

Fig. 2. Mean (\pm 95% CI): (a) forb cover, (b) low shrub cover, (c) hardwood/shrub cover, and (d) broadleaf vegetation height, for mature/old growth stands, long-interval burn stands, and short-interval burn stands (0, 1 and 2 recent burns, respectively). Heights were calculated as a weighted average based on cover \times height of each species.

Species richness increased with the number of recent fires and was highest in the SI burn (Table 1). This trend was similar when assessed at either the sample-wide (gamma) or plot (alpha) level. Fifty-nine species were detected in the SI

burn sample compared to 42 in the LI burn sample. The SI burn had 4.2–19.8 (95% CI) more species per plot than the LI burn. Some portion of the richness in the SI burn was likely associated with comparatively high forb/low-shrub abundance. There were no strong differences in species richness between the LI burn and M/OG stands (Table 1). The higher richness in the SI burn was not dominated by a few species; Shannon evenness was fairly high (0.75, 95% CI 0.67–0.83) and not different from the LI burn (0.73, 95% CI 0.66–0.79).

Species composition differed little between the LI burn and M/OG stands (MRPP: $A = 0.0095$, $P = 0.33$), but was strongly different in the SI burn compared to both the LI burn ($A = 0.13$, $P = 0.001$) and M/OG stands ($A = 0.12$, $P = 0.002$). Consistent with the patterns of increased abundance and diversity, the difference was due primarily to additions or increases in the abundance/frequency of several species in the SI burn, rather than species loss (Table 1). Most of the increases were of forb and low stature shrub species. Composition of hardwoods and shrubs showed a decreasing trend with number of recent burns in mean cover of *L. densiflorus* and *Q. chrysolepis*, the dominant hardwoods of these plant associations (Table 1). *Arbutus menziesii* and *Q. sadleriana* were mostly absent in the SI burn (Table 1). In contrast, *A. patula* occurred in greatest abundance in the SI burn (Table 1). The increase in low vegetation components, coupled with reduced cover of major hardwood species, resulted in overall lower-stature communities in the SI burn (Fig. 2d).

ISA results were also consistent with an additive effect of the SI fire (Table 1). Only two species, the fire-sensitive forbs *Goodyera oblongifolia* and *Chimaphila menziesii*, were uniquely associated with M/OG conditions and only one species, *A. menziesii*, was strongly associated with the LI fire. In contrast, seven species were strongly associated with the SI fire (Table 1). Thus, overall, most species found in M/OG forests occurred with similar abundance/frequency when subject to one or even two high-severity fires, with increases/additions of several disturbance-associated species in the SI burn.

HARDWOOD, SHRUB AND CONIFER RESPONSES

Sprouting was the dominant mode of regeneration for hardwoods and woody shrubs in both the SI and LI burn (Fig. 3). On average, a greater proportion of pre-fire individuals were killed (did not sprout) in the SI fire, but responses were highly variable (Fig. 3). At the individual level, sprouting probability was strongly positively associated with pre-fire size (GLME: $F_{1,732} = 24.9$, $P < 0.0001$), and there was no strong shift in this relationship between the SI and LI burns ($F_{1,10} = 1.78$, $P = 0.21$). Similarly, for individuals that sprouted, sprout biomass was strongly positively associated with pre-fire size (HLM: $F_{1,540} = 338.2$, $P < 0.0001$), and there was also no strong shift in this relationship between the SI and LI burns ($F_{1,10} = 1.12$, $P = 0.32$). However, relative to the LI burn, individuals in the SI burn were smaller at the time of the second fire (mean pre-fire basal area = 15.3 cm² shrub⁻¹ in SI burn, 52.2 cm² shrub⁻¹ in LI burn), which was associated with

