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Mixed-severity fire regimes: lessons and hypotheses from the Klamath-Siskiyou Ecoregion

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Abstract. Although mixed-severity fires are among the most widespread disturbances influencing western North American forests, they remain the least understood. A major question is the degree to which mixed-severity fire regimes are simply an ecological intermediate between low- and high-severity fire regimes, versus a unique disturbance regime with distinct properties. The Klamath-Siskiyou Mountains of southwestern Oregon and northwestern California provide an excellent laboratory for studies of mixed-severity fire effects, as structurally diverse vegetation types in the region foster, and partly arise from, fires of variable severity. In addition, many mixed-severity fires have occurred in the region in the last several decades, including the nationally significant 200,000-ha Biscuit Fire. Since 2002, we have engaged in studies of early ecosystem response to 15 of these fires, ranging from determinants of fire effects to responses of vegetation, wildlife, and biogeochemistry. We present here some of our important early findings regarding mixed-severity fire, thereby updating the state of the science on mixed-severity fire regimes and highlighting questions and hypotheses to be tested in future studies on mixed-severity fire regimes. Our studies in the Klamath-Siskiyou Ecoregion suggest that forests with mixed-severity fire regimes are characterized primarily by their intimately mixed patches of vegetation of varied age, resulting from complex variations in both fire frequency and severity and species responses to this variation. Based on our findings, we hypothesize that the proximity of living and dead forest after mixed-severity fire, and the close mingling of early- and late-seral communities, results in unique vegetation and wildlife responses compared to predominantly low- or high-severity fires. These factors also appear to contribute to high resilience of plant and wildlife species to mixed-severity fire in the Klamath-Siskiyou Ecoregion. More informed management of ecosystems with mixed-severity regimes requires understanding of their wide variability in space and time, and the particular ecological responses that this variability elicits.

Key words: Biscuit Fire; ecosystem response to fire; fire behavior; fire mosaic; fire regime; fire severity; Klamath-Siskiyou Ecoregion; post-fire ecology.

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Introduction

Fire regimes—the characteristic pattern and effects of wildland fire in a given area—are major drivers of the ecology of many vegetation types and are widely applied as a guiding framework for management of fire-prone ecosystems globally (Bond and van Wilgen 1996, Schoennagel et al. 2004, Noss et al. 2006). Fire regimes encompass several parameters, including fire frequency, seasonality, extent, and most often, severity. Typically defined as mortality of dominant vegetation (e.g., overstory trees), severity ranges from low, or non-lethal surface fires, to high, or stand-replacing crown fires (Agee 1993, Keeley 2009). To date, most information regarding forest fire regimes and their effects comes from the two ends of the severity spectrum, with much attention given to human-induced shifts from low- to high-severity fire regimes (e.g., Fulé et al. 2004, Graham et al. 2004). However, many forests experience mixed-severity fire regimes that differ from these extremes and instead are characterized by heterogeneous fire effects over a range of spatial and temporal scales.

Mixed-severity (M-S) fire regimes have been described for portions of several major forest types, including coastal Douglas-fir (*Pseudotsuga menziesii*) (Morrison and Swanson 1990), interior mixed-conifer (Arno et al. 2000, Fulé et al. 2003, Schoennagel et al. 2004, Hessburg et al. 2007), and ponderosa pine (*Pinus ponderosa*) (Shinneman and Baker 2003). M-S fire regimes are generally recognized as the most complex and least understood fire regimes in North America because of the varied importance of climate and fuels as drivers and the complex burn patterns that result (e.g., Schoennagel et al. 2004, Agee 2005, Lentile et al. 2005). Although M-S fires are defined as a combination of low- to high-severity fire effects within the perimeter of a single fire, their ecology may not be a simple intermediate between the two; rather, M-S fires and fire regimes (repeated M-S fires over time) are hypothesized to give rise to unique patch dynamics and ecosystem responses (see Agee 2005). M-S regimes are characterized by widely varying fire intervals and combinations of surface, torching, and crown fire behavior both within and between fires, resulting in intermixed patches of live and dead understory and overstory vegetation (Lentile et al. 2005). The concept of M-S fire is scale-dependent and is typically defined at meso-scales (e.g., forest stand or low-order watershed), because at the finest scales (e.g., individual tree), fire effects such as mortality are binary, while at a coarser scale (e.g., large or multiple watersheds), nearly all fires exhibit some degree of mixed fire effects (Turner and Romme 1994, Baker et al. 2007). To date, the causes and ecological consequences of variation in fire severity in M-S regimes remain inadequately explained.

The Klamath-Siskiyou Mountains of southwestern Oregon and northwestern California (Fig. 1) provide an excellent laboratory for studies of M-S fire effects. Fires in the area are variable in frequency and severity, both spatially and temporally (Agee 1993, Taylor and Skinner 1998). Situated at the convergence of major North American floristic zones (Whittaker 1960), the region is characterized by an exceptionally diverse flora, with strong components of broadleaf hardwood, coniferous, and herbaceous vegetation. Mosaics of these structurally diverse vegetation types foster and may, in part, arise from repeated exposure to variable fire frequency and severity (Agee 1991, 1993).

Over the last several decades, a number of M-S fires have occurred in the Klamath-Siskiyou region (Fig. 1), including the 200,000-hectare Biscuit Fire of 2002, the largest fire on record for the state of Oregon and one of the largest recorded forest fires in the United States. These fires present an opportunity to advance understanding of M-S fire regimes, similar to that provided by the 1988 Yellowstone Fires for high-severity fire regimes (Turner et al. 2003). Since 2002, we have engaged in studies of early ecosystem response to the fires, ranging from determinants of fire effects to responses of vegetation, wildlife, and biogeochemical dynamics. Here we synthesize results of our various studies, which focus on 15 fires that have occurred over the last twenty years in the Klamath-Siskiyou region. Our purpose is to highlight some important early discoveries from a model M-S fire region, and use these findings as a platform to develop hypotheses and research directions that may be explored in other systems influenced by M-S fires. In particular, we explore the ways in which M-S fire regimes may differ

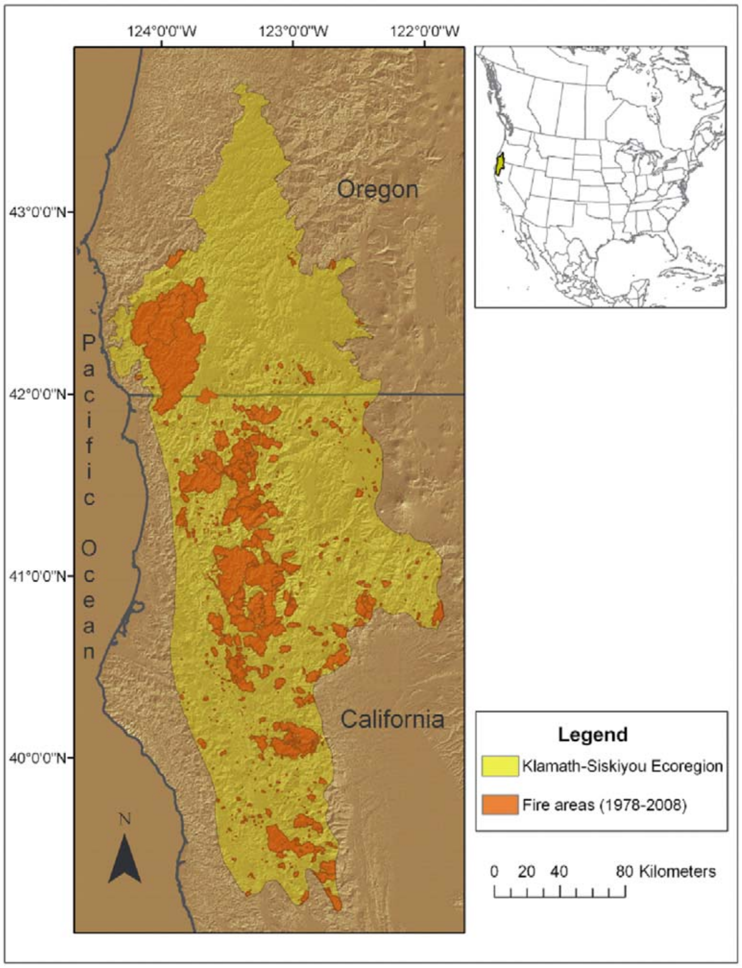

Fig. 1. Areas burned in the Klamath-Siskiyou Ecoregion of southwestern Oregon and northern California, 1978–2008. Fire regimes in the region are complex, variable in frequency, and generally of low- to mixed-severity. The region is characterized by an exceptionally diverse flora, which promote and likely arise from repeated exposure to variable fire frequency and severity.

from a simple intermediate between low- and high-severity regimes. Implications for management in M-S systems are discussed.

