Aridity and competition drive fire resistance trait covariation in mountain trees

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Abstract. Fire resistance traits drive tree species composition in surface-fire ecosystems, but how they covary at different scales of variation and with the environment is not well documented. We assessed the covariation of bark thickness (BT), tree height, and crown base-to-height ratio across Alpine forests, after accounting for the effects of tree diameter and competition for light on individual trait variation. Traits consistently correlated across individuals and communities, although the variance of BT mainly occurred among species, whereas crown elevation traits varied mainly within species. Aridity, temperature, and competition contributed to explain the variation of fire resistance traits among and within species, driving a trade-off between fire resistance and the ability to compete for light. Thick-barked species (fire-tolerant) that self-prune their lower branches (flame-avoiders) dominated the most fire-prone and flammable communities in sub-Mediterranean southern Alps, whereas thin-barked tree species that grow tall (competition for light) dominated the least fire-prone communities in the northern Alps. Our findings suggest a long-term interaction between mountain tree species and fire regime. Higher allocation to trunk elongation occurs in moist and shade environments, while higher allocation to thicken the bark and distancing the crown base from surface fuels occurs in open-canopy, dry forests where fire spreads with higher intensity.

Key words: bark thickness; crown basal height; height-diameter; interspecific; intraspecific; mountain forests; surface fire; trait covariation.

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INTRODUCTION

Fire is a major ecological factor that shapes the composition of plant communities and ecosystem functioning. The suite of functional traits that enables plant species to cope with wildfire diverges among ecosystems (Schwik and Ackerly 2001, Pausas 2015). While in crown-fire ecosystems regeneration strategies drive species persistence by vegetative resprouting or seedling recruitment (e.g., Pausas and Keeley 2014), in surface-fire ecosystems bark thickness (BT) provides fire tolerance by insulating the cambium and buds from lethal heating (Harmon 1984). In addition, tree height (TH) and the height to crown base (crown base-to-height ratio; CBR) enable trees to resist fire impacts by avoiding flames reaching the canopy (Lawes et al. 2011, Dantas and Pausas 2013). Taken together, fire resistance traits (BT, TH, and CBR) explain interspecific differences in post-fire tree survival (Lawes et al. 2011, Brando et al. 2012) and are used to predict the mortality likelihood of the aboveground biomass (Ibanez et al. 2013).
Plant ecological strategies are commonly defined by functional traits and their covariation among species (e.g., Westoby et al. 2002). Trait-based studies have been mostly based on species mean values to assess trait–environment relationships and infer plant ecological strategy. However, functional trait variation is not necessarily consistent across different scales of variation. For example, variation within species has been found larger than expected in the tropics (Messier et al. 2016), while global correlation patterns of the leaf economics spectrum do not necessarily occur within species (Niinemets 2015). Moreover, the study of environmental filtering processes needs to account for the variation of traits with ontogeny (e.g., size) and biotic interactions such as competition (Bennett et al. 2016). This variation is particularly important in the study of fire resistance traits from individuals to ecosystem dynamics, such as vegetation response to fire. For instance, it has been shown that fire-resistant pine species are tall with thick barks and high self-pruning (Schwilck and Ackerly 2001, Pausas 2015). However, it is not well documented how variation in fire tolerance (thick bark) and flame avoidance (elevated crown) is distributed across individuals, species, communities, and biomes. For instance, variation across scales of variation (e.g., logging) or disturbance (e.g., fire) are traditionally managed using natural regeneration. Therefore, trees were assumed to derive from the local gene pool, except the naturalized black pine (P. nigra) that has been introduced

