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RESEARCH REVIEW

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Are plant community responses to wildfire contingent upon historical disturbance regimes?

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Abstract

Background: Ecological disturbance is a major driver of ecosystem structure and evolutionary selection, and theory predicts that the frequency and/or intensity of disturbance should determine its effects on communities. However, adaptations of species pools to different historical disturbance regimes are rarely considered in the search for generalizable community responses to disturbance. To explore how the severity of disturbance affects plant diversity patterns, we review studies of understorey plant community responses to wildfire in conifer forests of western North America across a gradient of departure from historical fire regimes.

Review findings: We find that post-fire plant species richness may generally be maximized at disturbance severities that match the predominant historical disturbance regime in a given ecosystem. Studies that examined multiple spatial scales indicate that plant community responses to fire are likely to be scale dependent, suggesting that post-disturbance monitoring should consider community responses at multiple scales.

Synthesis: Our review highlights that consideration of historical disturbance regimes might improve the ability to predict the effects of disturbance on communities. We discuss future research needs; quantitative studies that compare community responses to fire at multiple scales across different historical fire regimes would be particularly useful. Ultimately, consideration of disturbance as a multivariate problem is likely to lead to greater inference than traditional bivariate approaches.

KEYWORDS
biodiversity, community assembly, dynamic ecosystem model, fire regimes, global change, intermediate disturbance hypothesis, scale dependence, understorey plants

1 | INTRODUCTION

Ecological disturbance is a major driver of ecosystem function, structure and composition, and the set of ecological disturbances that typifies an ecosystem also exerts powerful evolutionary pressures, often leading to characteristic adaptation syndromes in member species (Denslow, 1980; Grubb, 1977; Pickett & White, 2013; Sousa, 1979). Fire is the most important disturbance process in many global ecosystems, and it acts both as a powerful filter of the species pool and as a strong driver of evolutionary selection (Bond & van Wilgen, 1996; Bowman et al., 2009; Keeley, Bond, Bradstock, Pausas, & Rundel, 2011). The concept of the fire regime (i.e., the temporal and spatial patterns of burning that characterize an ecosystem, averaged over many fires over a long period of time) provides a useful framework for understanding the effects of fire on the ecosystem and how they can be modified by humans (Keeley & Safford, 2016; Sugihara, van Wagtendonk, Shaffer, Fites-Kaufman, & Thode, 2006). Many factors influence fire regimes on landscapes, including climate, fire adaptations in the regional species pool, the structure of fuels, topography, productivity and human interactions (Agee, 1993; Sugihara et al., 2006). The most widely used fire regime classifications, however, are based on only two factors, fire severity and frequency (e.g., Heinselman, 1981; Johnson & Van Wagner, 1985; Schmidt, Menakis, Hardy, Hann, & Bunnell, 2002), because they are major drivers of ecological and evolutionary response, they can be measured easily, and their relationship is broadly inverse (Connell, 1978; Huston, 1994; Pickett & White, 2013).

Anthropogenic pressures have caused changes in fire frequency and/or severity in many parts of the world, such that many fire regimes are now outside the historical range of variation (Cochrane et al., 1999; Harvey, Donato, & Turner, 2016; Miller, Safford, Crimmins, & Thode, 2009; Prichard, Stevens-Rumann, & Hessburg, 2017). For example, in certain forest ecosystems in western North America, the average size and severity of forest fires have increased over recent decades (Harvey et al., 2016; Miller et al., 2009). These changes are attributable to interactions between increasing fuels and forest density (a legacy of a century or more of fire suppression in ecosystems that supported high frequencies of low-severity fire before Euroamerican settlement) and climate change, which is warming and drying fuels while lengthening the fire season (Cansler & McKenzie, 2014; Harvey et al., 2016; Mallek, Safford, Viers, & Miller et al., 2013; Miller et al., 2009; Westerling, Hidalgo, Cayan, & Swetnam, 2006). Such dramatic shifts in fire regimes away from the historical range of variation are likely to have substantial impacts on ecosystem sustainability and biodiversity.

Altered fire regimes can have dramatic and long-persisting effects on ecosystems (e.g., regime shifts; Enright, Fontaine, Bowman, Bradstock, & Williams, 2015; Miller, Damschen, Ratajczak, & Özdoğan, 2017). For example, novel fire behaviour can alter forest structure and tree regeneration, potentially leading to alternative, non-forested vegetation states (Stevens-Rumann & Morgan, 2016; Tepley, Thompson, Epstein, & Anderson-Teixeira, 2017; Welch, Safford, & Young, 2016). The loss of large areas of forest as a consequence of larger, hotter fires can have significant effects on many forest ecosystem services that humans depend on, including water provisioning, timber, recreation and wildlife (CNRA, 2009). Comparatively little is known, however, about how shifting fire regimes affect forest biodiversity. Although much fire ecology research focuses on trees, understanding the effects of shifting fire regimes on understorey plants (the communities of forbs, graminoids and shrubs beneath forest canopies) is also particularly important, because these communities are a major component of forest biodiversity and support higher trophic levels.

A body of ecological theory predicts that effects of disturbances on communities may depend on interactions between disturbance frequency or intensity and plant productivity (Kondoh, 2001). In one specific example, the dynamic ecosystem model (DEM; Huston, 1979, 1994) predicts that increasing disturbance frequency or intensity will be needed to maintain diverse communities as productivity increases, because competitive exclusion will occur more rapidly in the absence of disturbance in productive environments. Modelling work has also supported this general hypothesis (Kondoh, 2001). The intermediate disturbance hypothesis (IDH) makes similar predictions and suggests that diversity should be maximized at intermediate disturbance frequencies or intensities, at least at intermediate levels of productivity (Connell, 1978; Huston, 2014; Sousa, 1979). The applicability of these theories has been debated widely, and empirical data do not consistently support a hump-shaped diversity response to disturbance frequency or intensity (Fox, 2013; Huston, 2014; Mackey & Currie, 2001). However, neither DEM nor IDH explicitly incorporates the possibility that life-history traits might interact with disturbance regimes to drive diversity responses.

