**Title**

Biogeography of fire regimes in western US conifer forests: a trait-based approach

**Running Title**

*Functional traits and forest fire regimes*

**Abstract**

Aim

Functional traits are a critical 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 presents 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 United States, present-day.

Major taxa studied

29 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 index, 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 with historically 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 US reveals agreement with independent assessments of historical fire regimes, while also identifying areas where community-wide species traits may 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 critical to evaluating 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 continental scale, and as such provides that link between functional traits and biogeography relevant to a critical ecosystem process.

**Keywords:**

Bark thickness, conifers, fire ecology, flammability, functional trait biogeography, resistance

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**Introduction**

Functional traits have become a critical 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 modeling 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 may select for and filter species at broad spatial scales, we apply a functional trait biogeography approach to describe regional variation in adaptations to frequent surface fire within conifer-dominated forests and woodlands of the western U.S.

Mapping of historical and contemporary fire regimes is useful to model spatial variation in 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, while 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 species’ natural history rather than a quantitative assessment of traits associated with surviving fire.

Frequent fire within the lifespan 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 following 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 where 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 U.S. (Safford and Stevens 2017; Steel et al. 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 et al., 2016). Bark thickness is strongly associated with tree survival of low- to moderate-intensity surface fires (Lutes & Keane, 2017; Pausas, 2015a), while 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 spread[.](#_ENREF_21) Under a two-dimensional flammability trait space (Pausas et al., 2017), “fast-flammable” evolutionary strategies are generally associated with greater flame lengths, percent consumption, and spread rates (Fig. S1 b,c, axis 1, Pausas et al. 2017), but with shorter duration of burning and total heat release (Fig. S1 b,c, axis 2). Conversely, “hot-flammable” strategies are generally associated with moderate flame lengths, percent consumption and spread rates, but longer duration of burning and more total heat release. “Non-flammable” species generally inhibit ignition and have lesser values for all flammability traits. Species with thick bark and high self-pruning also tend to have leaf litter conducive to “fast-flammable” fire behavior (Fig. S1a), which may promote tree survival by promoting rapid fire spread with lower residence times and minimizing cambial exposure to lethal temperatures (Pausas, 2015a; Varner, Kane, Kreye, & Engber, 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, due 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 species composition in some regions away from more fire-resistant species toward fire-sensitive species (Safford & Stevens, 2017). It is therefore critical to describe the current condition of forest communities as a function of constituent species’ ability to survive low-moderate intensity fire as adults. We quantified the biogeography of fire resistance (adult tree survival) in tree communities across the western United States by integrating functional traits with spatially-explicit data on species distributions and abundance. We use 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 focuses on data-rich conifer forests of the western U.S., 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).

**Methods**

*Quantifying 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 US 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 below). 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, percent consumption, and flame duration. We estimated the bark thickness of a 25.4 cm (10 in) diameter at breast height (dbh) 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 dbh, 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). 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), supplementing with data for other genera from the Fire Effects and Information System (FEIS, 2013).

Flammability data on maximum flame length, percent litter consumption, and flame duration were obtained from Fonda (2001), Fonda, Belanger, and Burley (1998), Banwell and Varner (unpublished data) and Kane (unpublished data). We conducted additional litter flammability trials for species in our database for which data did not exist. All flammability data included in this study followed consistent methods that have also been used in other regions (e.g., Kane, Varner, & Hiers, 2008). Flame length and percent consumption were tightly correlated (Pearson’s r = 0.93; Fig. S1), so to avoid double-counting we performed a principal component analysis of those two traits and used the first axis (PC1), which explained 96.7% of the variance, to account for these two traits simultaneously (Table 1). Flame length and percent consumption were non-linearly correlated with flame duration, with the shortest flame durations associated with both the lowest flame lengths and the highest flame lengths (Fig. S1). Together, PC1 and flame duration represent Pausas et al. (2017)’s two-dimensional trait space for litter flammability.

We aggregated the three fire-resistance 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 0-1). 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 1 and the least fire-resistant value assigned 0. 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 percent consumption using PC1 as described above. FRS for each species was then calculated as the average of its five percentile scores for the six traits (Table 1).

*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 US. Specifically, for each study species we used a geospatial raster layer of estimated basal area (m2 ha-1) at 250 m resolution across the western US (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 inference (conifer forests) by calculating the total basal area per pixel of all 29 study species, relative to the total basal area of all other western species from the same dataset, which primarily included hardwoods. We restricted our analysis to only those areas where >50% of the total tree basal area was comprised of our study species, and where the basal area of our study species exceeded 5 m2 ha-1. 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 0) to derive a community-weighted mean FRS at the pixel scale.