**Materials and Methods**

**Fire resistance traits**

An extensive sampling of TH (m), CBR, BT (mm), and tree diameter at breast height (dbh, cm) was carried out in the western Alps (N plots = 94) during summer 2012–2013. Nine out of the main European mountain tree species (Fig. 1) were sampled, including two angiosperm species (Fagus sylvatica L., Quercus pubescens Willd.) and seven gymnosperm species (Abies alba Mill., Larix decidua Mill., Picea abies (L.) Karst., Pinus nigra Arn., Pinus sylvestris L., Pinus cembra L., and Pinus uncinata Mill.). We followed a stratified random sampling within the four biogeographic regions of the western Alps (forest ecosystem type in Fréjaville et al. 2016): (1) sub-Mediterranean open forests (2), sub-Mediterranean closed forests, (3) subalpine open forests, and (4) moist montane forests (Fig. 1). Within each region, multiple locations along elevation, slope, and aspect gradients were sampled to capture a broad range of vegetation and habitat conditions. Locations showing recent evidence of management (e.g., logging) or disturbance (e.g., fire) were avoided. European mountain tree species are traditionally managed using natural regeneration. Therefore, trees were assumed to derive from the local gene pool, except the naturalized black pine (P. nigra) that has been introduced
Fig. 1. Map of sampling sites and biogeographic regions in the western Alps. The 94 plots (+) were clustered by biogeographic region using their geographical location: dry subalpine forests in the inner continental range (n = 27), moist montane forests of the northern Alps (n = 16), open-canopy sub-Mediterranean forests (n = 29) and closed-canopy sub-Mediterranean forests of the southern Alps (n = 27; modified from Fréjaville et al. 2016). Species relative abundance (basal area ratio) in the 94 plots is indicated by boxplots.
during the late-19th century to protect landscapes from erosion and landslides. We assumed that trait variation should reflect spatial divergence in current and recent environmental conditions.

Plot size was 200–400 m², depending on tree density. We used the percentage of basal area of each species as a measure of species relative abundance within each plot. For each tree, BT was averaged from two measurements at breast height (uphill and downhill) of the thickness of both inner and outer barks. The CBR was computed as the ratio between the crown basal height and TH to reflect the distance between the ground and canopy fuels relative to the height of the crown. Height measurements were performed using a vertex IV (Haglöf).

To characterize the environment at each sampled community, we used 30 arc-second (1 km at the equator) resolution data of climate and weather (Fréjaville and Curt 2015): the annual mean temperature and the annual drought code, both averaged over the period of 1979–2009. The drought code is a component of the fire weather index system that estimates fuel dryness from deep litter layers to living biomass (van Wagner 1987). Because this aridity index is highly correlated with fire activity in the Mediterranean Basin and mountain forests (Loepfe et al. 2014, Fréjaville et al. 2018), we used it to characterize the fire proneness of each community, rather than actual fire data that were not available over the entire study area at sufficient spatial resolution.

Finally, we used previous simulations of the fireline intensity (energy released per linear unit of the flaming front, in kW/m) under extreme weather conditions to characterize the potential fire intensity at each plot (Fréjaville et al. 2018) and to test whether fire resistance traits vary as a function of vegetation flammability in addition to temperature, aridity, and tree cover conditions. Fire simulations were performed on the basis of 30 arc-second resolution climate data and field measurement of surface fuel parameters across litter, grass, and shrub layers; fuel sampling and fire simulations are explained in detail by Fréjaville et al. (2018).

Variance partitioning

Variance component analyses were performed to compute the variance distribution of traits across nested ecological scales in the following increasing order: individual (intraspecific variance within species), species (interspecific variance within communities), community (among-community variance within regions), and biogeographic region (among-region variance). A linear mixed-effect model was fit to the variance of each trait (log-transformed) using a restricted maximum likelihood method. The 95% confidence interval (95% CI) was calculated for the percentage of variance explained at each nested level by bootstrapping, that is, 500 runs with 1000 randomly sampled data points with replacement (Messier et al. 2010).

Differences of explained trait variance among ecological scales were tested using ANOVA and Tukey post-hoc tests. To assess the relative importance of tree size (before standardizing its effect on trait variation), we added the dbh (log-transformed) as covariable in the model (fixed effect) and included it in the comparison.

Trait standardization

We standardized trait variation for the effects of dbh (ontogeny) before analyzing trait variation across scales and environmental gradients. First, we used linear mixed-effect models to fit species-specific allometric relationships. For each species j and each trait T, the allometric model Aj was fit by regressing log Tj against log dbhj. Plot was used as random effect to control for unaccounted variability among plots and to account for the nested design of individual trait measurements within plots. Species-specific model residuals were computed from fixed effects only (i.e., dbh) to extract the intraspecific trait variance which was not explained by tree size.

Second, the interspecific component of each trait was computed by using the Aj models to predict the species mean trait values for a given diameter (the mean dbh across all species). Third, intraspecific and interspecific components were summed to obtain the total trait variation, standardized for dbh, and corrected for potential sampling-induced differences in the among-species distribution of dbh. Community-level trait data were then computed by averaging standardized trait values of all sampled trees within each community for each component of trait variation (total, intraspecific, and interspecific).
Because dbh had no significant effects on CBR, we used measured data for standardization. Species mean traits were thus used to compute the interspecific component, and differences between individual values and species means were used to compute the intraspecific component.

