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Biogeography of fire regimes in western U.S. conifer forests: A trait-based approach

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Abstract

Aim: Functional traits are a crucial link between species distributions and the ecosystem processes that structure those species' niches. Concurrent increases in the availability of functional trait data and our ability to model species distributions present an opportunity to develop functional trait biogeography (i.e., the mapping of functional traits across space). Functional trait biogeography can improve process-based predictions about the resistance of certain species assemblages to changing environmental conditions across landscape scales. We illustrate this concept by developing the first trait-based, quantitative ranking of fire resistance (adult tree survival) in North American conifer species and mapping that fire resistance across space.

Location and time period: Western continental USA, present day.

Major taxa studied: Twenty-nine common conifer tree species.

Methods: We compiled six traits for each species: three relating to tree morphology and three relating to litter flammability. We combined these traits into a single fire resistance score and used community-weighted averaging to estimate the fire resistance scores of different forest communities, using interpolated species distribution and relative abundance data.

Results: Species associated historically with frequent fire have high fire resistance scores (e.g., *Pinus ponderosa*), reflected by thick bark, tall crowns and flammable litter. Species associated with subalpine or arid conditions have low fire resistance scores (e.g., *Picea engelmannii* and *Pinus edulis*), reflected by thin bark, short stature, poor self-pruning and low litter flammability. A map of forest community fire resistance across the western USA reveals agreement with independent assessments of historical fire regimes, while also identifying areas where community-wide species traits might be mismatched with historical fire regimes.

Main conclusions: Quantifying the functional traits that confer resistance to tree-killing fire provides a direct link between ecosystem disturbance and community resistance. Understanding this link is crucial to evaluation of the long-term resilience of different forest types under dynamic fire regimes. Our work represents the first known spatial representation of fire resistance traits at a regional scale and, as such,

provides a link between functional traits and biogeography relevant to a critical ecosystem process.

KEYWORDS
bark thickness, conifer, fire ecology, flammability, functional trait biogeography, resistance

1 | INTRODUCTION

Functional traits have become a crucial component of community ecology in the past decade, improving our understanding of how environmental niches are expressed by shared traits (McGill, Enquist, Weiher, & Westoby, 2006). Despite rapidly expanding databases of functional trait information, particularly for plants (Kattge et al., 2011), studies of niche dynamics using functional traits often focus at relatively fine spatial scales (Messier, McGill, & Lechowicz, 2010), and scaling up functional trait studies to describe ecosystem processes at broader landscape scales (from tens of hectares to continental scales) has been challenging (Funk et al., 2017). Advances in remote sensing and species distribution modelling have created an opportunity to integrate landscape models of species abundances with functional trait information via the concept of functional trait biogeography (Violle, Reich, Pacala, Enquist, & Kattge, 2014). To illustrate how ecosystem processes might select for and filter species at broad spatial scales, we apply a functional trait biogeography approach to describe the regional variation in adaptations to frequent surface fire within conifer-dominated forests and woodlands of the western USA.

Mapping of historical and contemporary fire regimes is useful to model spatial variation in the characteristic ecosystem response to wildland fire across a landscape (Schoennagel & Nelson, 2011). Such models are generally based on historical fire return intervals, climate, predominant vegetation and biophysical models that link these parameters (Rollins, 2009). Implicit in these models, particularly in forested ecosystems, is the recognition that there is functional trait variation among species of the predominant vegetation (e.g., trees) that influences the likelihood of the tree surviving a fire (Figure 1). Some functional traits of trees (e.g., thick bark) promote survival during fire through protective structures that reduce fire exposure, whereas others (e.g., flashy litter) can alter the fire spread and intensity by influencing the fuel environment (Hood, Varner, van Mantgem, & Cansler, 2018; Keeley, Pausas, Rundel, Bond, & Bradstock, 2011). It is common practice to rank species along a continuum from "fire tolerant" to "fire intolerant" (e.g., Brown & Smith, 2000; Safford & Stevens, 2017), but species rankings are often based on a qualitative understanding of the natural history of species rather than a quantitative assessment of traits associated with surviving fire.

Frequent fire within the life span of a tree can promote the selection of fire resistance traits over the evolutionary history of certain tree species (i.e., morphological characteristics that improve plant survival after a low- to moderate-intensity fire; Keeley et al., 2011; Pausas, 2015a). We conceptualize fire resistance (or fire tolerance) as the ability of mature trees to withstand surface fire; this is analogous to a "fire-tolerating" life-history strategy, in which traits promote the survival of aboveground biomass (Keeley, 2012; Pausas, 2015b). We distinguish this fire adaptation strategy from other fire-adapted life histories, such as "fire-embracing" strategies (Keeley, 2012), which involve loss of aboveground biomass and post-fire regeneration via resprouting or serotiny and may be adaptive under less frequent, higher-intensity fire regimes (Pausas, Keeley, & Schwilk, 2017; Schwilk & Ackerly, 2001), and fire-avoiding strategies, which involve ecosystems that burn infrequently and do not select for fire-adaptive traits. We chose to focus on fire resistance rather than fire-embracing traits in our analysis because the degree of fire resistance of different species is hypothesized to be strongly associated with the frequency and spatial extent of surface fire in forests of the western USA (Safford & Stevens, 2017; Steel, Safford, & Viers, 2015), and there is strong morphological variation among widespread species. Furthermore, the question of post-fire recovery, which is influenced by fire-embracing traits, dispersal traits and seedling niche requirements, is distinct from the question of which species are best adapted to survive frequent fires, which is the dimension of fire regimes we are considering here.

A set of traits associated with fire resistance (thick bark, a high degree of self-pruning lower branches and tall maximum heights) are often correlated with one another (Schwilk & Ackerly, 2001; Varner, Kane, Hiers, Kreye, & Veldman, 2016). Bark thickness is strongly associated with tree survival of low- to moderate-intensity surface fires (Lutes & Keane, 2017; Pausas, 2015a), whereas greater tree heights and self-pruning of lower branches reduce the likelihood that fire will enter the crown and kill the tree via crown scorching or torching (Schwilk & Ackerly, 2001).

