RESEARCH PAPER

Spatial and evolutionary parallelism between shade and drought tolerance explains the distributions of conifers in the conterminous United States

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ABSTRACT

Aim Gymnosperms do not follow a latitudinal diversity gradient across the Northern Hemisphere but are influenced by geography at continental scales. Tolerance to physiological aridity is thought to be the main driver of this distribution, yet through evolutionary time conifers have also faced conditions of frost, shade and fire. We tested four predictions to evaluate how environmental stressors and geographical and evolutionary patterns of traits influence conifer distributions: (1) environmental variables related to aridity are most important in explaining geographical patterns of traits; (2) traits responsible for survival in stressful conditions have evolved under a niche conservatism constraint; (3) phylogenetic correlations among traits as the result of complex evolutionary responses to multiple abiotic stressors are widespread; (4) there are parallelisms between spatial trait associations and correlated trait evolution.

Location The conterminous United States.

Methods We combined conifer occurrences with 10 traits related to drought, freezing, shade and fire. The spatial distribution of traits was mapped and the relationship between environment and the geographical patterns of traits was explored. Niche conservatism was assessed comparing patterns of trait evolution against Brownian motion. We computed geographical and phylogenetic correlations among traits to determine the correspondence between spatial and evolutionary trade-offs.

Results (1) Maximum temperature followed by precipitation were the environmental variables that best described the geographical distributions of traits. (2) Most traits contain a phylogenetic signal consistent with niche conservatism: major exceptions being fire-related traits and frost tolerance. (3) Drought and shade tolerances show one of the strongest negative phylogenetic correlations. (4) The drought–shade tolerance trade-off is mirrored at the biogeographical scale.

Main conclusions Unlike in angiosperms, cold does not seem to have been a major driver in the evolutionary history of temperate conifers. A strong trade-off between drought and shade tolerance is the simplest explanation for understanding the current distribution of conifers in North America.

Keywords
Conifers, National Forest Inventory, niche conservatism, phylogenetic correlations, southern North America, trait evolution, trait geographical patterns.

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INTRODUCTION

Tolerance to abiotic stresses is a major driver of species distributions. Among abiotic stresses, temperature extremes, water and light availability are considered to be the main factors limiting world-wide plant distributions and also affecting competitive relations between plants (Valladares & Niinemets, 2008; Martinez-Tilleria *et al.*, 2012; Kunstler *et al.*, 2016). At the biogeographical scale, fundamental differences in the distribution of angiosperms and gymnosperms in the Northern Hemisphere indicate that woody angiosperms follow a latitudinal diversity gradient – founded on the limited ability of angiosperm clades to adapt to mid-Tertiary cooling (Hawkins *et al.*, 2014; Zanne *et al.*, 2014). Conifer distribution, however, seems to be more influenced by geographical characteristics at continental scales (Leslie *et al.*, 2012). Indeed, whereas angiosperm-dominated forests of the north comprise species from younger clades than forests of the south (Hawkins *et al.*, 2014), recently diverged species in Northern Hemisphere gymnosperm lineages are broadly concentrated in mountainous areas of western North America and southern China (Leslie *et al.*, 2012). An explanation for this distribution pattern must encompass a variety of specific environments but also a history of trait evolution that is poorly known in comparison with the more diverse angiosperms (but see Willson *et al.*, 2008; Pittermann *et al.*, 2012; Cornwell *et al.*, 2015). Because adaptive shifts are inextricably linked through space and time (Prinzing *et al.*, 2001), functional traits of extant conifers should represent an evolutionary response to abiotic stressors operating at geographical scales ranging from a few metres to continental, and across deep evolutionary time. Further, macroecological patterns are not independent of the evolution of the lineages involved in generating them (Hernández *et al.*, 2013), so the identification of emergent geographical distributions in tree traits and the strongest underlying stressor(s) has obvious implications for explaining the predominance of conifers in some areas and not in others.

Gymnosperms, and conifers in particular, dominated terrestrial ecosystems during the Permian (*c.* 298–252 Ma), a period characterized by widespread aridity (Parrish, 1995). However, most Permian ancestors are extinct, and extant gymnosperms lineages (i.e. crown groups) largely comprise post-Eocene radiations (Crisp & Cook, 2011), suggesting that the current conifer-dominated north temperate forests are the combined result of retained ancestral characters plus evolutionary responses to environmental change during the last 34 million years of the Cenozoic. The cooler and drier events after the Eocene climatic optimum (*c.* 50 Ma), the uplift of the Rocky Mountains and competition with angiosperms (Bond, 1989; Ruddiman, 1990; Zachos *et al.*, 2008; Zanazzi *et al.*, 2007), among other events, represented a challenge for conifers in the Cenozoic, likely resulting in new adaptive responses. Throughout North America, for example, conifers are the dominant component of northern boreal forest, along the south-eastern Gulf Coast and on the mountain slopes of the west. With some exceptions (e.g. conifer-dominated areas of the Pacific Northwest), each of these regions is characterized by strong physiological aridity, even where precipitation is moderate or high, because water in the soil remains frozen for most of the year, rapidly percolates through sandy soils or its absorption is reduced by surface runoff from mountain slopes (Graham, 1999). Yet, along these regions, conifers have also had to face other physiological stresses like increase in shade and cold conditions or a paucity of nutrients, common, for instance, in sandy and slope soils. Adaptations of trees to multiple abiotic stresses are, however, highly complex, with mounting evidence suggesting that acquisition of tolerance to a given environmental stress compromises plant performance under a different stress (Ninemets & Valladares, 2006; Koehler *et al.*, 2012; Laanisto & Niinemets, 2015). Thus, for instance, adaptations that allow woody species to grow in shade can compromise their ability to grow in dry conditions, such that restricted co-tolerance of these two key stress factors is considered the main constraint limiting the combinations of species in forests across gradients of cold and water availability (Ninemets & Valladares, 2006; Laanisto & Niinemets, 2015).

