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# Functional diversity of North American broad-leaved trees is codetermined by past and current environmental factors

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**Abstract.** Modern and historical climate are known to codetermine broad-scale species richness and composition patterns in temperate regions. Nonetheless, is poorly understood the extent to which these effects individually or in combination determine functional diversity, many studies have simply assumed equilibrium between current climate and functional diversity. We estimated functional richness ( $F_{\text{Rich}}$ ) and dispersion ( $F_{\text{Disp}}$ ) of North American broad-leaved trees by combining distribution and trait information. Then, we determined if contemporary water-energy availability, current topographic variability, historical climatic stability, and lagged immigration from glacial refugia codetermined the functional diversity of North American broad-leaved trees. We did this by assessing the directionality, magnitude, and relative importance of various contemporary and historical environmental factors known to affect species diversity. Contrasts were performed across all North America (Mexico, United States, and Canada), and areas within this region that were glaciated or ice-free during the Last Glacial Maximum (~21 000 yr ago).  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  showed distinct geographic patterns that are strongly associated with both contemporary environmental conditions and glacial–interglacial climate change. Model averaged regression coefficients and AIC-based variable relative importance estimates show that contemporary productivity ( $F_{\text{Rich}}\text{-w}_{\text{AIC}}: 1.0$ ;  $F_{\text{Disp}}\text{-w}_{\text{AIC}}: 1.0$ ), annual precipitation ( $F_{\text{Rich}}\text{-w}_{\text{AIC}}: 0.81$ ;  $F_{\text{Disp}}\text{-w}_{\text{AIC}}: 1.0$ ), and accessibility to glacial refugia ( $F_{\text{Rich}}\text{-w}_{\text{AIC}}: 0.92$ ;  $F_{\text{Disp}}\text{-w}_{\text{AIC}}: 1.0$ ) have the strongest associations to  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$ . Furthermore, the association of functional diversity with topographic heterogeneity showed steeper slopes in ice-free regions. These findings suggest that, contrary to the expectation climate–diversity equilibrium, functional diversity of North America broad-leaved trees is codetermined by current climate and lagged immigration from glacial refugia.

**Key words:** climate velocity; ecosystem function; functional traits; glacial–interglacial climate change; history; species richness.

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## INTRODUCTION

There is increasing evidence that the marked geographic gradients in species diversity across the globe can be considered the result of the interacting effects of contemporary and historical

environmental conditions (Ricklefs 2004, Wiens and Donoghue 2004, Fritz et al. 2013). Functional diversity is a critical aspect of diversity, notably due to its influence on how ecosystems function (Díaz and Cabido 2001, Lavorel and Garnier 2002). For clarity, here we define functional

diversity as the range and dispersion of multiple functional traits within a species assemblage. These traits determine species sensitivity to changes in the environment (response traits) and its ecological role in an assemblage (effect traits). Our definitions of functional diversity and traits build on those of Lavorel and Garnier (2002).

Similar to species richness, phylogenetic diversity or beta-diversity, contemporary environment and historical conditions could mutually and independently determine current functional diversity patterns. Most studies explaining functional diversity variability at continental or global scales use contemporary climate as predictors (e.g., Thuiller et al. 2006, Swenson et al. 2012, Spasojevic et al. 2013, Šimová et al. 2014). However, the extent to which historical environmental conditions could also shape functional diversity is poorly known (but see Mathieu and Davies 2014, Ordonez and Svenning 2015, Svenning et al. 2015). Such lack of knowledge is the result of the prevailing idea of equilibrium between climate and functional diversity at large geographic scales.

Notably, there is evidence that paleoclimatic changes have led to the sorting of regional species pools according to both climate-tolerance (Svenning 2003, Eiserhardt et al. 2015) and dispersal traits (Normand et al. 2011, Nogués-Bravo et al. 2014). Such historical species sorting can result in deficits in the size and packing of the functional trait space of local assemblages when compared to those expected only contemporary restrictions. Such deficit has been shown for European plants by Ordonez and Svenning (2015). The prevalence of legacies of historical climate on contemporary functional diversity would indicate the possibility of long-term disequilibrium responses to current climate change. Therefore, understanding their importance is crucial for predicting how communities and ecosystems will respond to future climatic conditions (Chapin et al. 2000, Van Bodegom et al. 2012).

A recent review by Svenning et al. (2015) described how historical factors, as climate changes since the Last Glacial Maximum (LGM ~21 000 yr ago), could potentially affect biodiversity. In their review, the authors propose multiple mechanisms that may push the local and regional species pool and the functional composition of a species assemblage away from its environmental equilibrium state. Such mecha-

nisms include time-lagged movements of species across geographic space in response to postglacial warming (McLachlan et al. 2005, Svenning and Skov 2007a, Ordonez and Williams 2013) and historical filtering of species according to their environmental tolerances (Jansson 2003, Jetz et al. 2004, Williams et al. 2004, Svenning and Skov 2007b, Sandel et al. 2011).

