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Running title: Structure drives functional diversity

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Abstract

Functional diversity (FD), represented by plant traits, is fundamentally linked to an ecosystem's capacity to respond to environmental change. Yet, little is known about the spatial distribution of FD and its drivers. These knowledge gaps prevent the development of FD-based forest management approaches to increase the trait diversity insurance (i.e., the response diversity) against future environmental fluctuations and disturbances. Our study helps fill these knowledge gaps by (i) mapping the current FD distribution, (ii) and analyzing FD drivers across northeastern North America. Following the stress-dominance hypothesis, we expected a strong environmental filtering effect on FD. Moreover, we expected abundant species to determine the bulk of FD distributions as suggested by the mass-ratio hypothesis.

We combined a literature and database review of 44 traits for 43 tree species with terrestrial inventory data of 48,426 plots spanning an environmental gradient from northern boreal to temperate biomes. We evaluated the statistical influence of 25 covariates related to forest structure, climate, topography, soils, and stewardship on FD by employing an ensemble approach consisting of 90 non-parametric models.

Temperate forests and the boreal-temperate ecotone east and northeast of the Great Lakes were identified as FD hotspots. Environmental filtering by climate was of secondary importance, with forest structure explaining most of the FD distribution of tree species in northeastern North America. Thus, our study provides only partial support for the stress-dominance hypothesis. Species abundance weightings altered trait diversity distributions and drivers only marginally, supporting the mass-ratio hypothesis. Our results suggest that forest management could increase FD without requiring knowledge of functional ecology by fostering stand structural complexity

instead. Further, mixing species from different functional groups identified in this study can enhance the trait diversity insurance of forests to an uncertain future.

Keywords: boreal forests; functional diversity hotspots; mass-ratio hypothesis; stress-dominance hypothesis; temperate forests; trait diversity insurance

1. Introduction

Climate change is one of the greatest threats facing forest biodiversity (Bellard et al., 2012) and the provisioning of ecosystem services (Schröter et al., 2005). Consequently, scientists are investigating ecosystem traits (i.e., quantitative characteristics of organisms at the community level (He et al., 2019)) that lend resilience to climate change (Barros et al., 2016; Enright et al., 2014; Thom et al., 2019). One such measure is the functional diversity (FD) of plants coexisting in communities, which potentially renders a “functional trait insurance” against future changes, and is linked to the adaptive capacity of ecosystems (Aubin et al., 2016; Díaz et al., 2016; Stahl et al., 2013). Although future forest ecosystem dynamics and functioning will likely strongly depend on FD (Hisano et al., 2018), little is known about FD distributions, and their drivers.

FD is a measure of the diversity of functional traits that express morphological, physiological and phenological features affecting growth, survival, and reproductive success of plants (Violle et al., 2007). Thus, functional traits determine the tolerance ranges and competitive ability of plants within their biotic and abiotic environment (Lavorel and Garnier, 2002). FD is fundamentally linked to ecosystem functioning as species occupy different niches based on their traits (Goswami et al., 2017). Consequently, FD is a proxy for drivers of ecosystem dynamics and resilience (Kéfi et al., 2016), as well as the quantity and quality of services available for human well-being (Cadotte et al., 2011).

Functional richness (FR) and functional evenness (FE) are two principal components of FD (Chiu and Chao, 2014), providing different information about an ecosystem's resistance and resilience to environmental change (Kéfi et al., 2016). FR quantifies the total functional trait space occupied by a species community while FE describes how regular the functional trait space is filled by a plant community (Mason et al., 2005). We here define FD as the aggregated information provided by FR and FE. A number of indices have been developed to quantify FD (Schleuter et al., 2010). Hill numbers are increasingly used to assess FD as they combine FR and FE, have computational advantages over many other indices (e.g., they satisfy a replication principle which implies a linear relationship between species trait additions and the index), and are easy to interpret (Chiu and Chao, 2014). In effect, functional Hill numbers quantify the effective number of equally abundant and functionally distinct species (Chiu and Chao, 2014). Additionally, they allow variable emphasis to be placed on rare versus common species in estimating FD (e.g., by generalizing Shannon entropy and Rao's quadratic entropy). Such an abundance weighting can improve the understanding of community assembly rules (Chalmandrier et al., 2015). For instance, abundance weightings can indicate whether species occupy similar or diverging niches in forest ecosystems, and thus whether they contribute to ecosystem functioning proportionally to their abundance as proposed by the mass ratio hypothesis (Grime, 1998).

