



Using a trait-based approach to assess fire resistance in forest landscapes of the Inland Northwest, USA

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Abstract

Context Several plant traits are associated with resistance to fire, thus fire-resistant species may give rise to more fire-resistant landscapes. However, up-scaling from plant traits to landscape- and regional-scale fire effects remains a challenge.

Objectives We test two hypotheses: (1) forests composed of fire-resistant species experience lower fire severity than forests composed of less fire-resistant species; and (2) wildfires affecting forests with greater fire resistance experience smaller patches of high-severity fire.

Methods We used a predictive map of existing forest types (major tree species dominating forest composition) and a trait-based map of fire resistance. We examined large-scale spatial patterns of fire severity derived from Landsat imagery in 611 wildfires across the range of western larch in the Inland Northwest USA (1985–2014). We then applied structural equation modeling to study complex relationships between fire resistance and high-severity fire in each wildfire.

Results Forest types dominated by fire-resister species (e.g., ponderosa pine) experienced lower fire severity than forest types dominated by non-resister species such as lodgepole pine (fire-embracer) and subalpine fir (fire-avoider). We found a strong negative correlation between the fire resistance index and average values of the relative differenced normalized burn ratio, as well as an indirect relationship between fire resistance and high-severity patch size.

Conclusions The large-scale differences in fire severity among forest types generally reflect the degree of fire resistance that fire-related traits confer to individual trees species, providing evidence that incorporating plant traits has the potential to assist in assessing fire resistance at large spatial scales.

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Keywords Fire severity · Fire regime · Mixed-severity fire · Bark thickness · Patch size · Remote sensing

Introduction

Functional trait biogeography can improve the prediction of fire regimes in fire-prone ecosystems (Stevens et al. 2020). Certain plant traits (i.e., characteristics of plants and their organs) are associated with resistance to fire (Archibald et al. 2018; Stevens et al. 2020). However, up-scaling (i.e., predicting at larger scales with information from finer scales) from plant traits to landscape fire effects is challenging (Schwilk 2015; Pausas et al. 2017). As a result, research models have only recently begun to examine linkages between plant traits and fire severity across landscape scales (Pellegrini et al. 2017; Archibald et al. 2018). Here, we examine the influence of tree species composition on fire severity in forest ecosystems at broad spatial scales.

Tree species can be classified into five strategies according to their response to fire: resister, embracer, avoider, endurer, and colonizer (Rowe 1983; Agee 1993; Wirth 2005; Tautenhahn et al. 2016). Each strategy is associated with certain traits that enhance fitness (i.e., survival or reproduction success) under a given fire regime (Keeley et al. 2011; Keeley 2012; Pausas 2012, 2015b). In brief: (1) resisters survive frequent surface fires due to their thick bark, (2) embracers suffer crown fires but recover quickly from a canopy seed bank, (3) avoiders are easily killed by fire but occupy environments where fires are infrequent, (4) endurers are able to resprout after fire, and (5) colonizers establish on burned areas due to their long-distance seed dispersal (Appendix S1).

At individual plant level, fire resistance can be characterized by a suite of traits that decrease the likelihood of being injured or killed by fire (Stevens et al. 2020). Tree mortality is a major component of fire severity in forest ecosystems that arises from fire-caused injury to crown (branches, foliage and buds), stem (cambium) and root system (Agee 1993; Hood et al. 2018a). Recently, Stevens et al. (2020) created a quantitative fire resistance score (FRS) for conifer species in the western United States. The FRS ranges from zero to one and is based on six traits that confer resistance against surface fires: bark thickness, tree height, self-pruning, and three relating to litter flammability (Stevens et al. 2020). For instance, bark insulates the cambium from heat, where the degree of heat insulation by bark is proportional to the square of its thickness (Peterson and Ryan 1986; Pausas

2015a). Likewise, the absence of lower branches reduces the risk of crown fires, and thus decreases the exposure of foliage and buds to fire damage (Schwilk and Ackerly 2001; Keeley 2012; Pausas 2015b). The FRS is a standardized index that allows quantifying the relative resistance to surface fires of single species and forest communities where species distribution and abundance data are available.

The presence and dominance of fire-resistant species may give rise to more fire-resistant landscapes resulting in lower fire severity (Belote et al. 2015). For example, in the boreal forest biome, relative abundance of species with different fire strategies helps explain differences in fire severity between North American and Eurasian forests (Rogers et al. 2015). In this study, fire resistance refers exclusively to tree survival from fire (i.e., fire severity), as opposed to landscape-scale fire resistance that frequently refers to the capacity to limit fire spread (Fernandes 2013; DeRose and Long 2014). Although factors such as forest structure, topography, climate and weather are strong drivers of fire severity (Parks et al. 2018), generally we do not know how much variability in fire severity at landscape and regional scales is due to forest stand composition. Remote sensing studies document differences in fire severity patterns between potential vegetation zones (i.e., broad zones distinguished by the tree species that would dominate in late-successional stages; e.g., Miller et al. 2012; Harvey et al. 2016a; Reilly et al. 2017; Haugo et al. 2019). If current species composition and fire regimes are linked in forests of the western USA (Stevens et al. 2020), species-driven differences in fire severity should also manifest at regional scales from remote sensing data, even if species composition is the only driver taken into consideration.

Satellite images are essential tools for large-scale assessments of fire severity. Landsat Thematic Mapper/Enhanced Thematic Mapper Plus (TM/ETM+) images are an important data source to derive fire severity data due to several reasons, such as free images dating back to 1984, and the spatio-temporal resolution (30 m and 16 days). The differenced normalized burn ratio (dNBR) and its relative version (RdNBR) are common Landsat-based indices to quantify fire severity (Key 2006; Key and Benson 2006; Miller and Thode 2007; Parks et al. 2014). Remote sensing indices of fire severity help characterize fire effects when they are calibrated and

validated with field measures of fire effects (Wimberly and Reilly 2007; Miller et al. 2009; Cansler and McKenzie 2012; Kolden et al. 2015). Furthermore, remote sensing data can be classified into fire severity classes to derive maps of patches of distinct severity and landscape metrics that help explain the patterns and drivers of fire severity (Miller et al. 2009; Cansler and McKenzie 2012; Harvey et al. 2016a; Reilly et al. 2017). Advances in both remote sensing and trait databases (e.g., FRS) offer the opportunity to study the link between fire-resistant traits and fire severity at broad spatial scales.