Building on Svenning et al. (2015) ideas, we combined species distribution and trait information to quantify geographic patterns in two dimensions of functional diversity for broad-leaved trees across North America. We further assessed the relation between functional diversity with contemporary and historical environmental factors. Our goal was to determine the relative roles of contemporary environmental conditions and postglacial colonization lags in determining contemporary functional diversity patterns across North America for broad-leaved trees. In doing so, we make three predictions:

1. *Geographic patterns of functional richness and dispersion:* We expect a distinct spatial pattern in functional diversity that is related to glacier cover, with areas covered by ice during the last glaciation showing a smaller functional space, and a looser packing of traits within this space.
2. *Importance of contemporary and historical environmental conditions:* contrary to the climate and diversity equilibrium idea, historical climatic variables are as important as contemporary environment in determining the current functional space size and the packing of attributes within this functional space.
3. *Glaciation history effects on the importance of contemporary and historical environmental conditions:* We expect that contemporary environmental factors are the main functional diversity determinants within ice-free regions while the location of glacial refugia has a stronger effect on functional diversity patterns in formerly glaciated (cf. Normand et al. 2011).

## MATERIALS AND METHODS

### *Distribution data*

Our analyzes included 530 North America broad-leaved tree species, whose distributions were represented by range maps compiled by

the U. S. Geological Survey<sup>1</sup> (Critchfield and Little 1966, Little 1971, 1976, Little and Viereck 1977, 1978). These distribution maps represent the natural distribution of trees in North America (Mexico, United States, and Canada), allowing us to characterize functional diversity in the absence of recent human influence. Our analyses only included angiosperm trees, to avoid potential artifacts emerging from mixing angiosperms with the distantly related and functionally distinct gymnosperms. Each range map was summarized into  $\sim 100 \times 100$  km equal-area grids by overlaying a sampling grid over the distribution maps and selecting any cell that intersected the distribution polygon. The selected  $100 \times 100$  km grids were used as the geographic units in all the computations and analyzes done in this study.

#### *Trait information*

We used five ecomorphological traits: leaf area ( $L_{\text{Area}}$ ;  $\text{cm}^2$ ), specific leaf area (SLA,  $\text{cm}^2/\text{g}$ ), seed mass (SWT, mg), maximum stem height ( $H_{\text{max}}$ ; m), and wood density (WD,  $\text{kg}/\text{m}^3$ ). These traits were selected based on their importance for species' sensitivity to changes in the environment (response traits) and their environmental impacts (effect traits). These traits also characterize recognized plant functional strategies (Westoby et al. 2002, Wright et al. 2004, Chave et al. 2009), there is a known link between these traits and abiotic factors (Wright et al. 2005, McGill et al. 2006, Westoby and Wright 2006, Ordonez et al. 2009, Swenson et al. 2012, Ordonez and Olff 2013), and these traits are commonly used to predict the geographic distribution of vegetation types and ecosystem functions (Díaz and Cabido 2001, Lavorel and Garnier 2002, Lavorel 2013).

Mean trait values for each species were compiled from multiple data sets, namely Wright et al. (2004), Moles and Westoby (2006), Kleyer et al. (2008), Liu et al. (2008), Chave et al. (2009), Ordonez et al. (2010), and Ordonez and Olff (2013). We calculated a mean trait value for each species when multiple values were available. Gaps in the database ( $L_{\text{Area}}$ : 31%, SLA: 56%,  $H_{\text{max}}$ : 26%, SWT = 24%: WD: 56%) were filled using a taxonomically constrained Multivariate Imputation Chained Equations procedure (Buuren and Groothuis-Oudshoorn 2011). This

method involves specifying a multivariate distribution for the missing data using both the taxonomic hierarchy and known attributes to define a joint conditional distribution of possible trait values for those species with no information. Then we draw an imputation from this distribution using Markov Chain Monte Carlo (MCMC) techniques.

#### *Functional diversity estimation*

To represent the functional diversity of each assemblage, we here used two commonly used metrics: functional richness and dispersion. Functional richness ( $F_{\text{Rich}}$ ) describes the size of the functional space (Cornwell et al. 2006, Villéger et al. 2008). Functional dispersion ( $F_{\text{Disp}}$ ) describes the packing of species in a functional space around the functional space centroid (Laliberté and Legendre 2010). Normalized (mean = 0 and SD = 1) and then  $\log_{10}$  transformed traits were used for the estimation of functional diversity to control for the effects of different measurement units and the log-normal distribution in evaluated traits. Both  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  were estimated using the FD R-package (Laliberté and Shipley 2011).

As a complementary analysis, we also estimated the range (the difference between the minimum and maximum trait values) and variability (variance) for each of the used traits. These metrics can be seen as univariate versions of the  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  indices. The explained variance ( $R^2$ ) of single and multiple predictor models was used to assess the importance of evaluated traits range and variability as determinants of  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  respectively.

We evaluated the sensitivity of our estimates of  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  to taxonomic coverage using a jackknife procedure. For this, we removed all species within an order and then estimating  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  for each cell in the study region. Species removal was done iteratively over all the orders included in the database. We consider the convergence between these taxonomic restricted  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  estimates and those based on the full dataset indicate of the robustness of our functional diversity estimates to both incomplete taxonomic coverage, and the omission of particular phylogenetically lineages not included in the distribution maps (Appendix A).



### *Importance of contemporary and historical environmental conditions*

We evaluated the relation of North American broadleaved trees functional diversity to seven explanatory factors. The selected predictors encompass contemporary and historical environmental conditions related to the most supported hypotheses explaining both species diversity patterns at broad geographic scales; namely water–energy dynamics, habitat heterogeneity, lagged immigration from glacial refugia, and regional extinction/persistence in response to past climate change (Svenning and Skov 2007a, Weiser et al. 2007, Normand et al. 2011, Kerkhoff et al. 2014, Nogués-Bravo et al. 2014). Like species distributions, environmental predictors were summarized per  $100 \times 100$  km grids as the mean of all values from a source map intersecting a sampling grids.