The evolutionary history of a given regional flora may affect community responses to disturbance, because plants can have a variety of adaptations (or apparent adaptations) to disturbance, particularly in traits related to regeneration (Denslow, 1980; Grubb, 1977; Noble & Slatyer, 2012). For example, plants may regenerate rapidly in burned sites by resprouting from underground structures that can survive fire, or recolonize with seeds whose germination is cued by fire (Paula & Pausas, 2008; Sugihara et al., 2006). In some ecosystems, adaptations to disturbance have a major influence on the interactive effects of disturbance and productivity on diversity (Denslow, 1980, 1985; Milchunas, Sala, & Laurenroth, 1988; Safford & Mallek, 2010). Given that specific ecosystems (e.g., forest types) have generally experienced unique fire regimes for millennia, plants that grow in a given ecosystem have been filtered from the larger regional species pool based on their compatibility with the fire regime (Denslow, 1980; Stevens, Safford, Harrison, & Latimer, 2015).

Importantly, adaptations (or apparent adaptations) that make a plant well suited to one fire regime may not confer benefits in the context of different (or altered) fire regimes (Buma, Brown, Donato, Fontaine, & Johnstone, 2013; Denslow, 1980; Hobbs & Huenneke, 1992; Johnstone et al., 2016). For example, a plant that is adapted to survive low-intensity fire may not be able to survive a high-intensity fire, and plants with regeneration adaptations to infrequent but intense fire may experience population extirpations if fires are too frequent (and do not provide time for sufficient seed production and storage) or if they are not intense enough to stimulate germination (Keeley & Safford, 2016). This raises the crucial question of whether shifting fire regimes could have negative effects on plant diversity, which is a particularly relevant question given the wholesale changes in fire regimes in many global ecosystems in recent decades, including the increasing size of high-severity burn patches in many western North American forest types (Balch, Bradley, D'Antonio, & Gómez-Dans, 2013; Dennison, Brewer, Arnold, & Moritz, 2014; Prichard et al., 2017; Steel, Koontz, & Safford, 2018). Although understorey community responses to fire have been relatively well studied in some contexts, such as low-severity, prescribed fires (reviewed by Abella & Springer, 2015; Willms, Bartuszevige, Schwilk, & Kennedy, 2017), there has been less research on how the full spectrum of fire severity affects plant diversity across different fire regimes. There has been even less research specifically examining how shifts in fire regimes (such as increases in fire severity) affect communities and how the effects of changes such as increases in fire severity may vary among ecosystems with different historical fire regimes. Our understanding of the effects of fire on understorey plants is also limited by the narrow geographical focus of most existing studies to a single fire or a few fires within close proximity. Given that such studies rarely span broad ecological gradients, it is difficult to establish generalizable patterns of plant community responses to fire.

Here, we review the scientific literature to explore whether historical fire regimes influence post-fire plant diversity in forests in western North America that vary in their degree of departure from historical fire regimes. We expected that post-fire plant species richness would be maximized under disturbance severities that were most common historically in a given ecosystem. Specifically, we expected that high-severity fire would have negative effects on post-fire plant diversity relative to low- or moderate-severity fire in ecosystems that burned primarily at low severity historically, because regional species pools in these ecosystems should contain few plants with adaptations to high-severity fire. In ecosystems that have been characterized historically by a substantial component of high-severity fire, we expected that high-severity fire would have stronger positive effects on plant diversity than low- or moderate-severity fire (Figure 1). For moderate-severity fire regimes, we expected saturating (e.g., positive plateau) relationships between plant diversity and fire severity to be most common. Although we focus primarily on fire severity, our review is likely to have implications for other attributes of shifting fire regimes (e.g., fire size and frequency), which are often related to shifting fire severity (Steel, Safford, & Viers, 2015).

2 | STUDY SYSTEM

Western conifer forests are a good study system for examining the impact of altered fire regimes on plant communities because they support a range of fire regimes that vary in degree of departure from historical conditions of roughly the last 5,000 years (Betancourt & Van Devander, 1981; Table 1). Large areas of western North America historically supported fire regime group (FRG) I forests, which were dominated by "fire-resistant" trees with adaptations to frequent, low-severity fire, such as highly flammable foliage and cones, thick bark in adolescent stages, and self-pruning of lower branches. Given that large areas of high-severity (i.e., stand-replacing) fire were comparatively rare, most tree species in FRG I forests lack seed dormancy and fire-cued regeneration strategies (e.g., serotiny), and they depend on surviving trees to repopulate local areas after stand-replacing fires (Keeley & Safford, 2016; McCune, 1988; Safford & Stevens, 2017). In contrast, FRG IV and V forest types (Table 1) have been characterized historically by moderate- to low-frequency fires with a major component of high-severity effects, with long interfire periods tending to result in heavy accumulations of fuel (Agee, 1993; Schoennagel, Veblen, & Romme, 2004). Dominant tree species in these forest types are generally "fire avoiders" and include serotinous species in FRG IV and highly fire-sensitive species in FRG V. Serotiny is selected for in FRG IV forest types because the probability of mortality owing to fire is high, and seed release after death ensures population persistence. In FRG V forests, fire is rare enough that it is not a major selective force. As an intermediate between FRG I and IV, FRG III contains somewhat ecologically heterogeneous forest types that are thought to have supported moderately frequent fire and a more balanced mixture of fire severities. Such "mixed severity" fire regimes seem to be more common in topographically complex or climatically transitional regions and in forest types where hardwood and conifer species share dominance (Halofsky et al., 2011; Perry et al., 2011).