In this study, we apply remote sensing data to test the following hypotheses: (1) forests dominated by fire-resistant species experience lower fire severity than forests of species with a lower degree of fire resistance; and (2) wildfires affecting forest communities with a higher degree of fire resistance have smaller patches of high-severity fire. To do so, we selected 611 wildfires from the MTBS database that occurred in the Inland Northwest USA for a period of 30 years (1985–2014). Using predictive maps of existing forest species composition and fire resistance, we examined Landsat-derived metrics of fire severity and burned landscape patterns to verify whether fire-resistant traits can explain fire severity at large spatial scales.

Materials and methods

Study area and species

We tested the research hypotheses in forests of the northwestern USA. To delineate the study area, we used a species distribution model of western larch (*Larix occidentalis*; Rehfeldt et al. 2006; Rehfeldt and Jaquish 2010), one of the most fire-resistant tree species in the region (Table 1; Hood et al. 2018b). The distribution of western larch encompasses 12,980,388 ha (Fig. 1) and covers much of the mountain areas of the Inland Northwest USA region defined by Hessburg and Agee (2003). This area includes a great deal of variability in climate, topography, land use history, and historical fire regimes. According to the Fire Regime Groups (FRG) from Barrett et al. (2010), 34% of this area was historically characterized by low-severity (FRG I), 44% by mixed-severity (FRG III), and 18% by high-severity

(FRG IV) fire regimes. Refer to Hessburg and Agee (2003) for a more detailed description of the Inland Northwest USA.

Forests in the study area are dominated by a number of conifer species and forest types in which western larch occurs (Table S2). Dry forests types include those dominated by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and grand fir (*Abies grandis*). Cold forests types include those dominated by lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Other less common forest types include those dominated by Pacific silver fir (*Abies amabilis*), mountain hemlock (*Tsuga mertensiana*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and whitebark pine (*Pinus albicaulis*).

A fire strategy (see Table S1) was assigned to each species (Table 1). Western larch, ponderosa pine and Douglas-fir were classified as resisters; lodgepole pine as embracer; Engelmann spruce, subalpine fir, grand fir, Pacific silver fir, western hemlock, mountain hemlock and western redcedar as avoiders; and whitebark pine as colonizer. Some fire-related traits of these species are summarized in Table 1. Other relevant traits (not included in Table 1) that increase survival from fire, especially after crown fires, are protected buds and epicormic resprouting (Pausas and Keeley 2017; Hood et al. 2018a). For instance, buds of ponderosa pine are protected by thick, long needles (Hood et al. 2018b), and western larch is able to resprout from epicormic buds (Arno and Fischer 1995).

Existing forest type map

We used a national map of existing forest types to characterize the forest species composition of the area affected by wildfires (Fig. 2B). This dataset is a 250-m resolution map of the USA forest types generated from MODIS imagery and Forest Inventory and Analysis (FIA) plot data (Ruefenacht et al. 2008). Forest types are assigned to FIA plots using a decision tree based on the relative stocking values of tree species in the plot, which are primarily a function of basal area (Arner et al. 2003; Costanza et al. 2018). To provide additional validation for this map, we selected the most abundant forest types within the study area (Table 1), and used two

Table 1 Fire-related characteristics of twelve conifers from the Inland Northwest USA

Characteristic	WL	PP	DF	LP	ES	SF	GF	PF	WH	MH	WR	WP
Serotiny ^a	No	No	No	Yes	No	No	No	No	No	No	No	No
Basal resprouting ^a	No	No	No	No	No	No	No	No	No	No	No	No
Seed mass (mg) ^a	3.2	37.9	19.6	4.8	3.3	13.2	20.0	41.2	1.8	4.0	1.1	175.4 ⁱ
Shade tolerance ^{a,e}	1	1	2	1	2	5	4	5	5	5	5	1
Mature height (m) ^a	55	71	40	46	30	34	62	62	77	46	62	33
Bark thickness ^{a,e}	5	5	5	1	2	1	4	1	3	3	2	1
Self-pruning ^{b,f}	3	3	3	2	1	1	1	1	1	1	1	1
Crown density ^{b,f}	1	2	3	2	3	3	3	3	3	3	3	3
Foliage flammability ^{a,g}	3	1	4	2	5	4	3	4	5	3	4	–
Rooting depth ^{b,f}	3	3	3	3	1	1	1	1	1	2	1	3
Fire resistance score ^c	0.61	0.77	0.49	0.39	0.26	0.31	0.42	0.49	0.42	0.32	0.43	0.21
Fire strategy ^{d,h}	R	R	R	E	A	A	A	A	A	A	A	C

WL western larch (*Larix occidentalis*); PP ponderosa pine (*Pinus ponderosa*); DF Douglas-fir (*Pseudotsuga menziesii*); LP lodgepole pine (*Pinus contorta*); ES Engelmann spruce (*Picea engelmannii*); SF subalpine fir (*Abies lasiocarpa*); GF grand fir (*Abies grandis*); PF Pacific silver fir (*Abies amabilis*); WH western hemlock (*Tsuga heterophylla*); MH mountain hemlock (*Tsuga mertensiana*); WR western redcedar (*Thuja plicata*); WP whitebark pine (*Pinus albicaulis*). A few values not given by the cited sources were obtained from the Woody Plant Seed Manual (https://www.nsl.fs.fed.us/nsl_wpsm.html) and the Fire Effects Information System (<https://www.feis-crs.org/feis/>)

^aBased on: Baker (2009)

^bBased on: Flint (1925); Starker (1934); Minore (1979)

^cFrom: Stevens et al. (2020). Fire resistance score (FRS) ranges from 0 to 1

^dBased on: Agee (1993)

^eShade tolerance and bark thickness increase from 1 to 5

^fSelf-pruning height, crown bulk density and rooting depth increase from 1 to 3

^gFoliage flammability increases from 1 to 5; these values are indicative given that flammability has three major dimensions related to ignitability, flame spread rate, and heat released, which are not necessarily correlated, and thus it is difficult to measure flammability as a single fire trait (Pausas et al. 2017)

^hR: resister; E: embracer; A: avoider; C: colonizer

ⁱWhitebark pine seeds are dispersed mainly by animals

field plot datasets: 6068 FIA plots from Montana and Idaho, and 39,852 Gradient Nearest Neighbor (GNN) plots from Washington and Oregon. The overall accuracy was 49.2% for Montana and Idaho and 66.2% for Washington and Oregon. See Appendix S2 for more details on the accuracy assessment of the forest type map.