Contemporary predictors describing water–energy dynamics included mean annual temperature ( $^{\circ}\text{C}$ ), annual precipitation (mm/yr) and productivity (NDVI, unitless). Topographic variability (elevation standard variation, m) was used to describe contemporary habitat heterogeneity. Per-grid values were determined using the Worldclim database (Hijmans et al. 2005) and the FAO Annual Sum NDVI over the 1981 to 2003 period (FAO 2014). Predictors were obtained at a  $10 \times 10$  arc-minutes resolution (climate and elevation), or in the case of NDVI aggregated to this resolution from the original  $8 \times 8$  km resolution, before estimating grid means.

Historical predictors described two different mechanisms by which we can expect historical legacies in contemporary diversity patterns: lagged colonization dynamics (Svenning and Skov 2007a, Normand et al. 2011) and climatic instability-driven species extirpation (Svenning 2003). The effect of lagged colonization dynamics was measured using the accessibility to post-glacial re-colonization from LGM refugia. Historical climatic instability was measured using late-Quaternary glacial–interglacial temperature and precipitation change velocity. Historical predictors were derived individually for three of the Paleoclimatic Modeling Intercomparison Project Phase III (PMIP<sub>3</sub><sup>2</sup>) models providing predictions for the LGM. As commonly done in SDM to minimize the uncertainties and potential biases introduced by the modeling approach (cf. Araujo and

New 2007), estimates of accessibility and velocities were averaged across the evaluated climate reconstructions.

Following Sandel et al. (2011) approach, annual temperature and precipitation velocities between the LGM and the present were calculated as the ratio between the climate anomaly in this period and the spatial gradient in a  $3 \times 3$  grid cell neighborhood. Accessibility to postglacial recolonization from LGM refugia was determined following Svenning et al. (2010) approach, as the inverse distances between a grid cell and all cells considered suitable for temperate forest during the LGM. The statistical association between climatic conditions and current temperate forest distributions was used to define which areas were suitable for temperate broad-leaved trees during the LGM. Using the current distribution of temperate broad-leaved forests (derived from FAO land cover classification system; FAO 2011) as the response variable, and both mean annual temperature and annual precipitation as predictors a total of 800 statistical models (100 data partitions  $\times$  8 modeling approaches) were specified. Occurrences were randomly partitioned 100 times into calibration (80%) and evaluation (20%) data sets. The implemented modeling algorithms included: Generalized Linear Model, Boosted Regression Trees, Generalized Additive Model, Surface Range Envelop, Classification Tree Analysis, Multiple Adaptive Regression Splines, Flexible Discriminant Analysis, and Random Forests. The True Skill Statistic (TSS; Allouche et al. 2006) was used to both determine model accuracy and transform probability surfaces into presence/absences maps using a threshold maximizing TSS approach. Models were projected into LGM conditions, and weighted-averaged (using model accuracy as weights) to reduce uncertainties and potential biases introduced by model specifications (cf. Araujo and New 2007). Modeling, LGM projections and averaging were done using the biomod2 R-package default settings (Thuiller et al. 2014).

The relation between each of the seven evaluated predictors with  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  was initially assessed using Pearson's correlation coefficients, estimating significance using Dutilleul et al. (1993)'s spatially corrected degrees of freedom. Since multiple environmental predictors can interact, cancel or reverse the importance of other

factors, we also evaluated 256 spatial regressions describing all possible linear combinations of the four contemporary and three historical predictors evaluated in this study. To account for the spatial structure of the data, a spatial autoregressive error regression (SAR<sub>error</sub>) approach was used to model the relation between functional diversity and evaluated predictors. This approach provides unbiased parameter estimates, has strong type I error control and performs adequately independent of the kind of spatial autocorrelation in the data (Kissling and Carl 2008). The spatial weights matrix in our SAR<sub>error</sub> models was defined based the first neighbor of each grid cell. Before the correlation and regression analyses, annual precipitation, elevation variability and glacial temperature and precipitation velocities were log<sub>10</sub>-transformed because they were log-normally distributed. Single variable correlations and their significances were determined using the SpatialPack R-package (Cuevas et al. 2013) while SAR models were determined using the spdep (Bivand 2013) package.

Using Burnham and Anderson (2002)'s multi-model information-theory based approach, we first determined the relative importance of each of the seven evaluated predictors. We did this by summing Akaike weights ( $w_{AIC}$ ) of all the models including the variable of interest. We then determined the best estimates of the regression coefficients using Burnham and Anderson (2002) model averaging approach. For this, we averaged the standardized regression coefficients across all of the 256 evaluated models, weighting each value by the  $w_{AIC}$  for the model that contained it. Although model averages based on  $w_{AIC}$  has received serious criticisms (Cade 2015), multiple lines of evidence give us confidence in our averaged models' assessment of variable importance and directionality of changes. Specifically, there was no multicollinearity among the predictor variables, the dominant models, consistently included similar variables, and univariate analyzes supported the averaged model results (see Results).

