**Running Head**

*Functional traits and forest fire regimes*

**Title**

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

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**Journal requirements for “Research Communications”:**

Abstract: 150 words; Article: 2500 words; References: 20; figures/tables: 3 (+SI)

**Current stats:**

Abstract: 149 words; Article: 2486 words; References: 20; figures/tables: 3 (+SI)

**Abstract**

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 to improve process-based predictions about the resilience 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 in North American conifer species. Species associated with historically frequent fire have high fire resistance (e.g., *Pinus ponderosa*), while species associated with subalpine or desert conditions have low fire resistance (e.g., *Picea engelmannii* and *Pinus edulis*). 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.

**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 et al. 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 small spatial scales (Messier et al. 2010), and scaling up functional trait studies to describe ecosystem processes at the landscape scale 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 et al. 2014). To illustrate how ecosystem processes may select for and filter species at large spatial scales, we apply functional trait biogeography to describe regional variation in adaptive fire regimes 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 and Nelson 2011). Such models are generally based on historical fire return intervals, climate, predominant vegetation, and biophysical models that link these parameters together (Schoennagel and Nelson 2011). 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). Functional traits can influence tree survival during fire by mediating the direct physiological response of the tree to fire, or the way that fuel characteristics of the tree influence fire spread (Keeley et al. 2011). It is common practice to rank species along a continuum from “fire-tolerant” to “fire-intolerant” (e.g., Safford and Stevens 2017), but species rankings are often based on a qualitative understanding of species’ natural history rather than a quantitative assessment of traits that are associated with surviving fire.

Frequent fire over their evolutionary history of specific tree species can promote the selection of fire resistance traits, i.e. morphological characteristics that improve tree survival following a low to moderate intensity fire (Keeley et al. 2011, Pausas 2015). We conceptualize fire resistance (or fire tolerance) as the ability of mature trees to withstand surface fire. We distinguish this fire adaptation strategy from other fire-adapted life histories such as “fire embracing” or “fire resilient” strategies that involve loss of aboveground biomass and post-fire regeneration via resprouting or serotiny, which may be adaptive under less frequent, higher intensity fire regimes (Schwilk and Ackerly 2001, Pausas et al. 2017).

A set of traits associated with fire resistance – thick bark, a high degree of self-pruning lower branches, and tall maximum heights – are often strongly correlated with one another (Schwilk and Ackerly 2001). Bark thickness is strongly associated with tree survival of low- to moderate-intensity surface fires (Lutes and Keane 2017, Pausas et al. 2017), 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 and Ackerly 2001).

Litter flammability traits may also be associated with tree sensitivity to fire[.](#_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 heights, 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 and minimizing cambial exposure to lethal temperatures (Pausas 2015). In some cases, such leaf litter traits are associated with shade-intolerant and fire-dependent species that experience frequent fire (Schwilk and Caprio 2011), whereas species that are less likely to experience fire during their lifetimes, due to a combination of climate and fuel limitation, may have 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 suppression has shifted species composition in some regions away from more fire-resistant species toward fire-sensitive species (Safford and Stevens 2017). It is therefore critical to describe the current condition of forest communities as a function of constituent species’ ability to survive 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.

**Methods**

We assembled a quantitative trait database on six fire-adaptive traits that contribute to fire resistance of 29 widespread western conifer species (Supplemental Methods). 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 and Keane 2017). These multipliers assume a linear rate of bark accumulation with dbh, which is not realistic for many species, but they are currently the most widely-used trait in models of fire-caused mortality, and they capture general differences among species (Lutes and 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 Schwilk and Ackerly (2001), supplementing with data for other genera from the Fire Effects and Information System (FEIS 2013).