Patterns and Drivers of Severity in Mixed-Severity Fires

One of the major challenges to understanding M-S fire regimes is disentangling the various determinants of fire behavior and resulting mortality of dominant vegetation, or severity. Fire behavior and resulting severity is a product of interactions between weather, fuels, and topography (Agee 1993). Interactions between, and varying strength of, these three drivers of fire severity in the Klamath-Siskiyou region result in system behavior that is difficult to predict; M-S fires vary in spatial complexity of burn severity both within and among fires.

In predominantly high-severity fire regimes (stand-replacing), weather is generally attributed as the main driver of fire severity, with extreme weather events overriding the effects of fuel structure (Bessie and Johnson 1995, Turner et al. 2003, Schoennagel et al. 2004). In predominantly low-severity (surface fire) regimes, fine-scale fuel structure such as vertical and horizontal foliage continuity is a primary driver of fire effects

(Fulé et al. 2004, Graham et al. 2004). In contrast to these primarily weather-driven and fuel-driven fire regimes, the M-S regime is typified by relatively sensitive thresholds between fuel- and weather-driven fire behavior, even within a single fire.

The Biscuit Fire demonstrated the important role of these sensitive fuel-weather thresholds in M-S regimes. While fuel structure was an important driver over much of the burn area (see below), periods of strong, large-scale air flow at times overrode both fuels and locally generated wind in influencing fire severity (Thompson and Spies 2009). Biscuit Fire severity was highest and burn patches largest when prevailing winds were strong and out of the northeast. For the Klamath-Siskiyou region, the Biscuit Fire appears to have been unusually severe, as estimates of crown damage greatly exceed estimates from historical fires within the region (e.g., Weatherspoon and Skinner 1995, Odion et al. 2004, Alexander et al. 2006). The high severity of the Biscuit Fire was likely due in part to the dominance of weather as a driver; an earlier fire in the same area, the Silver Fire, burned under cooler conditions and resulted in generally lower fire severity (Thompson et al. 2007, Thompson and Spies 2010; Fig. 2). This importance of weather as a dominant driver of M-S fire is consistent with studies in other M-S fire regions (Bradstock et al. 2010; Schoennagel et al. in press).

In addition to weather influences, diversity of fuel (live and dead vegetation biomass) conditions in the Biscuit Fire area—itself dictated by sharp variation in climatic and edaphic conditions (Fig. 3; Whittaker 1960, Agee 1993)—also led to distinct patterns in burn severity. For example, high moisture conditions and associated vegetation/fuel conditions in riparian areas influenced fire behavior and effects; canopy and soil damage (but not tree mortality) were lower in riparian areas compared to uplands in the Biscuit Fire, particularly along larger streams (Halofsky and Hibbs 2008; T. Spies, *unpublished manuscript*). Evergreen hardwoods, an important structural and compositional component in forests in the region, experienced relatively high levels of burn damage in the subcanopies below conifers. However, there was no evidence that hardwood presence increased fire severity in

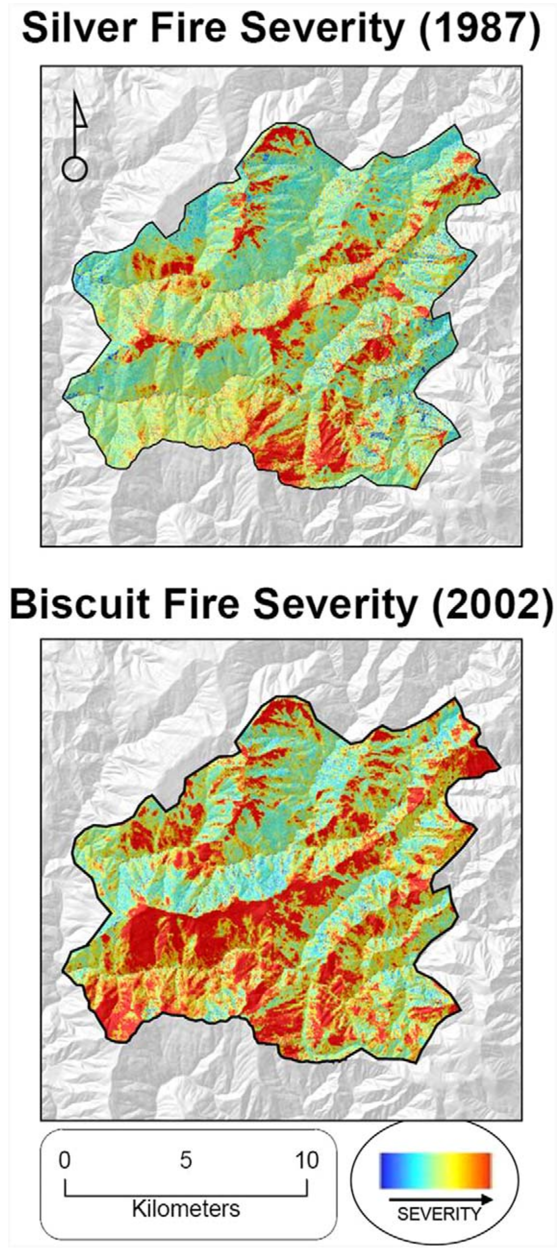

Fig. 2. Burn severity for the northern portion of the 1987 Silver Fire in southwestern Oregon, and burn severity for the same area in the 2002 Biscuit Fire. The burn patterns demonstrate the importance of both weather and vegetation (fuel) structure in driving fire effects. Both fires burned heterogeneously, leaving a mosaic of live and dead vegetation. Though the Biscuit Fire burned under more extreme weather conditions than the Silver Fire, resulting in more high severity area, fire severity in the Biscuit Fire was strongly influenced by that of the earlier Silver Fire after accounting for other biotic and abiotic factors.