**Interspecific trait differences, trait covariation, and trait–environment relationships**

To test interspecific trait differences, we used ANOVA and Tukey’s HSD post-hoc tests on the total variation of standardized traits (both inter- and intraspecific components). Log-transformation and standardization of traits satisfied normality assumptions.

To test correlations among traits, we used mixed-effect models with tree cover as covariate to control for competition, and plot as random factor:

\[
T_{1sc} = b_0 + a_1(T_{2sc}) + a_2(\text{tree cover}) + \text{random (Plot)} + \varepsilon
\]

To test whether trait correlations differed across scales, models were fit from standardized traits \( T \) at both individual and community levels for each component \( sc \) of trait covariation (total, intraspecific, and interspecific). Then, partial correlations were tested by computing Spearman’s rank coefficients between \( T_2 \) (the focal explanatory trait) and \( T_1 \) partial residuals (i.e., after accounting for tree cover on \( T_1 \)).

Similarly, to test trait variation with the environment at the community level, we used mixed-effect models to assess the relative effect of tree cover, annual drought, and temperature:

\[
T_{sc} = b_0 + a_1(\text{tree cover}) + a_2(\text{drought code}) + a_3(\text{annual temperature}) + \text{random (Plot)} + \varepsilon
\]

As supplementary analyses, we also tested the relative effect of fireline intensity (log-transformed) and the relative effect of tree basal area (cumulative basal area at breast height of all inventoried trees, in m²/ha) that is commonly used to infer tree competition (Kunstler et al. 2016).

To test whether correlations are consistent among and within species, models were fit for each component of trait variation \( sc \), and Spearman’s rank coefficients were computed between each environmental variable and \( T_{sc} \) partial residuals (i.e., after accounting for other environmental effects).

Finally, we applied ANOVA to explore the relative contribution of interspecific and intraspecific components of correlations among traits and trait variation with the environment, on the basis of sum of squares (Leps et al. 2011). All analyses and computations were carried out in the R software environment (R Core Team 2013), using lme function of nlme package for mixed-effect modeling (Pinheiro et al. 2015).

**RESULTS**

**Trait variation across ecological scales**

The variance partitioning analysis indicated that the relevance of each level to overall variation differed among traits (Fig. 2). Tree dbh was the main source of variation in TH (55%) and BT (47%), whereas it accounted for <5% in CBR. After accounting for tree size, BT varied first among species (32%), whereas CBR and TH varied first within species (33% and 15%, respectively, \( P < 0.05 \)). The intraspecific level accounted for 13% of variance in BT. The biogeographic level accounted for a substantial part of the variance in all traits (7–14%). Within regions, the plot level accounted for 21% in CBR and 13% TH and <1% in BT.

**Interspecific differences in fire resistance traits**

Allometric relationships used to standardize BT and TH are presented in Appendix S1: Table S1 and Fig. S1. Species dominating sub-Mediterranean forests (Pinus nigra, Pinus sylvestris, and Quercus) had thicker barks (Appendix S1: Fig. S2a), higher CBR (Appendix S1: Fig. S2b), and lower height (Appendix S1: Fig. S2c). Contrary, species dominating moist montane forests (Fagus, Abies, and Picea) were taller and had lower CBR and BT. In subalpine forests, Larix was taller and had thicker barks, Pinus uncinata and Pinus cembra had thinner barks, and P. cembra had the lowest CBR.

**Covariation among fire resistance traits**

Partial correlation analyses indicated that, once dbh and tree cover were accounted for, BT and CBR were positively correlated at the individual \( (r = 0.33, P < 0.001; \text{Fig. 3a}) \) and community levels \( (r = 0.58, P < 0.001; \text{Fig. 3b}) \), whereas BT and TH were negatively correlated at the individual
At both individual and community levels, Spearman coefficients indicated stronger correlations for the interspecific than the intraspecific component of trait covariation \((P < 0.001, \text{Fig. 3; Appendix S1: Table S2})\). At the community level, BT accounted for 6% of the variance in CBR and 20% in TH (Appendix S1: Table S2). At the individual level, within-species correlations between BT and CBR as well as between BT and TH were non-significant, positive or negative depending on the species (Appendix S1: Figs. S3, S4).