The evolutionary response to environmental stressors further depends on the tendency of lineages to retain niche-related traits through speciation events and over macroevolutionary time (phylogenetic niche conservatism, PNC) (Ackerly, 2003; Cooper *et al.*, 2010; Wiens *et al.*, 2010). Strong PNC results in similar evolutionary trajectories among closely related species, which are constrained to live in environments akin to those that permitted their ancestors to diversify (Prinzing *et al.*, 2001). For instance, PNC can explain in part why some geographical regions or environments support specific lineages (Crisp & Cook, 2012). In contrast, distantly related species will generally be found in different environmental conditions, although unrelated clades can have similar ecological requirements due to convergence or stasis (Paradis, 2012).

The present study uses a trait-based approach to identify the role of environmental stressors, evolutionary relatedness and phylogenetic conservatism in the current distribution of conifers across the southern half of North America. Specifically, we test four predictions. (1) We expect climatic variables related to aridity to weigh more heavily in explaining geographical patterns of conifer trait distributions, as conifer-dominated forests throughout North America occur under conditions of physiological aridity. If differences in drought tolerance primarily explain conifer distribution, then, (2) we expect strong PNC in drought tolerance and drought-related traits. We further expect that other traits responsible for conifer survival under abiotically stressful conditions show strong PNC patterns. (3) We additionally expect to find phylogenetic correlations among traits, most notably a drought–shade tolerance trade-off, as the result of complex evolutionary response of conifers to multiple abiotic stressors. (4) Finally, we expect parallelisms between the spatial association of traits and correlated trait evolution if PNC has had an important role in determining the distributions of conifers.

To test these four predictions, we combine local conifer occurrence data from the US Forest Inventory and Analysis (FIA) database with 10 traits believed to play key functional roles with respect to four selective forces that have affected the evolution of temperate-zone conifers: drought, freezing, shade and fire (Latham & Ricklefs, 1993; Ninemets & Valladares, 2006; He *et al.*, 2012; Keeley, 2012). We merge both data sets to: (1) map the spatial distributions of conifer functional traits, (2) quantify the relationship between environmental variables and community functional trait distributions, (3) assess phylogenetic niche conservatism for the traits, and (4) compute geographical and phylogenetic correlations among traits to determine the correspondence between environmental and evolutionary trade-offs.

MATERIALS AND METHODS

Forest inventory data and geographical analyses

Occurrences of conifers in the conterminous USA were extracted from the US Forest Service's FIA database (http://www.fia.fs.fed.us/; accessed July 2012). The FIA protocol records, per plot site and per species, the number of trees ≥ 12.7 cm diameter at breast in four subplots (168.3 m^2) 36.6 m apart, and the number of trees ≥ 2.54 cm in diameter in nested microplots (13.5 m^2). In this study we utilized the data from both the subplots and the microplots. For inclusion in the geographical analyses, a site had to support at least two conifer species and be coded as a 'natural stand' (i.e. tree plantations were not considered). Sites containing only one species were excluded, as the dependent variable in our community-level study is the average trait value per plot site (see below). This criterion did not bias site selection to any particular region. We also did not include any sites from Alaska. All angiosperm records were also removed and species records were merged under currently recognized names. We used The Plant List (http://www.theplantlist.org; accessed February 2014) as our source of information on synonyms. Our selection criteria produced a total of 53,160 sites containing 88 of the approximately 108 North American conifer species (the specific limits of some taxa remain unresolved).

Species trait information

We selected 10 traits for which data could be obtained for more than 60% of the species (see Appendix S1 in the Supporting Information). These traits represent axes of ecological strategies of trees with respect to drought tolerance, shade tolerance, frost tolerance and fire tolerance/resistance and were obtained from various sources (Appendix S2). We followed Shipley's (2010) definition and considered traits as 'any measureable property of a thing or an average property from a collection of things'. Therefore, our traits include a mixture of characteristics at different plant scales from physiology to morphology and plant performance. Five traits are continuous (wood density, seed size, height, bark thickness,

minimum number of frost-free days); three are ordinal (drought, shade and fire tolerance); and two are binary (seed dispersal mode and fire resistance). The minimum number of frost-free days was taken as a measure of frost tolerance (see Appendix S2). Realized cold tolerance (the minimum temperature at which species can be grown) was a priori also taken into account; however, it was highly correlated with frost ($P = 0.82$). We chose frost tolerance instead of cold tolerance because the former can be related to physiological aridity when water is not accessible because it is beginning to be or is frozen in the ground. Height, seed mass and bark thickness were log-transformed prior to analyses. Overall, our traits can be grouped into lower-level physiological/morphological functional traits like seed size, wood density and height, and higher-level performance traits like the various tolerance traits, which represent the whole integrated plant phenotype. These higher-level performance or tolerance traits may compensate for the absence in this study of other widely used plant functional traits, such as specific leaf area or percentage of nitrogen in leaves, which we decided not to include due to limited information (values for substantially fewer than 50% of the species were available).