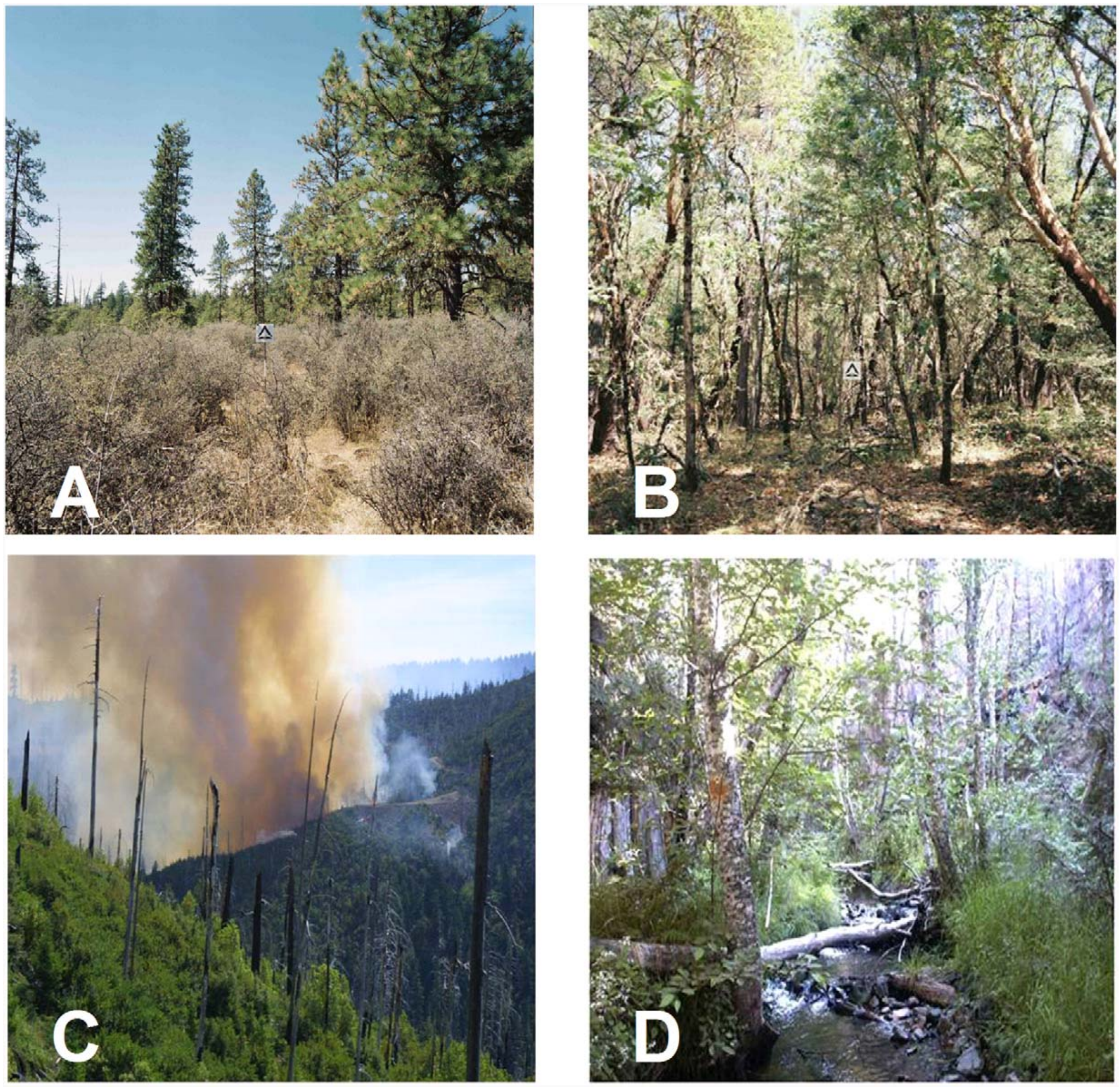

Fig. 3. Diversity of vegetation and fuel conditions in the Klamath-Siskiyou region that contributes to complex burn patterns, including (A) low productivity Jeffrey pine sites with open canopies and shrubby understories (relatively low canopy cover and high surface fuel loading); (B) productive mixed conifer forest with evergreen hardwood subcanopies (dense canopy cover and ladder fuels); (C) previously burned and managed forest with dense young conifers, standing snags, and high surface fuel loading; and (D) riparian areas dominated by deciduous hardwood species (generally high canopy cover, high surface and ladder fuel loading, and high fuel moisture). Photos 'A' and 'B' courtesy of the Digital Photo Series, Pacific Wildland Fire Sciences Laboratory, Fire and Environmental Research Applications Team, Seattle, WA; photo 'C' courtesy of T. Link.

overtopping conifers (Raymond and Peterson 2005, Thompson and Spies 2009). Somewhat surprisingly, low-productivity, sparsely treed sites on ultramafic soils experienced the highest rates of conifer crown damage (Thompson and Spies 2009). However, these sites were found to have high shrub cover, and there was a positive relationship between shrub cover and crown damage in the Biscuit Fire (Thompson and Spies 2009).

Few places within the Biscuit Fire perimeter were entirely unburned; 98% of the area was affected by surface fire (Campbell et al. 2007, Thompson and Spies 2009). Canopy mortality, on the other hand, was patchy and complex (Fig. 4). Patch sizes of overstory mortality exhibited a skewed distribution with many small patches created throughout the 4-month (July through October) burn period and fewer large patches created during a 9-day period of extreme weather. Across the entire fire, approximately half the conifer crowns remained intact, and there were few areas greater than several hectares that did not contain a mixture of both live and dead trees (Thompson and Spies 2009). This pattern was also found in other fires in the Klamath-Siskiyou region over the last 20 years (Shatford et al. 2007).

Topography in the Klamath-Siskiyou region generally results in drier and more flammable fuels on southwesterly aspects and in upper topographic positions, which generally leads to higher fire severity (Weatherspoon and Skinner 1995, Taylor and Skinner 1998, Alexander et al. 2006). Topography is also well documented to influence fire severity across several other fire-prone forest regions (e.g., Kushla and Ripple 1997, Oliveras et al. 2009, Bradstock et al. 2010). Surprisingly, however, severity patterns in the Biscuit Fire were not strongly associated with topography (slope, aspect, elevation), with weather and vegetation instead being the main drivers (Thompson and Spies 2009)—a finding similar to conclusions from the 1988 Yellowstone Fires. It is possible that dry winds out of the northeast and a maritime climate influence on west facing slopes confounded any positive relationship between southwest aspects and fire severity in the Biscuit Fire (Thompson and Spies 2009). Relationships between burn patterns and topography could thus vary by region and should be explored in future fires in the Klamath-Siskiyou and other regions with M-S fire regimes.

Biogeochemical Response to Mixed-Severity Fire

In general, the impacts of fire on biomass and geochemistry are expected to be proportional to fire severity and therefore should vary widely across M-S fires such as the Biscuit Fire. We found evidence both supporting and not supporting this expectation, depending on the ecosystem attribute considered. Supporting evidence included profound changes in soil properties in some stands subject to high-severity fire, where combustion temperatures over 660°C and convective erosion in the fire's plume apparently contributed to losses of about 2.5 cm of fine mineral soil and one-third of soil nitrogen (N) and half of soil carbon (C) (Bormann et al. 2008). Stands with partial or no fire mortality had lower C and N losses from mineral soil. The C and N losses were not significantly related to coarse woody fuel loads, but highly related (adj. $R^2 =$ 0.76–0.89) to consumption of fine (1–10 cm diameter) woody surface fuels (Homann et al., *unpublished manuscript*). In the only other forest wildfire study with pre- and post-fire soil sampling (Murphy et al. 2006, Johnson et al. 2007), carbon loss from O-horizon and wood in a moderate-severity fire compared well with the moderate-severity areas we studied in the Biscuit Fire, where few losses were observed from mineral soil.

The resulting contrast in soil productivity between low- and high-severity patches suggests the potential for long-term legacies of burn severity patterns. Such legacies of M-S fire could be one factor underlying the well-known variation in vegetation productivity, structure, and composition of the Klamath-Siskiyou region (e.g., conifer forest and broadleaf vegetation such as sclerophyllous shrubs). At our current state of knowledge, however, the long-term consequences of these soil changes remain unclear, and it is possible that N-fixing shrubs (e.g., *Ceanothus*)—which are often abundant in this region following severe fire (Shatford et al. 2007, Fontaine et al. 2009)—could help offset losses in some areas. Relationships between mixed-severity fire patterns, variation in soil properties (especially long-term legacy effects), and vegetation growth responses constitute an important direction for future research in M-S regimes.

Other geochemical dynamics varied surprisingly little across the mixed-severity mosaic of the Biscuit Fire, such as overall C emissions. Compared to the patchy nature of canopy combustion, the combustion of surface fuels

Fig. 4. Complex spatial patterns of the mixed-severity Biscuit Fire. Few places within the Biscuit Fire perimeter were entirely unburned. Canopy mortality, however, was patchy and complex across the Biscuit Fire. Across the entire fire, approximately half the conifer crowns remained intact, and there were few areas greater than several hectares that did not contain a mixture of both live and dead trees. This pattern was also found in other fires in the Klamath-Siskiyou region over the last 20 years. Photo: T.A. Spies.

(e.g., litter, duff, and fine woody debris) was relatively uniform and near complete across the entirety of the Biscuit (Campbell et al. 2007). This, combined with the fact that dead surface fuels have higher combustion efficiencies than do standing live components, meant that nearly 60% of the estimated 3.8 Tg C released to the atmosphere during the Biscuit arose from surface fuels (Campbell et al. 2007). This analysis of fuel consumption across a large M-S fire reveals that the majority of pyrogenic emissions are not strongly related to canopy mortality. As such, shifts in overall tree mortality, as perhaps affected by fuel structure or weather during the time of the fire, may strongly influence fire-wide crown mortality but have only a marginal influence on total pyrogenic emissions. How this trend may vary across other M-S regime forest types is largely unknown; this is an important knowledge gap in light of efforts to reduce wildfire C emissions by managing forest fuels (e.g., Hurteau et al. 2008, Mitchell et al. 2009).

Vegetation Response to Mixed-Severity Fire

Short-term (<5 yr) vegetation response to fire

Vegetation responses to M-S fire regimes are as complex as the burn patterns themselves. Spatial variation in fire severity has a vegetation legacy effect and perhaps a soil fertility effect. These fire effects coupled with variation in regeneration strategies by different plant groups—conifers by seed dispersal, broad-leaved trees primarily by sprouting, shrubs by both sprouting and seed banking—results in a diverse post-fire vegetation mosaic. For example, sprouting broadleaf vegetation cover four years after the Biscuit Fire ranged from 4–63%, depending on fire severity and elevation (Donato et al. 2009*a*). For conifers, the Biscuit Fire's M-S pattern resulted in generally well-distributed live seed sources, as ~81% of high-severity burn area was ≤400 m from live-tree edge (Fig. 5; Donato et al. 2009*a*). Within two years after fire, conifer regeneration was generally abundant (mean density >1000/ha) up to 400 m from live-tree edges but rapidly tapered with further distance. (In situ canopy seed banks such as serotinous cones are less important in this region than in many high-severity fire regimes such as Greater Yellowstone and the boreal zone; the main exception being knobcone pine (*Pinus attenuata*), which, although a minor forest component just prior to the Biscuit Fire, has now substantially increased in abundance [Donato et al. 2009*a*].)

As a result of these edge effects, small-to-medium burn patches and edges of large patches contained conifer seedlings and sprouting hardwoods, while interiors of large patches (>400 m from edge) were characterized by hardwood regeneration with delayed or no conifer establishment four years post-fire (Donato et al. 2009*a*). Burn patch size thus had a threshold effect on regeneration composition, resulting in potentially different successional pathways in the interior versus perimeter of larger patches.