Litter flammability traits may also be associated with tree sensitivity to fire in forests where litter fuels are important drivers of fire intensity and spread (Varner, Kane, Kreye, & Engber, 2015). Under a two-dimensional flammability trait space (Pausas et al., 2017), "fast-flammable" evolutionary strategies are generally associated with greater flame lengths, percentage consumption and rates of spreading (Supporting Information Figure S1b,c, axis 1; Pausas et al., 2017), but with a shorter duration of burning and total heat release (Supporting Information Figure S1b,c, axis 2). Conversely, "hot-flammable" strategies are generally associated with moderate flame lengths, percentage consumption and rates of spreading, but longer duration of burning and more total heat release. "Non-flammable" species generally inhibit ignition and have lower values for all flammability traits. Species with thick bark and high self-pruning also

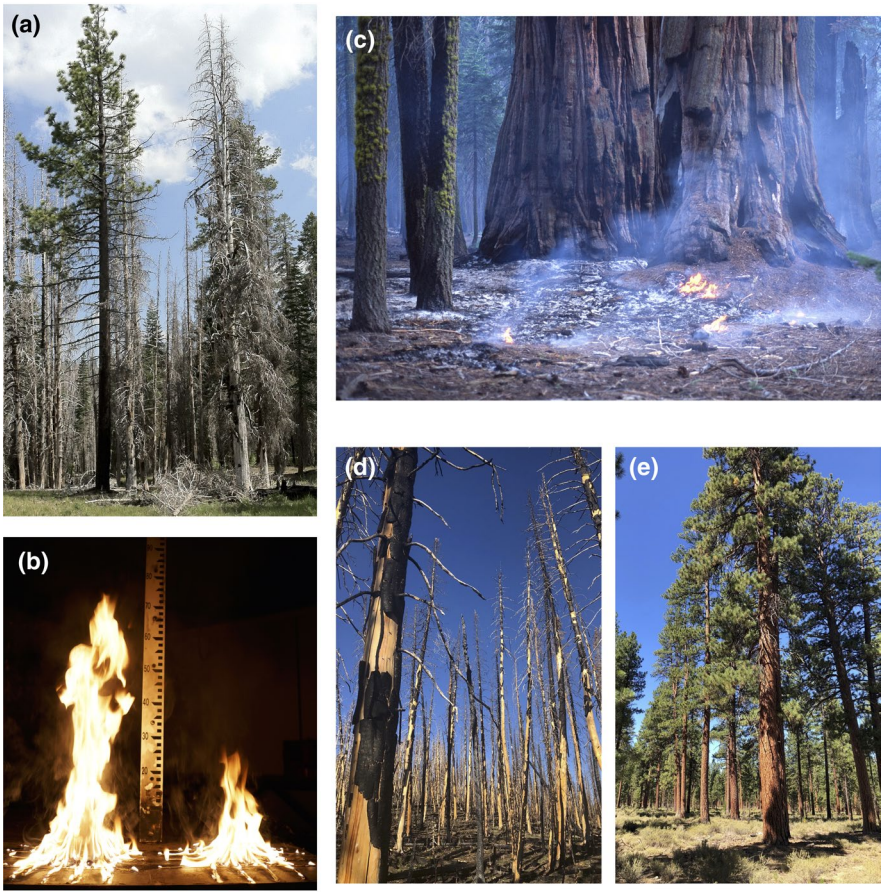

FIGURE 1 Examples of fire resistance and flammability traits of different conifer species. (a) *Pinus jeffreyi* (left) and *Pinus contorta* (right) after the 2012 Reading Fire, Lassen National Park, CA, USA. The two species experienced similar fuel environments (fairly open grown), with *Pinus jeffreyi* surviving and *Pinus contorta* dying. Note the lower profile of branches on *Pinus contorta*, indicating a lower degree of self-pruning. (b) Example of litter flammability differences in *Pinus jeffreyi* (left) and *Pinus contorta* (right), with *Pinus jeffreyi* having longer flame lengths and shorter flame durations than *Pinus contorta* for a given mass of fuel (Table 1). (c) The North American conifer with the thickest bark, *Sequoiadendron giganteum*, during a prescribed fire in Sequoia National Park, CA, USA. (d) Stand of fire-intolerant *Picea engelmannii* killed by fire, Fishlake National Forest, UT, USA. (e) Stand of fire-tolerant *Pinus ponderosa* that has survived several fires on the Deschutes National Forest, OR, USA. Photographic credits: (a) Jens Stevens; (b) Fred Ackerman; (c) Dylan Schwilk; and (d, e) J. Morgan Varner [Colour figure can be viewed at wileyonlinelibrary.com]

tend to have leaf litter conducive to "fast-flammable" fire behaviour (Supporting Information Figure S1a), which may promote tree survival by promoting rapid spread of fire with lower residence times and minimizing cambial exposure to lethal temperatures (Pausas, 2015a; Varner et al., 2015). In some cases, such leaf litter traits are associated with shade-intolerant and fire-dependent species that experience frequent fire (de Magalhaes & Schwilk, 2012; Schwilk & Caprio, 2011), whereas species that are less likely to experience fire during their lifetimes, owing to a combination of climate and fuel limitation, may experience less selective pressure to develop these "fast-flammable" traits (Keeley et al., 2011; Pausas et al., 2017).

The collective ability of trees to resist fire is one indicator of forest resilience to the increase in fire activity expected across western North America in the future under increased human development and climate change (Johnstone et al., 2016). Historical fire exclusion has shifted the composition of species in some regions away from more fire-resistant species and towards fire-sensitive species (Safford & Stevens, 2017). It is therefore crucial to describe the current condition of forest communities as a function of the ability of the constituent species to survive low- to moderate-intensity fire as adults.

We quantified the biogeography of fire resistance (adult tree survival) in tree communities across the western USA by integrating functional traits with spatially explicit data on species distributions and abundance. We used this approach to highlight important spatial variation in fire resistance across forested landscapes, to provide an independent assessment of other spatial models of fire regimes and to identify areas where the current species composition is mismatched with historical and future expected fire frequency. This study focused on data-rich conifer forests of the western USA, but the methods used here may be applied to other regions where variation in adaptive fire regimes is used to guide management decisions (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015).

2 | METHODS

2.1 | Quantification of functional traits

We assembled a quantitative trait database on six fire-adaptive traits that contribute to fire resistance of western North American conifer species. We selected conifer tree species for analysis based on the species database of the U.S. Forest Service Forest Inventory and Analysis (FIA) National Core Field Guide (USDA Forest Service FIA Program, 2014). We selected species classified by FIA as "Western" that also had spatially explicit basal area data available (see section 2.2). Our resulting trait database consisted of 29 widespread conifer species in western North America (our "study species"; Table 1).