We compared the community FRS map to LANDFIRE-derived indices of historical (pre-Euroamerican settlement) fire regimes (www.landfire.gov), using the fire regime group (FRG) and mean fire return interval (FRI) layers. FRG and FRI layers were resampled (from 30 m) 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=94901) subsample of the forested cells from the full landscape. For the FRG product, we compared community FRS scores among three forest FRG’s: 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 mean fire return intervals within a range of years (e.g., classes of 0-5 years, 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 mis-matches between historical fire regimes and current species composition, we identified forest areas where the current species composition may be more or less resistant to fire than expected given LANDFIRE-estimated historical fire frequency. Specifically, we sought to identify 1) fire-sensitive forests with frequent historical fire (“vulnerable-frequent”), 2) fire-sensitive forests with intermediate historical fire frequencies (“vulnerable-intermediate”), 3) fire-resistant forests with intermediate historical fire frequencies (“resistant-intermediate”) and 4) fire-resistant forests with infrequent historical fire (“resistant-infrequent”). Groups 1 and 2 are indicative of areas that may have experienced colonization by fire-sensitive species in response to fire suppression, whil groups 3 and 4 are indicative of areas where other factors may have limited 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 percent of pixels on either the fire-resistant or fire-vulnerable tails of the distribution within that fire frequency class.

**Results**

The trait values for our 29 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 (Fig. 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, Fig. 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 lawsonii*) 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, to *Pinus contorta* at the lower end, a borderline subalpine species that is known to have high post-fire mortality (Fig. 2). Finally, the ten lowest-ranking species occupy marginal forests 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.

Community fire resistance (FRS) varied across the western United States (Fig. 3), and was consistent with LANDFIRE estimates of fire regime group (FRG; Fig. S2) and fire return interval (FRI; Fig. S3). FRS was greater in FRG 1 (frequent) than either of the other FRG’s analyzed (Fig. 4; t = -115.1, df = 96205, P<0.0001). FRS also decreased significantly with increasing FRI (Fig. 4; t=-54.54, df=134451, P<0.0001), however the median FRS increased in the longest FRI class (greater than 300 years, classified as 500 years in our regression analysis; Fig. 4).

Some regions with long FRI’s (Fig. S3) were identified in our mismatched fire regime analysis as having more fire-resistant modern communities than independent assessments of fire regimes would suggest (Fig. 5). This is particularly true on the west slopes of the Cascade Range and inner Coast Range of Oregon (Fig. 5). Fire-resistant communities with intermediate rather than long FRI’s tended to be located on the margins of the Columbia Plateau and the Colorado Front Range (Fig. 5). Conversely, the most fire-intolerant modern communities with short FRI’s 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 (Fig. 5).

**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 spatial layers of geographic niche environments (in this case, adaptive niches structured by fire). Such approaches promise to be valuable for “scaling-up” functional traits to better understand 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 community. Functional traits such as those that confer fire resistance are *adaptive* under certain conditions (Schwilk & Ackerly, 2001), but may not be *adapted* to future conditions (Keeley et al., 2011). Thus, incorporating functional traits into biogeographic studies provides a direct link to the adaptive processes relevant to sustain particular species under a rapidly changing environment. In this study, we provide that direct link between traits that are adaptive to surviving relatively frequent low-moderate intensity surface fire (Fig. 3), and the prevalence of historical surface fire in those forest community types (Fig. 4).

While the spatial patterns of fire-resistant communities we identified are generally congruent with prior assessments of western fire regimes, locations where communities appear relatively mismatched to fire regimes (Fig. 5) are instructive of the ecology underlying the biogeographic 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 favorable conditions for fire spread. This area had the most fire-resistant functional traits of all infrequent FRI areas (“resistant-infrequent”, Fig. 5), and is dominated by the moderately fire-resistant Douglas-fir (*Pseudotsuga menziesii*, Table 1). However, if fuel loads are high and weather conditions are extreme, 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 quite high and would likely overwhelm trait-based fire resistance in these forests in the event of a fire. The redwood forests of coastal California are similarly 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 (Fig. S3), likely due in part to Native American influence and very close proximity to drier, fire-prone interior forests and woodlands (Steel, Safford, & Viers, 2015; Varner & Jules, 2017).

The modern abundance of fire-sensitive species in landscapes where dendroecological reconstructions indicate historically frequent fire (“sensitive-frequent”; Fig. 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 due to the absence of frequent surface fire if residual fire-resistant species are present (Stevens et al., 2016). In fire-prone regions where fire suppression has led to encroachment of fire intolerant species, the reduction of these species in mixed stands (via mechanical methods or prescribed fire) is often an objective of restoration (Larson, Belote, Cansler, Parks, & Dietz, 2013; Safford & Stevens, 2017). 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, as well as lower montane forests of the southwest where the fire-sensitive *Pinus edulis* often grades into fire-resistant *Pinus ponderosa* forest (Fig. 5).