Forest types are a discrete classification of forest stand composition based on dominant tree species, which simplify the species composition on the ground where heterogeneous mixtures of species occur. To account for this, we used raster maps of estimated tree basal area for each of the study species at 250 m resolution (Wilson et al. 2013) derived from MODIS imagery and FIA field plot data (Wilson et al. 2012). Table S6 includes a summary of the estimated

species composition of the main forest types within the burned areas.

Map of forest community fire resistance

In order to quantify fire resistance at large scales, we used a 250-m resolution raster map of forest community fire resistance (Stevens et al. 2020; Fig. 2A). This map was created by multiplying the trait-based FRS of 29 individual tree species by its relative abundance (based on estimated relative basal area fraction) to derive a mean community FRS at 250-m resolution across the western USA. Community FRS ranged from 0.20 to 0.79 in the burned areas of this study. Pixels with high community FRS values are indicative of forest stands dominated by species

Fig. 1 Distribution of fires that fell within the range of western larch (*Larix occidentalis*) from 1985 to 2014 (3,553,296 ha distributed across 611 fires)

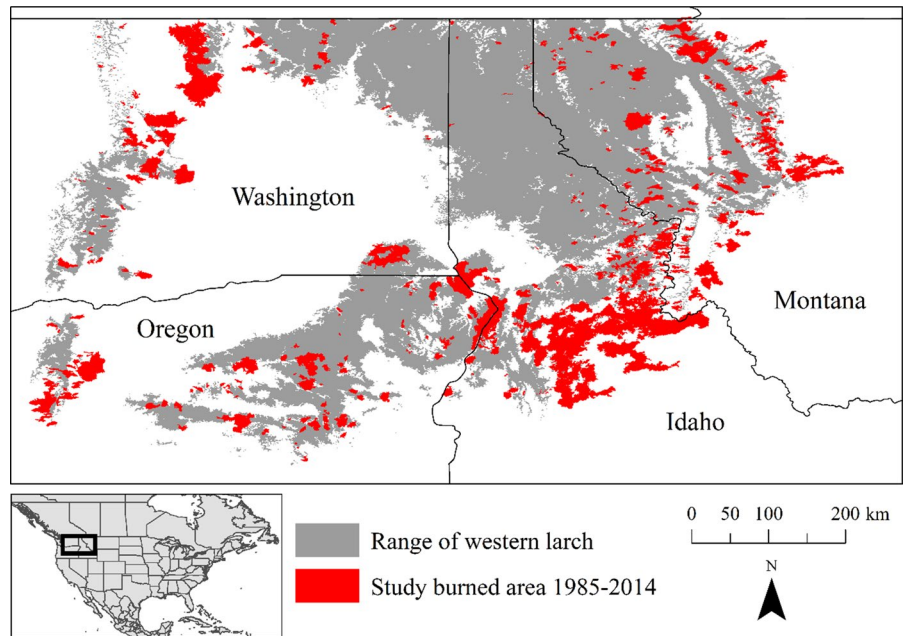
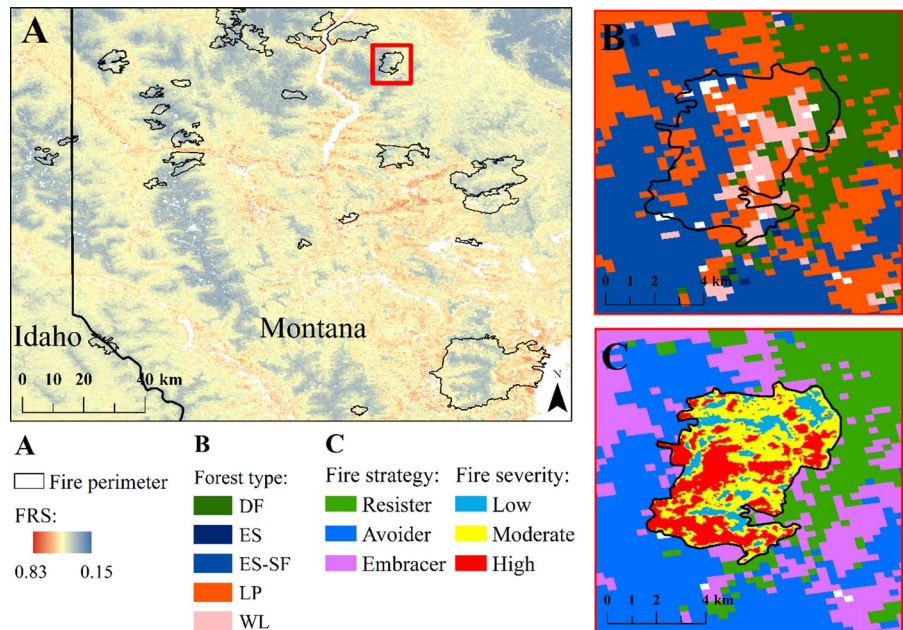


Fig. 2 Example of data used and derived in this study. **A** perimeters of wildfires and community fire resistance score map. **B** existing forest type map: WL western larch; DF Douglas-fir; LP lodgepole pine; ES Engelmann spruce; ES-SF Engelmann spruce-subalpine fir. **C** fire strategy map and fire severity patches: low (basal area mortality < 20%), moderate (20–80%) and high (> 80%)



with fire-resistant traits that increase tree survival probability.

Fire severity atlas

We derived fire severity maps from Landsat imagery. First, we acquired perimeters (i.e., fire polygons) from

the Monitoring Trends in Burn Severity (MTBS) database for all the fires (>400 ha) that occurred between 1985 and 2014. We selected fires that met the following criteria: (1) the fire perimeter was completely within or intersected partially the boundaries of the range of western larch; (2) >10% of the area within the fire perimeter was forest (according to the

forest type map); (3) the fire was not a prescribed fire. We retained 611 fires that burned 3,553,296 ha in total (Fig. 1).

Through pre-processing, we derived a Landsat time series stack. Briefly, all available L1T LEDAPS surface reflectance images from June to September for each year between 1984 and 2015 were used to derive annual composite images on Google Earth Engine. The annual composite images covered the area affected by the 611 wildfires and were created by selecting clear observations as close to day of year 215 as possible. Clouds and cloud shadows were identified with CFMask (Foga et al. 2017).