Our trait database included three traits relating to tree morphology (bark thickness, maximum tree height and degree of self-pruning) and three traits relating to litter flammability (flame length, percentage consumption and flame duration). We estimated the bark thickness of a 25.4 cm diameter at breast height (d.b.h.) tree using the species-specific bark thickness multipliers from the First Order Fire Effects Model (Lutes & Keane, 2017). These multipliers assume a linear rate of bark accumulation with diameter at breast height, which is an oversimplification for many species (Jackson, Adams, & Jackson, 1999), but they are currently the most widely used trait in models of fire-caused mortality, and they capture general differences among species (Lutes & Keane, 2017). Maximum tree height was derived from the TRY plant trait database (Kattge et al., 2011). The degree of self-pruning was assigned on an ordinal 1–10 scale, following the methods and data for the genus *Pinus* from Keeley and Zedler (1998) and Schwilk and Ackerly (2001), supplemented with data for other genera from the Fire Effects and Information System (FEIS, 2013).

Flammability data on maximum flame length, percentage litter consumption and flame duration for 16 conifer species were obtained from Fonda (2001; n = 2), Fonda, Belanger, and Burley (1998; n = 8), E. M. Banwell and J. M. Varner (unpublished data; n = 5) and J. M. Kane (unpublished data; n = 1); species-specific sources are shown in Table 1. We conducted additional litter flammability trials for 13 species for which data did not exist from previous studies. All flammability data included in this study followed consistent methods that have also been used in other regions (Kane, Varner, & Hiers, 2008; Varner et al., 2015). Flame length and percentage consumption were tightly correlated (Pearson's r = .93; Supporting Information Figure S1); therefore, to avoid double-counting, we performed a principal components analysis of those two traits and used the first axis (PC1; explaining 96.7% of the variance) to account for these two traits simultaneously (Table 1). Flame length and percentage consumption were correlated nonlinearly with flame duration, with the shortest flame durations being associated with both the shortest flame lengths and the longest flame lengths (Supporting Information Figure S1). Together, PC1 and flame duration represent two-dimensional trait space of Pausas et al. (2017) for litter flammability (Supporting Information Figure S1b,c).

We aggregated the three tree morphology traits and two flammability traits described above for each species by standardizing each trait and then averaging them into a single fire resistance score (FRS; range zero to one). Specifically, for each species we calculated the percentile of its trait value within the range of observed values for all species, with the most fire-resistant trait value assigned a percentile of one and the least fire-resistant value assigned a percentile of zero. We defined the most fire-resistant form of a trait as the thickest bark, tallest maximum height, greatest degree of self-pruning, shortest flame duration, and the combined tallest flame length and highest percentage consumption using PC1 as described above. The FRS for each species was then calculated as the average of its five percentile scores for the six traits (Table 1).

2.2 | Mapping and interpreting functional traits

We developed a community FRS layer by weighting the FRS of each individual species by its relative abundance in the community (range 0–100%, inclusive), using a layer of imputed basal area for each study species across the western USA. Specifically, for each study species we used a geospatial raster layer of estimated basal area (in square metres per hectare) at 250 m resolution across the western USA (Wilson, Lister, Riemann, & Griffith, 2013). These data are based on imputed basal area per species derived from FIA plots and remotely sensed data layers, using statistical relationships between basal area and climatic and topographic variables. Validation suggests fairly high accuracy, particularly for widespread species (Riemann, Wilson, Lister, & Parks, 2010; Wilson et al., 2013). We first identified our area of focus (conifer forests) by calculating the total basal area per pixel of all 29 study species, relative to the total basal area of all other tree species from the same dataset, most of which were hardwood (angiosperm) species. We restricted our analysis to only those areas where > 50% of the total tree basal area was composed of our study species, and where the basal area of our study species exceeded 5 m^2/ha. We then estimated the relative basal area fraction of each of our study species within each pixel and multiplied the FRS of each species by its relative abundance in a given pixel (which could include zero) to derive a community-weighted mean FRS at the pixel scale.

We compared the community FRS map with LANDFIRE-derived indices of historical (pre-Euro-American settlement) fire regimes (www.landfire.gov), using the fire regime group (FRG) and mean fire return interval (FRI) layers. The FRG and FRI layers were resampled (using the modal pixel value at 30 m resolution) to the same spatial resolution as our FRS data (250 m). We conducted statistical tests of FRS values by overlaying our map with maps of FRG and FRI and randomly selecting a 1% (n = 94,901) subsample of the forested cells from the full landscape. For the FRG product, we compared community FRS scores among three forest FRGs: high frequency/low severity (group 1); intermediate frequency and severity (group 3); and low frequency/high severity (group 5), testing for significant differences using an ANOVA in R. The FRI product classifies pixels as having

TABLE 1 Trait data and fire resistance scores for widespread western U.S. conifers used in the analysis