An emergent property of forest community fire resistance across the western U.S. is that the most fire-resistant stands often occupy mid-elevation montane forests (e.g., the northern Kaibab Plateau in Arizona, Fig. 3). This is consistent with the relationship between climate, fuels, and fire regimes where low fuel loads due 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 (Fig. 2), and thus even moderate intensity surface fires in these regions may lead to extensive tree mortality (Yocom-Kent et al., 2015).

The development of a standardized fire resistance score (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 similarly be developed for systems where crown-killing fire is the common fire regime, but would need to incorporate 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). Furthermore, fire-avoiding species (Keeley 2012) may also be resilient to stand-replacing fire if succession proceeds during sufficiently long fire-free intervals, and post-fire spatial mosaics of live tree refugia are complex enough for seed dispersal to initiate 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 western conifers (e.g., *Pinus contorta* var. *latifolia* in the Rocky Mountains; *Picea mariana* in the boreal shield, *Pinus attenuata*, *Pinus coulteri*, and *Hesperocyparis* spp. in California). 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 *P. contorta* var. *latifolia* and *P. mariana* (which is concentrated in Canada), these species often have narrow ranges and occupy marginal sites (FEIS, 2013). Resprouting in conifers in this region is similarly rare and mostly limited to species with narrow ranges across the western U.S. (e.g., *Juniperus deppeana* and *Pseudotsuga macrocarpa*), with the notable exception of *Sequoia sempervirens*, which has a fairly unique fire ecology among conifers (see below). Thus the geographic and across-species variation in fire-embracing traits is 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 captures a second dimension of fire regimes (the “hot-flammable strategy; Fig. S1; Pausas et al. 2017) that is also relevant in 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 behavior). 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 rates following fire, but rather to provide quantitative support to identifying which forest communities would be most resistant to surface fire *given* adequate fuel and climate conditions. Our FRS could also be further refined with improved data on bark thickness allometry across multiple species (Jackson et al., 1999), and additional parameters describing actual cambial exposure time or the ability of crowns to recover from scorch. Furthermore, availability of both trait data and spatial data for the traits and species we considered was generally limited to the species level, so we did not consider potentially important subspecies-level variation.

Importantly, the application of the FRS concept to landscape biogeography models is highly sensitive to the processes underlying the biogeographic models; contemporary distribution models like those we analyzed here (Wilson et al., 2013) reflect a long legacy of land use change and fire suppression, and do not necessarily reflect the potential vegetation type under a historical fire regime or a historical 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 critical 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.

**References**

Brown, J. K., & Smith, J. K. (2000). *Wildland fire in ecosystems: effects of fire on flora*. Retrieved from Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.:

de Magalhaes, R. M. Q., & Schwilk, D. W. (2012). Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology, 100*(5), 1153-1163. doi:10.1111/j.1365-2745.2012.01987.x

Enright, N. J., Fontaine, J. B., Bowman, D. M. J. S., Bradstock, R. A., & Williams, R. J. (2015). Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment, 13*(5), 265-272. doi:10.1890/140231

FEIS. (2013). Fire Effects Information System. Plant species descriptions. http://www.fs.fed.us/database/feis/plants/

Fonda, R. W. (2001). Burning Characteristics of Needles from Eight Pine Species. *Forest Science, 47*(3), 390-396.

Fonda, R. W., Belanger, L. A., & Burley, L. L. (1998). Burning characteristics of western conifer needles. *Northwest Science, 72*, 1-9.

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., . . . Wright, J. (2017). Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews, 92*(2), 1156-1173. doi:doi:10.1111/brv.12275

Hood, S. M., McHugh, C. W., Ryan, K. C., Reinhardt, E., & Smith, S. L. (2007). Evaluation of a post-fire tree mortality model for western USA conifers. *International Journal of Wildland Fire, 16*(6), 679-689. doi:10.1071/wf06122

Hood, S. M., Varner, J. M., van Mantgem, P., & Cansler, C. A. (2018). Fire and tree death: understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters, 13*(11), 113004. doi:10.1088/1748-9326/aae934

Jackson, J. F., Adams, D. C., & Jackson, U. B. (1999). Allometry of Constitutive Defense: A Model and a Comparative Test with Tree Bark and Fire Regime. *The American Naturalist, 153*(6), 614-632. doi:10.1086/303201

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., . . . Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment, 14*(7), 369-378. doi:10.1002/fee.1311

Kane, J. M., Varner, J. M., & Hiers, J. K. (2008). The burning characteristics of southeastern oaks: Discriminating fire facilitators from fire impeders. *Forest Ecology and Management, 256*(12), 2039-2045. doi:https://doi.org/10.1016/j.foreco.2008.07.039

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., . . . Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology, 17*(9), 2905-2935. doi:10.1111/j.1365-2486.2011.02451.x

Keeley, J. E. (2012). Ecology and evolution of pine life histories. *Annals of Forest Science, 69*(4), 445-453. doi:10.1007/s13595-012-0201-8

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science, 16*(8), 406-411. doi:10.1016/j.tplants.2011.04.002

Keeley, J. E., & Zedler, P. H. (1998). Evolution of life histories in *Pinus*. . In *Ecology and biogeography of Pinus* (pp. 219-250). Cambridge, U.K.: Cambridge University Press.

