

Aridity and competition drive fire resistance trait covariation in mountain trees

THIBAUT FRÉJAVILLE ^{1,2,3,†}, ALBERT VILÀ-CABRERA,⁴ THOMAS CURT ², AND CHRISTOPHER CARCAILLET ^{3,5,6}

¹BIOGECO (UMR 1202), INRA, Univ Bordeaux, F-33615 Pessac, France

²Irstea - UR RECOVER, 3275 route Cézanne - CS 4006, 13182 Aix-en-Provence cedex 5, France

³École Pratique des Hautes Études (EPHE) & PSL University, F-75014 Paris, France

⁴Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, FK9 4LA Stirling, UK

⁵Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés (UMR5023 CNRS), Université Lyon 1, F-69622 Villeurbanne, France

⁶LTER Zone Atelier Alpes, F-38000 Grenoble, France

Citation: Fréjaville, T., A. Vilà-Cabrera, T. Curt, and C. Carcaillet. 2018. Aridity and competition drive fire resistance trait covariation in mountain trees. *Ecosphere* 9(12):e02493. 10.1002/ecs2.2493

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.

Received 26 July 2018; revised 21 September 2018; accepted 25 September 2018. Corresponding Editor: Franco Biondi.

Copyright: © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† E-mail: thibaut.frejaville@gmail.com

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 (Schwilke and Ackery 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 strategies when considering TH which is also largely involved in competition for light (Falster and Westoby 2003, Kunstler et al. 2016). This variation beyond the species-level challenges our understanding of fundamental processes shaping plant ecological strategies and their application in predictive ecosystem models (Anderegg et al. 2018). Therefore, assessing whether covariation among functional traits is consistent across individuals, among species, communities, or biomes is essential to scale up individual variation 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 (Schwilke 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 biogeographic regions, and how this variation correlates with environmental gradients (Pausas 2017).

Here, we aim to investigate patterns of variation of fire resistance traits from individuals to biogeographic regions across the wide climatic and vegetation gradients of the western Alps. Alpine forests are mostly prone to surface fires (Genries et al. 2009, Moris et al. 2017), and fires are expected to increase in frequency and intensity with future warmer and drier conditions (Schumacher and Bugmann 2006, Dupire et al. 2017). Paleoecological analyses have shown long-term differences in fire activity between species

and plant communities in the Alps (Tinner et al. 2000, Blarquez et al. 2012). In accordance with recent evidence, we hypothesize that (1) most trait variation occurs at the species level (Messier et al. 2010, Siefert et al. 2015), (2) warmer and drier environments are dominated by species with thicker barks than in less fire-prone communities (Rosell 2016, Pellegrini et al. 2017), and (3) canopy closure drives variation of crown elevation traits (TH and CBR) in response to light availability. Furthermore, we question whether fire resistance traits are positively correlated along these fire proneness gradients, once individual trait variation with tree size and competition are accounted for, that is, whether fire-tolerant individuals (thick bark) exhibit both a flame avoidance strategy (high crown elevation) and a high ability to compete for light (tall trees relative to diameter) across Alpine forests, or alternatively whether these strategies trade-off across scales.