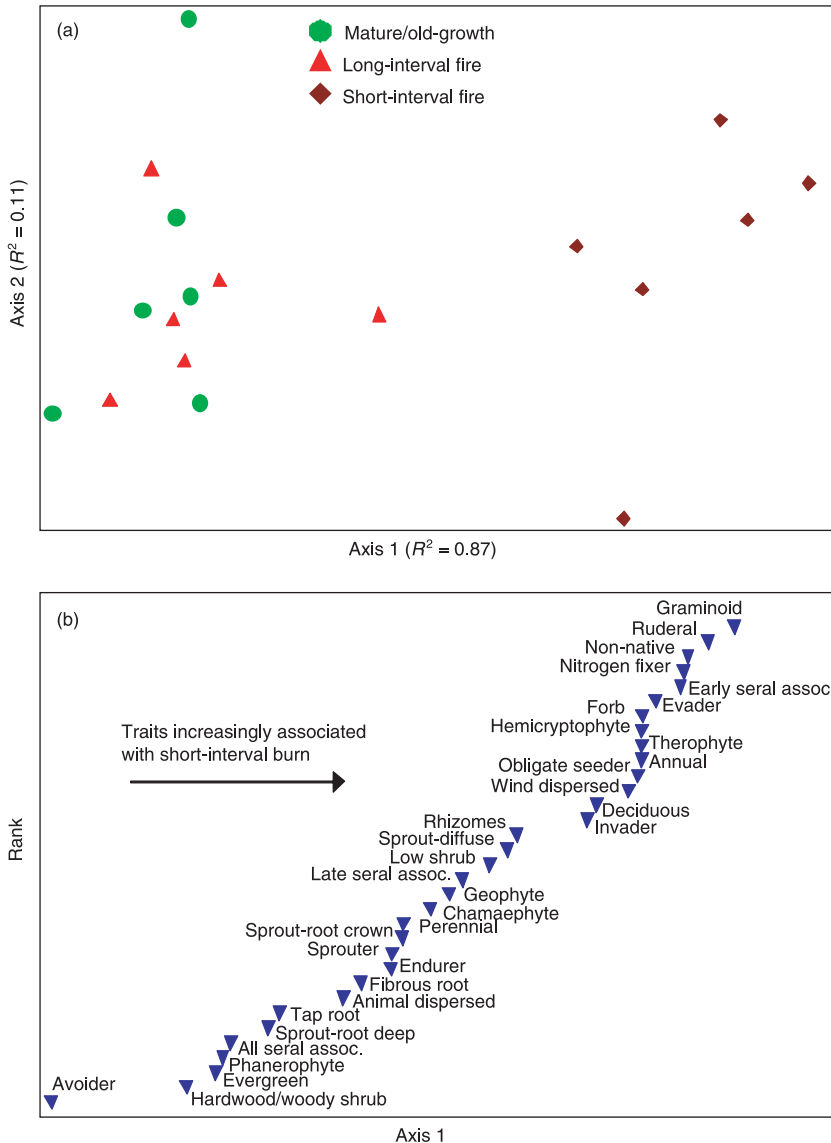


Fig. 5. (a) Ordination of plots in plant functional trait space. Larger distances between points represent larger differences in abundance of traits; SI burn plots are separated strongly from other treatments. R^2 values signify portion of original variance explained by each axis. Pearson's r correlations with environmental variables were (Axis 1, Axis 2, respectively): # burns (0.86, 0.04), elevation (0.22, 0.20), annual precipitation (−0.19, −0.14), annual solar heat load [aspect proxy] (−0.36, −0.35). (b) Ranks of plant functional traits along Axis 1. Attributes to the right are increasingly associated with (but not exclusive to) the SI burn, and vice versa. The 'Non-native' data point is due to minor occurrences of *Cirsium* spp. or *Senecio sylvaticus*.

shown) were well-distributed across axes, suggesting these factors were not major drivers of compositional gradients relative to disturbance history.

Discussion

The early post-fire data were most consistent with model 3: interval-dependent dynamics with no decline in diversity or abundance after SI fire (or 're-burn'). The SI fire resulted in unique post-fire communities containing nearly all species found in M/OG stands and in the LI burn, plus additions or increases in several disturbance-associated species (Table 1). This shift to higher richness and abundance, coupled with lower dominance by woody broadleaf components (Fig. 2), lends comparatively little support for model 1 (cyclical dynamics independent of fire interval) or model 2 (interval-dependent dynamics with major reductions in diversity/abundance). Regeneration of major structural species (e.g. conifers, hardwoods) in the SI burn suggested that, in the

absence of repeated severe fires, these stands retained the potential to develop toward mature forest condition.