Environmental data

We selected six environmental variables to examine the relationship between environment and the geographical structure of species traits across sites. We extracted two measures of temperature and two of precipitation from the 30 arcsec WorldClim database: BIO5 (maximum temperature of the warmest month), BIO6 (minimum temperature of the coldest month), BIO12 (annual precipitation), and BIO18 (precipitation in the warmest quarter or 'summer rainfall'). We also extracted a measure of solar insolation from the National Renewable Energy Laboratory (http://www.nrel.gov/gis/data_solar.html; accessed October 2014): summer normal direct insolation (summer radiation), at a *c.*10-km resolution. All of these climate variables vary over broad to intermediate scales, but because of the grain at which they are measured they have no variation at local scales. To represent proxies for potential local processes, we also generated two variables containing relatively small-scale variation: elevation and dominant soil type. The elevation of each site was estimated using the digital elevation model gtopo30 (http://ita.cr.usgs.gov/GTOPO30), whereas the dominant soil type was generated from the wss_gsmsoil_US_[2006-07-06] database, available from http://websoilsurvey.sc.egov.usda.gov (accessed October 2014). Spatial patterns of all environmental variables are mapped in Appendix S3. Because FIA sites on private land are shifted one to several kilometres in location to comply with Federal privacy laws, the local variables, especially elevation, contain an unknown amount of error.

Phylogeny

We obtained phylogenetic relatedness and divergences times for the sampled species by pruning the molecular-based

gymnosperm phylogeny of Burleigh *et al.* (2012). Briefly, this phylogeny was constructed incorporating core nucleotide sequence data from gymnosperms (Coniferophyta, Cycadophyta, Ginkgophyta and Gnetophyta) with sequences from the 'basal angiosperm' lineages (e.g. *Amborella*, Nymphaeales) and Moniliformopses taxa as outgroups. This included plastid and mitochondrial loci as well as nuclear 18S rDNA, 26S rDNA and internal transcribed spacers, which were aligned using Muscle (Thompson *et al.*, 1994). Maximum likelihood analyses to estimate the optimal topology and molecular branch lengths used the general time reversible nucleotide substitution model, and a final chronogram was obtained by incorporating the fossil constraints on seed plant clades of Won & Renner (2006). The final pruned phylogeny included 83 out of the 88 conifer species sampled by the FIA (Appendix S4).

Analytical protocols

Forest community data and geographical analyses

To obtain community data with species trait information we first generated a presence–absence matrix of the 88 conifer species across all sites. We then calculated an average value per plot site of each of the 10 traits. A common procedure when scaling traits from species to communities is to weight traits by species relative abundances or basal area within sites. However, we decided to take a conservative approach to presence–absence data to avoid confounding factors that can affect these relative weights but were not included in our study, such as pests, windbreaks or angiosperm trees.

Once the community trait matrix was obtained, the environmental relationships with the geographical distribution of each community trait were assessed with random forest (RF) models. Briefly, RF is a powerful machine-learning method for regression designed to produce accurate predictions that do not overfit the data (Breiman, 2001). In RF, bootstrap samples are drawn to construct multiple regression trees. Each tree is grown with a randomized subset of predictors, i.e. the number of predictors used to find the best split at each node is a randomly chosen subset of the total number of predictors. RF finally combines the predictions of these multiple independent regression trees into a robust composite model. The relative importance of the predictors is assessed by the decrease in explained variance resulting from permutations of the focal variable. We selected RF over more traditional parametric linear modelling approaches because it does not assume linearity and stationarity of relationships (i.e. it can model scale dependence). The non-stationarity violates a basic assumption of all parametric linear methods, whereas RF is able to disentangle interacting effects and identify nonlinear and scale-dependent relationships that often occur at the scale of the analysis performed here among multiple, correlated predictors (Cutler *et al.*, 2007).

We generated 10 RF models (one for each trait) in the R package 'RandomForest' (Liaw & Wiener, 2002) to statistically account for the spatial pattern of conifer traits across sites, using the climatic, elevation and soil-type variables as predictors. For each model we generated 200 regression trees and recorded the percentage of the explained variance (pseudo-R^2). We also ranked the importance of each variable ranging from 100 (the strongest predictor) to 0 (no predictive power) according to the node purity values. We assessed the sign of the relationship between the average community trait and environmental variables with Pearson correlations.