The Landsat data stack was the base to calculate the normalized burn ratio (NBR) annually from 1984 to 2015. NBR is a spectral index that contrasts Landsat TM/ETM+ bands four (near infrared [NIR]) and seven (shortwave infrared [SWIR]), which respond in opposite ways to fire (Key and Benson 2006). For each year, we used NBR images from the previous year (pre-fire) and images from the year after (post-fire) to calculate the relative differenced normalized burn ratio (RdNBR), a remote sensing index of fire severity that quantifies spectral change due to fire (Miller and Thode 2007). Formulae of remote sensing indices used in this study are included in Appendix S3. In short, we derived a Landsat NBR-based stack made up of annual RdNBR images from 1985 to 2014, with a 30-m resolution and an extent that covered the 611 fires selected. The NBR-based stack was clipped to fire polygons according to fire years to create the fire severity atlas.

Additionally, we reclassified the RdNBR data from the fire severity atlas into fire severity classes based on the proportion of basal area killed by fire (i.e., RdBA) as follows: low (RdBA < 20%), moderate (RdBA = 20–80%), and high (RdBA > 80%). We applied the model of Reilly et al. (2017; i.e., $RdNBR = 134.87 + 259.38 * RdBA + 567.68 * RdBA^2$) to define the remote sensing classes of fire severity: low (RdNBR < 209), moderate (RdNBR = 209–706), and high (RdNBR > 706). We acquired four field datasets to perform the accuracy assessment of these fire severity classes. These datasets come from studies published in Harvey (2015), Belote et al. (2015), Whittier and Gray (2016), and Reilly et al. (2017). In total, we had 401 field plots with information on RdBA, and all plots burned within the period and area studied here. RdNBR values were sampled at

plot locations from the fire severity atlas. The overall accuracy of this fire severity classification was 72.6% (Appendix S4).

Data analyses

Assessment of fire severity at forest type level

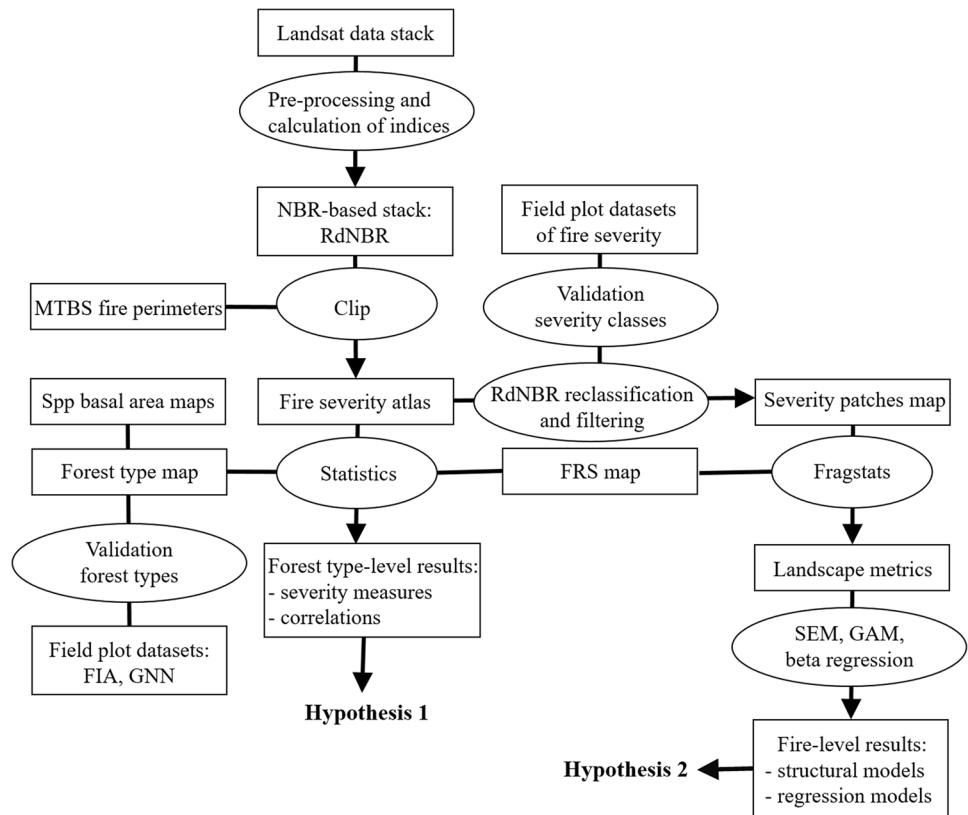
An overview of the methodology is presented in Fig. 3. To test the first research hypothesis, we used forest types as the unit of analysis. Only data corresponding to the first wildfire within reburned areas in the 30-year period were added to the analyses to avoid potential effects of successive wildfires on severity (Harvey et al. 2016b) and species subsequent changes (Shaw et al. 2017). Only forest types with a minimum burned area of 5000 ha were included in the analyses. We overlaid the forest type map with the fire severity atlas and the community FRS map to calculate the following metrics for each forest type: (1) mean RdNBR value; (2) proportions of pixels in the low (RdNBR < 209), moderate (RdNBR = 209–706) and high (RdNBR > 706) severity classes; and (3) mean community FRS value. Lastly, we correlated mean RdNBR values against both species- and mean community-level FRS values (Stevens et al. 2020).

Landscape patterns of high-severity fire in individual fires

Individual fires were used as the unit of analysis to test the second research hypothesis. We removed some of the initial 611 wildfires from the analyses due to different reasons. One fire burned partially in Canada and was excluded because we had no forest type information in the Canadian side of the border. Through manual inspection of individual fires, we detected issues associated with the Landsat 7 scan line corrector failure in 30 fires. While this affects a small amount of the area in the analyses, we excluded these fires because the spatial configuration of fire severity patches were likely affected. In addition, we restricted the analyses to fires with forest cover > 50%. In total, we included 545 fires in these analyses.

For each fire, the mean value of the community FRS was calculated. We reclassified the RdNBR images into fire severity classes: low (RdNBR < 209), moderate (RdNBR = 209–706) and high (RdNBR > 706). A 3 × 3 majority filter was

Fig. 3 Workflow to derive the results of this study. Rectangles represent data and ellipses represent processes



applied to smooth patches by reducing the influence of single pixels on severity patches delineation (Harvey et al. 2016a). After reclassification and filtering, a map of fire severity patches was obtained for each fire (Fig. 2C). We calculated three metrics for each fire: (1) fire size (i.e., total fire extent); (2) proportion of high severity (i.e., proportion of pixels in the high severity class); and (3) area-weighted mean patch size of high severity using an 8-pixel rule to define patches in Fragstats (McGarigal et al. 2012). Area-weighted means weight each patch by its size and provide a more landscape-centric representation than simple means of patch size because a random location in a landscape has a greater probability to be found at a large patch (McGarigal et al. 2012; Cansler and McKenzie 2014; Harvey et al. 2016a). Fire size and area-weighted mean patch size were log₁₀-transformed.