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Functional trait representation can vary considerably across a geographical region, depending on the distribution and relative abundance of constituent species (Butler et al., 2017; Ordonez and

Svenning, 2016). Regional differences in functional trait diversity imply variation in the insurance effect against future changes, with high diversity potentially buffering against environmental fluctuations and catalyzing reorganization after disturbance (Mori et al., 2013; Wüest et al., 2018). Tree species distribution in northeastern North America is generally limited by temperature to the north and precipitation to the west (Fei et al., 2017; McKenney et al., 2007). Current species distributions are largely the result of individual migration processes and biotic interactions since the last ice age (Clark, 1998). Pollen analyses indicate taxa-specific differences in migration, with the last major migration wave ending about 4,000 years ago (Webb, 1981). At the local scale, the species composition of northeastern North American forests is highly variable due to differences in soils, topography, and natural disturbance regimes (Lorimer and White, 2003; Nichols, 1935). Additionally, European colonization and land clearing during the 17th – 19th centuries, followed by agricultural abandonment and secondary forest succession, have strongly modified the forest composition and structure throughout this region (Foster et al., 1998; Thompson et al., 2013). Current management intensity varies markedly throughout northeastern North America, ranging from short-rotation, even-aged to uneven-aged, selection systems which, combined with other anthropogenic stressors, continue to alter successional trajectories (Donato et al., 2012) and forest structure (Thom and Keeton, 2020).

The relationship between species composition and FD has been described in several studies (e.g., Loreau et al. 2001; Lavorel and Garnier 2002; Hooper et al. 2005). However, the correlation between forest structure (e.g., variation in tree sizes, stand density, and canopy complexity) and FD remains poorly understood. Previous work has tested only a relative small number of explanatory variables related to forest structure (e.g., basal area) for their effects on FD (Whitfeld et al., 2014). This is surprising, as structural elements and ecosystem functions, such as Net

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Ecosystem Productivity and hydrologic regulation, change with forest stand development (Bormann and Likens, 1979; Franklin et al., 2002). For instance, an increase in structural complexity during forest development (e.g., including heterogeneity in tree dimensions and gap sizes) likely also causes an increase in FD by creating niches for a variety of species (Bauhus, 2009; Taylor et al., 2020). Canopy complexity of old forests supports species with very different life history traits (e.g., mixes of shade-tolerant and shade-intolerant species), and disturbance legacies (e.g., nurse trees and tip-up mounds) provide habitat for species with specialized traits (Fahey et al., 2018). Also, changes in forest structure during stand development can alter litter production and decomposition (Chen et al., 2017; O'Keefe and Naiman, 2006). Thus, edaphic conditions may support regeneration of different species as forests age.

Direct and indirect (e.g., intensifying natural disturbance regimes) climate change effects on forest ecosystems will alter nutrient and water cycles (Davis et al., 2019). Ecosystem responses (e.g., growth and competition) to these changes will depend on the functional traits of the species community (Stahl et al., 2013). Temperatures may rise by more than 4°C in most parts of North America by the end of the 21th century (Romero-Lankao et al., 2014). The boreal forest, which constitutes the northernmost forest zone of North America, is critical to regulating global carbon flux and climate (Pan et al., 2011). However, the inherently low biodiversity of the boreal biome (Brooks et al., 2006) renders it vulnerable to changes in climate and disturbance regimes (Liang et al., 2016; Paquette and Messier, 2011). Further, the boreal-temperate ecotone, linking the northern boreal to the more southerly temperate forests of North America, may be particularly susceptible to climate change as many constituent species are at their climatic range limits (Boulanger et al., 2017; Evans and Brown, 2017). A shift in climate could drive rapid changes in composition

(Taylor et al., 2017) and may induce decreases in biodiversity and ecosystem services, such as carbon storage (Thom et al., 2019).

Fostering FD offers a promising and yet still uncertain strategy for enhancing the adaptive capacity of ecosystems to environmental change (Messier et al., 2015). Integrating FD into proactive forest management planning to safeguard biodiversity and ecosystem services under climate change is increasingly encouraged (Aubin et al., 2016; Fahey et al., 2018; Messier et al., 2013). However, the concept of FD is not readily accessible to most forest practitioners, and knowledge gaps often limit its application to forest management. For instance, it remains uncertain which species combinations maximize FD, and which stand structures provide niches for those species.