As a complementary analysis, the same statistical evaluations described above were done using species richness-standardized  $F_{Rich}$  and  $F_{Disp}$  as response variables. Standardizations were done using a standardized effect size approach (SES; as in Swenson et al. 2012). This complementary

regression analyses used SES for  $F_{Rich}$  or  $F_{Disp}$  as response variables and all possible linear combinations of contemporary and historical environmental factors as predictor variables. Assessing the association of contemporary and historical factors with SES (presented as supplementary information; Appendix B) allowed us to determine richness-independent effects of current and historical predictors on functional diversity, as well as the relative importance of each of the seven evaluated factors as determinants of per-species effects. SES provides a standardized per/species changes in functional diversity at a given species richness. Qualitative, the results of SES based analyzes are similar to those based on raw values, so the results presented hereafter focus on raw functional diversity metrics.

Finally, the predictive power of contemporary and historical factors was evaluated using geographically independent validation approach. The goal here was to assess the predictive power of contemporary and historical variables beyond the calibration region. For this, the study region was divided along the 102 °W meridian, into two training and testing data sets (East-training vs. West-testing, and vice-versa). Models fitted on the training half of the data were then projected in the testing half. The Spearman-rank correlation between predicted and observed values was then used as a measure of predictive ability. Large Spearman-rank correlation coefficients would support the identified links between contemporary and historical factors and functional diversity.

## RESULTS

### *Geographic patterns of functional richness and dispersion*

High  $F_{Rich}$  were primarily concentrated in the Appalachians, southeastern Coastal Plains, and Northeast mixed wood temperate forests (Fig. 1b), a pattern closely matching that of species richness (Fig. 1a). In the case of  $F_{Disp}$  (Fig. 1a), maximum values were recorded in areas covered by the Laurentian shield 21 000 yr ago (defined by the red contour lines in Fig. 1), areas on the West western slopes of the Rocky Mountains and the Southwest (Fig. 1c). In comparison, species-rich areas in the Southeast and Central United States showed consistently low

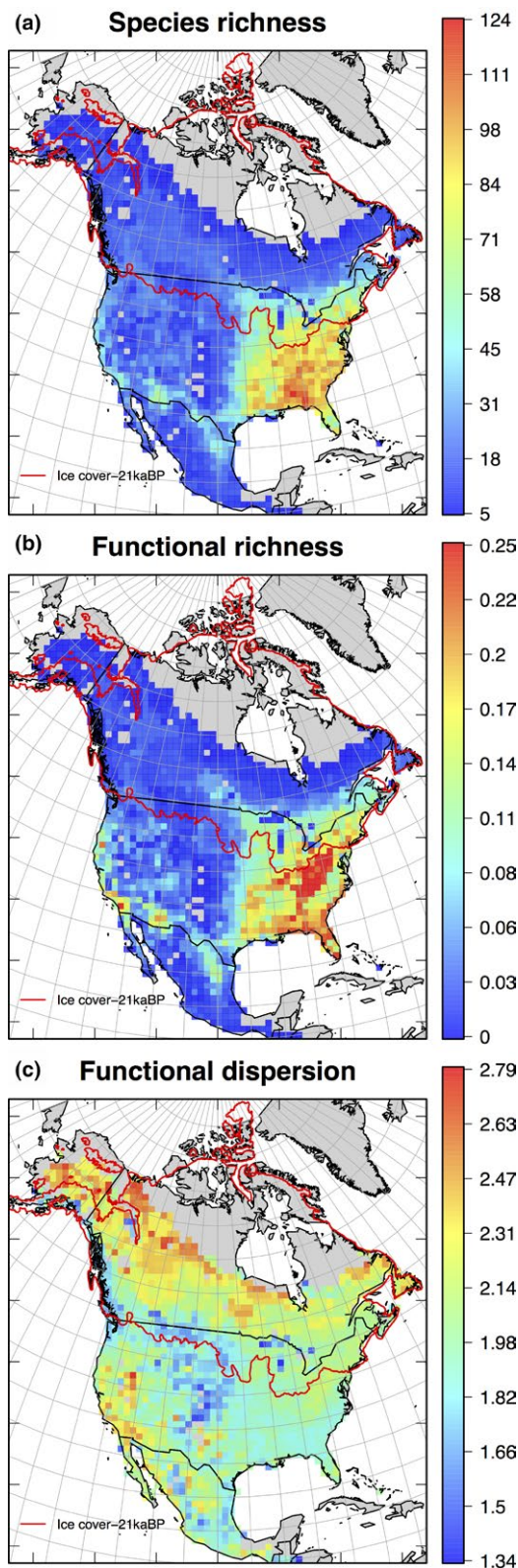


Fig. 1. Geographic patterns of species richness (a), functional richness (b), and functional dispersion (c) of broad-leaved tree species in North America. Distributions information based on Critchfield and Little (1966), Little (1971, 1976), Little and Viereck (1977, 1978) range maps. Red delimited areas show the maximum area of the Laurentide Ice Sheet during the Last Ice Age (21,000 yr ago).

$F_{Disp}$  (Fig. 1c). Notably, glaciated areas had significantly lower  $F_{Rich}$  and higher  $F_{Disp}$  than non-glaciated areas ( $F_{Rich} - F_{(1,1635)} = 101.19$ ,  $P < 0.001$ ;  $F_{Disp} - F_{(1,1655)} = 140.74$ ,  $P < 0.001$ ), indicating the potential importance of glaciation cover as a determinant of the functional diversity patterns in the region.