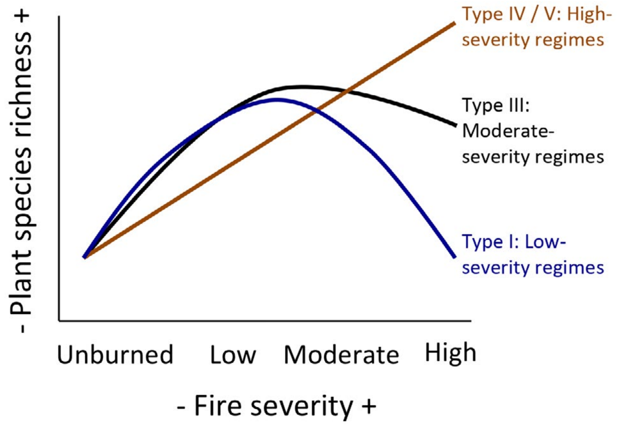

FIGURE 1 Hypothesized relationships between fire severity and plant alpha diversity in forests characterized by different historical fire regimes. The origin point of the trend lines on the *y* axis represents the pre-fire conditions. Portions of the lines to the right of the origin points represent hypothesized post-fire species richness

Since Euroamerican settlement, humans have altered fire regimes in western North American forests in three principal ways: indirectly, by changing the structure and amount of fuel (e.g., through timber harvest and livestock grazing); indirectly, by warming the climate (greenhouse gas emissions); and directly, by changing fire frequency and fire season. Historical timber harvest, which removed the largest trees, increased surface fuels and encouraged dense secondary growth of fire-intolerant species, often increased fire severity and resistance to control (i.e., made it more difficult to suppress fire; Brown, Reinhardt, & Kramer, 2003; Safford & Stevens, 2017), with the greatest impacts in FRG I and III. Importantly, historical timber harvest had very different effects on fire behaviour than contemporary forest thinning and fuel treatment management, which leave the larger trees, explicitly reduce surface fuels and cull small, fire-intolerant trees, thus tending to reduce fire severity (Safford, Stevens, Merriam, Meyer, & Latimer, 2012; Stephens et al., 2012). Domestic livestock grazing has also reduced fire frequency by removing flammable forage plants, primarily affecting forests in FRG I and III (Swetnam, Allen, & Betancourt, 1999). Climate warming has been ubiquitous, as have its effects on the fire regime in recent decades. Warmer temperatures lead to greater fuel drying and longer snow-free periods at high elevations, causing a longer fire season and, ultimately, leading to larger and more severe fires (Abatzoglou

TABLE 1 Historical and contemporary fire regimes for western North America based on LANDFIRE fire regimen classifications[a] and adapted from Steel et al. (2015)

Historical fire regime group[a]	Mean fire return interval[b] (years)	Modal fire severity[c]	Corresponding forest types	Current fire regime group
I	< 35	Low	Yellow pine, mixed-conifer, dry Douglas fir forests, oak woodlands	Rarely I, mostly III and IV
III	35–200	Mixed[d]	Mesic Douglas fir, mixed hardwood–conifer, some moist mixed-conifer forests, upper montane forests (e.g., red fir, some spruce–fir), redwood (under Native American burning)	III and IV
IV	35–200	High	Serotinous conifers (various species of pines and cypresses) and some upper montane spruce–fir	IV
V	≥ 200	High	Most subalpine forests, coastal spruce–fir–hemlock, redwood (under lightning ignition regime)	Mostly V, some IV

[a] Fire regime classes are from Schmidt et al. (2002).

[b] Fire return interval is the inverse of fire frequency and represents the average number of years between fire events.

[c] All fire regime groups support low-, moderate- and high-severity fire, but one of these components tends to dominate (the "modal" severity). Low severity = areas where canopy tree mortality is < 25%; moderate = canopy tree mortality between 25 and 90%; and high = canopy tree mortality > 90%.

[d] "Mixed" severity fire is intended to refer to those fire regimes where the balance between low-, moderate- and high-severity fire is more even than in fire regimes I, II or IV, but the term "mixed severity fire" is subjective and depends on the spatial scale of observation.

& Williams, 2016; Westerling et al., 2006). The most direct impacts to western North American fire regimes have come through human manipulation of fire frequency, either purposeful or involuntary. In most ecosystems, the presence of humans leads to an increase in the number of fire ignitions (Syphard et al., 2007; Safford & Van de Water, 2014). However, humans have also caused decreases in fire frequency in some ecosystems. The classic example is low- to mid-elevation FRG I forests of western North America, where low fuel loads and high vertical and horizontal discontinuity in forest structure led to easy suppression of fire for roughly a century after Euroamerican settlement (Mallek et al., 2013; Safford & Van de Water, 2014; Syphard, Keeley, Pfaff, & Ferschweiler, 2017; Tepley & Veblen, 2015).