An unresolved analytical issue with respect to the use of trait values averaged over entire communities is that similarities in species composition across communities can potentially generate spuriously strong associations among the variables themselves as well as with environmental gradients (Zelený & Schaffers, 2012). Therefore, we also conducted multiple regression analyses at the species level to test whether environmental predictors of spatial patterns of conifer traits were found at the species level as well as at the community level. For these analyses species were the units of analysis, in which traits comprised their species-level values and environmental variables were generated by calculating the average value of each variable across all sites where each species occurs. We generated eight multiple linear models and two models including a binomial function for the binomial traits (seed dispersal type and fire resistance). Environmental predictors were the same as in the RF models but the categorical variable 'soil type' was excluded. These analyses were also repeated to account for the phylogenetic relationships between species (Butler & King, 2004). The aim of the species-level analyses was to provide independent evidence that the statistical relationships among traits and environments identified at the community level were not due solely to the repeated co-occurrence pattern of species across sites (Zelený & Schaffers, 2012). When the community-level and species-level approaches generated substantially different models, interpretation of the former may not be robust.

Phylogenetic comparative analyses

We tested for niche conservatism in each trait using the general approach of Butler & King (2004). We used phylogenetic generalized least squares (PGLS) to fit three models of evolution: a white noise (WN) model of random variation, in which species trait differences are independent of their phylogenetic relatedness (i.e. the traits are labile), a Brownian motion (BM) model of gradual and continuous drift in species traits, which is sufficient to demonstrate PNC according to one definition (Blomberg *et al.*, 2003), and an Ornstein–Uhlenbeck (OU) model of constrained evolution where the random component of character evolution is pulled towards local optima, which satisfies the more stringent definition of PNC by Losos (2008). We used 'Geiger' in R (Harmon *et al.*, 2008) to calculate the log-likelihood of each model, and model fits were evaluated using the weights of the Akaike information criterion (AICw). We also calculated Pagel's λ and Blomberg's K for each tree trait for potential comparison with other studies. For seed dispersal type and fire resistance, we calculated the *D*-value, a measure of phylogenetic signal

for binary traits (Fritz & Purvis, 2010), and tested the estimated *D*-value for significant departure from both random association and the clumping expected under a BM model of evolution. For that, we used the R package 'Caper'.

Geographical and evolutionary correlations among traits

We computed Pearson correlations between the geographical distributions of each trait to assess geographical correlations. We further generated a single evolutionary variance–covariance matrix among traits to assess the degree of correlated evolution from ancestral characters to extant species (function *evol.vcv*; Revell, 2012). This function permits assessment of the evolutionary liability of each trait (diagonal elements) and between each pair of traits (off-diagonal elements), taking into account the non-independence of the data. To further compare the degree of correlated evolution among traits we calculated an evolutionary correlation matrix using PGLS (Butler & King, 2004).

RESULTS

Geographical patterns of the traits

Five traits (drought, shade and frost tolerance, wood density and seed size) show a strong geographical pattern across the conterminous USA (Fig. 1); there is a latitudinal gradient in the east and elevational gradients in both the eastern and western USA. In general, conifers comprising northern boreal and montane forests have lower wood density, produce smaller seeds and are more tolerant to shade and frost but less tolerant to drought. In addition, the strength of the strong trade-off found between shade and drought is lower at southern latitudes. RF models revealed that these geographical patterns are largely explained by maximum temperature, except for seed size which was best predicted by summer radiation (Table 1).

The two traits related to fire (tolerance and resistance) have regional patterns coinciding with those areas where fires are more frequent and/or intense (e.g. western and south-eastern forests). Yet, whereas in the south-eastern USA conifer-dominated forests are in general both tolerant and resistant to fire, this pattern is not found in the west, where conifers show low tolerance to fire despite being fire resistant (Fig. 1). Again, RF models found that temperature was the main predictor of fire tolerance and resistance (maximum temperature for the former and minimum temperature for the latter) (Table 1).

The three remaining traits (height, bark thickness, seed dispersal type) show geographical structure at regional or intermediate scales (Fig. 1). Conifers are tallest along the west coastal, western-montane and Appalachian forests, whereas trees are shortest in semi-arid habitats. Bark thickness shows a similar pattern to height, particularly in the western USA, where taller trees have thicker bark. Finally, conifers whose seeds are dispersed by animals tend to be more frequent in xeric and alpine environments. RF models found that precipitation was the main predictor for these traits. Specifically, annual precipitation was the main predictor of tree height and seed dispersal type, and summer

precipitation was the main predictor for bark thickness (Table 1).

Overall, the RF models explained high to very high levels of site-level variation of the observed geographical patterns for traits, with broad-scale climatic variables characterizing hot, dry habitats generating physiological aridity in trees (primarily temperature and secondarily precipitation) being the strongest predictors, as predicted.

Multiple regression analyses at the species level confirmed the RF results that temperature and precipitation were the most important predictors, though some traits were further explained by additional variables such as elevation (again associated with physiological aridity for trees growing on mountain slopes). Only seed traits, size and dispersal, and shade tolerance rendered different predictors. For instance, annual precipitation instead of maximum temperature better explains shade tolerance at the species level. Conversely, maximum temperature rather than annual precipitation and summer insolation better explained species seed traits (Appendices S5 & S6).