As expected, wider trait ranges and larger trait variances resulted in a higher  $F_{Rich}$  and  $F_{Disp}$ , respectively. Both univariate regression fits ( $R^2$  for SWT = 0.54, WD = 0.23,  $H_{max} = 0.01$ , SLA = 0.48,  $L_{Area} = 0.13$ ) and multivariate standardized regression coefficients (SWT = 0.03, WD = 0.007,  $H_{max} = -0.011$ , SLA = 0.021,  $L_{Area} = 0.011$ ) pointed to SWT and SLA ranges as the main determinants of  $F_{Rich}$ . In comparison, univariate regression fits ( $R^2$  for SWT = 0.01, WD = 0.09,  $H_{max} = 0.22$ , SLA = 0.001,  $L_{Area} = 0.18$ ) and multivariate standardized regression coefficients (SWT = 0.007, WD = 0.002,  $H_{max} = 0.023$ , SLA = 0.003,  $L_{Area} = 0.014$ ) indicated that  $F_{Disp}$  was mainly determined by variance in  $H_{max}$  and  $L_{Area}$ .

#### Importance of contemporary and historical environmental conditions

Pearson's correlations showed significant positive associations between  $F_{Rich}$  (Fig. 2) and a negative associations between  $F_{Disp}$  (Fig. 3) and almost all contemporary predictors. By comparison, Pearson's correlations indicated a generalized negative association of  $F_{Rich}$  (Fig. 2) and a positive association of  $F_{Disp}$  (Fig. 3) with historical climatic stability and accessibility to recolonization from LGM refugia. Multivariate SAR models including contemporary and historical environmental factors showed that variables in both sets of predictors were among the primary determinants of  $F_{Rich}$  and  $F_{Disp}$  (Table 1 and 2). The variables with strongest impacts on both  $F_{Rich}$  and  $F_{Disp}$  were NDVI,



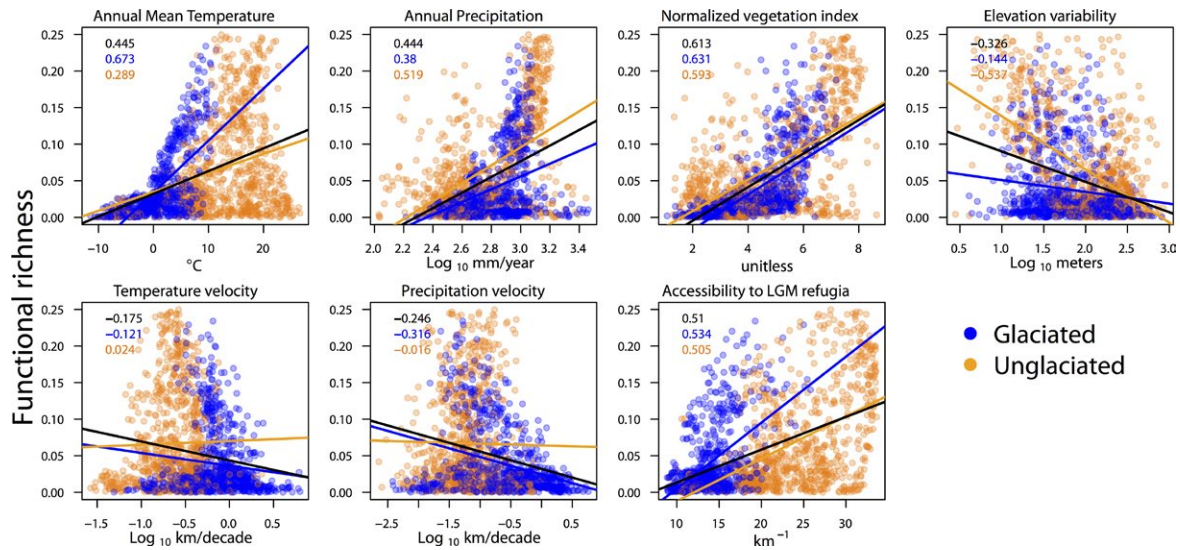


Fig. 2. Functional richness as a function of contemporary and historical environmental conditions. Functional richness estimates based on broad-leaved tree species in North America. The solid black line shows the linear regression using all observations, orange for areas south, and blue for areas north of the Laurentide ice sheet limit 21,000 yr ago BP. Values in the top left of each panel (color-coded according to area) represent the Pearson's correlation between functional richness and each explanatory variable.