Forests in western North America today represent a gradient of departure from historical fire regimes. Dry forests in FRG I (historically characterized by frequent, low-severity fire) have typically experienced increases in fuel loads and forest density and have often shifted to more shade-tolerant, flammable tree species, largely as a result of fire suppression (Agee, 1993; Safford & Stevens, 2017). As a consequence, high-severity fire has become more common in these ecosystems, such that the fire regime in many historical FRG I forests is now similar to FRG III and IV (less frequent fire, higher severity; Table 1; Mallek et al., 2013; Steel et al., 2015). Conversely, forests characterized historically by FRG IV and V (infrequent, sometimes high-severity fire), such as subalpine forests and other forests in relatively wet, cool environments, have not experienced strong departures from historical fire regimes. Forests in FRG III (characterized by infrequent, mixed severity fire) represent an intermediate level of departure from historical regimes, with some increases in fire severity (Mallek et al., 2013; Steel et al., 2015). The importance of historical fire regimes is currently recognized by land managers (DeMeo et al., 2012), but quantitative data on responses of entire plant communities have rarely been synthesized beyond the level of individual studies.

3 | REVIEW OF POST-FIRE PLANT COMMUNITY STUDIES

3.1 | Review methods

To find studies for review, we conducted multiple searches using the Web of Knowledge, and a US Forest Service research librarian located additional relevant papers. We used various combinations of the search terms "fire severity", "plant diversity", "species richness", "fire regime", "plant community" and "biodiversity". We also added papers from our personal research libraries and from references in other papers. To be included in the review, studies had to analyse post-fire plant communities from at least two levels of fire severity for purposes of comparison (one of which had to be the unburned condition) and had to report species richness as a response variable. Studies also had to include results from areas that did not involve management activities post-fire or immediately pre-fire so that results would not be confounded by management, although we included studies that tested management effects as long as untreated areas were also analysed. When we encountered multiple published papers that analysed the same data sets (or subsets thereof), we included only the most recently published paper that met our data needs. To represent the unburned community condition, most studies surveyed unburned control plots in forests adjacent to fire perimeters that were ecologically similar to areas that burned; a few studies compared pre- and post-fire data from long-term study plots. All studies that defined fire severity used a definition based on tree mortality. We did not attempt to standardize fire severity classifications among studies, because classifications were already similar among studies; high-severity fire was consistently defined as stand-replacing fire, and low-severity fire was defined by the survival of all or most trees.

We extracted information on plant community responses to fire severity from each paper. For papers that examined two or more levels of fire severity (in addition to the unburned condition), we classified papers into one of six possible response shapes (Figure 2), based on whether there were statistically significant differences between species richness at different fire severities. For example, a study was classified as "hump-shaped" if species richness at an intermediate fire severity was significantly higher than species richness at lower (or unburned) and higher fire severity. For papers that reported species richness responses only to unburned treatments and a single burn severity level, papers were classified as reporting positive, negative or no effect of fire on species richness (Supporting Information Table S1.1). When papers reported results at multiple time points, we generally focused on the latest time point reported. We also extracted information on the responses of beta diversity when it was reported (Supporting Information Table S1.2), in addition to information on other drivers of post-fire diversity that authors noted, including landscape context and productivity, although those topics were rarely examined and thus should be interpreted cautiously. We expected that beta diversity would be maximized at low to intermediate fire severities in all ecosystems, because these patchier, low-severity burns are likely to lead to more heterogeneous conditions. Given that exotic plants could potentially cause community response patterns that do not represent trait filtering by historical fire regimes, we also noted any patterns of exotic plant responses reported.

We assigned historical fire regimes to each study using reported data on forest type and the LANDFIRE fire regime classifications (Table 1; Schmidt et al., 2002). For purposes of discussion, throughout this paper we define high-severity fire as a stand-replacing fire where most (> 90%) trees are killed and low-severity fire as a fire where most (at least but usually ≫ 75%) trees survive. We primarily use the term "moderate severity" to describe the intermediate burn severity pattern, because the term "mixed severity" is scale dependent and has caused confusion (Tepley & Veblen, 2015).

3.2 | Review summary

We found 32 studies (comprising 34 separate study units, because some studies sampled multiple forest types) that met the criteria for inclusion in this review (Figure 3). Studies represented FRG I, III and IV, which is the full spectrum of fire regimes found in Western conifer forests, except for forests with average fire return intervals > 200 years (FRG V, which are relatively rare). Studies in historical FRG I generally took place in sites where fire has become (usually much) less frequent than under the historical regime, and many of these studies reported modern stand structures that were notably denser than was common in historical (pre-suppression) conditions. Of the 34 study units we reviewed, 14 explicitly examined high-severity fire in addition to low- or moderate-severity fire and the unburned condition (Table 2). The other studies examined only a single level of fire severity, usually low to moderate severity, and the unburned condition (Supporting Information Table S1.1). Most studies reported results from one or multiple time points in the first decade after fire, although some studies presented results for ≤ 30 years after fire. Studies that examined plant communities in the first 1–2 years after fire often found negative or non-significant