In this study, we analyzed the FD of forests in northeastern North America. Our objectives were to (i) map the current trait diversity distribution throughout northeastern North America, (ii) and quantify the drivers of FD. The “stress-dominance hypothesis” assumes that environmental filtering (i.e., abiotic factors selecting species with specific traits) is most distinct in harsh environments, only allowing adapted species with similar traits to establish (Chapman and McEwan, 2018a, 2018b; Swenson and Enquist, 2007). When conditions become more favorable, competitive interactions increasingly determine species establishment. As our study region consists primarily of boreal, and boreal-temperate forests, we hypothesized that environmental filtering, primarily climate, determines the trait diversity distribution. More specifically, we expected a distinct north-south gradient in the trait diversity distribution, with southern reaches being more diverse. Following the mass-ratio hypothesis, we further anticipated only moderate variation in our results when weighting FD by different species aggregation levels (i.e., we expected abundant species to determine the bulk of FD distributions) (Ohlmann et al., 2019).

2. Materials and methods

2.1. Study area

Our study spans a wide environmental gradient, encompassing five ecoregions. These range from Saskatchewan and Labrador in the north to Illinois and Ohio in the south (Fig. 1). Ecoregions are delineated around areas sharing similar vegetation, climate, and topography (EPA, 2016). Mean annual temperatures and annual precipitation vary considerably across the study region, ranging from -4.3 °C to 12.7 °C and 453 mm to 1,814 mm, respectively. Eastern boreal forests are dominated by cold-tolerant species, such as white spruce (*Picea glauca* [Moench]), black spruce (*Picea mariana* [Mill.]), balsam fir (*Abies balsamea* [L.]), trembling aspen (*Populus tremuloides* [Michx.]), and white birch (*Betula papyrifera* [Marsh.]). The boreal-temperate ecotone encompasses northern hardwood and mixed hardwood-conifer forest types that are more diverse, with sugar maple (*Acer saccharum* [Marsh.]), red maple (*Acer rubrum* [L.]), yellow birch (*Betula alleghaniensis* [Britton]), American beech (*Fagus grandifolia* [Ehrh.]), and eastern hemlock (*Tsuga canadensis* [L.]) being the dominant tree species. While those species also occur in temperate forests south of the ecotone, central hardwoods are rather dominated by oak species, particularly white (*Quercus alba* [L.]) and red oak (*Quercus rubra* [L.]).

2.2 Community data

We obtained relative species abundance from permanent sample plot (PSP) data. In particular, we employed the databases of the U.S. Forest Inventory and Analysis (FIA) Program, the Canadian National Forest Inventory (NFI), as well as PSP datasets from the Canadian provinces of

Saskatchewan, Manitoba, Ontario, Québec, New Brunswick, and Nova Scotia to collect data from the latest inventory (i.e., excluding earlier inventories). All individual datasets were harmonized and controlled for unrealistic entries, duplicates etc. before being compiled into a single comprehensive database. We omitted PSPs from the database if the 43 focal tree species did not comprise at least 95% of plot basal area, or if information for an explanatory variable (see below) was absent. In total, 48,426 PSPs were retained for analysis (Fig. 1).

2.3 Functional trait data

We collected functional trait data for 43 tree species (see Appendix S1, Supporting Information). Tree species were selected if they were abundant in the study region (i.e., relative basal area within the study region > 0.01%), or assumed to be of high ecological importance (e.g., due to a unique set of specialized functional traits). Following widely accepted systematics (Adler et al., 2014; Díaz et al., 2016), we categorized traits based on their hypothesized relevance for the three main demography processes: growth, recruitment, and survival of trees. These categories address different aspects for the overall adaptive capacity of species communities (Aubin et al., 2016). For instance, in a warmer world, growth traits (e.g., optimum temperature for photosynthesis) will influence productivity, recruitment traits (e.g., max. seed dispersal distance) will affect species migration speed, and survival traits (e.g., drought tolerance) enable existing organisms of an ecosystem to withstand environmental change.

To derive functional traits, we searched the TRY Plant Trait Database (Kattge et al., 2020, 2011), and performed an extensive literature review. The literature review did not follow a strict systematic approach (Nakagawa et al., 2017) as we aimed to include grey literature, for instance, books and reports (see also Thorn et al. 2018). Additionally, we used forest inventory data (see below) to estimate two traits (recruitment growth potential and top height growth). In total, we searched for 17 growth, 14 regeneration, and 13 survival traits (in sum 44 traits) of 43 species, i.e., 1892 trait parameter values. We found data for 1570 traits (83.0%) for the analysis (Fig. 2, Appendix S1). Most information was available for highly abundant tree species, such as red maple, sugar maple, paper birch, white spruce, and black spruce. In contrast, least traits were recorded for less common species, such as chestnut oak (*Quercus prinus* [Willd.]), pin cherry (*Prunus pensylvanica* [L.f.]), and slippery elm (*Ulmus rubra* [Muhl.]).