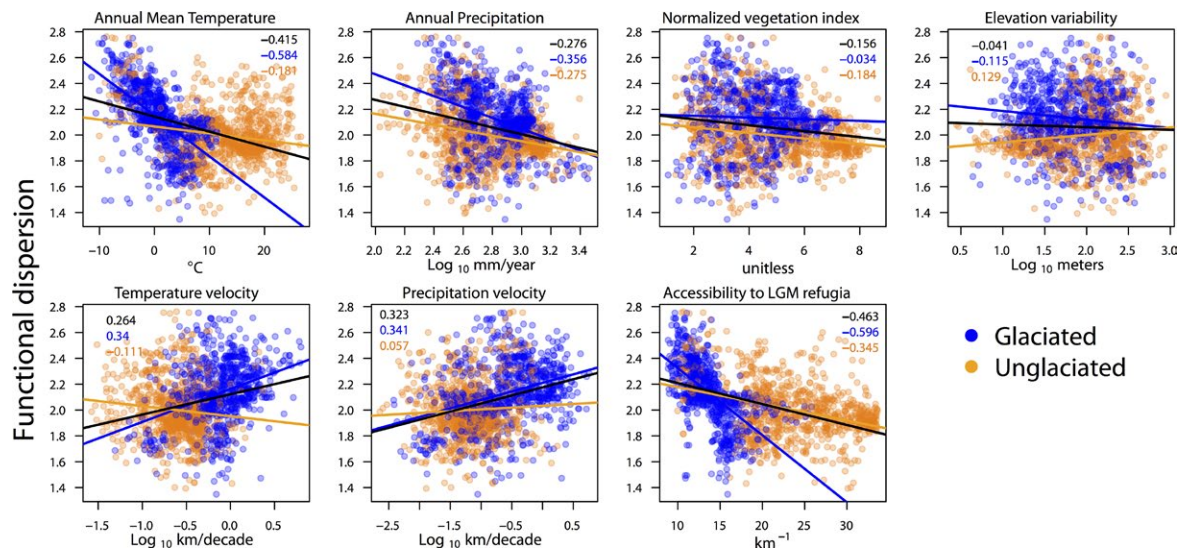


Fig. 3. Functional dispersion as a function of contemporary and historical environmental conditions. Functional dispersion estimates, color scheme, and correlation test as in Fig. 2.

accessibility to glacial refugia, and annual precipitation.  $F_{Rich}$  increased with annual precipitation, NDVI, and accessibility to glacial refugia (Table 1). Meanwhile,  $F_{Disp}$  increased with

annual precipitation and decreased with accessibility to glacial refugia and NDVI (Table 2). Based on Akaike weights ( $w_{AIC}$ ), NDVI, accessibility to glacial refugia, and annual



Table 1. Model averaged standardized regression coefficients for contemporary and historical predictors as predictors of  $F_{Rich}$  for North American broad-leaved trees. Coefficients were summarized using Burnham and Anderson (2002) model averaging approach. Akaike information criteria weights ( $W_{AIC}$ ) for each variable were calculated by summing the  $W_{AIC}$  of all the models including the variable of interest. Variables with strong support ( $W_{AIC} \geq 0.8$ ) are shown in bold.

	Functional richness					
	All		Ice-free		Glaciated	
	Coef	$W_{AIC}$	Coef	$W_{AIC}$	Coef	$W_{AIC}$
Contemporary predictors						
Mean annual temperature	-0.013	0.31	-0.029	0.40	0.016	0.32
Annual precipitation	<b>0.056</b>	<b>0.81</b>	<b>0.066</b>	<b>0.86</b>	-0.034	0.68
NDVI	<b>0.254</b>	<b>1.00</b>	<b>0.201</b>	<b>0.98</b>	<b>0.227</b>	<b>1.00</b>
Elevation variability	0.007	0.36	<b>0.086</b>	<b>0.96</b>	-0.002	0.28
Historical predictors						
Temperature velocity	-0.001	0.28	0.001	0.27	-0.008	0.31
Precipitation velocity	0.003	0.29	0.024	0.59	-0.017	0.37
Accessibility to LGM refugia	<b>0.242</b>	<b>0.92</b>	-0.11	0.56	0.13	0.63

Table 2. Model averaged standardized regression coefficients for contemporary and historical predictors as predictors of  $F_{Disp}$  for North American trees. As in Table 1, coefficients are model averaged values,  $W_{AIC}$  are summed weights across all evaluated models, and values in bold are variables with significant support.

	Functional dispersion					
	All		Ice-free		Glaciated	
	Coef	$W_{AIC}$	Coef	$W_{AIC}$	Coef	$W_{AIC}$
Contemporary predictors						
Mean annual temperature	-0.011	0.30	0.036	0.38	<b>-0.252</b>	<b>0.87</b>
Annual precipitation	<b>-0.317</b>	<b>1.00</b>	<b>-0.198</b>	<b>0.93</b>	<b>-0.266</b>	<b>1.00</b>
NDVI	<b>0.198</b>	<b>1.00</b>	-0.023	0.34	<b>0.271</b>	<b>1.00</b>
Elevation variability	-0.028	0.58	-0.062	0.69	-0.013	0.36
Historical predictors						
Temperature velocity	-0.023	0.45	<b>-0.133</b>	<b>0.98</b>	0.012	0.32
Precipitation velocity	0.013	0.35	-0.003	0.28	0.034	0.44
Accessibility to LGM refugia	<b>-0.445</b>	<b>1.00</b>	-0.138	0.66	-0.227	0.74

precipitation had the highest relative importance scores of all evaluated predictors for both  $F_{Rich}$  and  $F_{Disp}$  (Table 1 and 2). The best ten models (models with the ten lowest  $\Delta AIC$  values) for  $F_{Rich}$  and  $F_{Disp}$  always included both contemporary (NDVI and annual precipitation) and historical (accessibility) factors as predictors. Furthermore, the size of model averaged regression coefficients (Table 1 and 2) further supported the joint importance of contemporary factors and the influence accessibility to glacial refugia, as determinants of functional diversity.

A geographically independent validation approach confirmed the predictive power of the best models for  $F_{Rich}$  and  $F_{Disp}$ . Cross-longitudinal contrasts show that the effects of contemporary and historical factors were more transferable between testing and training regions for  $F_{Disp}$  than for  $F_{Rich}$ . Correlations between observed and predicted values for models trained west of 102 °W longitude were 0.27 and 0.57 for  $F_{Rich}$  and  $F_{Disp}$ , respectively. In comparison, correlations between observed and predicted values models trained east of 102 °W longitude were 0.27 and 0.78 for  $F_{Rich}$  and  $F_{Disp}$ , respectively.