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

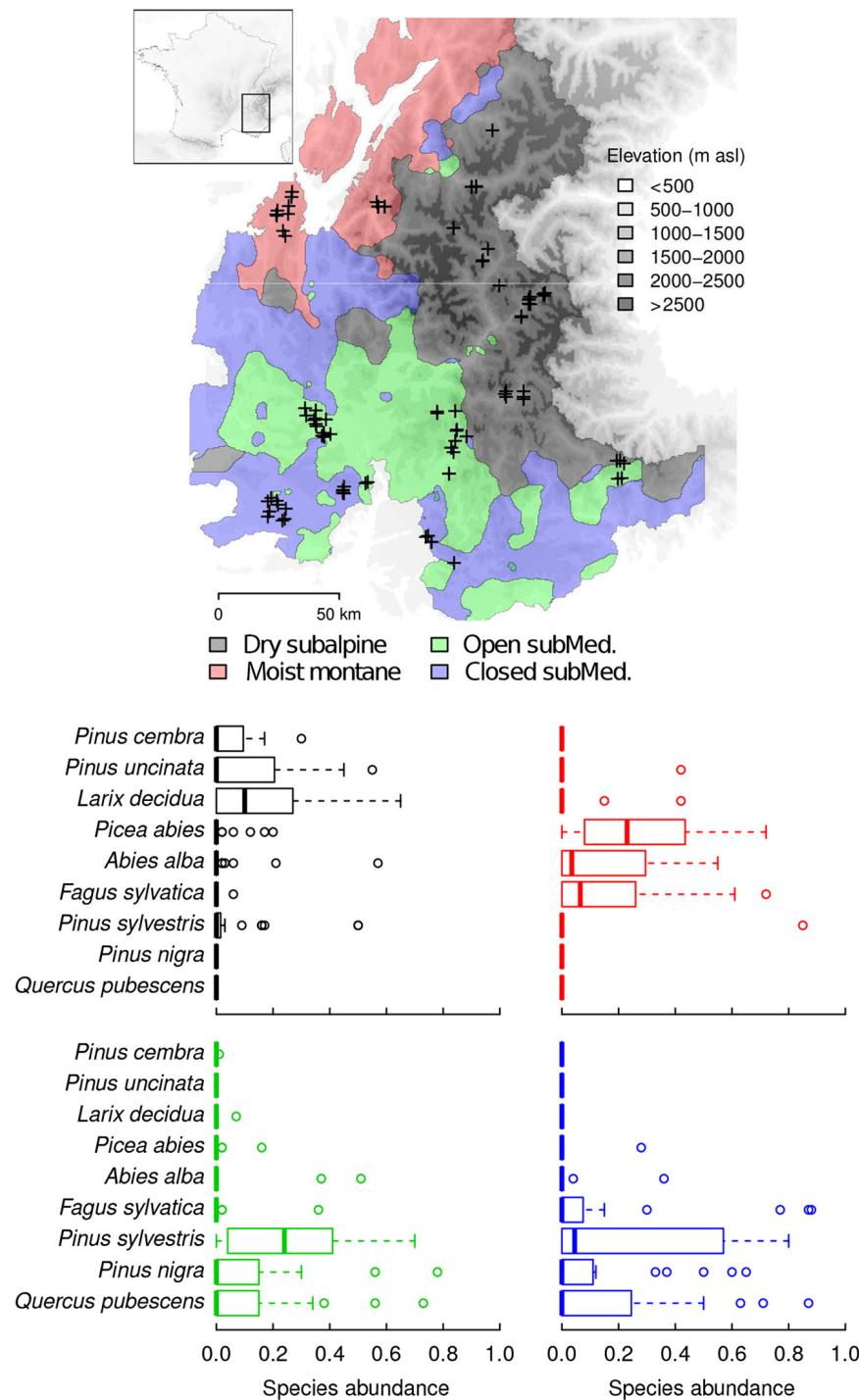


Fig. 1. Map of sampling sites and biogeographic regions in the western Alps. The 94 plots (+) were clustered by biogeographic region using their geographical location: dry subalpine forests in the inner continental range ($n = 27$), moist montane forests of the northern Alps ($n = 16$), open-canopy sub-Mediterranean 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 fire 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 and Curt 2017), 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 A_j was fit by regressing $\log T_j$ against $\log \text{dbh}_j$. 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 A_j 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 m^2/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 (Lepš 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 ($r = 0.33$, $P < 0.001$; Fig. 3a) and community levels ($r = 0.58$, $P < 0.001$; Fig. 3b), whereas BT and TH were negatively correlated at the individual