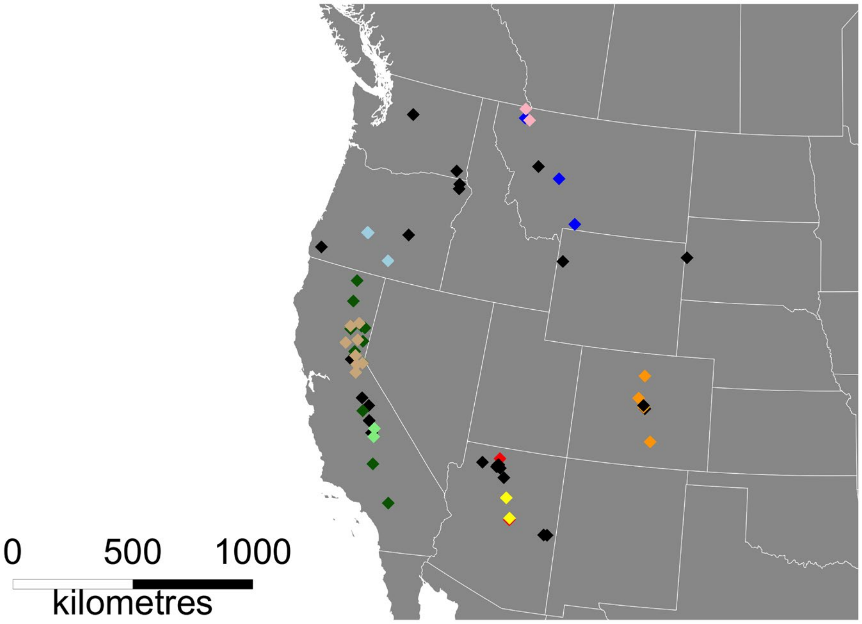

FIGURE 2 Types of relationships between fire severity and plant diversity described in the papers we reviewed

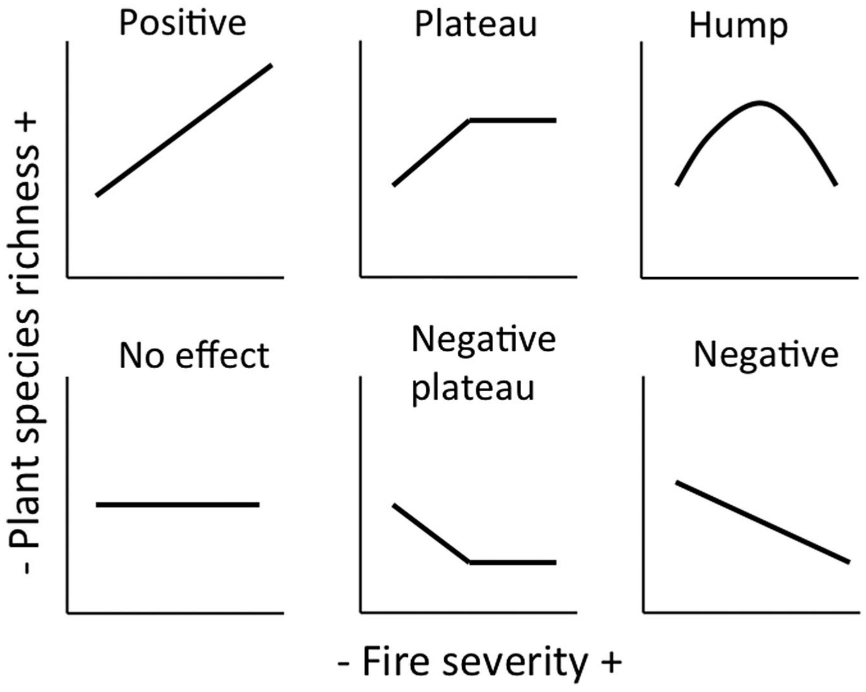

FIGURE 3 Map of approximate locations of study sites for the 32 studies we reviewed. Studies that included multiple study sites are mapped using multiple points of the same colour. Black points represent studies that took place at a single location

responses to fire, although responses generally became more positive after more time (Table 2; Supporting Information Table S1.1). Although most studies reported total species richness, including overstorey species, understorey species generally made up the majority of species richness. All studies analysed alpha (plot-level) diversity.

3.3 | Alpha diversity

Seven out of the eight studies that examined effects of multiple fire severities in forests historically characterized by FRG I found either hump-shaped or plateau-shaped relationships of plant diversity to fire severity. Three studies found hump-shaped relationships, where post-fire richness peaked in areas that burned at low or moderate severity and was lower in unburned areas and in areas that burned at high severity [DeSiervo, Jules, & Safford, 2015; Morgan et al., 2015; Richter et al., 2019; in the study by Morgan et al., 2015, the hump-shaped relationship was statistically signficant in the first year after fire and became a non-significant trend in subsequent years; in the study by Desiervo et al., 2015, the relationship was marginally significant ($p = .06$)]. Three studies found plateau-shaped relationships, where plant diversity was equivalent in low and high burn severities, but higher in both than in unburned areas (Burkle et al., 2015; Crawford, Wahren, Kyle, & Moir, 2001; Stevens et al., 2015). One study in FRG I also reported a linear positive species richness response to fire severity for the entire plant community (Keeley, Lubin, & Fotheringham, 2003), and one study reported results only for individual plant functional groups, which had varying response shapes (Griffis, Crawford, Wagner, & Moir, 2001).

Studies in FRG III and IV also had variable responses, but with an increasing proportion of positive relationships. Two of the three studies in FRG IV that included the unburned condition showed positive species richness responses to high-severity fire (Coop, Massatti, & Schoettle, 2010; Doyle, Knight, Taylor, Barmore, & Benedict, 1998; although the study by Doyle et al. (1998) is an unreplicated case study), whereas the other had a hump-shaped relationship (Strand et al., 2019: supplemental analyses). In FRG III, species richness response shapes to fire severity included linear positive (Abella & Fornwalt, 2015), hump-shaped (Burkle et al., 2015; significant for graminoids and marginally significant for forbs) and negative-plateau-shaped relationships (for forbs only; Burkle & Myers, 2015). The negative plateau relationship was reported from a study site that experienced rapid, abundant post-fire tree regeneration that apparently shaded out most herbaceous plants (Burkle et al., 2015).