Larson, A. J., Belote, R. T., Cansler, C. A., Parks, S. A., & Dietz, M. (2013). Latent Resilience in Ponderosa Pine Forest: Effects of Resumed Frequent Fire. *Ecological Applications*. doi:10.1890/13-0066.1

Lutes, D., & Keane, R. (2017). First Order Fire Effects Model: FOFEM 6.4, User’s Guide. In: USDA Forest Service, Missoula, Mont, USA.

Maxwell, R. S., Taylor, A. H., Skinner, C. N., Safford, H. D., Isaacs, R. E., Airey, C., & Young, A. B. (2014). Landscape-scale modeling of reference period forest conditions and fire behavior on heavily logged lands. *Ecosphere, 5*(3), art32. doi:10.1890/es13-00294.1

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution, 21*(4), 178-185. doi:10.1016/j.tree.2006.02.002

Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters, 13*(7), 838-848. doi:doi:10.1111/j.1461-0248.2010.01476.x

Pausas, J. G. (2015a). Bark thickness and fire regime. *Functional Ecology, 29*(3), 315-327. doi:10.1111/1365-2435.12372

Pausas, J. G. (2015b). Evolutionary fire ecology: lessons learned from pines. *Trends in Plant Science, 20*(5), 318-324. doi:https://doi.org/10.1016/j.tplants.2015.03.001

Pausas, J. G., Keeley, J. E., & Schwilk, D. W. (2017). Flammability as an ecological and evolutionary driver. *Journal of Ecology, 105*(2), 289-297. doi:10.1111/1365-2745.12691

Riemann, R., Wilson, B. T., Lister, A., & Parks, S. (2010). An effective assessment protocol for continuous geospatial datasets of forest characteristics using USFS Forest Inventory and Analysis (FIA) data. *Remote Sensing of Environment, 114*(10), 2337-2352. doi:http://dx.doi.org/10.1016/j.rse.2010.05.010

Rollins, M. G. (2009). LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire, 18*(3), 235-249. doi:http://dx.doi.org/10.1071/WF08088

Safford, H. D., & Stevens, J. T. (2017). *Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA*. Retrieved from Albany, CA: https://www.fs.fed.us/psw/publications/documents/psw\_gtr256/index.shtml

Schoennagel, T., & Nelson, C. R. (2011). Restoration relevance of recent National Fire Plan treatments in forests of the western United States. *Frontiers in Ecology and the Environment, 9*(5), 271-277. doi:10.1890/090199

Schwilk, D. W., & Ackerly, D. D. (2001). Flammability and serotiny as strategies: correlated evolution in pines. *Oikos, 94*(2), 326-336.

Schwilk, D. W., & Caprio, A. C. (2011). Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology, 99*(4), 970-980. doi:10.1111/j.1365-2745.2011.01828.x

Steel, Z. L., Safford, H. D., & Viers, J. H. (2015). The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere, 6*(1), art8. doi:10.1890/ES14-00224.1

Stevens, J. T., Safford, H. D., North, M. P., Fried, J. S., Gray, A. N., Brown, P. M., . . . Taylor, A. H. (2016). Average stand age from forest inventory plots does not describe historical fire regimes in ponderosa pine and mixed-conifer forests of western North America. *Plos One, 11*(5), e0147688. doi:10.1371/journal.pone.0147688

Turner, M. G., Braziunas, K. H., Hansen, W. D., & Harvey, B. J. (2019). Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proceedings of the National Academy of Sciences, 116*(23), 11319-11328. doi:10.1073/pnas.1902841116

USDA Forest Service FIA Program. (2014). *Forest Inventory and Analysis National Core Field Guide*. Retrieved from http://www.fia.fs.fed.us/library/field-guides-methods-proc/docs/2014/Core%20FIA%20field%20guide\_6-1.pdf

Varner, J. M., Arthur, M. A., Clark, S. L., Dey, D. C., Hart, J. L., & Schweitzer, C. J. (2016). Fire in Eastern North American oak ecosystems: filling the gaps. *Fire Ecology, 12*(2), 1-6. doi:10.4996/fireecology.1202001

Varner, J. M., & Jules, E. S. (2017). The enigmatic fire regime of coast redwood forests and why it matters. *Gen. Tech. Rep. PSW-GTR-258. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station: 15-18, 258*, 15-18.

