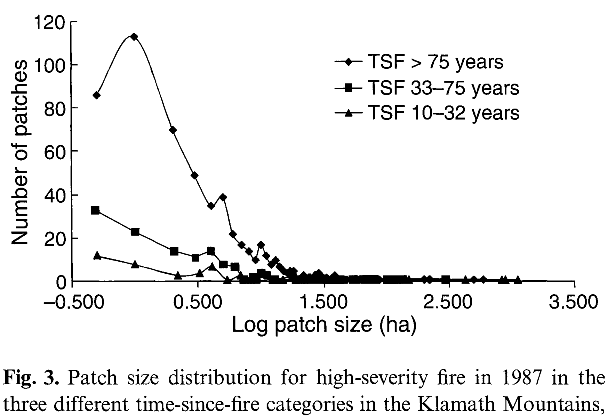

Fig. 3. Patch size distribution for high-severity fire in 1987 in the three different time-since-fire categories in the Klamath Mountains, northern California, USA.

Discussion

We found the vegetation in the Klamath Mountains to have different combustion properties and this was a function of TSF at the landscape scale. Consistent with the hypothesis that co-occurring vegetation states in this landscape can be maintained by different self-reinforcing relationships with fire, sclerophyll vegetation was pyrogenic, and its highest severity as well as relative abundance occurred where TSF was shortest. Conversely, the lowest fire severity and greatest abundance of forests occurred where TSF was longest (Fig. 2b,c). Therefore, our results support the model of alternative vegetation states maintained by different interactions between vegetation and fire, as discussed in early literature on California forests (Leiberg 1902; Show & Kotok 1924), and later, more formally, for landscapes in both California (Wilken 1967) and Australia that are characterized by wet Mediterranean or similar climate (Mount 1964; Jackson 1968). These two Mediterranean regions are well known to have remarkably convergent vegetation properties (di Castri & Mooney 1973).

One important limitation of our study is that we did not assess the effects of topography, aspect and soils on fire behaviour. The vegetation and TSF effects we identified were pronounced at spatially independent locations; however, disentangling the interdependent influences of the underlying environment would be difficult. High-severity fire in the study area is most common on drier and more southerly aspects and wind-exposed ridges (Weatherspoon & Skinner 1995; Taylor & Skinner 1998; Alexander *et al.* 2006). In these environments, succession to forest is slower, especially where soil productivity is lower as a result of the cumulative effects of fire history. Thus, climate, topography, soils, vegetation and fire tend to be mutually reinforcing determinants of landscape patterns. However, climate and topography, particularly as they affect wind, can override other factors and control fire–vegetation patterns (e.g. Geldenhuys 1994).

A MODEL OF FIRE-MEDIATED ALTERNATIVE COMMUNITY STATES

Disturbances that kill residents, stimulate recruitment events and vary stochastically in space and time are a key to the occurrence of alternative states (Petraitis & Latham 1999). In the study region, episodic weather-driven fire events kill patches of forest when severe drought and weather conditions may allow even the most fire-resistant stands to burn. Once sclerophyll vegetation replaces forests, its self-reinforcing relationship with fire can alter successional pathways to favour its retention (Fig. 4). Sclerophyll vegetation may effectively create a ‘fire trap’, preventing tree species from developing to adult sizes (Gignoux *et al.* 2009; Hoffmann *et al.* 2009). Pyrogenic, self-immolating plants that combine inhibition of late-successional species by fire damage with survival of regenerative