Both conifer and hardwood regeneration were also abundant in riparian areas four years after the Biscuit Fire; mean tree seedling density was >1600/ha and mean sprout density was >8200/ha (Halofsky and Hibbs 2009). Conifer- and hardwood-dominated riparian plant communities, each found in specific topographic settings, were self-replacing. In both riparian and upland sites, abundant regeneration and the self-replacement of pre-fire vegetation communities after the Biscuit Fire suggest high species and community resilience after M-S fire.

Long-term (>5 yr) vegetation response to fire

Vegetation establishes quickly after fire, but forest recovery extends over several decades. Working in several post-fire landscapes (n = 11 fires) throughout the Klamath-Siskiyou region, Shatford et al. (2007) found that conifer regeneration continued over a two-decade period across highly variable ecological settings. Shrub and sprouting hardwood communities were also abundant and diverse, forming a dominant to co-dominant canopy with conifers during early successional stages across a range of sites. Aspect, precipitation and elevation were found to be important predictors of all vegetation recovery processes (Lopez Ortiz 2007, Shatford et al. 2007). Only on very dry sites was conifer regeneration scarce or lacking, suggesting that early-colonizing shrubs and hardwoods are more likely to maintain long-term dominance in these locations. Interestingly, shrub cover and conifer growth were positively associated at low levels of moisture availability and negatively associated at high levels (Irvine et al. 2009, Shatford et al. 2007).

The interaction between patch-size and seed source dynamics was remarkably similar between small M-S fires and the exceptionally large Biscuit Fire; most high-severity burn area was <400 m from edge, and conifer regeneration was generally abundant within this distance (Shatford et al. 2007, Donato et al. 2009*a*). Coupled with early observations in both upland and riparian sites of the Biscuit Fire, these longer-term patterns indicate generally robust vegetation responses to M-S fire, as well as complex post-fire successional pathways that vary with both patchy fire effects and highly variable microsites.

M-S fire regimes appear to play a role in maintaining a significant hardwood presence in the Klamath-Siskiyou region. All of the hardwoods basal-sprout vigorously after fire; all except tanoak (*Lithocarpus densiflorus*) are at least moderately shade intolerant; and all have a mature height much shorter than the associated conifers. In coniferous forest, hardwoods form a shrub and mid-layer canopy (Franklin and Dyrness 1973, Agee 1993) that provides structural diversity and habitat for a large suite of wildlife species (Hagar 2007). Short intervals (less than 30 years) between fires maintain an open canopy in

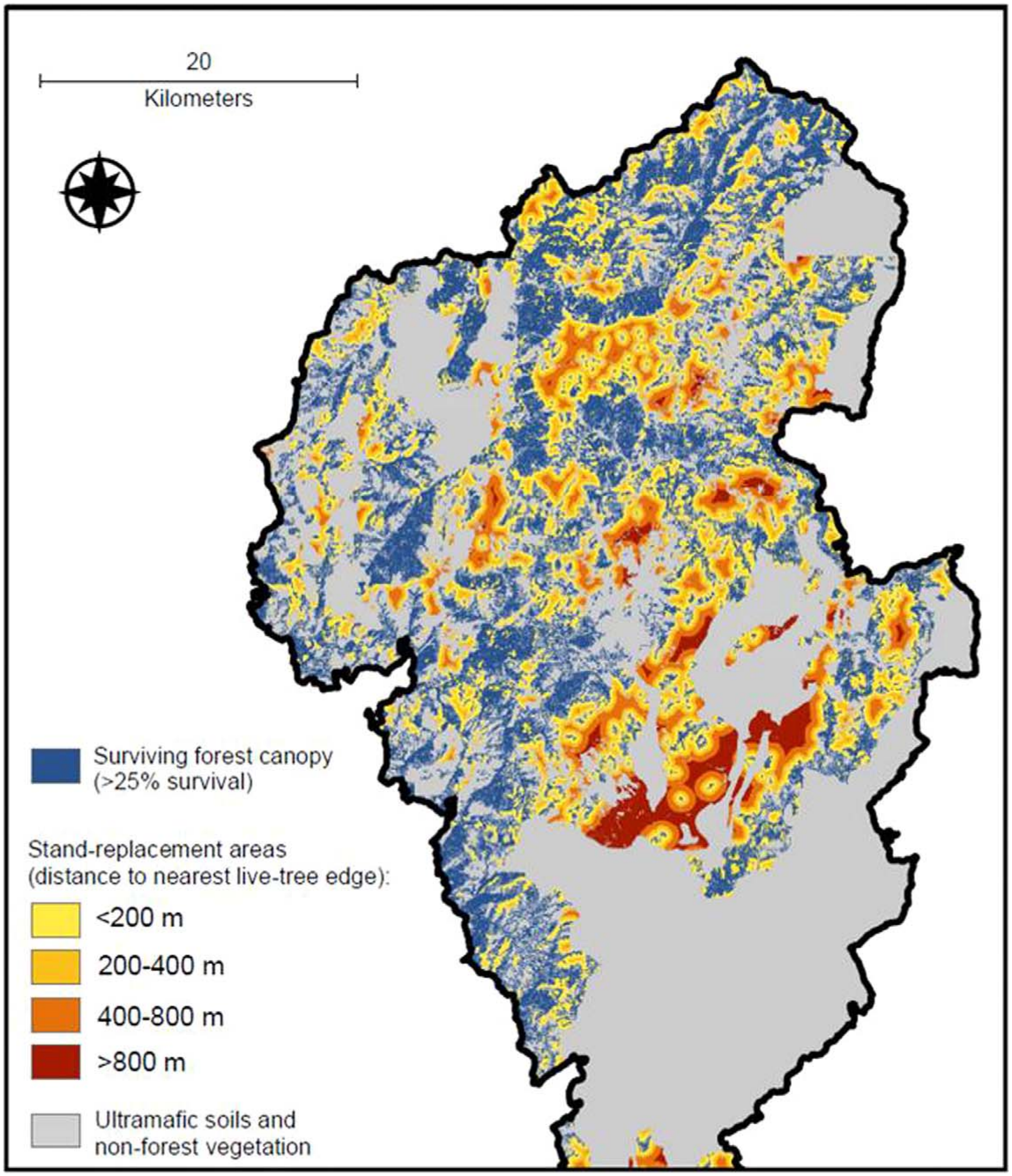

Fig. 5. Map of distance between stand-replacement areas of the Biscuit Fire and adjacent patches of surviving trees. Edge-to-interior ratios are often very large in mixed-severity fires. In the Biscuit Fire, ~58% of stand-replacement area was within 200 m of a live-tree edge, and ~81% was within 400 m. Assessment extensively ground-truthed to >90% accuracy via field reconnaissance and high-resolution aerial photo analysis (see Donato et al. 2009*a*). Perimeter is truncated at Oregon-California border due to insufficient or inconsistent spatial data to the south (<5% of burn area). Figure from Donato et al. (2009*a*). Copyright 2008 NRC Canada or its licensors. Reproduced with permission.

places, providing the ecological space for these species to persist (Agee 1993, Odion et al. 2010). We found that early post-fire hardwood cover is moderate to high (Shatford et al. 2007, Donato et al. 2009*a*, Fontaine et al. 2009), providing important habitat for open-cup nesting birds (Betts et al. 2010; M. Donaghy Cannon, *unpublished manuscript*) and contributing to soil function and mycorrhizal networks (Borchers and Perry 1990). By 20 years after fire, hardwood stem density can range up to 2000 ha^{-1}, with areal cover of 30% on north aspects and 13.5% on south aspects (Lopez Ortiz 2007).

M-S fire appears to maintain significant broadleaf presence in other regions as well. In western Montana forests, Fischer and Bradley (1987) found that occasional short fire return intervals allowed the sustained abundance of seral shrub and hardwood species, including aspen (*Populus tremuloides*), Scouler willow (*Salix scouleriana*), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), and redstem and evergreen ceanothus (*Ceanothus sanguineus* and *C. velutinus*) (Arno et al. 1985). Thus, variable fire return intervals in M-S regimes appear to promote species and structural diversity in vegetation communities, a hypothesis in need of broader and more mechanistic testing.