**Trait–environment relationships**

Partial correlation analyses indicated that BT decreased, whereas CBR and TH increased with tree cover (Fig. 4). In addition, BT and CBR increased, while TH decreased with increasing aridity and annual mean temperature \((P < 0.05; \text{Fig. 4; Appendix S1: Fig. S5})\). Trait–environment correlations were conserved at the interspecific and intraspecific levels, with few exceptions (Fig. 4; Appendix S1: Fig. S5). Variance analyses indicated that aridity was the main determinant of BT (23% of explained variance) mostly at the interspecific level, whereas tree cover accounted for the main part of the variance in CBR and TH (34% and 31%, respectively) mostly at the intraspecific level (Appendix S1: Table S3). In total, tree cover, drought, and annual temperature explained 33% of the variance in community mean BT, 51% in CBR, and 50% in TH (Appendix S1: Table S3). Supplementary analyses showed similar but higher correlations between traits and tree cover than between traits and tree basal area (Appendix S1: Fig. S6), indicating that tree cover captured the effect of tree basal area which is a more common index used to infer competition between trees. In addition, supplementary analyses indicated that traits did not vary with the fireline intensity once the drought code is accounted for, although weak but significant increase of BT and decrease of TH with increasing fireline intensity were found at the interspecific level (Appendix S1: Fig. S7).

**DISCUSSION**

Our results suggest that (1) fire resistance traits vary across different ecological scales and they correlate in the same direction across individuals and communities; (2) trait covariation mostly results from trait differences among species along gradients of tree cover and aridity, although intraspecific variation accounts for a substantial part of trait–environment relationships; and (3) fire resistance (thick bark and elevated crown base) and competition for light strategies (tall trees relative to diameter) trade-off in Alpine forests.

Fig. 2. Variance structure of log bark thickness (BT) (a), crown base-to-height ratio (CBR) (b), and log tree height (TH) (c) across ecological scales, once the effect of tree diameter (dbh) was accounted for. At each level, the relative variance distribution was computed by bootstrapping; bars (and lines) indicate mean (±SD) values. The conditional r-squared, that is, the amount of explained variance by fixed (dbh) and random effects (scales), is indicated; dbh accounted for 0.40, 0.03, and 0.45 of explained variance (marginal r-squared) in BT, CBR, and TH, respectively.

\(r = -0.27, P < 0.001; \text{Fig. 3c}\) and community levels \(r = -0.41, P < 0.001; \text{Fig. 3c}\).
most arid conditions across the western Alps and occur in flammable environments throughout their geographic range (Fréjaville et al. 2018). The resistance to surface fires of the dominant pines Pinus nigra and Pinus sylvestris is well documented in historical studies (Fulé et al. 2008, Leys et al. 2014). Contrary, taller trees are thin-barked species which dominate the least fire-prone communities across the wettest and shadiest forests of the Alps (Fréjaville et al. 2018). These findings provide additional evidence on interspecific variation of BT with fire activity (e.g., burned area) and precipitation (e.g., Rosell 2016, Pellegrini et al. 2017). Furthermore, we also show that BT increases and TH decreases with both aridity and potential fire intensity (Appendix S1: Fig. S7), suggesting that ecological patterns of forest flammability (Fréjaville et al. 2018) may partly explain fire resistance trait patterns in mountain forests. Our results suggest a well-documented trade-off in the allocation to bark vs. the ability to grow tall and compete for light between shade-intolerant and shade-tolerant species (Gignoux et al. 1997, Niinemets 1998, Lawes et al. 2011). In particular, fire tolerance through thick bark relative to diameter dominates in fire-prone ecosystems (e.g., open savannas), whereas resource acquisition strategies through plant height or height relative to diameter and specific leaf area dominate in