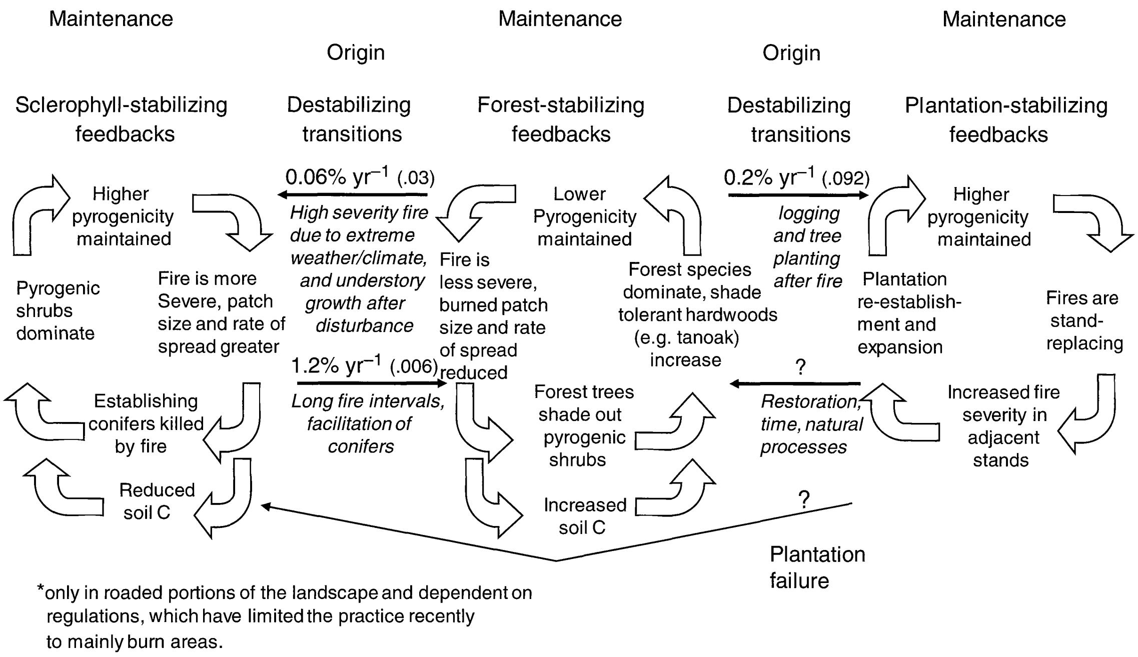

Fig. 4. Conceptual model showing the origin and maintenance of alternative stable states of vegetation in the study area with annual transition rates based on contemporary dynamics. The numbers in parentheses following the transition rate are standard errors of the mean decadal rate of fire from 1950 to 2000. Adapted from Petraitis & Latham (1999).

propagules are considered a 'special case' in which directional replacement of early species is prevented (Platt & Connell 2003). This occurred in our study area, for example, where patches burned severely in 1977 and reburned at high severity in 1987 (see also Donato *et al.* 2009).

Inhibition of late-successional species as a result of the pyrogenicity of early species may also involve indirect mechanisms related to fire. The cumulative effects of severe fire in reducing soil carbon and site productivity over time (Fig. 4) can slow growth rates of forest tree species (Waring & Schlesinger 1985), increasing the time they are vulnerable to the fire trap. This is an example of how sclerophyll vegetation can modify the underlying environment to favour its retention (Wilson & Agnew 1992). In addition, because conifers depend on dispersal to re-colonize burned patches, they can be inhibited if patch sizes exceed a dispersal distance threshold, beyond which conifer regeneration may diminish rapidly (Romme *et al.* 1998). We found that where TSF was short and sclerophyll vegetation more abundant, high-severity patches were significantly larger (Table 2). Thus, sclerophyll vegetation can promote relatively frequent, severe fire that operates together with reduced soil fertility and patch dynamics to directly and indirectly inhibit forests (Fig. 4).

Paradoxically, although the sclerophyll vegetation may inhibit forests through fire-related mechanisms, conifers can also be facilitated by shrubs. Conifer seedlings survive better under shrub canopies, where drought stress is reduced (Zavitkovski & Newton 1968; Dunne & Parker 1999) and their long-term growth potential may be increased by nitrogen-fixing *Ceanothus* spp. (Busse, Cochran & Barrett 1996). Conifer establishment may also be facilitated by provision of mycelia of mycorrhizal fungi by *Arctostaphylos* spp. (Horton, Bruns & Parker 1999). Facilitation of conifers by sclerophyll vegetation will help reduce the amount of time conifers are vulnerable to the fire trap and increase the frequency of fire needed for sclerophyll vegetation to be maintained.

With sufficiently long fire intervals conifers can escape the fire trap and reach a threshold beyond which positive feedbacks between reduced fire and vegetation pyrogenicity increasingly favour forests (Fig. 2b). These feedbacks lead to less fire-related mortality. We also found that fire intervals > 75 years led to a much lower probability and maximum size of large high-severity burned patches than where TSF was shorter (Figs 2b, 3 and Table 2). This effect of long fire intervals can help ensure that the seed is able to disperse from surviving conifers throughout severely burned areas. Forest areas that burned at high severity in the 1987 fires in the study area (Shatford, Hibbs & Puettmann 2007) and nearby in 2002 (Donato *et al.* 2009) and that were within 370 m of the surviving forest were found to have high levels of conifer regeneration. Donato *et al.* (2009) found that the area within this distance to seed sources constituted 70–90% of a large burn in the study region. Thus, long fire intervals may increase both the resistance of forests to fire and their resiliency after fire.