### *Glaciation history effects on the importance of contemporary and historical environmental conditions*

Region-specific analyses according to cover by the Laurentide Ice Sheet 21 000 yr ago (glaciated vs. ice-free areas) showed that  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  associations with evaluated environmental gradients were similar in direction for the two regions, but differed in magnitude (different slopes; Fig. 2 and 3). Differences in the strength of contemporary and historical effects between glaciated and ice-free areas were supported by a significant glacier cover-environmental interaction in ANCOVAs ( $P < 0.001$  for all comparisons). Functional diversity association with topographic heterogeneity was stronger in ice-free regions, whereas associations with water-energy availability showed more individualistic variation (Fig. 2 and 3). Differing lengths of the environmental gradients in the glaciated and ice-free regions could potentially be a reason for these differences between these regions. However, the differences remained when the analyses included only the overlapping parts of the environmental gradients (Appendix C).

Supporting our predictions, contemporary factors became more dominant as determinants of functional diversity in North American broadleaved trees when only considering ice-free regions areas (cf. model average regression coefficients and  $w_{\text{AIC}}$  for glaciated and ice-free areas; Table 1 & 2). For ice-free regions areas, NDVI was the variable with highest relative importance score for  $F_{\text{Rich}}$  while annual precipitation had the highest relative importance score for  $F_{\text{Disp}}$ . For glaciated areas, NDVI was the variable with highest relative importance score for  $F_{\text{Rich}}$  while NDVI, mean annual temperature and annual precipitation had the highest relative importance scores for  $F_{\text{Disp}}$ . Also supporting our predictions, historical factors were more important in formerly glaciated regions, indicating the historical effects of climatic stability and accessibility to glacial refugia are strongly linked to the overall glaciation history.

## DISCUSSION

### *Geographic patterns of functional richness and dispersion*

North America broadleaved trees  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  showed distinct spatial patterns, closely associated with the climatic history of this

region. Areas characterized by “harsher” glacial environments during the LGM, namely areas covered by the Laurentide Ice Sheet, showed smaller functional space sizes (low  $F_{\text{Rich}}$ ) and a lower packing of traits within this space (higher  $F_{\text{Disp}}$ ) than areas free of ice during the same period (e.g., Rocky Mountains and the South West). As shown in Šímová et al. (2014), the regions we characterize as glaciated during the LGM correspond to areas with smaller seeds and SLA, a wide variety of dispersal strategies (large range and variance in SWT), and a restricted (small range) but variable (large variance) range of heights. The strong representation of species with small seed in glaciated regions is consistent with strong filtering on dispersal traits through the need for colonization these regions via dispersal across large distances (cf. Normand et al. 2011). In the case of height, the observed structure in glaciated regions may reflect more open forest vegetation at high latitudes when compared to the dense broadleaved forests of the Southeast and regions of the Rocky Mountains. In contrast, formerly ice-free areas in the south show a large (high  $F_{\text{Rich}}$ ), but relatively evenly covered functional space (low  $F_{\text{Disp}}$ ). In this southern region, most of the species do not deviate much from the assemblage core, resulting in low  $F_{\text{Disp}}$ .

### *Importance of contemporary and historical environmental conditions*

As expected from other dimensions of diversity (e.g., Kreft and Jetz 2007, Svenning and Skov 2007b, Sandel et al. 2011, Jetz and Fine 2012, Ordonez and Svenning 2015), both contemporary and historical factors are closely correlated with contemporary functional richness and dispersion of North American woody angiosperms. Univariate and multivariate regressions reveal the importance of both contemporary and historical climate as determinants of the functional packing across large geographic regions via species pool effects and colonization lags. Water availability (precipitation), productivity (NDVI), and accessibility to glacial refugia showed the strongest association with functional diversity. Moreover, the similar magnitude of model average standardized regression coefficient for accessibility to glacial refugia, NDVI, and annual precipitation provides evidence that

both past and contemporary conditions equally shape the functional diversity in this region. Given the strong association between contemporary environmental conditions and functional traits (e.g., Wright et al. 2005, Ordonez et al. 2009, Ordonez and Olff 2013, Maire et al. 2015), the fact that the impact of historical environmental conditions on current functional diversity can still be recovered is surprising; more so given the distribution and composition stability of North American plants during the mid- to late Holocene (~11 000 yr ago, cf. Williams et al. 2004).

Our results show that  $F_{\text{Rich}}$  increases as precipitation and productivity and accessibility to glacial refugia increased. The influence of contemporary factors, either individually or in combination, reflects the importance of current conditions as determinants of the physiologically viable section of the regional functional trait space an assemblage occupies. These relations are most likely the result of broad-scale filtering of unsuitable parts of the continental functional space. Meanwhile, the association between  $F_{\text{Rich}}$  and accessibility to glacial refugia indicate the importance of postglacial migration lags not just for species distributions and diversity (Johnstone and Chapin 2003a, McLachlan et al. 2005, Payette 2007, Svenning and Skov 2007a,b, Gavin 2009, Ordonez and Williams 2013), but also for functional diversity. As shown by regression analyses, historical effects (colonization from past refugia) on  $F_{\text{Rich}}$  are comparable to those of the contemporary factors. Such similarity would result in analogous changes in the functional space size due to lags in colonization from glacial refugia, or changes in water availability and productivity. In summary, the importance of historical factors and determinants of  $F_{\text{Rich}}$  indicate how glacial–interglacial climatic changes have also defined which section of the possible trait space is realized in a location as well as the relative size of this space, even as a large proportion is environmentally viable under current conditions.