We used structural equation modeling (SEM) to investigate multiple relationships between the three landscape metrics (fire size, proportion of high severity, and area-weighted mean patch size of high severity) and fire resistance (mean community

FRS). We began with the full model proposed by Harvey et al. (2016a; Fig. 6 left). We removed statistically non-significant paths (i.e., linear relationships between variables with $p > 0.05$) and final model selection was based on the Akaike (AIC) and Bayesian information criterion (BIC). Model parameters were estimated with the maximum likelihood method and bootstrapped standard errors were used to deal with multivariate non-normal distribution (Gana and Broc 2019). SEM was carried out using the function *sem* from the R package *lavaan* (Rosseel 2012).

To graphically represent non-linear relationships, we conducted beta regressions and generalized additive modeling (GAM) on the predictors and response variables utilized in the SEM. Beta regression was used to model the proportion of high-severity fire as a function of fire size and mean community FRS. A logit link was applied in the *betareg* function from the R package *betareg* (Cribari-Neto and Zeileis 2010). GAM was used to model area-weighted mean patch size of high severity as a function of fire size and proportion of high

severity. A Gaussian error distribution was applied in the *gam* function from the R package *mgcv* (Wood 2011). We check model assumptions (i.e., normality, homogeneity and independence) graphically with Pearson residuals (Zuur et al. 2009). We performed all the statistical analyses within the R framework (R Core Team 2018). All sources of data used in this study are listed in Appendix S5.

Results

Fire severity of forest types

Mean fire severity in forest types dominated by resister species (i.e., western larch, ponderosa pine and Douglas-fir) was lower than in forest types dominated by other species, including embracers (lodgepole pine), colonizers (whitebark pine) and avoiders (e.g., Engelmann spruce and subalpine fir), with the exception of grand fir (Table 2). Despite classifying grand fir as an avoider, severity values in the grand fir forest type were at the same level of forest types

dominated by resister species. The mean community FRS of the grand fir forest type was the second highest among the forest types, only behind ponderosa pine (Table 2). In fact, resister species were estimated to be abundant in the grand fir forest type (Table S6).

There were differences in the proportions of fire severity classes between forest types of fire-resister and non-resister species. “Moderate” was the most abundant severity class in forest types of resister species and grand fir, whereas in the rest of forest types “high” was the dominant severity class (Table 2). In forest types of resister species, low- and moderate-severity fire accounted for approximately 75% of the burned area. Forest types of resister species had less high-severity fire (about 25% of the burned area) than the other forest types (except grand fir), in which high-severity fire reached more than 40% of the burned area. Distributions of RdNBR values of the major forest types also show the difference in fire severity between these two groups, fire-resisters and non-resisters. Forest types of resister species had unimodal distributions and peaked between the low and moderate classes, while distributions in forest types

Table 2 Summary of remote sensing measures of fire severity for the main burned forest types and fire strategies

Fire Strategy	Forest Type	Burned Area (ha)	Mean RdNBR	Fire severity class ^a			Mean ^b FRS
				Low	Moderate	High	
Resister	WL	21,971	491	0.23	0.51	0.27	0.46
	PP	382,360	339	0.37	0.46	0.17	0.59
	DF	1,056,881	463	0.29	0.45	0.26	0.48
	All	1,461,212	431	0.31	0.45	0.24	0.50
Embracer	LP	447,873	627	0.21	0.37	0.42	0.40
Avoider	ES	27,707	704	0.18	0.32	0.50	0.39
	ES-SF	477,868	610	0.23	0.36	0.41	0.36
	SF	38,011	640	0.20	0.34	0.45	0.37
	GF	144,053	430	0.36	0.40	0.24	0.49
	PF	5742	648	0.18	0.36	0.46	0.43
	MH	25,272	671	0.17	0.30	0.53	0.39
	All	718,653	582	0.25	0.36	0.39	0.41
Colonizer	WP	17,048	691	0.19	0.30	0.50	0.32
	Non-forest	441,320	180	0.55	0.35	0.10	

WL western larch; PP ponderosa pine; DF Douglas-fir; LP lodgepole pine; ES Engelmann spruce; ES-SF Engelmann spruce-subalpine fir; SF subalpine fir; GF grand fir; PF Pacific silver fir; MH mountain hemlock; WP whitebark pine. Resisters: WL, PP, DF; Embracer: LP; Avoiders: ES, ES-SF, SF, GF, PF, MH; Colonizer: WP

^aProportion of pixels in the low (RdNBR < 209), moderate (RdNBR = 209–706) and high (RdNBR > 709) classes

^bMean FRS are calculated from the forest community FRS map and should not be confused with the FRS values assigned to each species in Table 1

of non-resister species were bimodal with one of the peaks located in the high severity class or flat-topped (Fig. 4).

Species-level FRS and mean RdNBR values of forest types were negatively and highly correlated (Fig. 5 left). The negative correlation between mean community-level FRS and mean RdNBR was even higher (Fig. 5 right), and shows how the top-ranking forest types in community fire resistance (ponderosa pine, grand fir, Douglas-fir and western larch) had the lowest fire severity values.

Landscape drivers of high-severity fire

At fire level, we did not find a direct significant relationship between community FRS and mean patch size of high severity, although there was an indirect link between both variables through the effect on proportion of high-severity fire (Fig. 6 right). Mean community FRS was a significant predictor of the proportion of high severity (Fig. 6 right). Proportion of high-severity fire clearly decreased with increasing FRS (Fig. 7b). On the other side, proportion of high-severity fire was a strong predictor of mean patch size of high severity (Fig. 6 right). Figure 7d shows