Fig. 3. Partial correlations between standardized traits at individual (a, c) and community levels (b, d). Within each panel, the total (left), intraspecific (top-right), and interspecific (bottom-right) components of trait covariation are shown. Trait variation with the tree cover was prior accounted for to control for competition; variance analyses of trait covariation components are reported in Appendix S1: Table S2. Mean values (and SD) by species (a, c) and biogeographic regions (b, d) are indicated by large circles (and bars). Spearman’s rank correlation coefficients (r) are indicated: ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05. Regression lines are shown for illustrative purpose.
Our findings suggest that drought and tree cover structure the species-level trade-off between growing tall in low fire-prone environments vs. unburned dense forests (Cavender-Bares and Reich 2012, Hoffmann et al. 2012, Dantas et al. 2013).
thickening the bark and distancing the crown base from surface fuels in dry, open-canopy environments. On the contrary, the lower flammability and shadier conditions of moist montane forests (Fréjaville et al. 2016) may have promoted a higher allocation to height against the promotion of fire resistance in *Fagus*, *Picea*, and *Abies* (thin barks and low self-pruning), which reflects their high sensitivity to fire (Colombaroli et al. 2007, Maringer et al. 2016). These correlative observations in mountain forests suggest that both BT and CBR reflect a strategy to resist fire by heat tolerance and flame avoidance, respectively, whereas TH relative to diameter (stem elongation) reflects a strategy to compete for light.

In subalpine forests of the inner Alps, communities are dominated by mixed strategies: *Pinus uncinata* and especially *Pinus cembra* are fire-sensitive (thin barks, low crown bases, and moderate heights), while the co-dominant *Larix* presents competitive and fire-resistant traits, in addition to a lower bark flammability (Fréjaville et al. 2013). These differences in fire resistance traits likely explain the dominance of *Larix* over *P. cembra* in periods of higher fire occurrence over the last 18,000 yr (Carcailllet and Blarquez 2017). Climate change together with the high fire intensity in subalpine forests (Fréjaville et al. 2016) might induce population decline of *P. cembra* in the Alps, if fire return intervals become shorter than the time required to reach maturity (Blarquez et al. 2012).

Our results show that intraspecific variability accounts for a substantial part of the variance in fire resistance traits (Fig. 1), as it has been observed in other traits and biomes (Siefert et al. 2015, Vilà-Cabrera et al. 2015). The intraspecific variation mostly accounts for community differences in flame avoidance (CBR) and competition for light strategies (TH) along tree cover conditions (Fig. 4), and it accounts for the increase in community fire tolerance (BT) in parallel to the decrease of TH with annual temperature (Appendix S1: Fig. S5), showing that canopy conditions and individual variation have more influence on fire resistance traits than expected. Moreover, our results show a consistent correlation between traits and environmental conditions among- and within species. These findings suggest that competition is an environmental filter that shapes fire resistance trait variability between- and within species, and across communities, in addition to fire (Cavender-Bares and Reich 2012, Siefert et al. 2015). This role of competition on fire-related traits has been also demonstrated in the forest–savanna transition. For example, the lower flammability and higher competitive environment of closed-canopy forests promotes the dominance of thin-barked, tall species, while the high flammability of open savanna forests promotes the dominance of thick-barked, small stature species (Hoffmann et al. 2012).

Finally, we found that correlation among traits was not consistently conserved within each species (Fig. 3; Appendix S1: Figs. S3, S4), suggesting an ecological trade-off between competitive and fire-resistant traits rather than a physiological or evolutionary trade-off. That is, our results indicate that a higher allocation to trunk elongation is not always concomitant with a lower allocation to bark (e.g., *Larix*), but that both vary with environmental conditions in opposite directions (Fig. 4). However, considering all species together our results show that trait covariation was invariant from individuals to species and communities in the Alps (Fig. 3), suggesting that environmental drivers of fire resistance consistently drive trait coordination across scales. These findings highlight that the trade-off observed at the individual and species levels between competition for light and fire resistance strategies may be scaled up to communities and biogeographic regions in European mountain forests, to predict vegetation response to fire. Together with the absence of fire-resistant traits in the competitive environments of moist montane forests, our results suggest long-term interplays between species and fire regime in Alpine forests. At the same time, our results show that trait–environment correlations were stronger at the interspecific than intraspecific level, and that the latter reduced the strength of correlations based on differences between species traits (Fig. 4; Appendix S1: Figs. S5–S7; Anderegg et al. 2018). Our results thus emphasize the importance of individual variability in understanding community assembly processes (Laughlin et al. 2012) that may be critical for predicting how changing fire regimes (Fréjaville and Curt 2017) will shift the distributions of fire-sensitive and fire-resistant mountain tree species. The increasing severity of fire weather conditions (Dupire et al. 2017) together with higher fire intensity and crown fire likelihood at the dry
range margin of mountain trees (Fréjaville et al. 2018) may increase the importance of fire resistance traits driving the composition of mountain forests, and the response of their communities to climate change.