Other studies have also reported abundant conifer regeneration after M-S fires, with the mechanism and spatial pattern varying by region, forest type, and regeneration characteristics of dominant tree species (Chappell and Agee 1996, Greene and Johnson 1999, 2000, Bonnet et al. 2005, Larson and Franklin 2005, Lentile et al. 2005, Jayen et al. 2006). In mesic forest types such as the Klamath-Siskiyou and western Cascade Mountains, regeneration densities are often high in areas burned with low- to moderate severity and several hundred meters into high-severity patches (Shatford et al. 2007, Chappell and Agee 1996, Donato et al. 2009*a*), while in drier forest types such as ponderosa pine, regeneration can be mostly absent from high-severity patches except near edges (Bonnet et al. 2005, Lentile et al. 2005, but see Haire and McGarigal 2010). Mixed-severity regimes occur over a range of climatic regimes, from fairly dry to fairly moist, and regeneration abundance varies widely but somewhat predictably (positively) over this range of moisture availability. Thus, the long-term importance of burn patch structure may vary along a spectrum of forest types, from dry interior pine forests in which burn mosaics may persist strongly (with purported state changes in patch interiors), to moist forest types in which burn mosaics may have an important but more ephemeral effect on gross vegetation composition. (Note that forests with canopy seed banks such as serotinous cones often exhibit abundant regeneration across very large high-severity burn areas due to the presence of in situ seed sources [Greene and Johnson 1999, Pausas et al. 2003, Larson and Franklin 2005]; in these regions burn patch structure likely has little effect on gross ecosystem composition over time.) The Klamath-Siskiyou region would appear to lie near the middle of the moisture-regeneration continuum among forests affected by M-S fire. Long-term spatial tracking of forest regeneration dynamics in M-S fires across multiple forest types is needed to fully assess this hypothesis.

Wildlife Response to Mixed-Severity Fire

Research on wildlife response to fire has been predominantly focused at the stand-scale on low- or high-severity disturbance, with limited explicit focus on complex patterns of burn severity in M-S disturbances (see review by Kennedy and Fontaine 2009). A handful of studies have begun to show how different levels of burn severity influence habitat suitability for birds (e.g., Smucker et al. 2005, Kotliar et al. 2007). However, the importance of juxtaposition of patches of differing severity (and thus successional stage) is not well understood, and may have especially important consequences for wildlife given the capacity of many species to utilize a range of conditions simultaneously (e.g., the threatened Northern spotted owl, *Strix occidentalis* caurina, Franklin et al. 2000).

Data from the Klamath-Siskiyou region suggest that the vegetation mosaic and broadleaf abundance associated with the M-S regime are important drivers of wildlife response to fire (Fontaine et al. 2009, Meehan and George 2003, Betts et al. 2010; Clark et al. in press). Avian community composition and abundance within high-severity portions of the Biscuit Fire were remarkably resilient relative to unburned, late-successional reference forests outside the fire (Fontaine et al. 2009). While avian communities in unburned and burned patches were distinct in composition, species richness was not reduced by high-severity fire and density was reduced by

~50%, likely a consequence of the fine-grained burn mosaic and regenerating broad-leaved vegetation (Betts et al. 2010, Fontaine et al. 2009). Following disturbance, many broad-leaved species resprout and may rapidly grow (>2 m in height 4 yrs post-fire, J. Fontaine, *unpublished data*), providing foraging and nesting substrates for a range of species. This effect may persist for two decades or longer following fire (Fontaine et al. 2009). Species such as lazuli bunting (*Passerina amoena*), Nashville warbler (*Vermivora ruficapilla*), and black-headed grosbeak (*Pheucticus melanocephalus*) heavily utilize this regenerating vegetation (Betts et al. 2010, Fontaine et al. 2009).

Certain species thought of as late-successional forest specialists may also use recently burned areas, a response likely associated with the presence of a complex burn mosaic. For example, interspersion of low- and high-severity patches allowed for the persistence of birds that nest and forage in canopy foliage (e.g., hermit warbler (*Dendroica occidentalis*) M. Donaghy Cannon, *unpublished data*). Amount of edge habitat was positively associated with olive-sided flycatcher (*Contopus cooperi*) prevalence post-fire (Meehan and George 2003). Of high management relevance, northern spotted owls and California spotted owls (*S. o. occidentalis*) may also utilize the M-S mosaic. In the Klamath-Siskiyou region, Northern Spotted Owl fitness is higher in landscapes containing a mixture of old forest and younger brushy vegetation (Franklin et al. 2000), suggesting that in this part of its range, the spotted owl is well suited to a M-S fire regime. However, in the short term, a large extent of high-severity fire within owl territories may provoke negative short-term responses (e.g., displacement, lower survival). While partially confounded by salvage logging, Clark et al. (in press) found that survival of northern spotted owls within fires was lower than in adjacent unburned habitat in the initial years (1–4 yrs post-fire) following high-severity fire. However, in the Sierra Nevada mountains of central California, the probability of territory occupancy by California spotted owls was unaffected by recent fire events (3–16 yrs post-fire across a range of severities and extents; Roberts et al. 2010) suggesting that this southern sub-species also is adapted to fire disturbances within a M-S fire regime.

Many important questions remain in the context of wildlife and mixed-severity fire regimes, not the least of which is expanding the taxonomic breadth of the literature beyond birds and small mammals (Kennedy and Fontaine 2009). Over long time scales it is evident that fire maintains the broad-leaved vegetation and landscape heterogeneity on which many bird species depend (Betts et al. 2010, Franklin et al. 2000, Schlossberg and King 2008). However, in the short-term further research is required to test questions addressing the relative importance of the post-fire mosaic (coarse-scale) and vegetation regeneration patterns (fine-scale) for determining post-fire wildlife abundance across a range of fire severities (see Kotliar et al. 2007, 2008). For example, one of the best studies on the topic (Smucker et al. 2005) classified 'moderate' severity as 20–80% tree mortality using a 30-m radius plot and excluded unburned islands within fires (also an important area of future research), analyzing stand-scale patterns with no landscape component to their analysis. Despite such limitations, Smucker et al. (2005) and Kotliar et al. (2007) both found intriguing wildlife dynamics such as hump-shaped patterns of response to varying fire severity following M-S fires in forests of western Montana and New Mexico, respectively. This higher abundance in moderate/mixed severity conditions suggests a suite of species responds most positively to increased edge and heterogeneity in fire effects. Examples reported such as dark-eyed junco (*Junco hyemalis*) and western tanager (*Piranga rubra*) also showed high abundances in the Biscuit Fire (Fontaine et al. 2009). Similarity in species responses to fire across regions, some of which have very different vegetation composition and understory structure (Kennedy and Fontaine 2009), further suggests that burn mosaic structure may be a dominant driver of wildlife response across M-S fire regions.

Disturbance Interactions (Reburn)

In contrast to low-severity fire regimes where repeated fire is known to maintain biodiversity and ecosystem function (van Lear et al. 2005), the role of recurrent, mixed- to high-severity fires is not well understood (Agee 1993, Gray and

Franklin 1997, Johnstone 2006, Collins et al. 2009). These short-interval (<30 year) events ("reburns") are likely the norm in fire-prone forests with high productivity, such as those in the Klamath-Siskiyou region. A great deal of management effort on publicly-owned lands has been devoted to minimizing the occurrence or effects of these reburn events, as they are generally assumed to be ecologically deleterious (e.g., USDA 1988).

Recent evidence from the Klamath-Siskiyou region suggests that the interval between fires, and thus successional stage when burned, is a key determinant of how strongly sequential fires interact. Where the Biscuit Fire burned over the 15-year-old M-S Silver Fire, fire severity was strongly influenced by the severity mosaic of the earlier fire, after accounting for other biotic and abiotic factors. Low-severity patches were more likely to reburn with low severity, and high-severity patches reburned with high severity (Thompson et al. 2007, Thompson and Spies 2010; Fig. 2). Thus, sequential disturbances separated by 15 years exhibited a positive feedback, reinforcing the spatial pattern on the landscape. This pattern may or may not occur after other reburns in this and other regions characterized by M-S fire regimes, but was also observed in the Gila National Forest of New Mexico (Holden et al. 2010). Shorter intervals (<9 years) between fires were negatively associated with fire severity in the low-severity (and fuel-limited) fire regime of the south-central Sierra Nevada (Collins et al. 2009). However, the relatively high productivity and post-fire abundance of sprouting evergreen hardwoods in the Klamath-Siskiyou region may allow repeated high-severity fires even with relatively short fire return intervals. The shrub and hardwood dominated vegetation that establishes after fire in this region is highly combustible and can maintain dominance for up to approximately 30 years without fire (Odion et al. 2010).

Examining the effects of longer fire intervals, Odion et al. (2004) concluded that severity of the 1987 fires in the Klamath-Siskiyou region was lower in closed forests where fire had been absent since 1920 compared to areas burned more recently. Odion et al. (2004) suggest that as combustible understory fuels (i.e., shrubs and evergreen hardwoods) decrease with succession due to shading and as height to live crown increases in the absence of fire in this region, the likelihood of a fire transitioning to the canopy decreases. Thus, following a stand-replacing fire, there may be a temporal threshold in the likelihood of additional stand-replacing fires, with positive feedbacks (i.e., high-severity fire followed by high-severity fire) over short time-scales (<30 years) owing to the rapid growth and dominance of evergreen hardwoods and shrubs, and negative feedbacks (i.e., high-severity fire followed by low-severity fire) over longer time-scales (>75 years) owing to the development of higher crown base heights and less continuous understory fuels. The nature and timing of such a threshold would have important implications for long-term landscape structure (see Odion et al. 2010) and is an important direction for further research on M-S regimes.