	Trait values[1]						Percentile of range (standardized values)					
Scientific name	Bark thickness	Plant height	Self-pruning	Flame length[2]	Percentage consumed[2]	Flame duration[2]	Bark thickness	Plant height	Self-pruning	PC1[3] of fl and pc	Flame duration[4]	FRS
Sequoia sempervirens	2.06	95.2	5	59.4[a]	86.1	73.4	1.00	1.00	0.44	0.85	0.87	0.83
Pinus jeffreyi	1.73	51.4	10	67.3[b]	90.0	79.2	0.78	0.48	1.00	0.93	0.82	0.80
Pinus ponderosa	1.60	41.2	10	77.0[b]	92.0	79.7	0.69	0.35	1.00	1.00	0.81	0.77
Pinus lambertiana	1.83	62.3	10	55.6[a]	77.1	128.5	0.85	0.61	1.00	0.76	0.48	0.74
Sequoiadendron giganteum	2.06	85.6	8	42.6[a]	75.8	148.5	1.00	0.89	0.78	0.67	0.38	0.74
Larix occidentalis	1.60	51.1	9	27.9[d]	34.6	89.9	0.69	0.47	0.89	0.27	0.73	0.61
Pinus monticola	0.89	62.1	6	75.1[c]	82.8	90.3	0.22	0.60	0.56	0.92	0.72	0.60
Chamaecyparis lawsoniana	2.06	50.0	6	21.7[d]	31.4	115.6	1.00	0.46	0.56	0.21	0.55	0.55
Calocedrus decurrens	1.52	48.1	5	25.3[d]	46.6	105.0	0.64	0.44	0.44	0.34	0.62	0.50
Abies amabilis	1.19	51.3	5	38.4 [a]	32.0	79.8	0.42	0.47	0.44	0.31	0.81	0.49
Pseudotsuga menziesii	1.60	54.3	5	26.2[a]	26.6	105.8	0.69	0.51	0.44	0.20	0.61	0.49
Abies concolor	1.22	46.3	4	22.9[d]	44.5	97.3	0.44	0.42	0.33	0.31	0.67	0.43
Thuja plicata	0.89	51.2	5	42.4[a]	45.7	113.2	0.22	0.47	0.44	0.44	0.57	0.43
Abies grandis	1.17	59.4	4	15.1[d]	14.2	88.9	0.41	0.57	0.33	0.03	0.74	0.42
Abies procera	1.14	55.1	5	14.6[d]	22.8	101.4	0.39	0.52	0.44	0.10	0.64	0.42
Tsuga heterophylla	1.02	48.1	4	24.6[a]	18.8	68.4	0.31	0.44	0.33	0.13	0.92	0.42
Abies magnifica	0.99	46.8	5	18.0[d]	32.1	101.7	0.29	0.42	0.44	0.19	0.64	0.40
Pinus contorta	0.71	26.1	3	58.1[c]	79.9	101.2	0.10	0.17	0.22	0.79	0.64	0.39
Chamaecyparis nootkatensis	0.56	35.4	6	48.0[d]	65.7	134.1	0.00	0.29	0.56	0.63	0.45	0.38
Tsuga mertensiana	1.02	25.0	5	15.4[d]	27.9	118.0	0.31	0.16	0.44	0.14	0.54	0.32
Abies lasiocarpa	1.04	27.4	2	16.7[a]	25.6	79.8	0.32	0.19	0.11	0.13	0.81	0.31
Picea sitchensis	0.69	27.1	2	10.0[e]	13.7	60.9	0.08	0.19	0.11	0.00	1.00	0.28
Pinus flexilis	0.76	17.1	2	55.3[c]	71.7	154.6	0.14	0.07	0.11	0.71	0.35	0.28
Juniperus scopulorum	0.84	11.6	2	32.4[d]	55.3	117.9	0.19	0.00	0.11	0.45	0.54	0.26
Picea engelmannii	0.91	37.2	2	17.1[d]	28.7	122.9	0.24	0.31	0.11	0.16	0.51	0.26
Juniperus occidentalis	0.64	15.9	2	25.7[d]	47.9	107.7	0.05	0.05	0.11	0.36	0.60	0.23
Pinus albicaulis	0.76	17.6	1	48.4[c]	63.4	182.9	0.14	0.07	0.00	0.61	0.23	0.21

(Continues)

TABLE 1 (Continued)

Scientific name	Trait values[1]						Percentile of range (standardized values)					
	Bark thickness	Plant height	Self-pruning	Flame length[2]	Percentage consumed[2]	Flame duration[2]	Bark thickness	Plant height	Self-pruning	PC1[3] of fl and pc	Flame duration[4]	FRS
Picea glauca	0.64	16.3	2	16.0[d]	29.1	102.3	0.05	0.06	0.11	0.15	0.64	0.20
Pinus edulis	0.81	13.5	1	40.0[c]	62.2	253.9	0.17	0.02	0.00	0.55	0.00	0.15

Note: The table is ordered by decreasing fire resistance score (FRS). The first set of values reflects measured values and the second reflects standardized values.

1. Units for measured trait values are centimetres (bark thickness; for a 25.4 cm d.b.h. tree), metres (tree height), scale of 1–10 (self-pruning), seconds (flame duration), centimetres (flame length) and percentage consumed of 0–100 (percentage consumed).
2. Sources for flammability data (footnotes in Flame length column only) are as follows:
   a. Fonda et al. (1998).
   b. Fonda (2001).
   c. E. M. Banwell and J. M. Varner, unpublished data.
   d. Measured for this study.
   e. J. M. Kane, unpublished data.
3. Flame length (fl) and percentage consumed (pc) were closely correlated (r = .93); traits were combined in ordination, and the first principal component (PC1) was used to calculate FRS.
4. Percentiles of range for flame duration calculated on a logarithmic scale.

mean fire return intervals within a range of years (e.g., classes of 0–5 and 6–10 years); we simplified this classification by merging them into fewer classes and assigning the median fire return interval of the merged classes to the pixel value (5, 15, 25, 35, 50, 100, 200 and 500 year return intervals). For the FRI product, we tested whether community FRS values decreased as a function of lengthening fire return intervals, using linear regression in R.

To quantify potential mismatches between historical fire regimes and current species composition, we identified forest areas where the current species composition might be more or less resistant to fire than expected given LANDFIRE-estimated historical fire frequency. Specifically, we sought to identify: (a) fire-sensitive forests with frequent historical fire ("vulnerable–frequent"); (b) fire-sensitive forests with intermediate historical fire frequencies ("vulnerable–intermediate"); (c) fire-resistant forests with intermediate historical fire frequencies ("resistant–intermediate"); and (d) fire-resistant forests with infrequent historical fire ("resistant–infrequent"). Groups 1 and 2 are indicative of areas that might have experienced colonization by fire-sensitive species in response to fire suppression, whereas groups 3 and 4 are indicative of areas where other factors might have limited the historical fire frequency despite the presence of species capable of surviving fire. We defined frequent fire as 1–20 year FRI, intermediate fire as 41–150 year FRI, and infrequent fire as 151–300 year FRI, based on LANDFIRE classifications. We calculated the FRS percentile of every pixel of a given fire frequency class and identified the 20% of pixels on either the fire-resistant or fire-vulnerable tails of the distribution within that fire frequency class.