Studies that examined only low-severity fire, mostly in FRG I, usually found neutral to positive effects of fire on species richness relative to unburned controls (Supporting Information Table S1.1). Only two studies reported negative effects, both of which took place in the year after fire. Many of the low-severity fire studies took place in stands with higher than historical tree density and/or basal area, where light limitation might dampen herbaceous responses to fire. Several studies that reported neutral or slight positive effects of low-severity fire on plant diversity in unmanaged stands found that thinning stands before burning produced larger increases in species richness (e.g., Dodson & Peterson, 2010; Dodson, Peterson, & Harrod, 2008; Strahan, Stoddard, Springer, & Huffman, 2015; Wayman & North, 2007).

3.4 | Beta diversity

Only four studies (comprising six study units) explicitly reported effects of fire on beta diversity that could be distinguished by fire regime, although two others provided results from which beta diversity responses could be inferred (Supporting Information Table S1.2). All of these studies indicated that beta diversity (defined as differences

TABLE 2 Summary of plant diversity responses for studies that examined unburned conditions and at least two other fire severity classes in conifer forests of western North America

Study	State	Forest type	Time since fire (years)	Number of plots	Number of fire severity categories	Fire regime group	Negative	Negative plateau	Hump	Plateau	Positive	No effect
Burkle et al. (2015), Helena	MT	Yellow pine	10	54	3	I				■		
Crawford et al. (2001)	AZ	Yellow pine	2	102	3	I				■		
DeSiervo et al. (2015)	CA	Yellow pine–mixed conifer–leather oak	5	130	6	I			■			
Griffis et al. (2001)	AZ	Yellow pine	3–11	160	3	I			NG		EF	NF, EG
Keeley et al. (2003)	CA	Yellow pine–mixed conifer	1–5	103	3	I					■	
Richter et al. (2019)	CA	Yellow pine–mixed conifer	5–14	630	6	I			■			
Stevens et al. (2015)	CA	Yellow pine–mixed conifer	5	664	3	I				■		
Morgan et al. (2015)	MT	Douglas fir–lodgepole pine and yellow pine	1–6	72	4	I			■			
Abella & Fornwalt (2015)	CO	Yellow pine	1–5, 10	20	4	III					■	
Burkle et al. (2015), Paradise Valley	MT	Lodgepole pine–Douglas fir	6	54	3	III			■			
Burkle et al. (2015), Whitefish	MT	Larch–lodgepole pine–mixed conifer	12	54	3	III		F				G
Coop et al. (2010)	CO	Subalpine forest	30	200	3	IV					■	
Strand et al. (2019) (subalpine sites in two fires)	WA	Subalpine forest	10 to 12	41	4	IV			■			
Doyle et al. (1998)	WY	Rocky Mountain fir–lodgepole pine–Apache pine	1,2,3, 9, 17	3	3	IV					■	

Note: Studies are organized by historical fire regime in order of increasing fire severity. All studies examined unburned, low- and/or moderate-severity and high-severity sites. Black boxes represent responses of the entire plant community, the entire understorey plant community or all herbaceous species. Grey boxes represent subsets of the plant community (i.e., functional groups: E = exotic; F = forbs; G = graminoids; and N = native). For Strand et al. (2019), we conducted an additional analysis of fire regime group IV sites in two fires that were not specifically reported in the paper. The number of fires for each study and *p*-values from analyses are shown in the Supporting Information (Table S1.3) in species composition between plots in the same fire severity class in all cases) tends to increase or remain unchanged after low- to moderate-severity fire in comparison to the unburned condition. All of the three studies that examined both high- and low/moderate-severity fire found higher beta diversity in areas that burned at lower fire severities than in areas that burned at higher severities, suggesting that high-severity fire might have a homogenizing effect on plant communities relative to lower-severity burns, which might be more patchy [Burkle et al., 2015 (forbs only); Richter et al. 2019; Stevens et al., 2015]. One study that reported species richness responses to low-severity fires from multiple scales (i.e., nested plots) found stronger increases in richness in larger plots, indicating increased beta diversity post-fire, although beta diversity was not quantified explicitly (Metlen & Fiedler, 2006). Another study of low-severity, prescribed fire found that beta diversity increased after fire only in stands that had been thinned previously, but not in unthinned stands (Dodson & Peterson, 2010).

3.5 | Species composition and functional groups

Several studies examined post-fire species composition in addition to species richness. Across all historical fire regimes, annual herbs were often found to be more abundant in burned than unburned areas, and in some cases the annual herb response explained post-fire spikes in species richness (Abella & Fornwalt, 2015; Huisinga, Laughlin, Fule, Springer, & McGlone, 2005; Laughlin et al., 2004). Annuals often peaked in the first few years after fire and then decreased, but sometimes persisted for longer (e.g., Doyle et al., 1998). Several studies noted compositional differences among areas that burned at different fire severities and/or unburned areas, highlighting that different fire severities might select for plants with different traits (Coop et al., 2010; Crawford et al., 2001; DeSiervo et al., 2015; Donato, Fontaine, Robinson, Kauffman, & Law, 2009). Stevens et al. (2015) found that plants with northern temperate evolutionary origins (better adapted to mesic habitats) were less likely to be present after high-severity than low-severity fires in forests historically characterized by a primarily low-severity fire regime, and found that the loss of northern temperate species led to decreased species richness after high-severity fire.

Exotic species could potentially cause community responses to fire severity that are not representative of the evolutionary history of the local flora, and roughly half the studies we reviewed specifically reported responses of exotic species to fire. Although some studies noted increases in exotic species cover and richness after fire, the post-fire abundance of exotics was generally low relative to natives, with exotics rarely becoming dominant (e.g., Abella & Fornwalt, 2015; Dodson et al., 2008), and only one study specifically reported that post-fire plant richness patterns were driven by exotics (Crawford et al., 2001). Several studies reported results for unique plant functional groups independently (e.g., grasses and forbs; Table 2). Given that the group definitions varied among studies, it was difficult to draw generalizable patterns about responses of unique functional groups, except perhaps that they seemed to be more variable than responses of the community as a whole.