Regeneration patterns after two sequential fires in the Klamath-Siskiyou region also highlighted the importance of the severity mosaic in influencing vegetation composition and structure. Because the mosaic pattern was largely reinforced through the Silver-Biscuit sequence, most live-tree seed sources were retained, apparently facilitating reseeding of conifers even in this twice-burned area (Donato et al. 2009*b*). Hardwoods and shrubs also regenerated after two fires, with a similar proportion of individuals sprouting as after a single fire (Donato et al. 2009*b*). Surprisingly, two sequential fires led not to a depleted forest community, but rather to an increase in plant species richness, with little evidence of species extirpation (Donato et al. 2009*b*). Increases in species richness were largely due to increases in fire-ephemeral species (e.g., *Epilobium* spp.). This observation differs from observations of declining vegetation cover, productivity, and/or diversity in other Mediterranean ecosystems subject to recurrent wildfires, which may have been uncharacteristic disturbance behavior in those systems (Zedler et al. 1983, Diaz-Delgado et al. 2002, Eugenio et al. 2006). In our study area, we hypothesize that species composition of twice-burned plant communities may eventually converge with that of once-burned communities. Testing of this hypothesis, along with examination of post-fire vegetation patterns after reburn in this and other regions, is needed to further characterize the effects of recurrent M-S fires.

Wildlife showed similar responses to recurrent M-S fires. Compared to once-burned areas, bird species richness and density in twice-burned areas were higher and dominated by shrub- and hardwood-nesting species (Fontaine et al. 2009). Shrub- and hardwood-nesting and disturbance-adapted bird species (e.g., lazuli bunting (*Passerina amoena*)) were strong indicators of twice-burned habitats. Small mammal species richness and community structure in twice-burned areas were similar to once-burned areas but with significantly higher densities (Fontaine 2007). Again, further examination of these patterns after reburn in other regions would help to determine whether these patterns are typical for all M-S fire regimes.

Conclusions

Observed ecological patterns in mixed-severity fires

Characterizing 'typical' dynamics of M-S fires has been difficult because they are highly variable in both space and time (Agee 2005). For example, mean fire return intervals may have much less importance than the range of fire intervals in a given area. Observations in the Klamath-Siskiyou region suggest that variation in dominant drivers of fire behavior (fuels, topography, and weather) leads to varied burn patterns both within and among M-S fires. The range in fire effects—fire severity, patch size, and legacy generation—appears to be a major driver of ecosystem dynamics in these systems, as we have described here. Our observations support the idea that wide variation in fire return interval, dominant drivers of fire behavior, and fire effects is one of the defining characteristics of the M-S fire regime.

Are M-S fires simply intermediate between low- and high-severity regimes, or are they unique? Low-severity fire regimes are typically described as "stand-maintaining" because they are dominated by fine-scale mortality that results in uneven-aged stands (Agee 1993). In contrast, high-severity regimes are described as "stand-replacing" because they are dominated by large mortality patches that result in even-aged stands (Agee 1993). Fundamentally, M-S regimes are characterized by a combination of these effects, but what may distinguish them and give rise to unique properties (Table 1) are: (1) the degree and scale of inter-mixing of diverse patch ages and structures; and (2) particularly high variability in fire parameters (e.g., return interval, dominant drivers, fire effects) relative to central tendencies. The edge-to-interior ratio of burn patches is typically much higher in M-S fires than in low- and high-severity fires (Agee 2005); i.e., edge abundance is non-linearly related to severity regime. The M-S fire is therefore characterized by the mixing at relatively fine scales (tens to a few hundreds of meters) of patches of vegetation burned to varied levels of severity. Similarly, the irregularity of the fire return interval leads to highly variable patch age.

The intimate mixing of fire effects and patch age (and related structure and species composition) in M-S fires drives most of the ecological processes and properties we have described and suggests that forest systems with M-S fire regimes may be distinct from those developed under low- or high-severity regimes (Table 1). This is not to say that M-S forests do not share characteristics with forests under other regimes. Because both low- and mixed-severity regimes experience relatively frequent fire, both forest systems contain many plant and animal species with adaptations suited to frequent post-fire regeneration. In addition, in high-severity regimes, very large wildfires can exhibit qualitatively similar patch/edge effects to what we describe here for M-S fires (Turner et al. 1994, 2003, Schoennagel et al. 2008). Nonetheless, our studies in the Klamath-Siskiyou region suggest that, taken together, the suite of M-S fire characteristics may give rise to unique ecological dynamics in M-S regimes (Table 1). We observed that varied fire effects result in (and result from) fine-scale variation in patch age and composition, which provides habitat for a variety of species in relatively close proximity.

Many factors appear to have a role in fostering the patchy nature of fire behavior and post-fire vegetation in the Klamath-Siskiyou region, and many of these factors interact. First, the patchy nature of fire severity can be affected by the spatial and temporal patterns in weather, topography, and fuels—the latter affected by local severity of the last fire, variation in fertility, time since the last fire (vegetation development stage), and shrub cover. Second, the spatial variability of

Table 1. Observed characteristics in, and vegetation response to, mixed-severity fires in the Klamath-Siskiyou and other regions, as compared to observations from low- and high-severity fires.

	Mixed-Severity Fires	Low-Severity Fires
Fire Characteristics	Relatively sensitive thresholds between influence of weather and fuels as dominant drivers of fire behavior and effects—fuel structure plays an important role in patch-scale effects, but periods of extreme weather can override other factors	Dominant influence of fuels as a driver of fire behavior and effects
	A tendency toward scale-independence, with generally similar burn patch sizes within both small and large fire perimeters	Scale-dependence, with larger surface-burn patch sizes in larger fires
	Occurrence of high-severity fire even with a relatively short fire return interval	Short intervals between fires are primarily associated with low-severity surface fires
	Reported positive fire-vegetation feedbacks in which the spatial mosaic of a fire tends to be reinforced through subsequent fires over the short term (<30 years), with implications for long-term landscape forest structure	Negative fire-vegetation feedbacks in these fuel-driven regimes; fires consume surface fuels and make additional fires less likely for a period
	High amount of edge between seral stages due to repeated and spatially heterogeneous burns	Low amount of edge between seral stages due to more homogeneous burns
System response	Generally abundant post-fire conifer regeneration (by virtue of seed source proximity) in all but the largest high-severity patches and on the driest sites	Moderate to high conifer regeneration under intact canopies after surface fires and in small fire-created openings, relatively little regeneration in occasional larger openings
	Juxtaposition of early and later seral vegetation, which provides habitat for a range of wildlife species in relatively close proximity	Limited intermixing of seral stages; early seral patches typically confined to small areas within mature forest cover
	Extensive vegetation regeneration even after repeated high-severity fires	Reported delays in regeneration after repeated high-severity fires
	High community resilience owing to the presence of species adapted to regenerate after disturbance, spatial intermixing of seral stages, and close proximity of seed sources	Reported state changes after uncharacteristically severe fire in ponderosa pine

many factors affects vegetation development. Fertility may vary because of inherent site characteristics, because of past fire severity, and because of the heterogeneity of *Ceanothus* species cover. Disturbance and management history and site characteristics can affect the abundance of *Ceanothus* species in the seed bank and the abundance of sprouting hardwoods (Lopez Ortiz 2007). Finally, patch size created by fire affects species composition through seed dispersal limitations. From one fire to the next, these factors may reinforce the spatial pattern of fire and vegetation, although this may depend on time between fires. The relative importance of these and other factors in regulating the patchy nature of fire behavior and vegetation characteristics varies across the Klamath-Siskiyou landscape.

A consistent finding among the diverse ecosystem responses summarized here is the high resilience of plant and wildlife species composition in Klamath-Siskiyou forests to M-S fire. Although the 2002 Biscuit Fire made national headlines and was considered to be outside characteristic ranges in terms of size and severity, several studies of this and nearby fires showed rapid and sustained response of both flora and fauna, even in areas that had burned twice with high-severity within a 15-year period. These responses were closely tied to the fine-scale juxtaposition of seral stages, vegetation structure, and live and dead legacies associated with the M-S burn mosaic.

Management implications

Because M-S regimes give rise to unique ecosystem properties, different approaches may be required to sustain the unique ecological characteristics in forests with M-S regimes. Based on the observations presented here, M-S fires

Table 1. Extended.