In the case of  $F_{\text{Disp}}$  we found it decreased as precipitation and accessibility to glacial refugia increased, and productivity increased. These patterns reveal the importance of both contemporary and historical climate as determinants of the functional packing across broad geographic regions, most likely via species pool effects

and physiological tolerances. While the impact of present environmental conditions on  $F_{\text{Disp}}$  is most likely via species pool effects, the impact of accessibility is most likely via lagged postglacial colonization and the permanent removal species with unsuitable physiological or ecological traits. Contemporary and historical environmental factors have been proposed to codetermine of the number of species that can occur in an assemblage (Svenning and Skov 2007b, Svenning et al. 2010, Kerkhoff et al. 2014). However, co-occurring species need to divide the available functional space among them as a function of the number of species in the regions and the similarity between them. The interaction between species richness and physiological tolerances define how contemporary and historical environmental conditions have determined the functional space packing of an assemblage.

Recently, Šimová et al. (2014) showed how individual trait variance (the univariate analog of our  $F_{\text{Disp}}$  metric) was not universally affected by changes in contemporary climatic harshness in this region. As a result, it could be assumed that the relative position of species within a predefined functional space would not be related to environmental conditions. In contrast, we found a significant association between  $F_{\text{Disp}}$  and both contemporary and historical environmental conditions. From a methodological perspective, this illustrates how a series of small non-significant univariate differences in the variability in traits can add up to generate multivariate divergence of traits. From an ecological perspective, this illustrates the need to evaluate multiple functional dimensions/strategies when aiming to determine meaningful ecological differences among species, and how the importance of current and historical environmental factors as determinants of an assemblage the functional space and composition.

#### *Glaciation history effects on the importance of contemporary and historical environmental conditions*

The possibility that dispersal-mediated effects determine the observed  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  patterns for North America broadleaved trees are in line with the observed differences in migration capacity of plant species in this region (McLachlan et al. 2005, Gavin 2009, Ordonez and Williams 2013). Such migration lag has been also used



to explain the change in the lagged response in realized climatic niche of North America broadleaved trees over the last 16 000 yr (Ordóñez 2013). This broad assortment of dispersal dynamics has resulted in modern ranges of some North America trees, and other plant species still being constrained by postglacial re-colonization (Johnstone and Chapin 2003a, Payette 2007, Gavin 2009, Blonder et al. 2015). For example, the northern limit of lodgepole pine (*Pinus contorta*) is not climatically determined, and therefore not in equilibrium with current climate (Johnstone and Chapin 2003a). Furthermore, the importance of climatic constraints on species ranges is exemplified by *Picea critchfieldii*, the only plant known to become globally extinct due to climate change during the Late Pleistocene (Jackson and Weng 1999). As a result, species in areas glaciated during the LGM shown a lower filling of their potential geographic range particularly in the Rocky Mountains and the South West and Northeast (cf. Blonder et al. 2015). Such a lag could translate into only a fraction of the possible functional space being realized in glaciated regions, as shown by Ordóñez and Svenning (2015) for the European flora.

The fact that the analyses for the glaciated and unglaciated subregions separately indicate that contemporary environmental factors are the main determinants of functional diversity within both areas implies that the effect of long-term climate stability and postglacial migration lags are linked to overall glacier coverage. Moreover, the differences in functional diversity between glaciated and ice-free regions can be considered as clear evidence that limited postglacial dispersal plays an important supplementary role. Likewise, we found steeper relations between elevation variability and  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  in ice-free regions when compared to glaciated areas, indicating a historical legacy in the relation between functional diversity and contemporary environment relationships. These patterns are consistent with Svenning et al. (2009) for plant species richness in Europe, with the shallower relations between richness and topographic variability in formerly glaciated regions explainable from the reduced regional species pools due to glacial losses.

## CONCLUSION

In this study, we have shown how that both contemporary and historical environmental conditions determine the  $F_{\text{Rich}}$  and  $F_{\text{Disp}}$  of North American broad-leaved trees, contrary to the expectation of equilibrium between climate and diversity. This relation implies that the functional characteristics of North American broad-leaved trees are still partially controlled by climate conditions experienced during the Last Ice Age. Our results are consistent with the recent finding of generalized range disequilibrium in North American trees (Blonder et al. 2015), and the functional deficits, as shown for the European flora by Ordóñez and Svenning (2015).

Multiple mechanisms can explain the relations of contemporary functional diversity with historical conditions. Among these, differences in postglacial migration rates between North American broad-leaved trees (McLachlan et al. 2005, Ordóñez and Williams 2013), climate-driven species extinctions (Svenning 2003, Eiserhardt et al. 2015), and trait-related filtering via physiological or ecological tolerances (Mouillot et al. 2013, Zanne et al. 2013) have the most support in the literature. Such mechanisms have left lasting historical legacies on contemporary functional diversity, by shifting the trajectory of an assembly functional composition away from an equilibrium situation. Our work is one of the first studies that present evidence showing that both contemporary and historical factors simultaneously determine the functional richness and dispersion patterns at a continental scale. Given the current rates of climate and land use change, present and future losses in local and regional functional diversity can be expected to have long recovery times.

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## NOTES

<sup>1</sup> <http://esp.cr.usgs.gov/data/atlas/little/>

<sup>2</sup> <http://pmip3.lsce.ipsl.fr/>

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