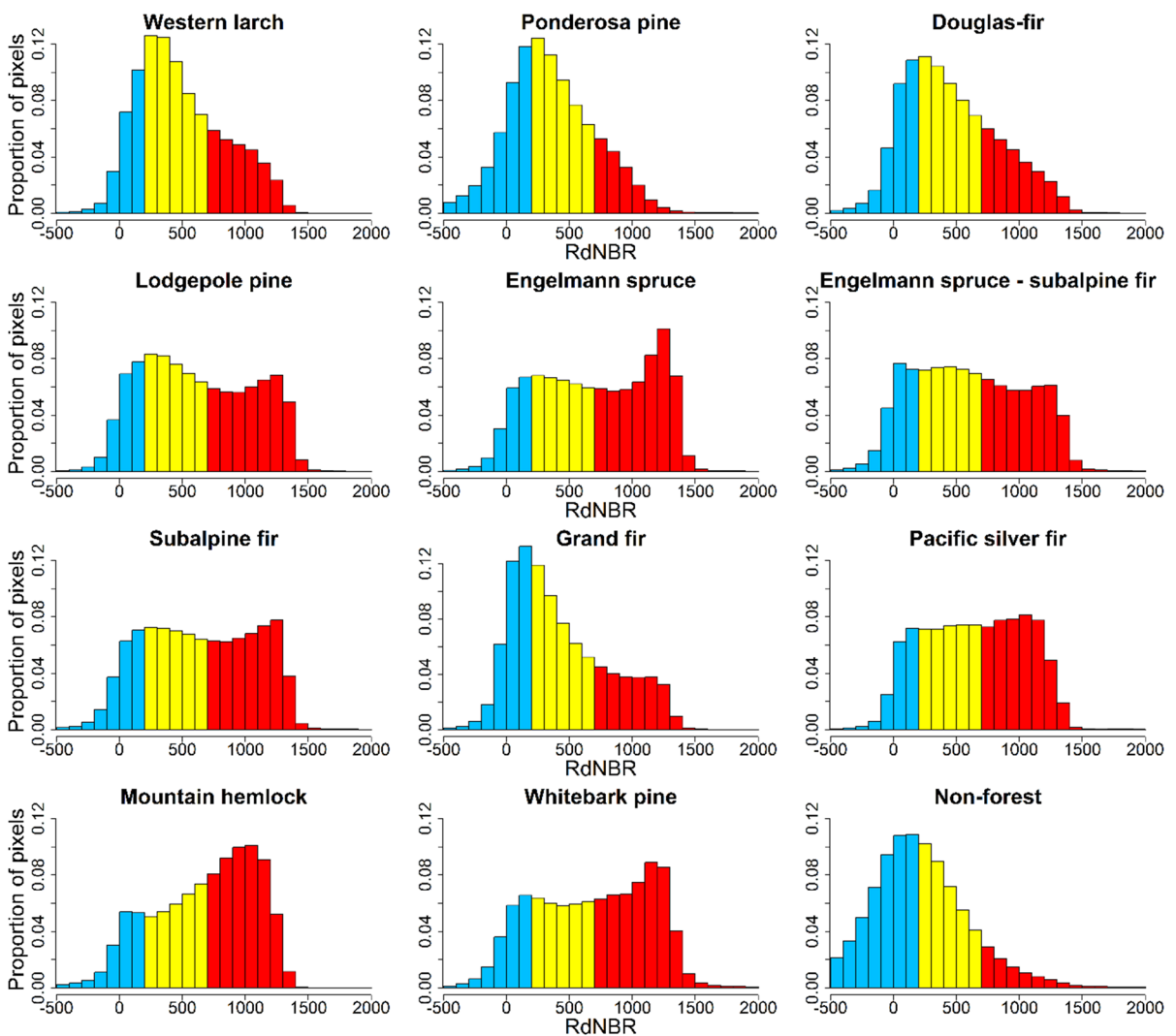


Fig. 4 Distributions of RdNBR values of the main burned forest types. Colors indicate fire severity classes: blue (low: RdNBR < 209), yellow (moderate: RdNBR = 209–706), red (high: RdNBR > 706)

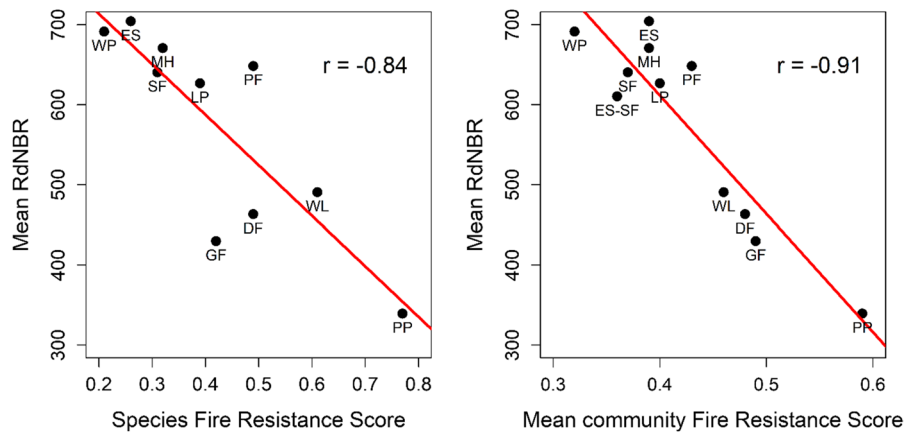


Fig. 5 Correlations between FRS and mean RdNBR for the main burned forest types. Left: single-species FRS values from Stevens et al. (2020) assigned to the reference species of each forest type; right: mean FRS values calculated from the map of community FRS (Stevens et al. 2020). *r*: Pearson’s correla-

tion coefficient (in both cases $p < 0.01$). *WL* western larch; *PP* ponderosa pine; *DF* Douglas-fir; *LP* lodgepole pine; *ES* Engelmann spruce; *SF* subalpine fir; *GF* grand fir; *PF* Pacific silver fir; *MH* mountain hemlock; *WP* whitebark pine

that the mean size of high-severity patches tended to grow non-linearly with proportion of high severity. Finally, the proportion of high-severity fire increased with fire size (Fig. 7a), and mean patch size of high severity was positively and directly related to fire size (Fig. 7c).