Varner, J. M., Kane, J., Kreye, J., & Engber, E. (2015). The Flammability of Forest and Woodland Litter: a Synthesis. *Current Forestry Reports*, 1-9. doi:10.1007/s40725-015-0012-x

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., & Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences, 111*(38), 13690. doi:10.1073/pnas.1415442111

Wilson, B. T., Lister, A. J., Riemann, R. I., & Griffith, D. M. (2013). *Live tree species basal area of the contiguous United States (2000-2009)*. Retrieved from: http://www.fs.usda.gov/rds/archive/Product/RDS-2013-0013

Yocom-Kent, L. L., Fulé, P. Z., Bunn, W. A., & Gdula, E. G. (2015). Historical high-severity fire patches in mixed-conifer forests. *Canadian Journal of Forest Research*, 1587-1596. doi:10.1139/cjfr-2015-0128

**Data availability**:

Aggregated trait data are made available in the paper itself (Table 1). The spatial fire resistance layer (Figure 3) and all analysis code will be made available in a repository on the USGS ScienceBase system (https://www.sciencebase.gov/catalog/). Current code used to generate the manuscript is available at https://github.com/matthewkling/fire\_traits

**Table 1**: Trait data and fire resistance scores (FRS) for widespread western US conifers used in the analysis. Table is ordered by decreasing FRS. The first set of values reflects measured values and the second reflects standardized values

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Trait values1 | | | | | |  | Percentile of range (standardized values) | | | | |  |
| Scientific name | Bark thickness | Plant height | Self pruning | Flame length | Percent consumed | Flame duration |  | Bark thickness | Plant height | Self pruning | PC12 of fl and pc | Flame duration3 | **FRS** |
| *Sequoia sempervirens* | 2.06 | 95.2 | 5 | 59.4 | 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 | 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 | 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 | 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 | 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 | 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 | 82.8 | 90.3 |  | 0.22 | 0.60 | 0.56 | 0.92 | 0.72 | 0.60 |
| *Chamaecyparis lawsonia* | 2.06 | 50.0 | 6 | 21.7 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 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 | 63.4 | 182.9 |  | 0.14 | 0.07 | 0.00 | 0.61 | 0.23 | 0.21 |
| *Picea glauca* | 0.64 | 16.3 | 2 | 16.0 | 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 | 62.2 | 253.9 |  | 0.17 | 0.02 | 0.00 | 0.55 | 0.00 | 0.15 |

1: Units for measured trait values are cm (bark thickness; for a 25.4 cm dbh tree), m (tree height), scale of 1-10 (self-pruning), seconds (flame duration), cm (flame length), and percentage consumed of 0-100 (percent consumed).

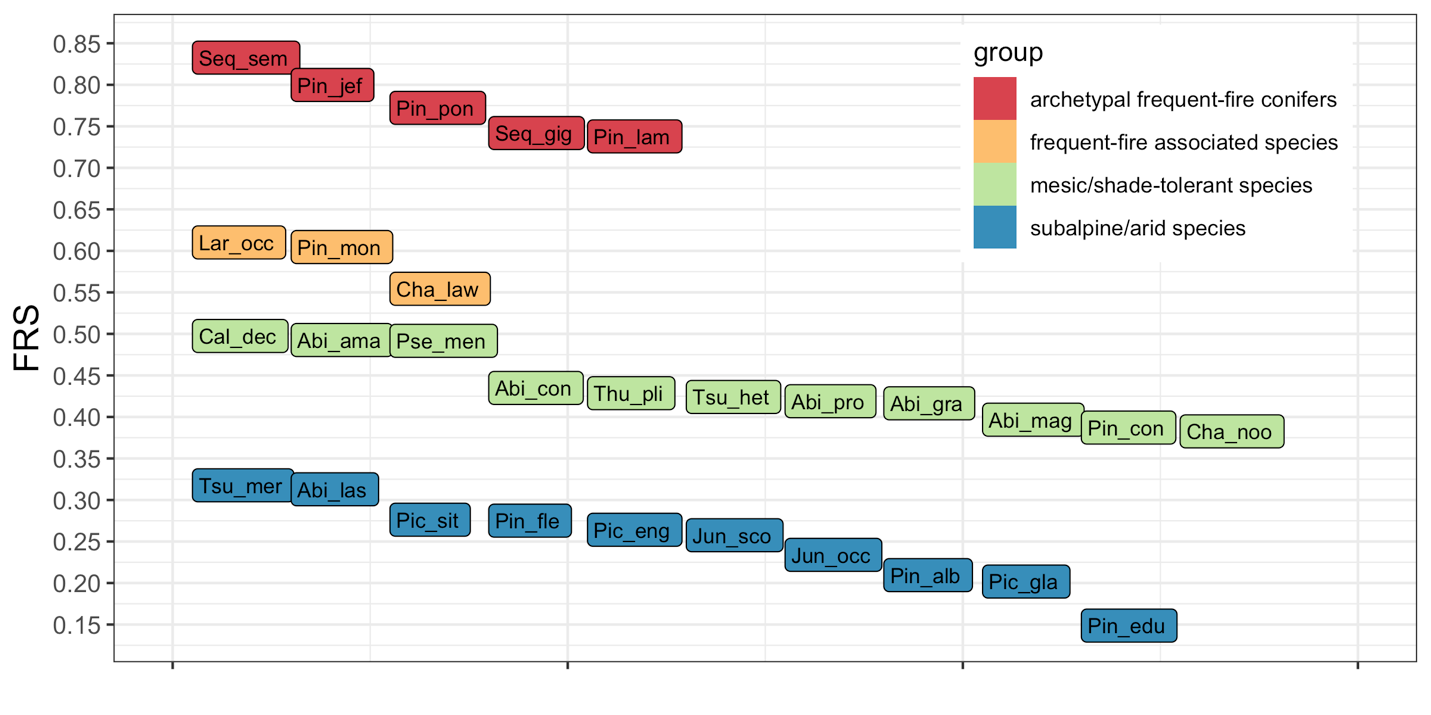
2: flame length (fl) and percent consumed (pc) were closely correlated (r = 0.93); traits were combined in ordination and the first principal component (PC1) was used to calculate FRS.