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LITERATURE CITED

Anderegg, L. D. L., L.T. Berner, G. Badgley, M. L. Sethi, B. E. Law, and J. HilleRisLambers. 2018. Within-species patterns challenge our understanding of the leaf economics spectrum. Ecology Letters 21:734–744.

Bennett, J. A., K. Riibak, R. Tamme, R. J. Lewis, and M. Pärtel. 2016. The reciprocal relationship between competition and intraspecific trait variation. Journal of Ecology 104:1410–1420.

Blarquez, O., C. Carcaillet, T. M. Elzein, and P. Roiron. 2012. Needle accumulation rate model-based reconstruction of palaearctic tree biomass in the western subalpine Alps. Holocene 22:579–587.

Brando, P. M., D. C. Nepstad, J. K. Balch, B. Bolker, M. C. Christman, M. Coe, and F. E. Putz. 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. Global Change Biology 18:630–641.

Carcaillet, C., and O. Blarquez. 2017. Fire ecology of a tree glacial refugium on a nunatak with a view on Alpine glaciers. New Phytologist 216:1281–1290.

Cavender-Bares, J., and P. B. Reich. 2012. Shocks to the system: community assembly of the oak savanna in a 40-year fire frequency experiment. Ecology 93:552–569.

Colomboari, D., A. Marchetto, and W. Tinner. 2007. Long-term interactions between Mediterranean climate, vegetation and fire regime at Lago di Massaciuccoli (Tuscany, Italy). Journal of Ecology 95:755–770.

Dantas, V. de L., M. A. Batalha, and J. G. Pausas. 2013. Fire drives functional thresholds on the savanna–forest transition. Ecology 94:2454–2463.

Dantas, V. de L., and J. G. Pausas. 2013. The lanky and the corky: fire-escape strategies in savanna woody species. Journal of Ecology 101:1265–1272.

Dupire, S., T. Curt, and S. Bigot. 2017. Spatio-temporal trends in fire weather in the French Alps. Science of the Total Environment 595:801–817.

Falster, D. S., and M. Westoby. 2003. Plant height and evolutionary games. Trends in Ecology & Evolution 18:337–343.

Fréjaville, T., and T. Curt. 2015. Spatiotemporal patterns of changes in fire regime and climate: defining the pyroclimates of south-eastern France (Mediterranean Basin). Climatic Change 129:239–251.

Fréjaville, T., and T. Curt. 2017. Seasonal changes in the human alteration of fire regimes beyond the climate forcing. Environmental Research Letters 12:035006.

Fréjaville, T., T. Curt, and C. Carcaillet. 2013. Bark flammability as a fire-response trait for subalpine trees. Frontiers in Plant Science 4:466.

Fréjaville, T., T. Curt, and C. Carcaillet. 2016. Tree cover and seasonal precipitation drive understorey flammability in alpine mountain forests. Journal of Biogeography 43:1869–1880.

Fréjaville, T., T. Curt, and C. Carcaillet. 2018. Higher potential fire intensity at the dry range margins of European mountain trees. Journal of Biogeography 45:2003–2015.

Fulé, P. Z., M. Ribas, E. Gutiérrez, R. Vallejo, and M. W. Kaye. 2008. Forest structure and fire history in an old Pinus nigra forest, eastern Spain. Forest Ecology and Management 255:1234–1242.

Genries, A., X. Morin, S. Chauchard, and C. Carcaillet. 2009. The function of surface fires in the dynamics and structure of a formerly grazed old subalpine forest. Journal of Ecology 97:729–741.

Gignoux, J., J. Clobert, and J. C. Menaut. 1997. Alternative fire resistance strategies in savanna trees. Oecologia 110:576–583.

Harmon, M. E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National-Park. Ecology 65:796–802.

Hoffmann, W. A., E. L. Geiger, S. G. Gotsch, D. R. Rossatto, L. C. R. Silva, O. L. Lau, M. Haridasan, and A. C. Franco. 2012. Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. Ecology Letters 15:759–768.

Ibanez, T., T. Curt, and C. Hely. 2013. Low tolerance of New Caledonian secondary forest species to savanna fires. Journal of Vegetation Science 24:177–188.