There are several reasons why forests in the study region become less pyrogenic with TSF and with stand age. Understorey shrubs and small conifers are increasingly excluded by the forest canopy (Azuma, Donnegan & Gedney 2004). Closed forests also have a microclimate that is less favourable to fire (Countryman 1955). Larger trees and fallen logs act as heat sinks during fires (Azuma, Donnegan & Gedney 2004).

Biomass that is most available to flaming combustion, canopy foliage and fine wood on the forest floor, may reach equilibrium (Jenny, Gessel & Bingham 1949; Kittredge 1955; Waring & Schlesinger 1985), but support lower fire severity because the height of the canopy above the forest floor increases (Azuma, Donnegan & Gedney 2004). Tanoak and other hardwoods have also been associated with low fire severity in long-unburned stands in the study region (Azuma, Donnegan & Gedney 2004; Odion *et al.* 2004). Hardwoods in the oak family often have high lignin content and have generally been found to be much less pyrogenic than conifers (Mutch 1970; Williamson & Black 1981; Rebertus, Williamson & Moser 1989; Pausas *et al.* 2004).

As forests develop, tanoak is not excluded like pyrogenic shrubs. Instead, it transforms from shrubby, xerophytic forms with dense, small, thick and waxy leaves to more arborescent, mesophytic forms with large, shade-tolerant leaves. Phenotypic plasticity, as exemplified by these changes, is a key trait among species that are important immediately after disturbance and can remain so late in succession despite a change in the environment (Platt & Connell 2003). High-severity FRIs in forests of the study area under fire exclusion (1740 years) exceed the life spans of the conifer species (Burns & Honkala 1990). Because tanoak can both persist and also recruit new canopy stems in mature forests in the absence of fire (Hunter 1997), whereas conifers like Douglas-fir rely on cohort regeneration after fire (Wills & Stuart 1994), tanoak may eventually become more dominant in the study region with fire exclusion. However, fire exclusion may increase the susceptibility of tanoak, as well as California black oak, to a highly virulent non-native pathogen causing Sudden Oak Death disease (Moritz & Odion 2005). Thus, other hardwoods that also do not require fire for reproduction may eventually increase if fire exclusion persists, which would further reduce forest pyrogenicity. Although climate change could potentially reverse these ongoing forest changes by increasing rates of burning, this may not apply to the study region (Krawchuk *et al.* 2009). Moreover, decreases in vegetation pyrogenicity can override effects of changing climate on fire (Higuera *et al.* 2009).

Conclusions

Alternative community states are difficult to demonstrate at the spatial and temporal scales of many landscape studies and, consequently, may be underappreciated in natural vegetation (Petraitis & Latham 1999). We found that alternative states of pyrogenic and non-pyrogenic vegetation are maintained in the same environment by different self-reinforcing relationships with fire. In fire-prone environments, such self-organizing dynamics between vegetation and fire may lead to sharp vegetation boundaries that do not correspond to underlying environmental gradients (Wilson & Agnew 1992). Our work also points out the extensive effects of spatial autocorrelation that need to be considered to make inferences about fire behaviour. Our samples needed to be 2 km apart to be independent. An obvious limitation of our study was the inability to account for interacting topographic, soil and weather effects; however, these likely reinforce the vegetation influences on fire that we found.

Our findings that fire exclusion leads to afforestation and loss of vegetation that is dependent on frequent fire are consistent with global patterns (Bond, Woodward & Midgley 2005). However, our results conflict with assumptions regarding fire-prone forested landscapes of the study region (Spies *et al.* 2006) and western United States of America that fire exclusion leads to more pyrogenic forests, increasing the probability of high-severity fire. Current management based on these prevailing views, such as thinning forest stands, constructing fuelbreaks and establishing plantations after fire, does not address the rapid decrease in fire-dependent sclerophyll vegetation and changes to forests that are caused by fire exclusion in the study region. Addressing the ongoing effects of fire exclusion will require a better understanding of these effects. It will also require that society develop a less adversarial relationship towards fire and adapt to better accommodate its natural role in shaping vegetation and biodiversity (Jensen & McPherson 2008; Baker 2009). Managing for ecological processes, which have shaped vegetation and biodiversity, is consistent with conservation objectives in the Klamath region (Taylor & Skinner 1998; DellaSala 2006) – a renowned centre of vegetation and floristic diversity in western North America (Whittaker 1961; DellaSala *et al.* 1999).

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