VEGETATION ABUNDANCE, DIVERSITY AND COMPOSITION

The consistent presence of a core assemblage including nearly all species found in mature forests suggests high community resilience following one and even two stand-replacing fires. The increase in species richness in the SI burn was unanticipated and mainly due to additions of ruderal or disturbance-associated flora such as *Rubus* spp. and bracken fern (*Pteridium aquilinum*), the latter also noted by Isaac (1940) following recurrent burning of cutover areas in the Douglas-fir region. The pattern we observed – SI fire leading to lesser dominance by woody broadleaf components, generating gaps in which additions of ruderal/low-stature species lead to higher species richness and cover – is similar to that observed by Delitti *et al.* (2005) in a Spanish Mediterranean ecosystem.

The mechanisms for increases in early seral species and total richness in the SI burn could be abiotic, such as changes to soil properties that favour such species, or biotic, as in the development of a propagule bank for early seral species during the 15 years between fires (Noble & Slatyer 1980). Based on the abundance in the SI burn of short-lived, rapidly maturing species (ruderal, annual), and those with long-lived seed banks (evaders) (Table 2, Fig. 5), we infer that increases in early seral species were driven primarily by the biotic mechanism of propagule availability. This mechanism represents a positive feedback legacy effect, whereby small compositional changes following a single fire (minor increases in early seral species and associated seed banks) lead to greater modifications following a second fire (major increases in these species).

Pre-existing variability among treatments could explain the differences we observed, particularly because of the lack of spatial interspersion of treatments. However, a nearly identical core set of species was found in all three treatments which provides supporting evidence that the sample groups were comparable before recent disturbance. Moreover, the primary difference observed in the SI burn – addition of disturbance-associated components – is logically consistent with a fire response.

HARDWOOD, SHRUB AND CONIFER RESPONSES

Hardwood and shrub regeneration

Hardwood and shrub individuals of a given size had similar sprouting probability and biomass in the SI and LI burns. A 15-year interval between fires appears sufficient for below-ground carbohydrate reserves to support sprouting following top-kill for the species examined in this study. Similarity of sprouting between treatments also suggests there was no difference in heat-related damage to below-ground tissues; thus fire severity was apparently similar across treatments in this respect. Nevertheless, it is possible that a shorter interval fire, or further repeated fires, could reduce the sprouting response relative to what we observed (Delitti *et al.* 2005).

Because the relationship between post-fire sprouting biomass and pre-fire size was the same across treatments, the lower post-fire hardwood/shrub cover and biomass in the SI treatment may be due to the smaller size of individuals at the time of the second fire (Fig. 4). This may be associated with: (i) the conversion by the first fire of large hardwood trees to smaller, multi-stemmed sprouts with lower leaf/basal area (see Bond & van Wilgen 1996); (ii) a compositional shift toward smaller species that colonized the site over time following the first burn (e.g. *A. patula*) (Table 1); or (iii) pre-existing differences in hardwood/shrub sizes. The conversion by the first fire of tree forms to sprout-shrub forms, and its feedback to re-burn response (smaller subsequent sprouts), is a possible mechanism by which recurrent burning could reduce dominance by hardwoods and shrubs during early succession, creating growing space for other vegetation (model 3, see Fig. 2).