3.6 | Landscape context and productivity

Only one of the studies we reviewed examined effects of heterogeneity of fire severity in landscapes surrounding study plots or the size and spatial configuration of high-severity burn patches. Coop et al. (2010) found that species richness increased along transects running across the edges of fires into the core area of high-severity burn patches in an FRG IV fire. Many studies discussed interactions between productivity and disturbance as potentially important drivers of post-fire plant diversity patterns, although few studies tested this relationship quantitatively, presumably because few studies spanned a substantial regional productivity gradient. Burkle, Myers, and Belote (2015) found that post-fire species richness was negatively associated with productivity, apparently because rapidly regenerating trees quickly out-competed herbs. Coop et al. (2010) reported that compositional difference between unburned and high-severity burn patches increased with productivity, and DeSiervo et al. (2015) reported interactive effects of productivity and fire severity on species composition.

4 | DISCUSSION

Our review suggests that contemporary plant diversity responses to fire severity in western North American forests could be contingent, at least in part, on historical disturbance regimes and modern departures from those regimes. However, the substantial variation among results in each fire regime makes it difficult to establish clear differences among patterns in different fire regimes. In ecosystems where high-severity fire was historically uncommon (i.e., FRG I), total post-fire species richness often peaks in areas that burn at low to moderate severity, as we expected, or shows a qualitatively similar saturating (plateau) pattern. In ecosystems where high-severity fire was historically a more sizeable component of the fire regime (i.e., FRG IV), post-fire diversity peaks at high severity, as we expected, in two of the three studies we examined. A role for historical contingency in determining diversity responses to fire severity has been postulated previously (Denslow, 1980), and there is empirical evidence for a similar role of historical contingency in plant community responses to grazing disturbance (Milchunas et al., 1988; Olff & Ritchie, 1998). Further quantitative studies that span multiple historical fire regimes using a common study design will be needed to provide a more definitive test of the importance of historical contingency for post-fire diversity responses.

Historical contingency in plant community responses to fire severity may arise because regional species pools in different forest types contain species with different adaptations to fire severity, and altered disturbance regimes may filter out species without appropriate traits (Denslow, 1980; Johnstone et al., 2016). Ecosystems that have historically been characterized primarily by low-severity fire typically contain few understorey species with adaptations to high-severity fire, such as fire-induced germination, whereas these adaptations are more common in systems that have had a large component of high-severity fire (Keeley & Safford, 2016). Given that fire regimes in many global ecosystems have shifted outside their historical range of variation in recent decades or centuries, patterns of historical contingency in community responses to fire raise substantial questions about the long-term maintenance of biodiversity amid interactive global change pressures.

Understanding the mechanisms that link plant community responses to disturbance is crucial for elucidating generalizable disturbance–diversity relationships. High-severity fire typically led to greater relative increases in alpha diversity in ecosystems that historically supported mostly moderate-frequency, high-severity fire (e.g., FRG IV) than in those historically characterized primarily by high-frequency, low-severity fire (e.g., FRG I), raising the question of how plant adaptations to fire vary between these ecosystems. For species to occur in the post-fire landscape, they must either survive the fire *in situ* (as seeds or living plants) or (re)colonize after fire; therefore, both dispersal ability and the presence and types of fire adaptations in the flora are important factors (Catano, Dickson, & Myers, 2017). Ruderal species with high dispersal ability are common after severe disturbances in most ecosystems (Grime, 2006), but in contrast to many FRG IV and some FRG III ecosystems, species with specific adaptations to survive or rapidly recruit after severe fire are not abundant in FRG I forests (Keeley & Safford, 2016). For example, many pine and cypress (*Cupressus* and *Hesperocyparis*) species that dominate FRG IV forests around the world exhibit partial or complete serotiny, and their understories often support species whose germination is fire cued (Keeley et al., 2011). Fire-cued germination is also sometimes found in FRG I forests, but it is comparatively rare. Stevens et al. (2015) reported that species with traits resulting in lower environmental stress tolerance (e.g., low specific leaf area) were more likely to disappear after high-severity fire in FRG I forests, highlighting that high-severity fire might produce warmer, drier environmental conditions that might be intolerable to plants adapted primarily to low-severity fire and the relatively mesic conditions provided by forest canopies. Recent research has indicated that altered environmental conditions after high-severity fire in FRG I/III forests may also cause diversity losses in lichens, another taxonomic group sensitive to large-scale loss of tree cover (Miller, Root, & Safford, 2018).

Ecological theory predicts that diversity will be maximized at an intermediate severity (or frequency) of disturbance, at least at sites with intermediate biological productivity (Huston, 2014). In our review, hump-shaped responses of diversity to fire severity do appear to be common in ecosystems that historically experienced predominantly low- and moderate-severity disturbance, along with qualitatively similar saturating (positive-plateau) relationships. However, diversity peaks more commonly after high-severity disturbance (relative to undisturbed conditions and low-severity disturbance) in ecosystems that historically experienced primarily high-severity fire, although such forests are often less productive than those historically characterized by low-severity disturbance. This contrasts with theory that predicts more negative effects of disturbance on diversity at lower productivity (Huston, 1979, 2014). Thus, traditional disturbance theory does not seem to explain the patterns we observe (although they are not fully explained by historical contingency either). Our review suggests that historical contingency should be integrated into theory as a predictor alongside the frequency/intensity of disturbance and productivity.