Discussion

The results confirm the two hypotheses. First, forest types dominated by fire-resistant species experienced lower fire severity than non-resister forest types. We found a strong negative correlation between the fire resistance index developed by Stevens et al. (2020) and Landsat-based average values of the RdNBR. Second, burned landscapes with higher degree of fire resistance tended to have less high-severity fire,

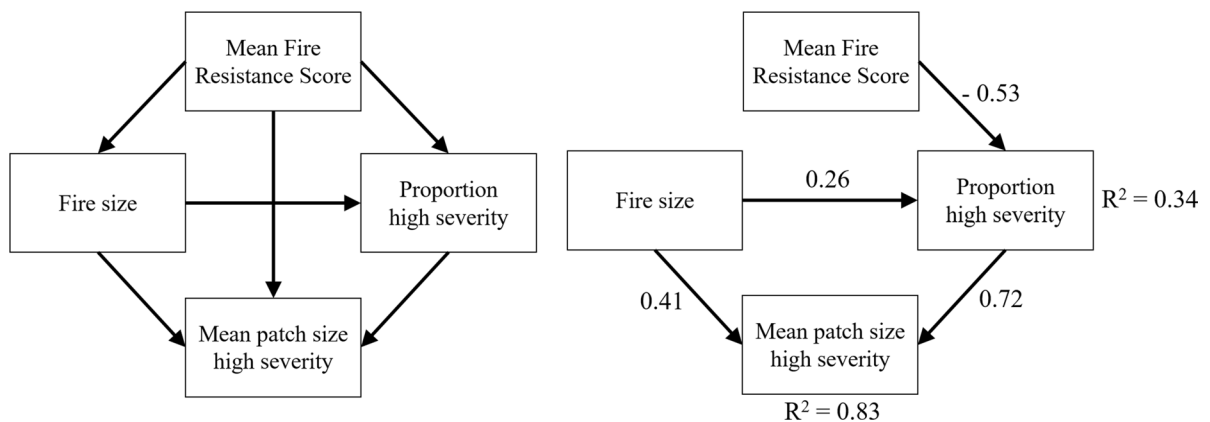
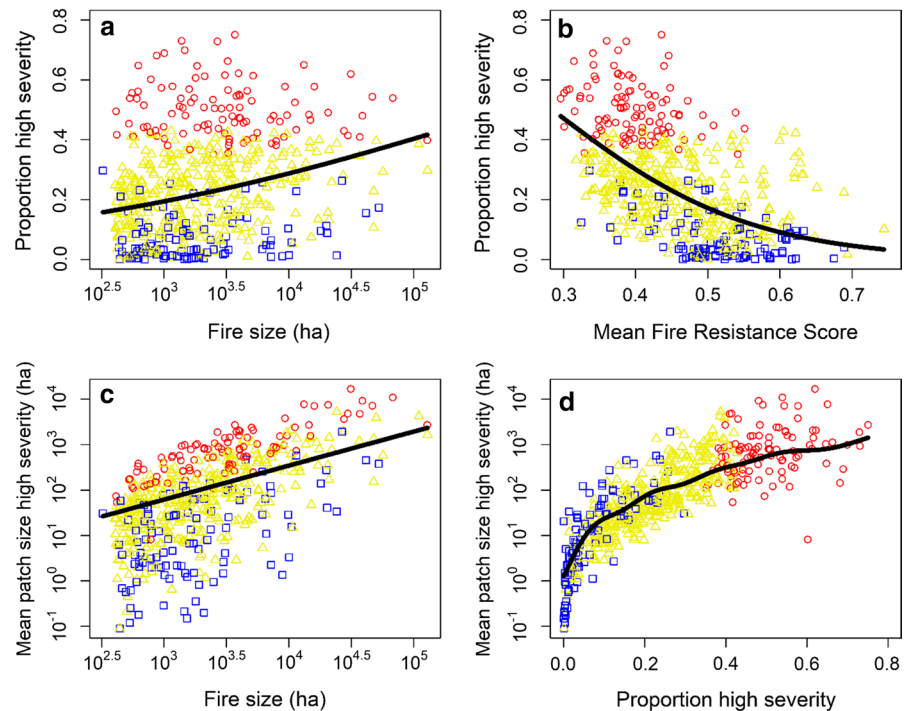


Fig. 6 Initial conceptual model (left) and final model built with SEM (right). Observed variables are represented by rectangles. Single-headed arrows indicate relationships between predictors (arrow tail) and response variables (arrow head)

and are labeled with standardized path coefficients. R^2 refers to the proportion of variance in response variables explained by predictors. Additional results and measures of model fit are reported in Tables S8-S9

Fig. 7 Scatterplots and regression curves fitted with beta regressions (proportion of high-severity fire) and GAM (area-weighted mean patch size of high severity). Red dots represent high-severity fires (i.e., wildfires in which high-severity fire is the dominant severity class), yellow triangles moderate-severity fires, and blue squares low-severity fires. Summaries of the models are reported in Table S10



and we detected an indirect relationship between high-severity patch size and fire resistance mediated by the abundance of area burned at high severity. These results suggest that plant traits may be useful for anticipating fire effects at regional scales, even though the effects of individual fires may be variable and difficult to predict by using exclusively species composition data.

Hypothesis 1 Fire severity of forest types at regional scale

The Landsat-derived metrics showed that fire severity in forest types dominated by fire-resister species (ponderosa pine, western larch and Douglas-fir) was lower than in forest types dominated by fire-embracer and fire-avoider species (Table 2). These findings support the hypothesis that forests dominated by species with fire-resistant traits undergo less fire-caused mortality. These results are consistent with the patterns described by Rogers et al. (2015) in boreal forests, who found that species-level traits explained differences in fire severity between North American forests with a high-severity crown fire regime and Eurasian forests with a lower-severity, surface fire regime. Our results suggest that a trait-based approach may be

broadly applicable across a wide range of forest types and fire regimes.

Taking into consideration mixed-species composition in forest communities, rather than only the dominant species of the forest type, improved the prediction of regional-scale values of fire severity in temperate coniferous forests of the Inland Northwest USA (Fig. 5). The grand fir forest type had severity values at the same level of forest types dominated by fire-resister species despite grand fir was classified as a fire-avoider species. To a lesser extent, the western larch forest type had severity values slightly higher than anticipated from the high resistance degree of western larch at species level. These results may be due a mismatch between the level of traits (assigned to species) and the level of forest data (assigned to forest types). While in some forest types (e.g., ponderosa pine, Douglas-fir, lodgepole pine, mountain hemlock) the species representing these types are the dominant component in terms of basal area, other species, such as western larch and grand fir, are less dominant in their corresponding forest types (Table S6), which are often collectively referred to as mixed conifer. For example, lodgepole pine, Engelmann spruce and sub-alpine fir are a substantial component of the burned western larch forest type, reducing its overall fire

resistance, while Douglas-fir and ponderosa pine are abundant species in the grand fir forest type, increasing the overall fire resistance. The estimated relative abundance of species at 250-m resolution within forest types explains why overall community FRS match fire severity better than single-species FRS attributed to each forest type. In other words, relative abundance of tree species with different fire-related traits largely explains the regional-scale differences in fire severity among forest types.