Conifer establishment

Initial post-fire conditions were apparently not limiting to total conifer establishment in the Silver-Biscuit SI burn. Thus, if differences emerge later between conifer regeneration in the SI vs. LI burns (*sensu* Gray & Franklin 1997), it could be inferred that latent differences (e.g. competition, herbivory, soil properties) drove the difference. Dense early conifer establishment in the SI burn suggests that the availability of seed sources and suitable germination substrate was similar to that in the LI burn. Distance to contiguous seed source ranged from 85–300 m for SI burn plots compared to 80–370 m for LI burn plots, a range applicable to 70–90% of the stand-replacement portions of the Biscuit Fire excluding serpentine areas (based on US Forest Service GIS data; see Donato 2008). (Note that precipitation during post-fire growing seasons, an important factor for regeneration and one that may vary widely among years, likely did not contribute abnormally to regeneration, as it was generally within one S.D. of 30-year mean, and if anything was generally below average [Donato 2008]).

A mixed-severity fire typically produces complex patterns of tree mortality on the landscape (Agee 1993, 2005). These patterns result in much of a burned area being close to live-tree seed sources, even in large fires with substantial stand replacement (Turner *et al.* 1994). In the Silver-Biscuit SI burn, areas that burned with low severity in the initial fire tended to re-burn with low severity (Thompson *et al.* 2007), such that the mosaic of available seed sources largely persisted through the second fire. The persistence of the mosaic over certain time scales may result in well-dispersed seed sources following repeated mixed-severity fires. This dynamic differs from observations of sparse regeneration following SI fires in ecosystems reliant on *in situ* re-seeding from serotinous conifers (fire interval < reproductive age) (Eugenio *et al.* 2006; Johnstone & Chapin 2006) or on off-site seed sources as in this system, but with seed sources reduced by the second fire (Isaac & Meagher 1936). Our inference of off-site source in this study is based on nearly all seedlings establishing 2 years post-fire, too late for a dead-tree canopy seed bank source.

TRAIT ANALYSIS

Analysis of plant functional traits showed several strong associations with recent fire history, providing support for the use of functional traits in predicting vegetation response to short-interval severe fires (Table 2, Fig. 5). Some associations were intuitive while others were unanticipated. As we hypothesized, several disturbance-associated traits and functional types were highly associated with the SI burn. Broadly applicable examples included invader and evader regenerative strategies, ruderal/early seral associates, and wind-dispersed seeds.

Several different regenerative mechanisms were important in the SI burn, including vegetative sprouting, *in situ* seed banks, and dispersal from *ex situ* seed sources. Assessing Noble and Slatyer's (1980) vital attributes against the 15-year

fire interval, forbs and low shrubs were 'G' types (rapid maturation time and stored soil seed banks), hardwoods and shrubs were 'S' and/or 'V' types (vegetative sprouting ability and/or long-lived soil seed banks), and conifers were 'D' types (well-dispersed propagules from surrounding live tree sources). This diversity of available mechanisms likely in part underlies the robust vegetation response to SI fire.

Rapid time to reproduction was a major factor in species that increased following SI fire. Ruderal and low-stature community components including many low shrubs and forbs (mainly hemicryptophytes and therophytes) – particularly those with rapid maturation and shorter-lived tissues such as annuals and deciduous species – responded positively to the SI fire (Table 2). Delitti *et al.* (2005) also observed increases in low shrubs and forbs, especially hemicryptophytes, following recurrent fires in a Spanish Mediterranean ecosystem. For broadleaf evergreen woody vegetation, however, there was little association with any fire history, although these tended to have lower mass/cover in the SI burn – also similar to Delitti *et al.* (2005). Thus, species investing more resources in early reproduction, and less in long-lived leaves and secondary tissues (wood), may be expected to be relatively dominant immediately following recurrent stand-replacing fires (Table 2; Noble & Slatyer 1980).

Consistent with observations made by Lloret *et al.* (2005) in a Spanish Mediterranean ecosystem, seeder species were associated with recurrent fires while sprouter species (particularly those that sprout from central root crowns or burls) did not show strong associations with recent fire history (Table 2). The exception in our study was that species sprouting from diffuse rhizomatous structures responded positively to the SI fire. Diffuse sprouters may have increased due to a legacy effect associated with the establishment of these species after the first fire, or due to increased lateral growth associated with repeated top (apical) kill (Riba 1998).