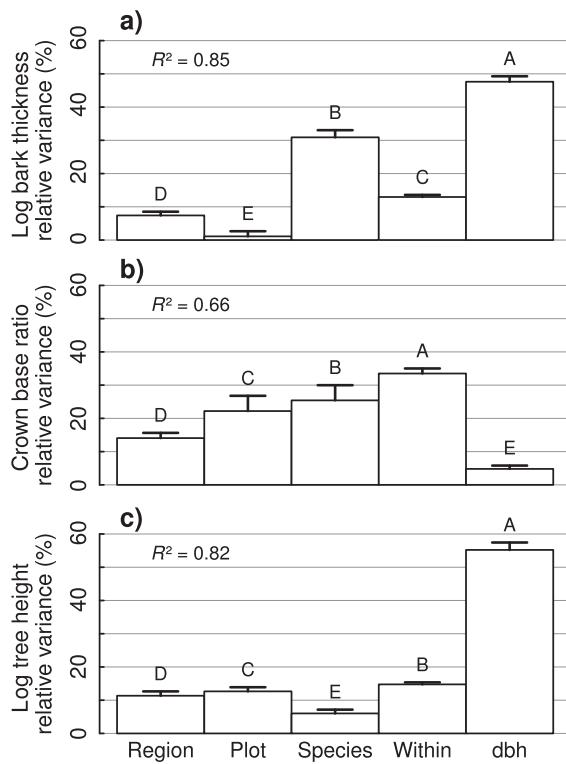


Fig. 2. Variance structure of log bark thickness (BT) (a), crown base-to-height ratio (CBR) (b), and log tree height (TH) (c) across ecological scales, once the effect of tree diameter (dbh) was accounted for. At each level, the relative variance distribution was computed by bootstrapping; bars (and lines) indicate mean (\pm 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.

($r = -0.27$, $P < 0.001$; Fig. 3c) and community levels ($r = -0.41$, $P < 0.001$; Fig. 3c).

At both individual and community levels, Spearman coefficients indicated stronger correlations for the interspecific than the intraspecific component of trait covariation ($P < 0.001$, 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 ($P < 0.05$; 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.

Trait covariation was explained at the biogeographical level by the dominance of thick-barked species that self-prune their lower branches (resistance strategy by fire tolerance and flame-avoidance, respectively) in fire-prone, sub-Mediterranean forests. These species inhabit the