The patterns of fire severity found in the grand fir forest type are also likely associated to structural and composition changes caused by a strong deficit of fire. Land use changes in the nineteenth and twentieth centuries, including fire exclusion, livestock grazing and timber harvesting, favored the expansion of grand fir in the study area (Hessburg and Agee 2003; Merschel et al. 2014; Johnston et al. 2018). In many ponderosa pine forests maintained historically by a high frequency, low-severity fire regime, the transition towards denser forests dominated by Douglas-fir and grand fir would explain why ponderosa pine and Douglas-fir still compose a significant proportion of basal area in the grand fir forest type, and many maintain large, old, fire-resistant ponderosa pine trees (Johnston et al. 2021; Merschel et al. 2021). Therefore, the particular structure and composition of these “recent” grand fir forests (e.g., Merschel et al. 2014), with an important presence of large-diameter trees of fire-resistant species, may provide latent fire resistance (Larson et al. 2013).

Species with traits that fall under multiple fire strategies are likely beneficial under mixed-severity fire regimes (Poulos et al. 2018). Consequently, fire resistance indices and fire severity estimates may mismatch for regions and forest types characterized by mixed-severity fire regimes (Halofsky et al. 2011; Perry et al. 2011). Western larch is an example of how variability in fire-related traits may be beneficial under a mixed-severity fire regime. Low- to moderate-severity fire favors western larch, a shade-intolerant species, by thinning out competition, while high-severity fire creates suitable conditions (i.e., canopy gaps and mineral seedbed) for larch regeneration (Arno and Fischer 1995; Schmidt and Shearer 1995). As in fire-colonizer species, western larch has long-distance dispersal capacity due to its light, wind-dispersed seeds, and generally stand-replacing fire favors post-fire regeneration of western larch over other tree

species (Scher 2002; Harvey et al. 2016c; Urza and Sibold 2017; Hood et al. 2018b).

Hypothesis 2 Spatial patterns of high-severity fire at landscape scale

The relationship between fire resistance and severity was weaker at the scale of individual fires than at the regional scale. Wildfires affecting forest communities with higher fire resistance tended to have lower proportions of high-severity fire and smaller high-severity patches. Nevertheless, the relationship between fire resistance and high-severity patch size was not direct but mediated by the abundance of stand-replacing fire within the wildfires (Fig. 6).

The strong, positive, non-linear relationship found between proportion of high-severity fire and high-severity patch size supports the understanding that high-severity wildfires (i.e., wildfires in which high-severity fire is the dominant severity class) tend to have larger stand-replacing patches by a few orders of magnitude than moderate- and low-severity wildfires (Agee 1998). To a lesser extent, the size of high-severity patches also increased with fire size. All these results are consistent with findings of other studies in the Inland Northwest USA (Cansler and McKenzie 2014; Harvey et al. 2016c; Reilly et al. 2017).

The great variability in both proportion of high-severity fire and high-severity patch size along the gradient of mean community FRS, (1) shows the limitations of the fire resistance score when averaged over the whole wildfire extent (i.e., burned landscape) to predict the spatial configuration of high-severity fire, and (2) highlights that large stand-replacing patches (> 100 ha) are part of all the contemporary fire regimes in the region. Other top-down (e.g., weather, climate) and bottom-up factors (e.g., topography, fuel) must play an important role driving high-severity fire (Cansler and McKenzie 2014; Harvey et al. 2016a; Reilly et al. 2017; Parks et al. 2018). In brief, we should expect a lower predictive capacity of fire resistance indices at relatively small scales (e.g., forest stand, severity patch, single fire).

Implications for linking plant traits and large-scale fire effects

The FRS index was meant to quantify fire resistance of forests to surface fires (Stevens et al. (2020), but may be more broadly applied to other fire regimes. However, some aspects may hinder the association between trait-based resistance and fire severity. First, the community FRS map does not take into consideration tree size or forest structure, but only relative species composition. Fire resistance increases with age due to increased bark thickness and crown base height (Schmidt et al. 1976), and thus there may be differences in fire severity between young (less resistant to fire) and mature stands of fire-resistant species. For instance, large grand fir trees can have a relatively thick bark (Howard and Aleksoff 2000; Hood et al. 2018b). In fact, Flint (1925) highlighted that grand fir can have a degree of fire resistance nearly equal to Douglas-fir. Similarly, open and heterogeneous forest structures of fire-resistant species are likely to experience lower fire severity (Johnston et al. 2021; Merschel et al. 2021; North et al. 2021). Applying forest structure spatial data (e.g., based on basal area and tree size classes) across broad scales could complement the FRS concept (Reilly et al. 2018). Second, it is common to find large variability in fire-related traits within and among populations of the same species (Pausas 2015a, b). Third, some species occur across a broad range of environments, and low-severity fires may be more relevant in warm-dry sites than in cool or moist sites (Arno and Fischer 1995; Naficy et al. 2016). Despite the inherent limitations of the FRS to predict tree mortality, we found that mean community-level FRS was highly correlated with mean fire severity at forest type level. This indicates that trait-based indices seem a suitable tool to link forest resistance to fire severity at large spatial and temporal scales (e.g., from thousands to millions of hectares, and from several fire seasons to decades).

Conclusions

This study provides further evidence that fire-related traits are useful for up-scaling attributes of

fire regimes such as spatial patterns of fire severity (Rogers et al. 2015; Pellegrini et al. 2017; Stevens et al. 2020). The correlations found between trait-based fire resistance and fire severity at regional and landscape scales confirm our two hypothesis, but also reveals that the strength of the relationship is scale-dependent. Satellite-based, large-scale differences in fire severity among forest types match the degree of fire resistance that fire-related traits provide to individual tree species. We interpret this finding as an evidence that tree species composition, as proxy of fire resistance due to the influence of plant traits on tree survival from fire, is an important driver of fire severity at large spatial scales. Therefore, the concept of fire resistance score of Stevens et al. (2020) allows models to include data on organ- and plant-level traits to predict fire effects at broad scales. This is a significant step forward in comparison with broad vegetation classes that simplify species composition and mask the potential response to fire. Trait-based fire resistance indices are a new tool quantifying the relative capacity of forest ecosystem to deal with fire disturbances, which can potentially help researchers and managers up-scale pyrosilviculture (North et al. 2021). The same or similar approaches can be used in other regions around the globe to study the relationships between plant traits and fire regimes at large scales.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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