3: percentiles of range for flame duration calculated on a log scale.

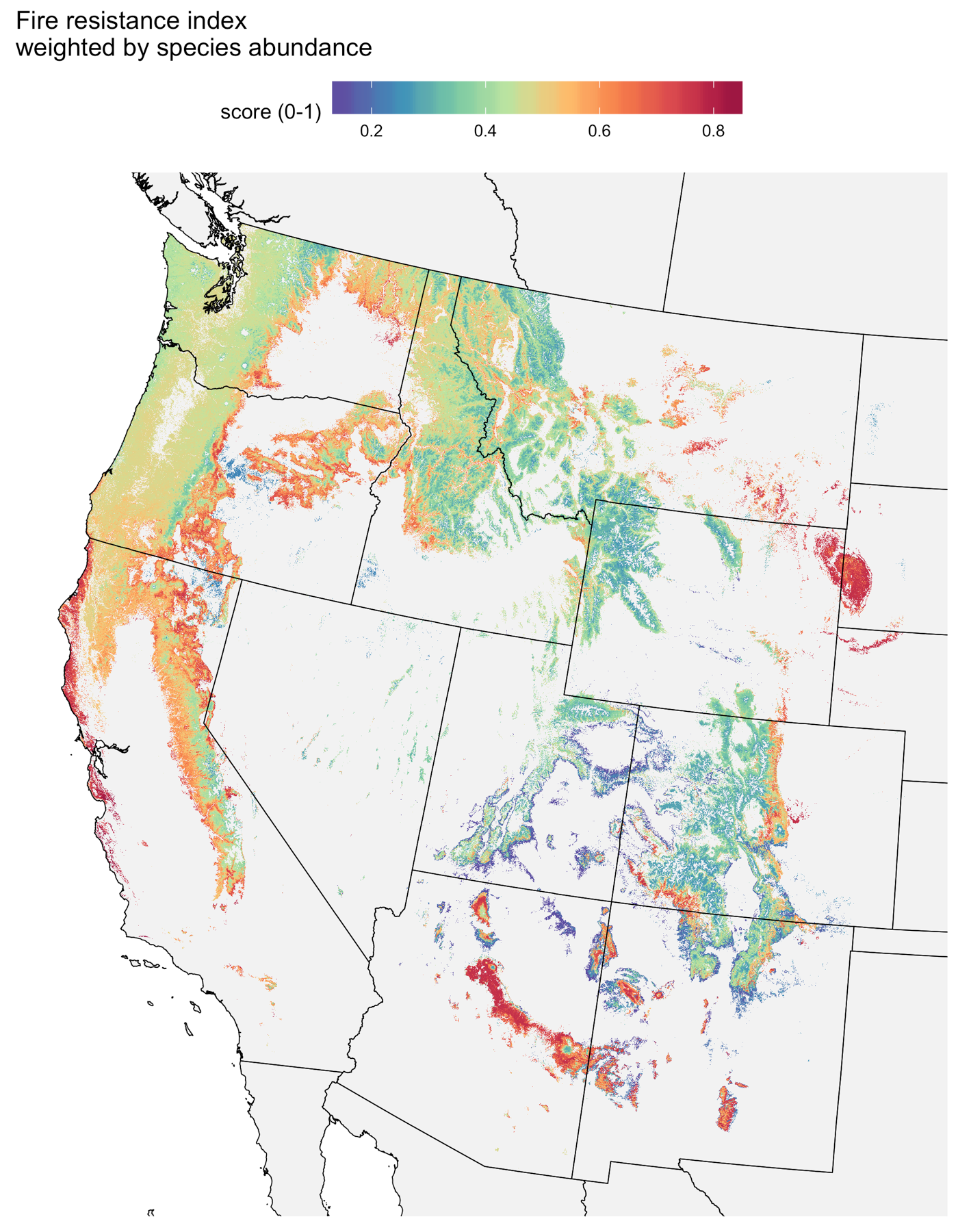


**Figure 1**: Examples of fire resistance and flammability traits of different conifer species. (a): *Pinus jeffreyi* (left) and *Pinus contorta* (right) following the 2012 Reading Fire, Lassen National Park, California. The two species experienced similar fuel environments (fairly open-grown), with *P. jeffreyi* surviving and *P. contorta* dying. Note the lower profile of branches on *P. contorta*, indicating a lesser degree of self-pruning. (b): example of litter