Phylogenetic comparative analyses

The phylogenetic analyses indicate that conifer trait evolution has been strongly constrained. An OU model describing trait evolution under stabilizing selection best fitted the trait values across species in six of the eight continuous traits (Table 2). The best fit could not be determined unambiguously for fire tolerance (OU and WN models provided similar fits). For frost tolerance, AICw suggests an OU model to be the best, but its higher α-values (Table 2) and large evolutionary variances (Table 3) compared with the other traits provides little evidence of conservatism. For the two binary traits, we obtained a *D*-value of 0.010 for seed dispersal type, which indicates this trait is phylogenetically conserved (according to a BM model of evolution). On the other hand, a *D*-value of 0.855 suggests that fire resistance is labile. In short, drought and shade tolerance of conifers currently inhabiting North America have evolved in a manner consistent with niche conservatism (defined by constrained evolution). The same is true for wood density, seed size, height and bark thickness, which likely represent adaptive traits related to conifer survival when exposed to aridity and/or shade conditions.

Geographical and evolutionary correlations among traits

Phylogenetic correlation analyses indicate multiple correlated evolutionary processes among traits (Table 3). As predicted, one of the strongest relationships found was between shade and drought tolerance, targeting this trade-off as one the most important determinant of recent conifer evolution. Wood density shows negative evolutionary correlations with frost and shade tolerance. However, the phylogenetic correlation between wood density and drought was not significant. Seed size also shows strong evolutionary correlations with wood density, drought tolerance and shade tolerance. Finally, height and bark thickness show positively correlated evolution, probably due to
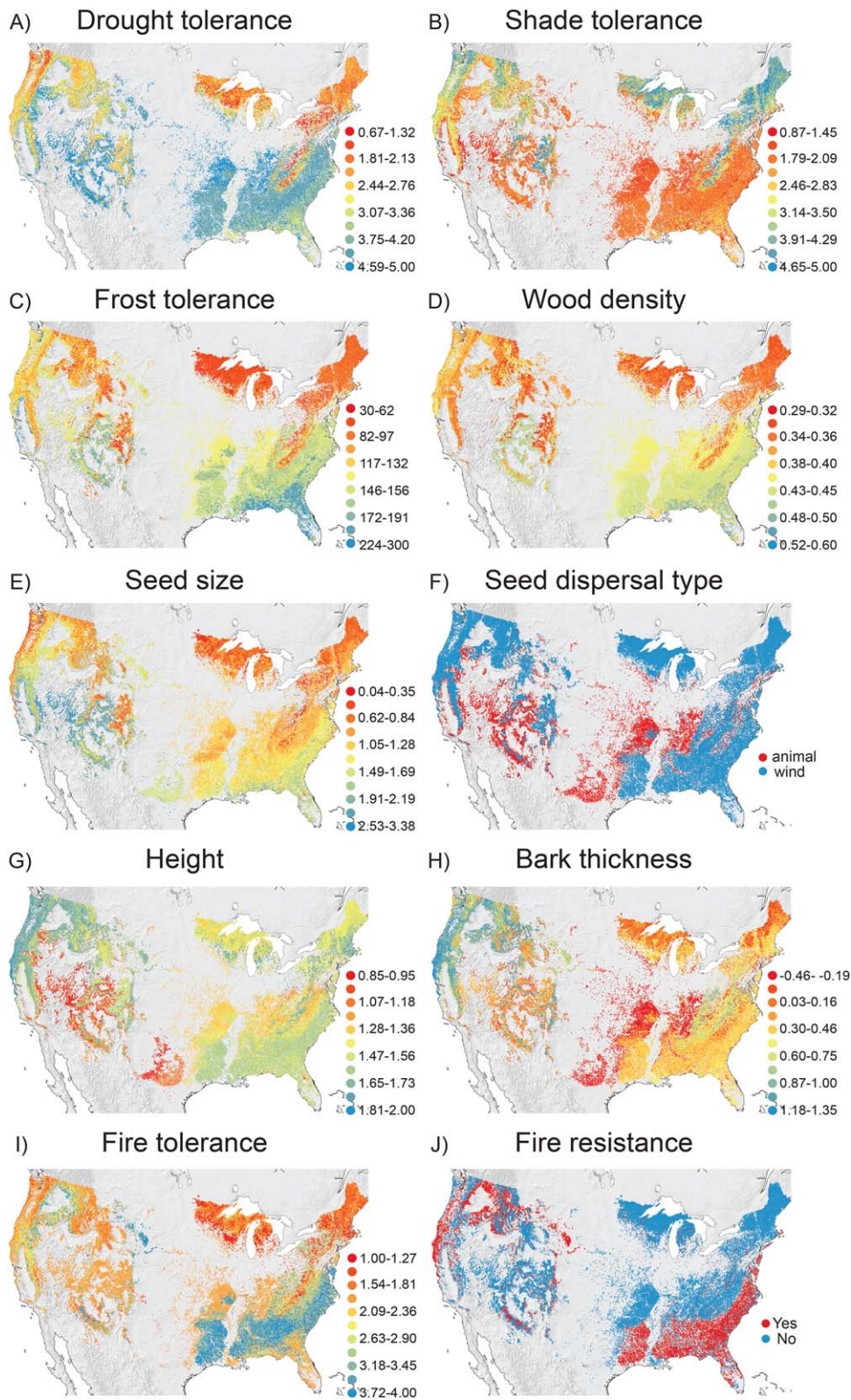
Figure 1 Geographical patterns for 10 traits across 98,400 plots for southern North American conifers. For illustrative purposes natural stands with one species are also included to show their geographical patterns although they were not included in the analysis.

allometric scaling; surprisingly, fire tolerance shows no evolutionary correlation with any trait.