3 | RESULTS

The trait values for our 29 conifer species (Table 1) were significantly correlated among bark thickness, tree height and self-pruning, but less so amongst flammability traits of flame length and flame duration (Supporting Information Figure S1). Fire resistance scores ranged from a high of 0.83 for *Sequoia sempervirens* (coast redwood) to a low of 0.15 for *Pinus edulis* (piñon pine). The fire resistance scores segregated ordinally into four groups, which reflected our a priori knowledge of the species in question (Table 1; Figure 2). The five highest-ranking species inhabit historically frequent-fire ecosystems (e.g., fire regime group 1) and have well-documented fire scar records, including *Pinus ponderosa* and *Sequoiadendron giganteum* (FEIS, 2013). The next three species (*Larix occidentalis*, *Pinus monticola* and *Chamaecyparis lawsoniana*) are commonly found in mixed-conifer stands with historically frequent fire, but are rarely the dominant species in those stands. A large group of 11 species in the middle of the rankings includes many species found in more mesic mixed-conifer stands that often occupy shade-tolerant and late-seral niches, ranging from *Calocedrus decurrens* at the high end, a common secondary component of *Pinus ponderosa* forests in California that is fire-resistant as an adult, to *Pinus contorta* at the lower end, a borderline subalpine species that is known to have high post-fire mortality (Figure 2). Finally, the 10

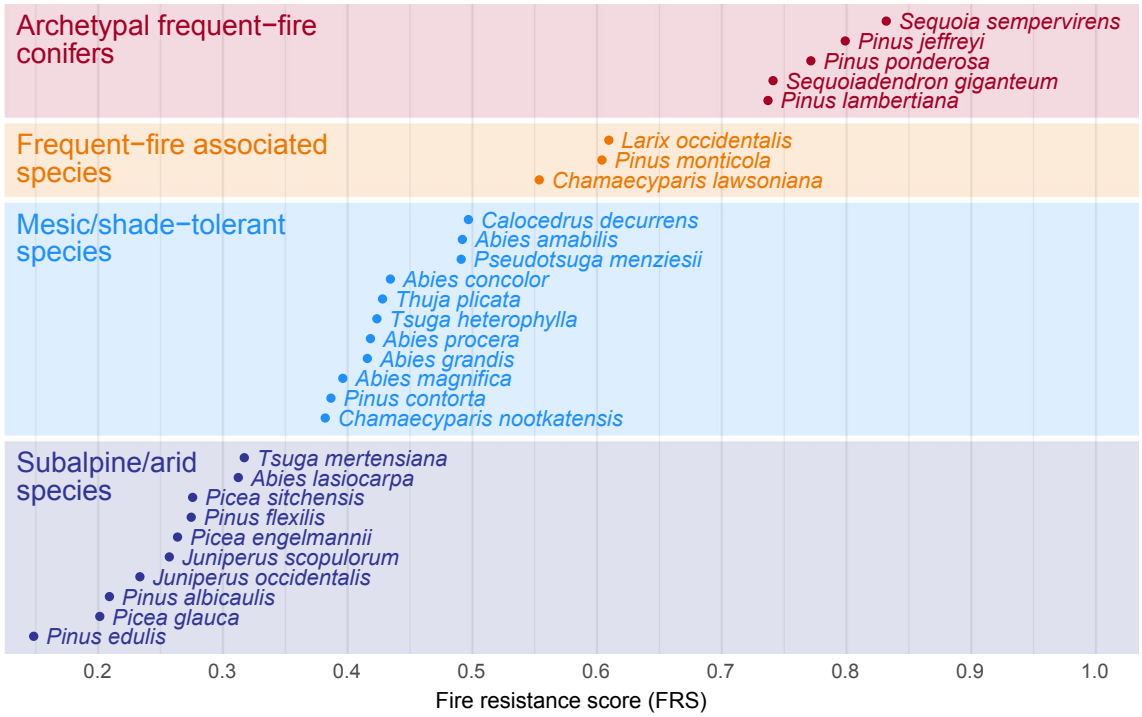

FIGURE 2 Ecological grouping of 29 conifer species by fire resistance scores (FRS). Scores on the *x* axis are derived from a combination of six functional traits for each species. Species are rank ordered on the *y* axis and categorized broadly by their fire ecology associations; groupings do not imply functional equivalence within groups [Colour figure can be viewed at wileyonlinelibrary.com]

lowest-ranking species occupy marginal forests and woodlands at either higher subalpine elevations (e.g., *Abies lasiocarpa* and *Picea engelmannii*) or lower arid elevations (e.g., *Juniperus scopulorum* and *Pinus edulis*), where fires are historically less common (e.g., fire regime group 5). We note that the breakpoints among these groups are rather arbitrary because fire resistance traits are continuous; we intend these groupings to be a heuristic to reflect common species groupings rather than fixed communities.

Community fire resistance (FRS) varied across the western USA (Figure 3) and was consistent with LANDFIRE estimates of FRG (Supporting Information Figure S2) and FRI (Supporting Information Figure S3). The FRS was greater in FRG 1 (frequent) than in either of the other FRGs analysed (Figure 4; t = −115.1, d.f. = 96,205, p < .0001). The FRS also decreased significantly with increasing FRI (Figure 4; slope significantly different from zero; t = −54.54, d.f. = 134,451, p < .0001); however, the median FRS increased in the longest FRI class (> 300 years, classified as 500 years in our regression analysis; Figure 4).

Some regions with long FRIs (Supporting Information Figure S3) were identified in our mismatched fire regime analysis as having more fire-resistant modern communities than independent assessments of fire regimes would suggest (Figure 5). This is particularly true on the west slopes of the Cascade Range and inner Coast Range of Oregon. Fire-resistant communities with intermediate rather than long FRIs tended to be located on the margins of the Columbia Plateau and the Colorado Front Range. Conversely, the most fire-intolerant modern communities with short FRIs tended to be located on arid woodland margins and in mixed-conifer stands in the Southwest, mixed-conifer stands of California, and mixed ponderosa pine–lodgepole pine stands of eastern Oregon.

4 | DISCUSSION

By mapping functional traits across a landscape and comparing patterns with independent data on relevant ecosystem processes, we illustrate how functional trait biogeography can be used to construct geographical layers of adaptive niche environments; in this case, niches structured by and adaptive to frequent surface fire. Such approaches promise to be valuable for scaling up functional traits to gain a better understanding of ecosystem processes (Funk et al., 2017). In this study, changes to those processes, such as increasing fire frequency with climate change or increases in fuel loads that promote high-severity fire, may result in niche shifts that result in further disequilibrium between environmental conditions and the adaptive traits of the dominant trees in the community. Functional traits, such as those that confer fire resistance, are adaptive in certain conditions (Schwilk & Ackerly, 2001), but might not be adapted to future conditions (Keeley et al., 2011). Thus, the incorporation of functional traits into biogeographical studies provides a direct link to the adaptive processes relevant to sustaining particular species in a rapidly changing environment. In this study, we provide that direct link between traits that are adaptive to survival of relatively frequent low- to moderate-intensity surface fire (Figure 3), and the prevalence of historical surface fire in those forest community types (Figure 4).