High-Severity Fires	References
Dominant influence of weather as a driver of fire behavior and effects	Bessie and Johnson (1995), Turner et al. (2003), Fulé et al. (2004), Graham et al. (2004), Schoennagel et al. (2004), Thompson and Spies (2009)
Scale-dependence, with larger burn patch sizes in larger high-severity fires	Agee (2005), Lentile et al. (2005), Shatford et al. (2007), Donato et al. (2009a)
When short-interval fires occur, they tend to be small and of low severity; however this dynamic is not well quantified across regions and likely varies with system productivity	Romme (1982), Agee (1993) and references therein, Hessburg et al. (2007), Thompson et al. (2007)
Lack of distinct fire-vegetation feedbacks due to dominance of weather as a driver	Agee (1993) and references therein, Bessie and Johnson (1995), Turner et al. (2003), Hessburg et al. (2007), Thompson et al. (2007), Odion et al. (2010),
Low amount of edge between seral stages due to more homogeneous burns	Morrison and Swanson (1990), Agee (2005)
Limited conifer regeneration in large stand-replacing fires if live-tree seed sources are eliminated over broad areas (except in forest types with canopy seed banks, which can support successful regeneration across large burn areas)	Chappell and Agee (1996), Turner et al. (1997, 1999), Greene and Johnson (1999, 2000), Larson and Franklin (2005), Lentile et al. (2005), Shatford et al. (2007), Donato et al. (2009a)
Limited intermixing of seral stages; early seral patches may cover large areas after fire	Agee (1993), Franklin et al. (2000), Meehan and George (2003), Schlossburg and King (2008), Fontaine et al. (2009), Clark et al. (in press), Donaghy-Cannon (*unpublished data*)
Reported delays in, or altered, regeneration after repeated high-severity fires	Gray and Franklin (1997), Eugenio et al. (2006), Johnstone (2006), Donato et al. (2009b)
High species and community resilience after high-severity fire	Turner et al. (2003), Lentile et al. (2005), Lopez Ortiz (2007), Shatford et al. (2007), Donato et al. (2009a,b), Fontaine et al. (2009), Halofsky et al. (2009), Irvine et al. (2009) Haire and McGarigal (2010)

lead to dynamic ecosystem responses (sometimes referred to as "recovery" depending on objectives or values in question), such as regeneration of forest vegetation, creation of wildlife habitat, and maintenance of biodiversity (Noss et al. 2006). These responses may sometimes render certain management activities redundant with natural responses. For example, studies in the Klamath-Siskiyou region suggest that some common post-fire management actions—such as tree planting, snag removal, and vegetation control—may not always be needed to meet the management objectives of providing wildlife habitat, promoting forest regeneration, and reducing fire hazard (Donato et al. 2006, Lopez Ortiz 2007, Shatford et al. 2007, Thompson et al. 2007, Kayes 2008). Conversely, situations may arise where the recovery rate or pathway exhibited by a particular site is inconsistent with a desired outcome (e.g., delayed conifer regeneration or slow initial growth caused by climatic variability, dry site conditions, seed year variability, intense broadleaf competition, or low seed dispersal to the centers of large high-severity patches; Hobbs et al. 1992, Shatford et al. 2007, Donato et al. 2009*a*). In such situations, targeted silvicultural intervention may be effective at redirecting or expediting a particular outcome. These relationships illustrate the importance of clarity in objectives and consideration of site-specific context when designing and implementing post-fire management.

Future research directions

Numerous important questions remain regarding the processes and interactions that regulate post-fire recovery and the ecological functioning of landscapes structured by M-S regimes. A basic issue still being explored is the extent of M-S fire regimes in North America and other temperate zones. Evidence of M-S fire dynamics continues to emerge in a wide range of forest types (e.g., Schoennagel et al. in press), with significant implications for our understanding and management of these systems. Uncertainties also exist regarding the influence of anthropogenic factors on M-S regimes in the Klamath-Siskiyou and other regions, especially the role of 20th-century fire exclusion on current fuel loads, landscape patch dynamics and ecosystem responses. For example, it is difficult to assess whether conditions have significantly diverged from historic conditions when the inherent range in system behavior was likely very wide (Schoennagel et al. 2004). The role of climate change and its effects on fire behavior are also poorly understood within the context of the variable M-S fire regime. As wildfire activity will likely increase in North America in the coming decades (McKenzie et al. 2004), an important challenge is developing management strategies that are suited to the complexities of the M-S fire regime. Increasing understanding of M-S fire regimes through further research and testing of hypotheses described here will aid the development of effective management strategies for these complex systems.

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Literature Cited

Agee, J. K. 1991. Fire history along an elevational gradient in the Siskiyou Mountains, Oregon. Northwest Science 65:188–199.

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Agee, J. K. 2005. The complex nature of mixed severity fire regimes. Pages 1–10 *in* L. Lagene, J. Zelnik, S. Cadwallader, and B. Hughes, editors. Mixed Severity Fire Regimes: Ecology and Management. Volume AFE MISC03. Washington State University Cooperative Extension Service/The Association for Fire Ecology, Spokane, Washington, USA.

Alexander, J. D., N. E. Seavy, J. C. Ralph, and B. Hogoboom. 2006. Vegetation and topographical correlates of fire severity from two fires in the Klamath-Siskiyou region of Oregon and California. International Journal of Wildland Fire 15:237–245.

Arno, S. F., D. J. Parsons, and R. E. Keane. 2000. Mixed-severity fire regimes in the northern Rocky Mountains: Consequences of fire exclusion and options for the future. RMRS-P-15-VOL-5. USDA Forest Service, Ogden, Utah, USA.

Arno, S. F., D. G. Simmerman, and R. E. Keane. 1985. Forest succession on four habitat types in western Montana. USDA Forest Service GTR-INT-177. USDA Forest Service, Ogden, Utah, USA.

Baker, W. L., T. T. Veblen, and R. L. Sherriff. 2007. Fire, fuels and restoration of ponderosa pine–Douglas fir forests in the Rocky Mountains, USA. Journal of Biogeography 34:251–269.

Bessie, W. C., and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology 76:747–762.

Betts, M. G., J. C. Hagar, J. W. Rivers, J. D. Alexander, K. McGarigal, and B. C. McComb. 2010. Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. Ecological Applications 20:2116–2130.

Bond, W. J., and B. W. van Wilgen. 1996. Fire and plants. Chapman and Hall, London, UK.

Bonnet, V. H., A. W. Schoettle, and W. D. Shepperd. 2005. Post-fire environmental conditions influence the spatial pattern of regeneration for *Pinus ponderosa*. Canadian Journal of Forest Research 35:37–47.

Borchers, S. L. and D. A. Perry. 1990. Growth and ectomycorrhiza formation of Douglas-fir seedlings grown in soils collected at different distances from pioneering hardwoods in southwest Oregon clear-cuts. Canadian Journal of Forest Research 20:712–721.

Bormann, B. T., P. S. Homann, R. L. Darbyshire, and B. A. Morrissette. 2008. Intense forest wildfire sharply reduces mineral soil C and N: the first direct evidence. Canadian Journal of Forest Research 38:2771–2783.

Bradstock, R. A., K. A. Hammill, L. Collins, and O. Price. 2010. Effects of weather, fuel and terrain on fire severity in topographically diverse landscapes of south-eastern Australia. Landscape Ecology 25:607–619.

Campbell, J. L., D. C. Donato, D. Azuma, and B. E. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research 112:G04014.

Chappell, C. B., and J. K. Agee. 1996. Fire severity and tree seedling establishment in *Abies magnifica* forests, southern Cascades, Oregon. Ecological Applications 6:628–640.

Clark, D. A., R. G. Anthony, and L. S. Andrews. in press. Survival rates of northern spotted owls in post-fire landscapes of southwest Oregon. Journal of Raptor Research 45.

Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. van Wagtendonk, and S. L. Stephens. 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. Ecosystems 12:114–128.

Diaz-Delgado, R., F. Lloret, X. Pons, and J. Terradas. 2002. Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. Ecology 83:2293–2303.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Postwildfire logging hinders regeneration and increases fire risk. Science 311:352.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009*a*. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Canadian Journal of Forest Research 39:823–838.

Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009*b*. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology 97:142–154.

Eugenio, M., I. Verkaik, F. Lloret, and J. M. Espelta. 2006. Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). Forest Ecology and Management 231:47–54.

Fischer, W. C., and A. F. Bradley. 1987. Fire ecology of western Montana forest habitat types. USDA Forest Service GTR-INT-223. USDA Forest Service, Ogden, Utah, USA.