Correlations among geographical distributions of traits range from non-existent to very high (Table 4). However, as a result of the large number of sites included in the analysis ($n = 53,160$), all correlations were significant. Therefore, we decided to consider as sufficiently robust those correlations with $r > 0.70$. Among these, the correlation between shade

Table 1 Random forest models (200 trees) for mean trait values of 88 conifer species across the conterminous United States.

	R^2	Max. T	Min. T	Ann. P	Sum P	Sum insol.	Elev.	Soil
Frost tolerance	0.88	**100 (+)**	68.7	23.3	27.8	12.6	20.1	36.1
Drought tolerance	0.85	**100 (+)**	28.2	33.2	16.2	26.8	24.6	38.3
Wood density	0.81	**100 (+)**	68.5	34.9	19.6	16.4	27.3	26.7
Fire tolerance	0.78	**100 (+)**	67.9	33.9	26.9	37.4	34.8	47.1
Seed size	0.76	76.1	74.2	57.1	55.2	**100 (+)**	62.6	63.3
Shade tolerance	0.76	**100 (−)**	26.5	34.1	19.2	21.1	21.5	32.1
Seed dispersal type	0.73	71.2	30.9	**100 (−)**	32.9	33.2	52.4	29.9
Height	0.72	65.6	50.8	**100 (+)**	57.4	44.3	67.6	16.6
Bark thickness	0.69	58.1	62.5	42.3	**100 (−)**	68.3	59.2	27.9
Fire resistance	0.66	52.9	**100 (+)**	42.4	48.1	46.1	65.9	21.3

The most important predictor variables for each trait (>90) are highlighted in bold and the sign of the correlation provided. Results are ranked by the explanatory power (R^2) of the model. Predictor variables are: maximum temperature of the warmest month (Max. T), minimum temperature of the coldest month (Min. T), annual precipitation (Ann. P), summer precipitation (Sum. P), summer normal direct insolation (Sum insol.), elevation (Elev.) and soil type (Soil).

and drought tolerance was remarkable. Correlations between shade tolerance and wood density, drought and frost tolerance, drought tolerance and wood density, frost tolerance and wood density, and height and bark thickness were also noteworthy (all > 0.71; Table 4).

DISCUSSION

In this study, we combined geographical and phylogenetic approaches to investigate the ecological and evolutionary drivers of conifer distribution through the conterminous USA. The benefits of such combination were clear. Both types of analyses independently point to the trade-off between shade and drought tolerance as the main driver of recent conifer

Table 2 Comparative fits of eight continuous and ordinal conifer traits to three alternative evolutionary models.

Trait	AICw–BM	AICw–OU	AICw–WN	λ	K	α
Drought tolerance	0	1	0	0.863	0.103	0.043
Wood density	0	1	0	0.953	0.161	0.041
Seed size	0	1	0	0.963	0.117	0.028
Shade tolerance	0	1	0	0.900	0.123	0.043
Bark thickness	0	1	0	0.916	0.083	0.036
Height	0	1	0	0.919	0.086	0.038
Frost tolerance	0	0.822	0.178	0.520	0.030	0.242
Fire tolerance	0	0.554	0.446	<0.001	0.033	0.241

Ornstein–Uhlenbeck process (OU; constrained evolution), Brownian motion (BM; drift) and white noise (WN; no phylogenetic signal) models. Model fits are evaluated using Akaike weights (AICw) and express the probability that each model is the best among those compared. Pagel's λ, Blomberg's K and the α of the OU model are also provided.

evolution and distribution. Moreover, the strong phylogenetic conservatism found for shade and drought tolerance provides a link to connect this ecological–evolutionary parallelism, suggesting that the current environmental variation of the continental USA sorts different conifer lineages according to their conserved tolerance. Therefore, this strongly conserved trade-off has been key to promoting conifer evolution, but it has simultaneously limited lineage distribution, not allowing drought-tolerant lineages of southern latitudes (e.g. *Pinus*, *Juniperus*) to occur at higher elevations and latitudes, whereas the reverse is true for shade-tolerant lineages (e.g. *Abies*).

More specifically, our four predictions are fulfilled to varying degrees. First, temperature (followed by precipitation) is the strongest climatic variable explaining contemporaneous geographical patterns of functional traits and stress tolerances of North American conifers (see Table 1), although relationships between particular traits and environmental variables vary somewhat depending on whether a community- or species-focus approach is used. This is a predictable result, as both temperature and/or precipitation have been documented to explain broad geographical patterns of many organisms (Gaston, 2000). More significantly, however, when compared with woody angiosperms, whose distributions across North America are explained by adaptations to cold (Hawkins *et al.*, 2014), maximum instead of minimum temperatures become the major factor influencing the responses of conifers to freezing, shade, drought and fire. This can be explained by the different stressors that angiosperm and gymnosperm trees have to cope with. While angiosperm trees face cold as the major abiotic filter, conifers generally occur in environments where several environmental stressors co-occur simultaneously.