Surprisingly, very few traits were strongly negatively associated with the SI burn (Table 2). Avoiders were the primary negative responders, but the community we studied only included four such species – the forbs and low shrubs *G. oblongifolia*, *C. menziesii*, *C. umbellata*, and *Pachystima myrcinites*. However, most species typically associated with late seral conditions (e.g. in the FEIS data base) were present with similar relative abundance/frequency in M/OG, LI burn, and SI burn stands. This response, coupled with the low number of species classified as avoiders, likely reflects a flora well-suited to the variable fire regime of the Klamath–Siskiyou region.

The functional trait patterns we quantified may provide insight into differing responses to recurrent fires among ecosystems. Regions in which negative overall responses have been reported (e.g. Kutiel 1997; Diaz-Delgado *et al.* 2002) may be drier and/or less productive than the Klamath–Siskiyou region, with greater proportional representation of sprouting woody species with slower maturation, and fewer low-stature herbaceous components (e.g. hemicryptophytes, therophytes), ruderal species, or species with invader/evader regenerative strategies. Also, interactions with recent management history are important (Paine *et al.* 1998) and

vary widely by region; our study areas were relatively uninfluenced by recent forest management activities such as timber harvest. Perhaps most importantly, the Silver-Biscuit SI fire occurred in a mixed-severity fire regime context, in which wide variations in fire interval and severity have likely occurred for millennia.

SI FIRE, SUCCESSION AND MIXED-SEVERITY FIRE REGIMES

Post-fire succession can be divided into two phases (Noble & Slatyer 1980): the first, immediately post-fire, when competition for resources is low and species abundance is driven primarily by regenerative processes (the focus of this study); and the second, after this initial pulse, when resource competition becomes progressively important. Variations in the first phase may strongly influence the second. The results of this study suggest that SI fires produce unique post-fire communities relative to a single LI fire, but the degree to which this affects long-term trajectories remains an interesting hypothesis to test. Moreover, it remains possible that elements of models 1 and 2 could manifest themselves as these stands develop. For example, the presence in the SI burn of regenerating conifers and hardwoods (the major structural species of these forest types) suggests that in the absence of continued stand-replacing fires, succession may converge with that following a LI fire, trending toward mature forest condition (i.e. elements of model 1). Alternatively, if, for example, soil chemistry is dramatically altered by two fires (beyond the scope of this study), tree growth and thus canopy development may eventually differ in the SI burn (i.e. model 2).

The abundance, character and landscape distribution of SI fires have likely varied widely over time. Important factors in this variability may include long-term climatic variability (Whitlock *et al.* 2003) as well as recent fire exclusion which may have influenced pre-fire vegetation conditions (Agee 1991; Taylor & Skinner 1998). Also, stand-scale variation in fire interval may be important since feedbacks between multiple fires may exhibit threshold behaviour, with increased probability of high-severity re-burning over short-time scales (Thompson *et al.* 2007), but decreased probability over longer time scales that allow for canopy closure and large stature trees (Odion *et al.* 2004). Where positive feedbacks exist, continual SI fires could lead to further shifts and altered successional trajectories. Lastly, differences in fire severity among short-interval events would likely produce very different outcomes to what we observed.

Post-fire management activities are often focused, in part, on reducing anticipated adverse effects of repeat high-severity fires (expectation of model 2; USDA 1988). For certain objectives, such as the rapid attainment of late-successional condition, recurrent stand-replacement fires are clearly counter-productive in the short term. However, these events may be consistent with objectives for maintaining characteristic disturbance processes and regional vascular plant diversity (see Landres *et al.* 1999). These results indicate that much of the native biota is resilient to 'extreme' events such as recurrent

severe fire. Given the Klamath–Siskiyou region's characteristic patterns of fire severity, productivity, and ignition source, there is good reason to believe that short-interval severe fires have historically been a component of the fire regime. These events contribute to the landscape heterogeneity inherent to mixed-severity fire regimes, in which variability in fire frequency, severity, and pattern can be more important than central tendencies (Agee 2005). Where consistent with land-use objectives, process-based disturbance management could include this variation, perpetuating a diversity of conditions across the landscape.

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