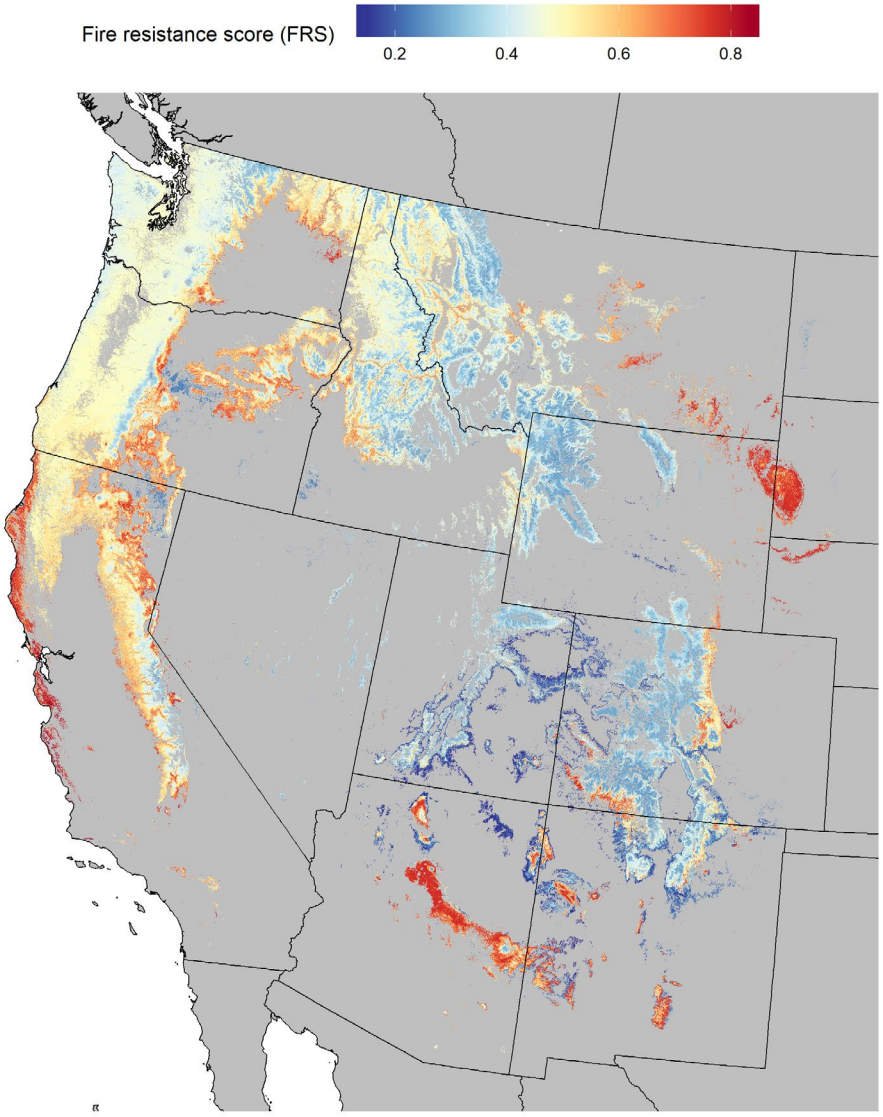

FIGURE 3 Community-weighted mean fire resistance scores (FRS) across the western USA. Scores range from low fire resistance (zero) to high fire resistance (one); FRS raster layer resolution is 250 m [Colour figure can be viewed at wileyonlinelibrary.com]

Although the spatial patterns of fire-resistant communities we identified are generally congruent with prior assessments of historical fire regimes, locations where communities appear relatively mismatched to fire regimes (Figure 5) are instructive about the ecology underlying the biogeographical patterns. For instance, FRI values > 300 years (generally associated with FRG 5) are common in the western slopes of the Cascade Range in the Pacific Northwest, where forest biomass is very high, but high precipitation and atmospheric moisture limit favourable conditions for fire spread. This area has the most fire-resistant functional traits of all infrequent FRI areas ("resistant–infrequent"; Figure 5) and is dominated by the moderately fire-resistant Douglas fir (*Pseudotsuga menziesii*; Table 1). However, if fuel loads are high and weather conditions extreme, the resulting crown fires can overwhelm the adaptations of even the most fire-resistant species (Rollins, 2009). Fuel loads in the western Cascades, for instance, are generally fairly high and would be likely to overwhelm trait-based fire resistance in these forests in the event of a fire. Likewise, the redwood forests of coastal California are dominated by a very fire-resistant species (*Sequoia sempervirens*) in a region where fire is often ignition limited; however, traits are not mismatched because this region has a record of historically frequent fire (Supporting Information Figure S3), probably attibutable, in part, to Native American influence and the very close proximity to drier, fire-prone interior forests and woodlands (Steel et al., 2015; Varner & Jules, 2017).

The modern abundance of fire-sensitive species in landscapes where dendroecological reconstructions indicate historically frequent fire ("sensitive–frequent"; Figure 5) might suggest past high-severity fire if residual fire-resistant species are absent (Yocom-Kent, Fulé, Bunn, & Gdula, 2015), or infilling by fire-sensitive species owing to the absence of frequent surface fire if residual fire-resistant species are present (Margolis, 2014; Stevens et al., 2016). We identified such "sensitive–frequent" areas that include mixed-conifer forests of northern California, the eastern slopes of the northern Cascade Range and the southern Rocky Mountains, in addition to lower montane forests of the Southwest, where the fire-sensitive *Pinus edulis* and several *Juniperus* species often grade into fire-resistant *Pinus ponderosa* forest (Figure 5). Many of these mismatches