Kunstler, G., et al. 2016. Plant functional traits have globally consistent effects on competition. Nature 529:204–207.

Laughlin, D. C., C. Joshi, P. M. Bodegom, Z. A. Bastow, and P. Z. Fulé. 2012. A predictive model of
community assembly that incorporates intraspecific trait variation. Ecology Letters 15:1291–1299.
Lawes, M. J., H. Adie, J. Russell-Smith, B. Murphy, and J. J. Midgley. 2011. How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. Ecosphere 2:42.
Leps, J., F. de Bello, P. Smilauer, and J. Doležal. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. Ecography 34:856–863.
Leys, B., W. Finsinger, and C. Carcaillet. 2014. Historical range of fire frequency is not the Achilles’ heel of the Corsican black pine ecosystem. Journal of Ecology 102:381–395.
Llopfè, L., A. Rodrigo, and F. Lloret. 2014. Two thresholds determine climatic control of forest fire size in Europe and northern Africa. Regional Environmental Change 14:1395–1404.
Maringer, J., D. Ascoli, M. Küffer, S. Schmidtlein, and M. Conedera. 2016. What drives European beech (Fagus sylvatica L.) mortality after forest fires of varying severity? Forest Ecology and Management 368:81–93.
Messier, J., B. J. McGill, B. J. Enquist, and M. J. Lechowicz. 2016. Trait variation and integration across scales: Is the leaf economic spectrum present at local scales? Ecography 40:685–697.
Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. Ecology letters 13:838–848.
Moris, J. V., G. Vacchiano, S. R. Enri, M. Lonati, R. Motta, and D. Ascoli. 2017. Resilience of European larch (Larix decidua Mill.) forests to wildﬁres in the western Alps. New Forests 48:663–683.
Niinemets, Ü. 1998. Growth of young trees of Acer platanoides and Quercus robur along a gap-understory continuum: interrelationships between allometry, biomass partitioning, nitrogen, and shade tolerance. International Journal of Plant Sciences 159:318–330.
Niinemets, Ü. 2015. Is there a species spectrum within the world-wide leaf economics spectrum? Major variations in leaf functional traits in the Mediterranean sclerophyll Quercus ilex. New Phytologist 205:79–96.
Pausas, J. G. 2015. Evolutionary fire ecology: lessons learned from pines. Trends in Plant Science 20:318–324.
Pausas, J. G. 2017. Bark thickness and fire regime: another twist. New Phytologist 213:13–15.
Pausas, J. G., and J. E. Keeley. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. New Phytologist 204:55–65.
Pellegrini, A. F. A., W. R. L. Anderegg, C. E. T. Paine, W. A. Hoffmann, T. Kartzinel, S. S. Rabin, D. Sheil, A. C. Franco, and S. W. Pacala. 2017. Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. Ecology Letters 20:307–316.
Pinheiro, J., D. Bates, S. DeBroy, D. Sarkar, and R Core Team. 2015. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–120. http://CRAN.R-project.org/package=nlme
R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rosell, J. A. 2016. Bark thickness across the angiosperms: more than just ﬁre. New Phytologist 211:90–102.
Schumacher, S., and H. Bugmann. 2006. The relative importance of climatic effects, wildﬁres and management for future forest landscape dynamics in the Swiss Alps. Global Change Biology 12:1435–1450.
Schwikl, D. W., and D. D. Ackerly. 2001. Flammability and serotiny as strategies: correlated evolution in pine. Oikos 94:326–336.
Siefert, A., et al. 2015. A global meta-analysis of the relative extent of intraspeciﬁc trait variation in plant communities. Ecology Letters 18:1406–1419.
Tinner, W., M. Conedera, E. Gobet, P. Hubschmid, M. Wehrli, and B. Ammann. 2000. A palaeoecological attempt to classify forest sensitivity of trees in the southern Alps. Holocene 10:565–574.
von Wagner, C. E. 1987. Development and structure of the Canadian Forest Fire Weather Index System. Technical Report 35. Canadian Forestry Service, Ottawa, Ontario, Canada.
Vilà-Cabrera, A., J. Martínez-Vilalta, and J. Retana. 2015. Functional trait variation along environmental gradients in temperate and Mediterranean trees. Global Ecology and Biogeography 24:1377–1389.
Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33:125–159.

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