Flammability data on mean flame length, percent litter consumption, and flame duration were obtained from Fonda (2001), Fonda et al. (1998), Banwell and Varner (unpublished data) and Kane (unpublished data). Flame height 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 height and percent consumption were non-linearly correlated with flame duration, with the shortest flame durations associated with both the lowest flame heights and the highest flame heights (Fig. S1). Together, PC1 and flame duration represent the two-dimensional trait space for litter flammability (Pausas et al. 2017).

We aggregated the three fire-resistance traits and two flammability traits described above into a single “fire resistance score” (FRS; range 0-1) by averaging the five traits above for each species (Supplemental Methods). 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 (Supplemental Methods).

We compared the community FRS map to LANDFIRE-derived indices of historical fire regimes (www.landfire.gov), using the fire regime group (FRG) and mean fire return interval (FRI) layers. FRG and FRI layers were resampled to the same spatial resolution as our FRS data (250 m). We conducted statistical tests of FRS values on a random 1% subsample (N=94901) of the full landscape. For the FRG product, we compared 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). 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 FRS values decreased as a function of lengthening fire-return intervals.

To quantify potential imbalances between historical fire regimes and current 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 (“vulnerable-intermediate”), 3) fire-resistant forests with intermediate historical fire (“resistant-intermediate”) and 4) fire-resistant forests with infrequent historical fire (“resistant-infrequent”). 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 and Discussion**

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 height 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. S2). The five highest-ranking species inhabit historically frequent-fire ecosystems and have well-documented fire scar records, including *Pinus ponderosa* and *Sequoiadendron giganteum* (FEIS 2013). The next three species 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 low end, a borderline subalpine species that is known to have high post-fire mortality (Fig. S2). Finally, the ten lowest-ranking species occupy marginal forests at either higher subalpine elevations (e.g., *Abies lasiocarpa* and *Picea engelmannii*) or lower desert elevations (e.g., *Juniperus scopulorum* and *Pinus edulis*) where fires are rare.

Community fire resistance (FRS) varied across the landscape (Fig. 2), and was generally consistent with LANDFIRE estimates of fire regime group (FRG; Fig. S3) and fire return interval (FRI; Fig. S4). FRS was greater in FRG 1 (frequent) than either of the other FRG’s analyzed (Fig. S5; t = -115.1, df = 96205, P<0.0001). FRS also decreased significantly with increasing FRI (Fig. S5; 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. S5).

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 infrequent FRI areas (“resistant-infrequent”, Fig. S6), 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 (Safford and Stevens 2017). 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 climate-limited, however this region has a record of historically frequent fire (Fig. S4), likely due in part to Native American influence and close proximity to drier interior forests (Steel et al. 2015).

A quantitative assessment of community fire resistance at a landscape scale has practical implications. The modern abundance of fire-sensitive species in landscapes where dendroecological reconstructions indicate historically frequent fire (“sensitive-frequent”; Fig. S6) might suggest past high-severity fire if residual fire-resistant species are absent (Yocom-Kent et al. 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 (Safford and 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. S5).

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. 2). 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 forests where fuel conditions could otherwise support fire spread (Steel et al. 2015, Safford and Stevens 2017). The least fire-resistant species occupy these elevational extremes (Fig. S2), and thus even moderate intensity surface fires in these regions may lead to extensive tree mortality (Yocom-Kent et al. 2015)[.](#_ENREF_27)

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 case, 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 and Ackerly 2001)[, but may not be](#_ENREF_20) *adapted* to future conditions. 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.

**Acknowledgments**: Early discussions with Malcolm North, Andrew Latimer, and Scott Stephens helped refine these ideas.

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**Table 1**: Trait data and fire resistance scores (FRS) for widespread western US conifers used in the analysis. Table is ordered by decreasing FRS.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Values1 | | | | | |  | Percentile of range | | | | |  |
| Scientific name | Bark thickness | Plant height | Self pruning | Flame height | Percent consumed | Flame duration |  | Bark thickness | Plant height | Self pruning | PC12 of fh 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 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 height), and percentage consumed of 0-100 (percent consumed).

2: flame height and percent consumed 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.