Fontaine, J. B. 2007. Influences of high severity fire and post-fire logging on avian and small mammal communities of the Siskiyou Mountains, Oregon, USA. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Fontaine, J. B., D. C. Donato, W. D. Robinson, B. E. Law, and J. B. Kauffman. 2009. Bird communities following high-severity fire: response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. Forest Ecology and Management 257:1496–1504.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs 70:539–590.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. GTR-PNW-8. USDA Forest Service, Pacific Northwest Forest and Range and Experiment Station, Portland, Oregon, USA.

Fulé, P. Z., A. E. Cocke, T. A. Heinlein, and W. W. Covington. 2004. Effects of an intense prescribed forest fire: Is it ecological restoration? Restoration Ecology 12:220–230.

Fulé, P. Z., J. E. Crouse, T. A. Heinlein, M. M. Moore, W. W. Covington, and G. Verkamp. 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. Landscape Ecology 18:465–485.

Graham, R. T., S. McCaffrey, and T. B. Jain, editors. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. RMRS GTR-120. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Gray, A. N., and J. F. Franklin. 1997. Effects of multiple fires on the structure of southwestern Washington forests. Northwest Science 71:174–185.

Greene, D. F., and E. A. Johnson. 1999. Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. Canadian Journal of Forest Research 29:462–473.

Greene, D. F., and E. A. Johnson. 2000. Tree recruitment from burn edges. Canadian Journal of Forest Research 30:1264–1274.

Hagar, J. C. 2007. Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests—a review. Forest Ecology and Management 246:108–122.

Haire, S. L. and K. McGarigal. 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. Landscape Ecology 25:1055–1069.

Halofsky, J. E. and D. E. Hibbs. 2008. Determinants of riparian fire severity in two Oregon fires, USA. Canadian Journal of Forest Research 38:1959–1973.

Halofsky, J. E. and D. E. Hibbs. 2009. Controls on early post-fire woody plant colonization in riparian areas. Forest Ecology and Management 258:1350–1358.

Hessburg, P. F., R. B. Salter, and K. M. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecology 22 (Supplement 1):5–24.

Hobbs, S. D., S. D. Tesch, P. W. Owston, R. E. Stewart, J. C. Tappeiner II and G. E. Wells, editors. 1992. Reforestation practices in Southwestern Oregon and Northern California. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.

Holden, Z. A., P. Morgan, and A. T. Hudak. 2010. Burn severity of areas reburned by wildfires in the Gila National Forest, New Mexico, USA. Fire Ecology 6:77–85.

Hurteau, M. D., G. W. Koch, and B. A. Hungate. 2008. Carbon protection and fire risk reduction: toward a full accounting of forest carbon offsets. Frontiers in Ecology and the Environment 6:493–498.

Irvine, D., D. E. Hibbs, and J. P. A. Shatford. 2009. Competition and facilitation in a post-fire landscape: young conifer growth in the Klamath-Siskiyou Region. Northwest Science 83:334–347.

Jayen, K., A. Leduc, and Y. Bergeron. 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Quebec, Canada. Ecoscience 13:143–151.

Johnson, D. W., J. D. Murphy, R. F. Walker, D. Glass, and W. W. Miller. 2007. Wildfire effects on forest carbon and nutrient budgets. Ecological Engineering 31:183–192.

Johnstone, J. F. 2006. Response of boreal plant communities to variations in previous fire-free interval. International Journal of Wildland Fire 15:497–508.

Kayes, L. J. 2008. Early-successional vegetation dynamics and microsite preferences following post-fire forest restoration in southwestern Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Kennedy, P. L., and J. B. Fontaine. 2009. Synthesis of knowledge on the effects of fire and fire surrogates on wildlife in U.S. dry forests. Special Report 1096. Oregon State University Agricultural Experiment Station, Corvallis, Oregon, USA.

Kotliar, N. B., P. L. Kennedy, and K. Ferree. 2007. Avifaunal responses to fire in southwestern montane forests along a burn severity gradient. Ecological Applications 17:491–495.

Kotliar, N. B., E. W. Reynolds, and D. H. Deutschman. 2008. American three-toed woodpecker response to burn severity and prey availability at multiple spatial scales. Fire Ecology 4:26–45.

Kushla, J. D. and W. J. Ripple. 1997. The role of terrain in a fire mosaic of a temperate coniferous forest. Forest Ecology and Management 95:97–107.

Larson, A. J., and J. F. Franklin. 2005. Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. Forest Ecology and Management 218:25–36.

Lentile, L. B., F. W. Smith, and W. D. Shepperd. 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. Canadian Journal of Forest Research 35:2875–2885.

Lopez Ortiz, M. J. 2007. Plant community recovery after high severity wildfire and post-fire management in the Klamath Region. Thesis. Oregon State University, Corvallis, Oregon, USA.

McKenzie, D. H., Z. Gedalof, D. L. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. Conservation Biology 18:890–902.

Meehan, T. D., and T. L. George. 2003. Short-term effects of moderate- to high-severity wildfire on a disturbance-dependent flycatcher in northwest California. Auk 120:1102–1113.

Mitchell, S. R., M. E. Harmon, and K. E. B. O'Connell. 2009. Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. Ecological Applications 19:643–655.

Morrison, P. H., and F. J. Swanson. 1990. Fire history and pattern in a Cascade Range landscape. PNW-GTR-254. USDA Forest Service, Pacific Northwest Research Station. Portland, Oregon, USA.

Murphy, J. D., D. W. Johnson, W. W. Miller, R. F. Walker, E. F. Carroll, and R. R. Blank. 2006. Wildfire effects on soil nutrients and leaching in a Tahoe Basin watershed. Journal of Environmental Quality 35:479–489.

Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. Frontiers in Ecology and the Environment 4:481–487.

Odion, D. C., E. J. Frost, J. R. Strittholt, H. Jiang, D. A. Dellasala, and M. A. Moritz. 2004. Patterns of fire severity and forest conditions in the western Klamath Mountains, California. Conservation Biology 18:927–936.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. Journal of Ecology 98:96–105.

Oliveras, I., M. Gracia, G. More, and J. Retana. 2009. Factors influencing the pattern of fire severities in a large wildfire under extreme meteorological conditions in the Mediterranean basin. International Journal of Wildland Fire 18:755–764.

Pausas, J. G., N. Ouadah, A. Ferran, T. Gimeno, and R. Vallejo. 2003. Fire severity and seedling establishement in *Pinus halepensis* woodlands, eastern Iberian Peninsula. Plant Ecology 169:205–213.

Raymond, C. L., and D. L. Peterson. 2005. Fuel treatments alter the effects of wildfire in a mixed-evergreen forest, Oregon, USA. Canadian Journal of Forest Research 35:2981–2995.

Roberts, S. L., J. W. Van Wagtendonk, A. K. Miles, and D. A. Kelt. 2010. Effects of fire on spotted owl site occupancy in a late-successional forest. Biological Conservation. [doi: 10.1016/j.biocon.2010.1011.1002]

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199–221.

Schlossberg, S., and D. I. King. 2008. Are shrubland birds edge specialists? Ecological Applications 18:1325–1330.

Schoennagel, T., R. Sherriff, and T. Veblen. In press. Fire history and tree recruitment in the Colorado Front Range upper montane zone: implications for forest restoration. Ecological Applications. [doi: 10.1890/10-1222.1]

Schoennagel, T., E. A. Smithwick, and M. G. Turner. 2008. Landscape heterogeneity following large fires: Insights from Yellowstone National Park, USA. International Journal of Wildland Fire 17:742–753.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. BioScience 54:661–676.

Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: how much, how soon? Journal of Forestry 105:139–46.

Shinneman, D. J., and W. L. Baker. 2003. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. Conservation Biology 11:1276–1288.

Smucker, K. M., R. L. Hutto, and B. M. Steele. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15:1535–1549.

Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management 111:285–301.

Thompson, J. R., and T. A. Spies. 2009. Vegetation and weather explain variation in crown damage within a large mixed severity wildfire. Forest Ecology and Management 258:1684–1694.

Thompson, J. R., and T. A. Spies. 2010. Factors associated with crown damage following recurring mixed-severity wildfires and post-fire management. Landscape Ecology 25:775–789.

Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. Proceedings of the National Academy of Sciences USA 104:10743–10748.

Turner, M. G., W. W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5:731–742.

Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9:59–77.

Turner, M. G., W. H. Romme, and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and the Environment 1:351–358.

USDA (United States Department of Agriculture). 1988. Silver Fire Recovery Project Final Environmental Impact Statement. USDA Forest Service, Siskiyou National Forest, Medford, Oregon, USA.

van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk. Forest Ecology and Management 211:150–165.

Weatherspoon, C. P. and C. N. Skinner. 1995. An assessment of factors associated with damage to tree crowns from the 1987 wildfires in northern California. Forest Science 41:430–451.

Whittaker, R. H. 1960. Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30:279–338.

Zedler, P. H., C. R. Gautier, and G. S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64:809–818.