Although few studies we reviewed explicitly examined community responses to fire severity at multiple spatial scales, those that did consistently found scale-dependent responses, indicating that studying post-fire communities at multiple spatial scales might be crucial for understanding the mechanisms underpinning the effects of fire on biodiversity. A substantial proportion of the plant community response to fire is likely to occur via changes in beta diversity, which might be independent of alpha diversity responses. For example, low- and moderate-severity burning in forests leaves many plants alive and often produces a mosaic of burned and unburned patches in the understorey, increasing landscape-scale diversity via increased community heterogeneity, even, in some cases, where fire has no effect on local-scale richness relative to unburned areas (Dodson & Peterson, 2010; Metlen & Fiedler, 2006). Conversely, beta diversity is often observed to decrease after high-severity fire (as with other severe disturbances; Chase, 2007; Hobbs & Huenneke, 1992), sometimes even while alpha diversity increases (Burkle & Myers, 2015). Homogenization of plant communities after high-severity fire might be a product of homogenized post-fire environmental conditions; ecosystems with a flora adapted to high-severity fire might compensate for this effect via a post-fire surge in alpha diversity. The relative lack of remaining unburned or lightly burned refuges after high-severity fire might, however, enhance its negative effects on floras with few specific adaptations to severe fire (Stevens et al., 2015).

The spatial heterogeneity of burn severity in the landscape surrounding focal communities is another potentially important but often overlooked influence on post-fire plant communities (Martin & Sapsis, 1991). In an ecosystem historically characterized by infrequent high-severity fire, Coop et al. (2010) showed that local species richness increases with distance into the core area of high-severity burn patches, where light availability is greatest after fire. The advent of "mega-fires" highlights the importance of understanding how understorey plant communities will respond to the increasing size of high-severity burn patches in forests historically characterized by high-frequency, low-severity (FRG I) fire regimes (Steel et al., 2015, 2018). Although there has been little research into the effects of the increasing size of high-severity burn patches for understorey plants in North America, there is evidence that plant–pollinator networks can be more diverse at sites with greater pyrodiversity, a metric of spatial and temporal heterogeneity in fire severity (Martin & Sapsis, 1991; Ponisio et al., 2016). Recent research shows that tree regeneration can fail in the core area of large, high-severity burn patches because of dispersal limitation, highlighting potential negative effects of homogeneous high-severity burn patterns (Shive et al., 2018; Stevens-Rumann & Morgan, 2016; Tepley et al., 2017; Welch et al., 2016). Similar effects seem plausible for understorey plants, especially in the early years after fire, because plants in historical low-severity fire regimes generally must disperse in from outside the high-severity patches, given that few species have adaptations to survive high-severity fire *in situ* (Keeley & Safford, 2016). Indeed, understanding the consequences of the growing size of high-severity burn patches for biodiversity appears to be among the most pressing contemporary challenges for fire ecologists (Steel et al., 2018).

Demonstrating quantitative evidence for an influence of historical contingency on post-fire plant diversity patterns is challenging, because few studies span multiple fire regimes, and it is difficult to compare studies that use different field sampling methods directly. This review highlights a need for geographically extensive studies that span regional gradients in productivity and severity of disturbance and examine community responses at multiple scales to distinguish local- and landscape-level patterns. Dispersal, persistence and stress-tolerance traits might all influence plant community composition in post-fire landscapes (Catano et al., 2017; Hobbs & Huenneke, 1992), but more research is needed to determine the relative importance of each of these in different forest types. Likewise, although it is known that species from certain biogeographical lineages may respond differently to fire (Stevens, Miller, & Fornwalt, 2019; Stevens, Safford, Harrison, & Latimer, 2015), more research using quantitative community phylogenetic diversity patterns in post-fire landscapes could provide deeper insight into the responses of different evolutionary lineages to disturbance. Many studies in our review relied on space-for-time substitutions, where species richness in unburned areas adjacent to fires was assumed to be equivalent to pre-fire richness. Studies that directly compare pre- and post-fire plant communities, however, might allow for more precise estimations of the effects of fire.

In conclusion, our review suggests that plant richness responses to fire severity might correspond to species adaptations to historical fire regimes, but further studies coordinated across multiple fire regimes are needed to address this question.

4.1 | Implications for restoration and management

Planning forest management priorities amid shifting disturbance regimes and other global change pressures represents a substantial conservation challenge. Historical disturbance regimes are an important consideration for conservation planning, but they represent a general starting place rather than a universal blueprint for disturbance management (Safford, Hayward, Heller, & Wiens, 2012). Restoration of historical fire regimes does not necessarily reproduce desired conditions, especially under an altered climate, and can even lead to undesirable state changes (Flatley & Fulé, 2016). Many studies we reviewed from FRG I found that fire alone had weak effects on plant diversity in dense forest stands, but that plant diversity increased substantially when thinning and fire were applied sequentially (Supporting Information Table S1.1; Dodson et al., 2008; Dodson & Peterson, 2010; Wayman & North, 2007), highlighting that active restoration practices can help to make up for a century of missed fire cycles more rapidly. Thinning also reduces the probability of future high-severity fires (Safford, Stevens, et al., 2012; Strom & Fulé, 2007), thereby providing further potential long-term benefits to plant diversity in FRG I forests that have become denser than under historical conditions. Conversely, although it might be justified from the standpoint of the fire risk to humans, thinning that reduces fire severity could potentially have negative effects on plant diversity in forests historically characterized by high-severity fire (Noss, Franklin, Baker, Schoennagel, & Moyle, 2006).

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DATA AVAILABILITY STATEMENT

All data used in this review are included in the manuscript and the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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