Second, most of the traits we examined contained a phylogenetic signal consistent with niche conservatism (see Table 2). Clearly, the strongest evolutionary trait association was the negative correlation between shade tolerance and drought tolerance, which in its interaction with current environmental

Table 3 Variance (diagonal), covariance (upper triangular matrix) and correlation (lower triangular matrix) values resulting from the evolutionary variance–covariance matrix and phylogenetic correlation analysis for eight continuous and ordinal conifer traits.

	Shade tolerance	Drought tolerance	Frost tolerance	Fire tolerance	Wood density	Seed size	Height	Bark thickness
Shade tolerance	0.166	−0.086	0.950	−0.061	−0.001	−0.019	0.012	0.009
Drought tolerance	**−0.625**	0.170	−0.169	0.016	0.001	0.021	−0.004	−0.007
Frost tolerance	0.191	−0.293	484.495	−2.747	−0.113	−1.486	0.586	0.433
Fire tolerance	−0.145	0.132	−0.165	0.327	0.0001	0.0001	0.002	0.036
Wood density	**−0.577**	0.459	**−0.235**	−0.139	0.0003	0.001	−0.0005	−0.0005
Seed size	**−0.334**	**0.569**	**−0.199**	0.015	**−0.625**	0.039	−0.003	−0.0003
Height	**0.377**	−0.456	**0.290**	0.136	**−0.560**	−0.319	0.008	0.007
Bark thickness	−0.097	−0.217	0.170	0.064	−0.212	−0.122	**0.544**	0.020

Significant correlations ($P < 0.05$) for the phylogenetic correlations are highlighted in bold.

variability generates the basis of the conifer pattern across the conterminous USA (see Table 4, Fig. 1). At the other extreme, fire tolerance and resistance represent major exceptions to niche conservatism patterns. More unexpectedly, however, frost tolerance exhibits a pattern of minimal evolutionary significance. In part, these findings suggest that cold was not a major driver in the evolutionary history of North American conifers. In other words, potential adaptation to cold during the mid-Tertiary cooling of the global climate does not explain the current distribution of conifers across the southern half of North America, although obviously frost tolerance is an adaptive trait of conifers at continental scales, differentiating geographically those species that can survive in high latitudes and elevations from those that cannot (Fig. 1). Given our results, it seems more probable that the evolutionary tendency of some shade-adapted lineages allowed the colonization of higher latitudes and elevations by conifers after retreat of the ice sheets, as boreal coniferous forests started to assemble in the western volcanic highlands and in the high latitudes by the mid-Eocene (Graham, 1999). Likewise, the evolutionary tendency to be drought adapted allowed more xeric clades (e.g. *Juniperus* and *Pinus*) to radiate into the increasingly dry post-Eocene habitats of the continental interior. In any case, selection towards shade or drought tolerance proves rather stable (Table 2) and geographically well correlated with wood density. Wood density

has been identified as a key trait in woody species distributions (Chave *et al.*, 2009), and for North American conifers wood density seems to summarize the combination of the shade–drought spectrum that involves multiple morphological and physiological adaptations acting in combination (Valladares, 2003; Cescatti & Niinemets, 2004). Low wood density in boreal clades (e.g. *Chamaecyparis*, *Thuja*, *Abies* and *Picea*) is consistent with their adaptation to shady conditions. Certainly, the attainment of low wood density would allow species living in dense forests to be taller (note that wood density is negatively correlated with height; Table 3) and compete better for light (Bigler & Veblen, 2009). Moreover, although it is known that drought tolerance in conifers is associated with an increase in wood density (Pittermann *et al.*, 2012), the phylogenetic correlation between drought tolerance and wood density was not significant, even though its value was relatively high (see Table 3). Since the association of high wood density with drought-induced embolism resistance is widely accepted (Chave *et al.*, 2009), we acknowledge that in this specific case the more taxonomically restricted information available for wood density in comparison with drought tolerance might account for the lack of significance in the phylogenetic correlation.

Our results also indicate that other traits probably play an important role in determining conifer distributions; this is the case for seed size, which broadly shows a latitudinal

Table 4 Correlation coefficients resulting from Pearson correlation analysis for eight continuous and ordinal conifer traits.

	Shade tolerance	Drought tolerance	Frost tolerance	Fire tolerance	Wood density	Seed size	Height
Drought tolerance	**−0.911**						
Frost tolerance	0.678	**−0.723**					
Fire tolerance	−0.530	0.594	−0.641				
Wood density	**−0.774**	**0.716**	**−0.840**	0.552			
Seed size	−0.561	0.639	−0.558	0.311	0.458		
Height	0.156	−0.262	0.017	0.183	−0.068	−0.050	
Bark thickness	−0.235	0.135	−0.060	0.239	0.174	0.283	0.630

Coefficients higher than 0.7 are highlighted in bold.