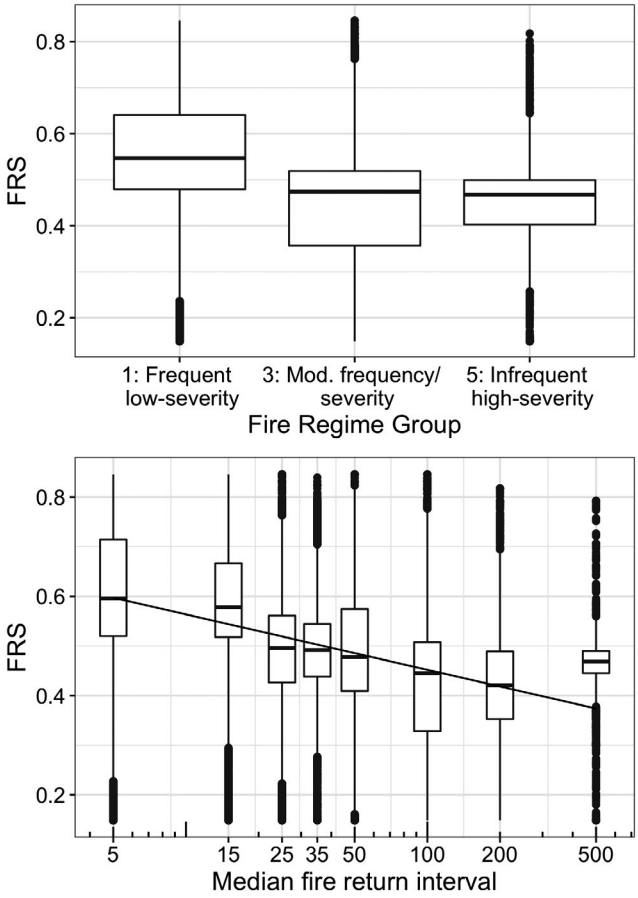

FIGURE 4 Comparison of community fire resistance scores (FRS) for three different fire regime groups (top; see Supporting Information Figure S2) and for a range of different fire return intervals (bottom; see Supporting Information Figure S3)

in historically frequent-fire areas are likely to be attributable to the exclusion of fire and the subsequent encroachment of fire-intolerant species (Margolis, 2014); in such areas, the reduction of these fire-intolerant species (via mechanical methods or prescribed fire) is often an objective of restoration (Larson, Belote, Cansler, Parks, & Dietz, 2013; Safford & Stevens, 2017).

An emergent property of forest community fire resistance across the western USA is that the most fire-resistant stands often occupy mid-elevation montane forests (e.g., the northern Kaibab Plateau in Arizona; Figure 3). This is consistent with the relationship between climate, fuels and fire regimes, in which low fuel loads attributable to arid conditions limit fire spread in lower montane regions (e.g., piñon–juniper woodlands) and climate (cold and/or wet conditions) limits fire spread in subalpine or coastal forests where fuel conditions could otherwise support fire spread (Safford & Stevens, 2017; Steel et al., 2015). The least fire-resistant species occupy these elevational extremes (Figure 2), and thus even moderate-intensity surface fires in these regions may lead to extensive tree mortality and rapid community changes (Yocom-Kent et al., 2015).

The development of a standardized FRS allows for future comparative research to account for general but imperfect correlations among different traits that confer resilience to tree-killing fire. Additional traits could be integrated into the FRS, but the traits we present here form the basis for most modern process-driven models of tree response to fire (Hood, McHugh, Ryan, Reinhardt, & Smith, 2007; Pausas et al., 2017). A fire resilience index could also be developed for systems where crown-killing fire is the common fire regime, but would need to incorporate the variation in regeneration methods and optimal fire return intervals (Enright et al., 2015). In general, fire-embracing species possessing either serotiny or resprouting ability are resilient to stand-replacing, high-severity fire, although with ongoing anthropogenic and climate-driven shortening of fire return intervals in such crown-fire-adapted ecosystems, these species are also at risk of population declines (Enright et al., 2015; Turner, Braziunas, Hansen, & Harvey, 2019; Whitman, Parisien, Thompson, & Flannigan, 2019). Furthermore, fire-avoiding species (Keeley, 2012) may also be resilient to stand-replacing fire if tree establishment proceeds during sufficiently long fire-free intervals and if post-fire spatial mosaics of live tree refugia are complex enough for seed dispersal to initiate forest succession.

We focused on fire resistance (crown survival) rather than fire-embracing strategies (post-fire regeneration *sensu* Keeley, 2012) in part because regeneration strategies such as serotiny, which is adaptive under crown fire, occur in relatively few widespread western conifers, such as *Pinus contorta* var. *latifolia* in the Rocky Mountains (Clements, 1910) and *Picea mariana* in the boreal shield (Zasada, 1986). A larger number of serotinous species occur in California (*Pinus attenuata*, *Pinus coulteri*, *Pinus muricata*, *Pinus radiata*, *Pinus torreyana* and several *Hesperocyparis* spp.), but these are generally found in isolated stands, often associated with shrublands (Barbour, 2007). These "fire-embracing" species also tend to score low on measures of fire resistance, such as bark thickness (Schwilk & Ackerly, 2001) and, with the exception of *Pinus contorta* var. *latifolia* and *Picea mariana* (which is concentrated in Canada), these species are not sufficiently widespread to influence biogeographical patterns at the scale we are analysing here. Resprouting in conifers in this region is likewise rare and mostly limited to species with narrow ranges across the western USA (e.g., *Juniperus deppeana* and *Pseudotsuga macrocarpa*), with the notable exception of *Sequoia sempervirens*, which has an unusual fire ecology among conifers (as described above). Thus, the geographical extent and variation among species for fire-embracing traits are less than for fire resistance traits, presenting a unique set of challenges for extending functional trait biogeography to that dimension of fire regime adaptations.

Even within the traits we selected, our FRS index has its limitations. The use of litter flammability in our FRS reflects the second dimension of fire regimes discussed above [the "fire-embracing" (Keeley, 2012) or "hot-flammable" (Pausas et al., 2017) strategy; Supporting Information Figure S1b,c]. This strategy is relevant to crown-fire-dominated systems, but litter fuels are not typically the dominant fuels in those ecosystems, where live fuels from shrubs and trees are stronger drivers of fire behaviour. Forest physiognomy is therefore a driver of fire regimes that is related to, but not captured by, our methodology. We again emphasize that fuels and climate conditions can override trait influences on tree survival during fire, and our FRS index is not meant to be predictive of tree survival