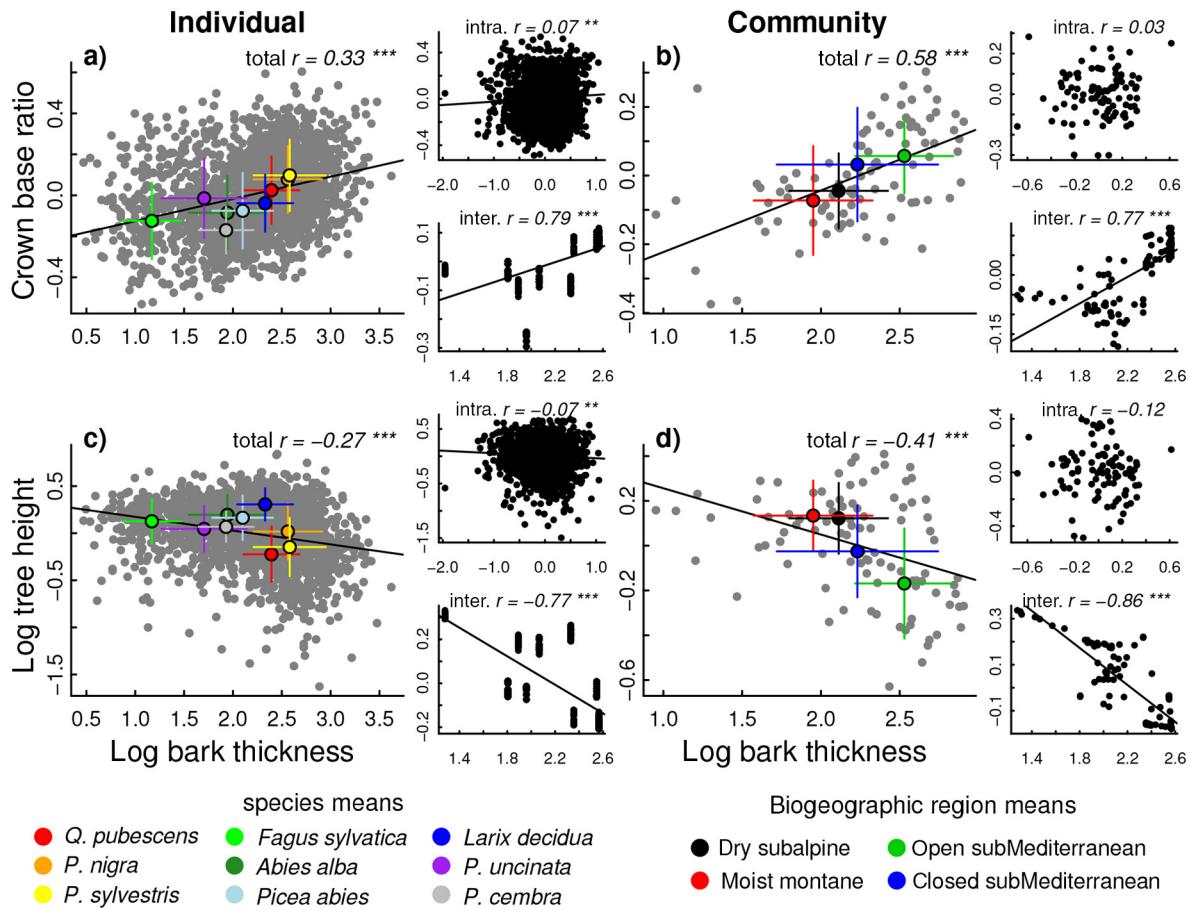


Fig. 3. Partial correlations between standardized traits at individual (a, c) and community levels (b, d). Within each panel, the total (left), intraspecific (top-right), and interspecific (bottom-right) components of trait covariation are shown. Trait variation with the tree cover was prior accounted 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: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. Regression lines are shown for illustrative purpose.