flammability differences in *P. jeffreyi* (left) and *P. contorta* (right), with *P. jeffreyi* having greater flame lengths and shorter flame durations than *P. 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, California. (d): stand of fire-intolerant *Picea engelmannii* killed by fire, Fishlake National Forest, Utah. (e): stand of fire-tolerant *Pinus ponderosa* that has survived several fires on the Deschutes National Forest, Oregon.

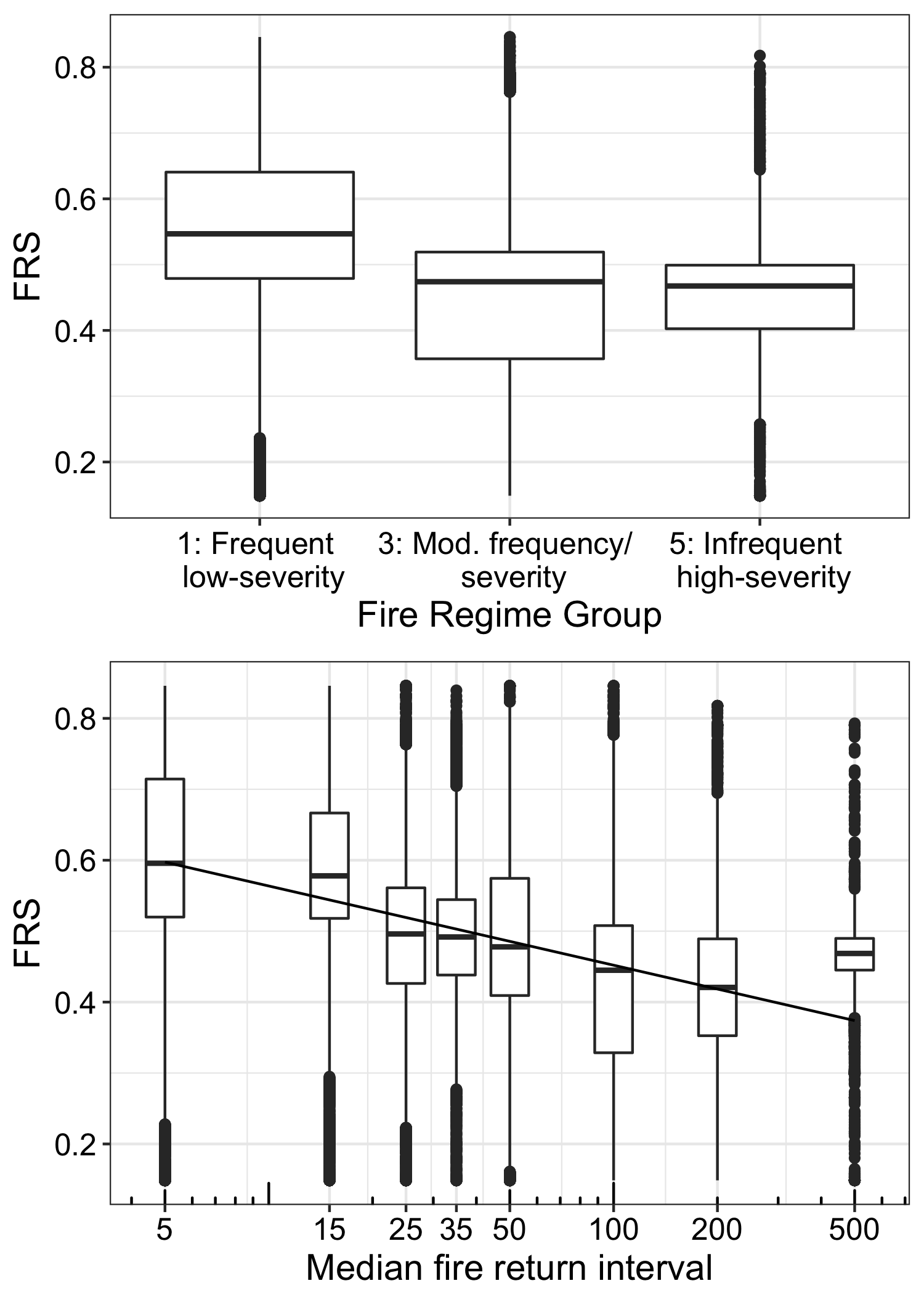
Photo credits: (a) Jens Stevens, (b) Fred Ackerman, (c) Dylan Schwilk, (d, e) J. Morgan Varner