pattern in the east and an elevational pattern in the west of the USA (Fig. 1). Maximum insolation instead of maximum temperature explains the geographical pattern of seed size, consistent with the fact that conifers with proportionally larger seeds are present in those areas where summer radiation is intense, namely the desert areas of the west and the highest, nearly bare, peaks of the Rockies. Geographical differences are partly driven by the strong PNC shown by seed size (see Table 2). Small seeds found in those clades living in higher latitudes (e.g. *Chamaecyparis*, *Picea*, *Tsuga*, *Thuja*) could be interpreted as a pre-adaptation to cold, as a rapid recolonization after the Last Glacial Maximum was facilitated for those ancestors with smaller, wind-dispersed seeds (e.g. MacDonald *et al.*, 1998). However, given the negative evolutionary correlation between seed size and frost tolerance (Table 3), our findings point more to an adaptation to the lack of large animal dispersers at colder high latitudes (Willig *et al.*, 2003). Likewise, the larger seeds observed in *Juniperus* and pines associated with xeric open habitats, both piñon–juniper woodland and the timber line, are consistent with the adaptation to seed dispersal by animals, particularly birds, in very dry environments (note the high positive phylogenetic correlation between drought tolerance and seed size in Table 3). Large seeds filled with large quantities of nutrients for seedlings are more attractive to animals, which constitutes an evolutionary advantage to species growing in such stressful habitats (Lanner, 1998).

There is a general consensus that fire has historically been a significant environmental stressor that has shaped conifer-dominated forests and has selected for adaptations to fire in the majority of conifers (Bond & Scott, 2010; He *et al.*, 2012; Cornwell *et al.*, 2015). Indeed, in the Northern Hemisphere, fire-controlled woodland fossils can be traced to the mid-Eocene (Graham, 1999) or earlier (He *et al.*, 2012). However, and despite this evidence, we found no phylogenetic signal of conservatism in fire resistance and tolerance. The geographical pattern of both traits suggests instead current species-specific adaptations to the two fire regimes – infrequent crown fires and frequent low-intensity surface fires – common in the USA (see Fig. 1). It could be that adaptations to fire tolerance and/or resistance are masked by selection for greater height and bark thickness. Survival of surface fires may be enhanced by greater height and bark thickness (Jackson *et al.*, 1999; He *et al.*, 2012; Keeley, 2012), whereas species adapted to intense crown fires usually have much thinner bark (Keeley, 2012). Geographical patterns of height and bark thickness, with taller conifers having thicker bark being located in the western USA, might support this scenario, but these could also reflect differences in primary productivity. On the other hand, other specific traits not considered here may drive evolutionary adaptations to fire. Cornwell *et al.* (2015) found that attributes of gymnosperm litter have a phylogenetic component that may have a large influence on fire behaviour in surface fire regimes. Their study notes the low flammability of the non-*Pinus* Pinaceae, mainly components of the boreal forest (e.g. *Picea*, *Abies*, *Larix*, *Tsuga*), suggesting that the small needles dropped by these species form densely packed litterbeds that help suppress surface fires. This would explain why areas in California dominated by the non-*Pinus* Pinaceae burned less frequently in the past than similar areas dominated by larger-leaved species (e.g. Schwilk & Caprio, 2011).

Finally, it should be noted that some of the phylogenetic patterns we found and mismatches between geographical and evolutionary trait associations might be artefacts of differential extinction rather than identifying, for example, conservatism of the trait of interest (Crisp & Cook, 2012). This is because researchers assume that extinct species represent intermediate states of extant species, but there is no guarantee of this and the former can possess unique combinations of traits that no longer exist (see Diniz-Filho *et al.*, 2013), biasing understanding of patterns. Obviously, phylogenetic analyses could be improved by using phylogenies that explicitly incorporate fossil data (Crisp & Cook, 2012; Slater & Harmon, 2013), but in most cases combining fossil and phylogenetic data is challenging due to gaps in the fossil record. An additional limitation of this study is that trait values are assigned at species level, that is, potential adaptation at the population level or intraspecific trait variation are not taken into account. This constraint has no easy solution, given the lack of information at the intraspecific level for species extending over broad scales. On the other hand, the importance of accounting for intraspecific variation at macroecological scales when interspecific variation is expected to be large is still debated (Albert *et al.*, 2012; Siefert *et al.*, 2015).

To conclude, in contrast to the angiosperms, many aspects of gymnosperm evolution, ecology and biogeography remain poorly studied (but see Leslie *et al.*, 2012; Fragnière *et al.*, 2015). Here, we have shown that the strong trade-off between drought and shade tolerance, which is summarized in wood density as a key functional trait, is the simplest explanation for understanding the current distribution of conifers across southern North America. In addition to the already well-known drought tolerance of conifers, essential for the colonization of the xeric habitats of the continental interior and sandy coastal soils, the acquisition of tolerance to shade was key in the colonization of higher latitudes by gymnosperms, whereas (the perhaps taken for granted) frost tolerance is pushed into the background. Surprisingly, other factors thought key in the evolutionary history of North American conifers, such as the tolerance of and resistance to wildfires, do not appear relevant but still show strong geographical structure. Future questions need to address the evolutionary rates of traits through the phylogeny. This would be helpful for understanding which traits are more evolutionarily constrained at a macroecological scale as well as for quantifying possible evolutionary trajectories of future conifer responses in the face of global change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species list and trait values.
Appendix S2 Trait explanation and data sources.
Appendix S3 Geographical patterns of the environmental variables.
Appendix S4 Phylogenetic topology.
Appendix S5 Results from multiple regression models for the continuous trait values.
Appendix S6 Results from phylogenetic least squares models for the continuous trait values.

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