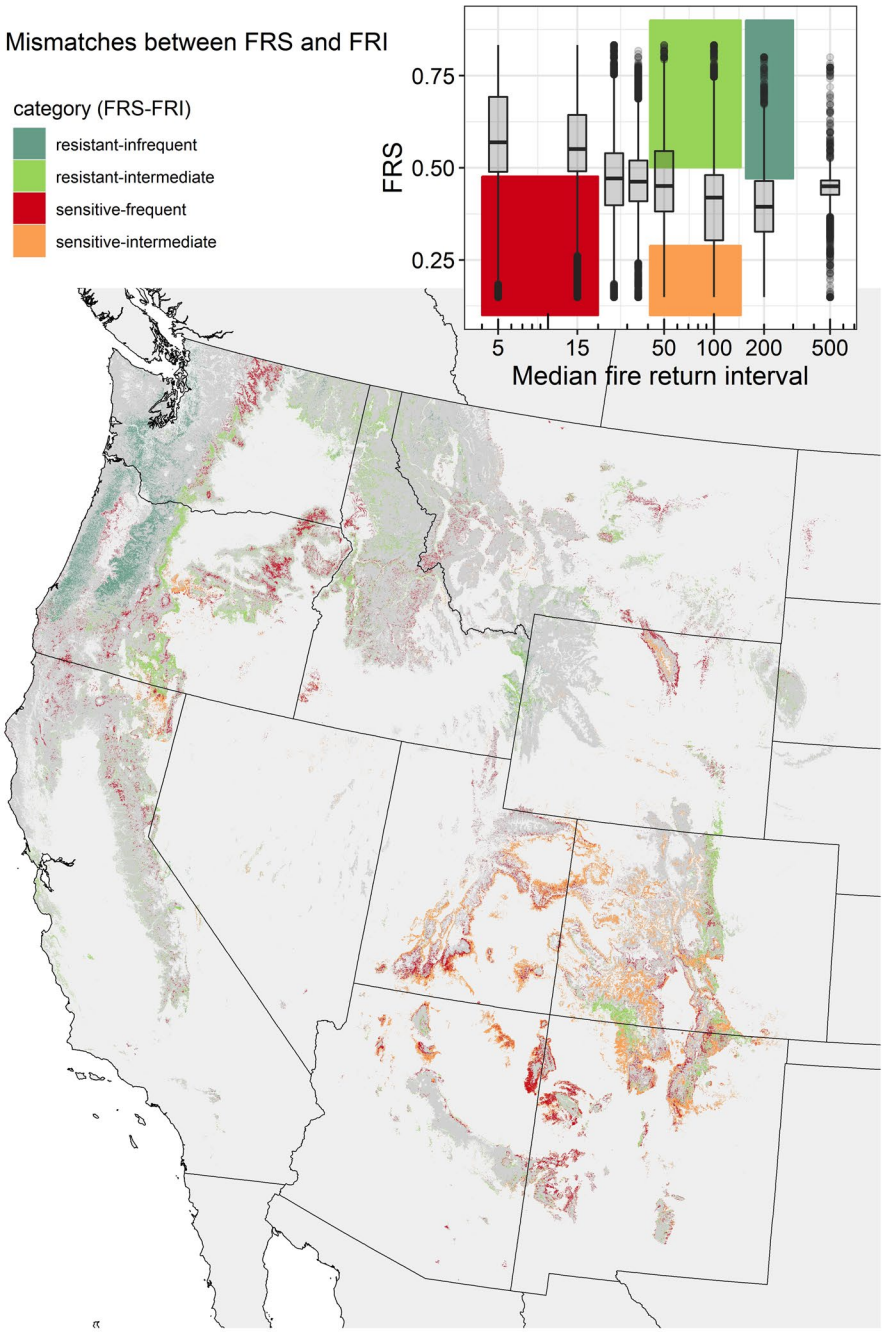

FIGURE 5 Potential mismatches between contemporary fire resistance score (FRS) and historical fire return interval (FRI). "Resistant" areas are defined as the 20% of forested areas with the highest fire resistance scores in areas defined as either intermediate (41–150 year) or infrequent (151–300 year) historical fire return intervals. "Sensitive" areas are defined as the 20% of forested areas with the lowest fire resistance scores in areas defined as either intermediate or frequent (< 20 year) historical fire return intervals [Colour figure can be viewed at wileyonlinelibrary.com]

rates after fire, but instead to generate quantitative support to identify which forest communities would be most resistant to surface fire, given adequate fuel and climate conditions. Our FRS could also be refined with improved data on bark, via better vertical allometry and roughness across multiple species (Jackson, Adams, & Jackson, 1999) that provide a better indication of cambial exposure time to heat from fires. Additional work that quantifies differential sensitivity of species to crown scorch and other fire injuries could be added as those data are developed (Hood et al., 2018). Lastly, availability of both trait data and spatial data for the traits and species we considered was generally limited to the species level (and not to widespread subspecies, as in the diverse *Pinus ponderosa*, *Pinus contorta* and *Pseudotsuga menziesii*); therefore, we did not consider potentially important subspecies-level biogeographical variation that could be incorporated into future work.

Importantly, the application of the FRS concept to landscape biogeographical models is highly sensitive to the processes underlying the biogeographical models; contemporary distribution models, such as those we analysed here (Wilson et al., 2013), reflect a long legacy of change in land use and fire exclusion and do not necessarily reflect the potential type of vegetation under a historical fire regime or a past climate. Future research could apply the FRS concept, and functional trait biogeography more broadly, to reconstructed forest stands such as those generated by predictive vegetation mapping (Maxwell et al., 2014) or other reconstruction methods (Yocom-Kent et al., 2015). Such applications of functional trait biogeography provide a crucial

and often-missing link between individual-scale processes driving plant responses to their environment and synoptic patterns of environmental conditions at much broader spatial and temporal scales.

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DATA AVAILABILITY STATEMENT

Aggregated trait data are made available in the paper itself (Table 1). The spatial fire resistance layer (Figure 3) and data contained in Table 1 are also available via USGS ScienceBase at: https://doi.org/10.5066/P97F5P7L

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BIOSKETCH

The research team is interested in the processes driving forest fire regimes at multiple spatial and temporal scales. The authors have expertise on plant responses to fire, ranging from individual scales (e.g., flammability traits and resistance traits) to landscape scales (e.g., impacts of fire on population, community and ecosystem processes). The authors have also researched plant–fire interactions from relatively short time-scales (e.g., fuel management and ecosystem resilience to disturbance) to long time-scales (e.g., evolutionary responses to climate-driven fire patterns). The main objective of the team is to integrate processes that operate at small scales to gain a better understanding of patterns observed at large scales and, ultimately, to improve decision-making around adaptive management of ecosystems under rapidly changing fire regimes.

SUPPORTING INFORMATION

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

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