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

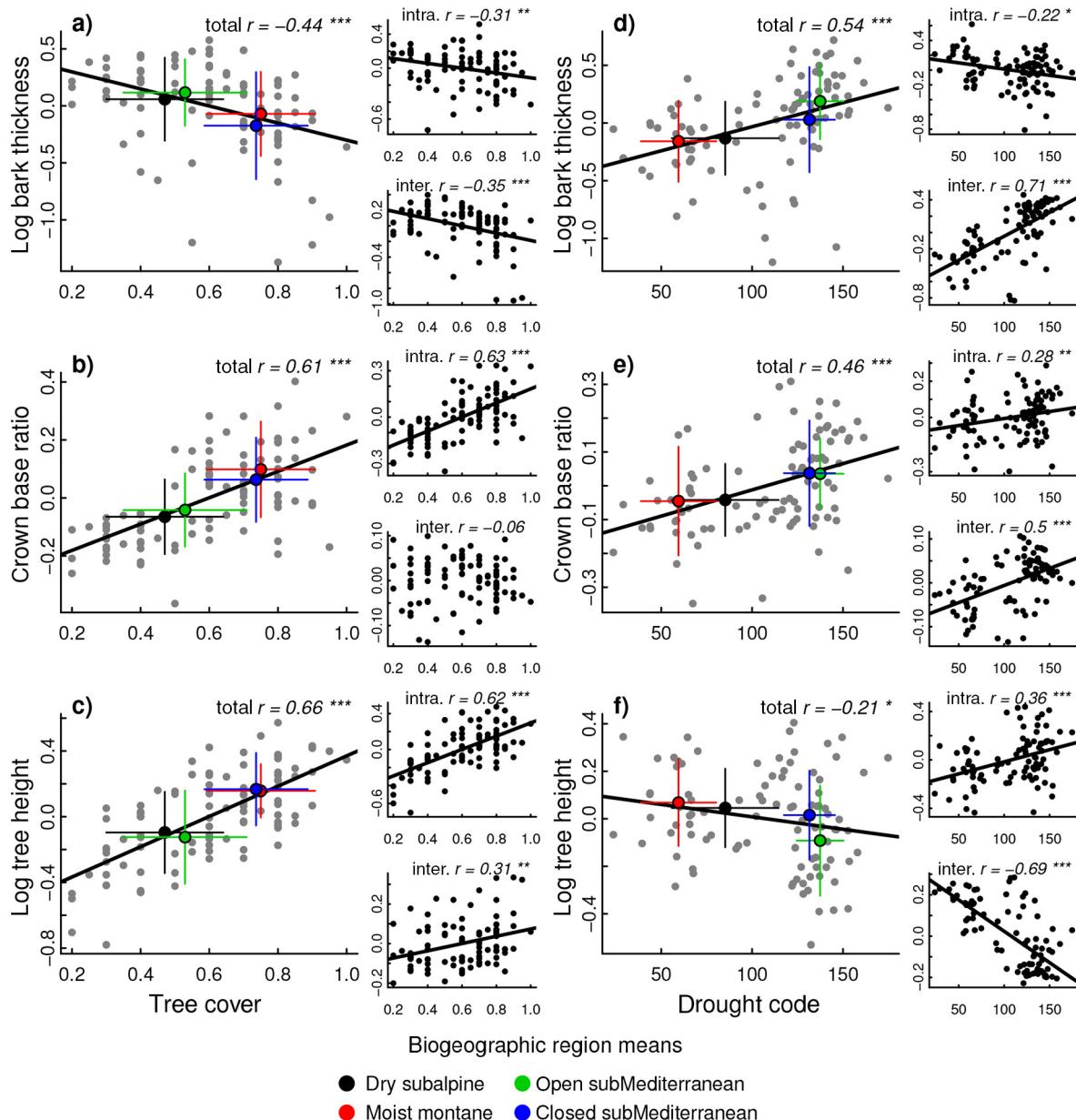


Fig. 4. Partial correlations between community mean standardized traits and the environment: tree cover (a–c) and the drought code (d–f). Within each panel, the total (left), intraspecific (top-right), and interspecific (bottom-right) components of trait–environment correlations are shown. Trait variation with other environmental factors (than the focal one) was prior accounted for; variance analyses of trait–environment correlation components are reported in Appendix S1: Table S3. Mean values (and SD) by biogeographic regions are indicated by large circles (and bars). Spearman’s rank correlation coefficients (r) are indicated: *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$. Regression lines are shown for illustrative purpose.

unburned dense forests (Cavender-Bares and Reich 2012, Hoffmann et al. 2012, Dantas et al. 2013).

Our findings suggest that drought and tree cover structure the species-level trade-off between growing tall in low fire-prone environments vs.

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 (Carcaillet 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.

ACKNOWLEDGMENTS

Financial support was provided by the FUME project (EU' 7th Framework Programme) and by grants from the National Research Institute of Science and Technology for Environment and Agriculture (Irstea) to T.F. A.V.C was funded by the European Union's Horizon 2020 research and innovation programme under Marie Skłodowska-Curie grant agreement No. 656300. This manuscript forms part of a PhD internship at the Autonomous University of Barcelona (CREAF) supported by the EU' 7th Framework Programme through the Marie Curie IRSES program NewForests (PIRES-GA-2013-612645).

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 palaeo-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: S52–S69.
- Colombaroli, 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* 97:728–741.
- 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. Rosatto, 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.
- Lepš, J., F. de Bello, P. Šmilauer, 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.
- Loepfe, 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, N. Küffer, S. Schmidlein, 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. Kartzin, 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.
- Schwilk, D. W., and D. D. Ackerly. 2001. Flammability and serotiny as strategies: correlated evolution in pines. *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 fire sensitivity of trees in the southern Alps. *Holocene* 10:565–574.
- van 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.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2493/full>