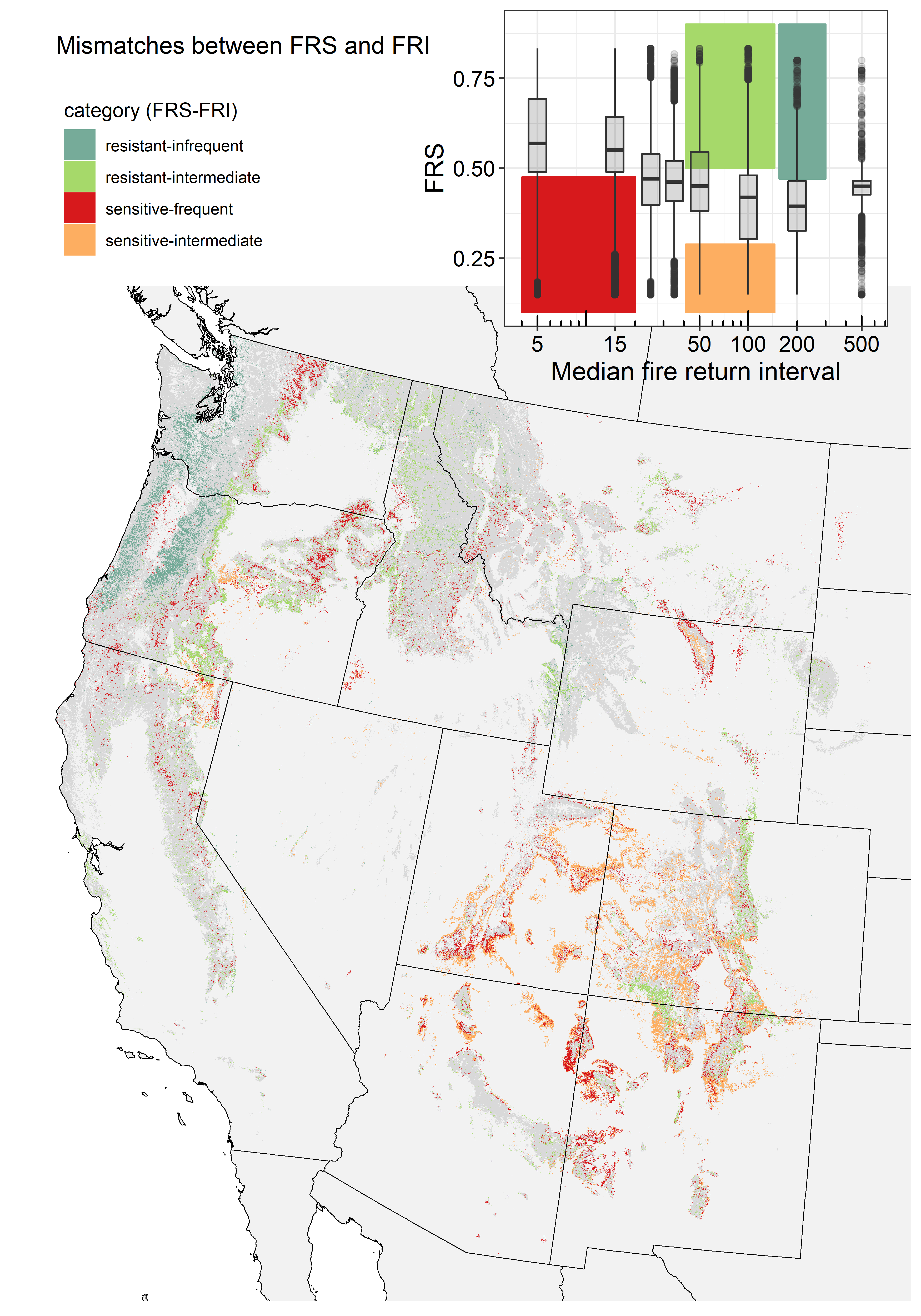
**Figure 2**: Ecological grouping of 29 conifer species by fire resistance scores (FRS). Species names are listed in Table 1. The x-axis is not numeric and is presented to allow visualization of all species codes, extending to the right in order of decreasing FRS.



**Figure 3**: Fire resistance scores (FRS) mapped across the western United States. Scores range from low fire resistance (0) to high fire resistance (1); FRS raster layer resolution is 250 m.



**Figure 4:** Comparison of community fire resistance scores (FRS) at three different fire regime groups (top; see Figure S3) and at a range of different fire return intervals (bottom; see Figure S4)



**Figure 5**: Potential imbalances between contemporary fire resistance traits and historical fire regimes. “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.