We confirmed our theoretical assumption of selected traits by testing their effects on stand growth, regeneration, and mortality. We derived annual basal area increment and tree mortality rate, as well as stand density of trees with a dbh < 10 cm as indicator for established tree regeneration for a subset of 19,039 plots for which no management intervention was recorded between the two latest inventories (note that field interpretations of past management exhibit uncertainty to some degree). Regression models indicated a positive relationship between growth trait diversity (computed as Hill numbers, see below) and stand growth ($p<0.001$), a positive relationship between regeneration trait diversity and regeneration success ($p<0.001$), as well as a negative relationship between survival trait diversity and mortality rate ($p<0.001$).

2.4 Drivers of functional diversity

2.4.1. Forest structure

Data for potential FD drivers were obtained from various sources. Drivers were related to forest structure, climate, topography, soils, and stewardship. In total, we tested the effects of 25 potential explanatory variables on FD (Table 1).

We derived information on forest structure directly from PSPs. Structural attributes are characteristic for diverging successional development stages and ecological niches associated with mixes of different tree species (Frelich and Reich, 1995; Pulsford et al., 2016), and thus different trait combinations. In northeastern forests, basal area of live trees increases almost linearly with stand age during the first decades to centuries and levels off after approximately two centuries, though with considerable variation (Keeton et al., 2011; McGee et al., 1999). Further, variation (here the standard deviation) in tree diameter at breast height (*SD dbh*) and in tree height (*SD height*) is usually highest in older forests (Taylor et al., 2013; Urbano and Keeton, 2017). In contrast, *stand density* is frequently high in young forests, decreases over time with stand development, but again may increase through gap regeneration in older forests (Oliver, 1981; Tyrrell and Crow, 1994; Urbano and Keeton, 2017).

2.4.2. Climate

Climatic conditions influence species' geographic distributions, forest community composition, and associated FD (Ordonez and Svenning, 2016; Thuiller et al., 2006). We derived baseline climate normals (1970-2000 observation period) from WorldClim with a resolution of 1 km (WorldClim, 2016). In addition to mean annual temperature (*T mean*) and annual precipitation (*P sum*), we also differentiated between meteorological seasons. For instance, summer temperature (*T summer*) has a strong impact on tree growth, while low temperatures during winter (*T winter*) restrict seedling survival of many species. Hence, seasonal climatic effects on FD likely differ. Moreover, we computed *seasonality* to account for climate variation during the year, as species growing in continental regions are likely better adapted to wider temperature fluctuations than those in maritime climates. Following O'Donnell and Ignizio (2012), *seasonality* was defined for temperature as the standard deviation (SD), and for precipitation as the coefficient of variation (CV) across all months of a year.

2.4.3. Topography

Topography may influence plant performance through its modulating effect on local environmental conditions. All topographic variables were derived from a digital elevation model (DEM) with a resolution of 25 m downloaded using the 'elevatr' package in R (Hollister and Shah, 2018). For computational efficiency, we aggregated the data to 1 km resolution. Based on the disparities of DEM grid cells we derived *slope* and *aspect*, which influence the amount of radiation reaching the forest. Moreover, we computed the Terrain Ruggedness Index (*TRI*), which is the mean of the absolute differences between the value of a cell and the value of its eight surrounding cells (in Meters) as well as the Topographic Position Index (*TPI*) which is the difference between the value of a cell and the mean value of its eight surrounding cells (in Meters) (Wilson et al., 2007). *TRI* informs about abrupt change, whereas *TPI* defines more general topographic changes. Higher *TRI* and *TPI* indicate greater heterogeneity in environmental conditions, which may influence levels of FD through greater niche differentiation.

2.4.4. Soils

Soil conditions can have strong effects on community structure (Nilsson et al., 2008). Forest communities in northeastern North America have been found to vary a lot where soil conditions differ locally (Arii and Lechowicz, 2002). For instance, balsam fir, and black spruce can dominate poorly drained soils where species such as sugar maple or eastern hemlock would otherwise dominate (Nichols, 1935; Whittaker, 1975). Harsh soil conditions (e.g., low soil moisture and nutrients) have been found to support specialized species communities of low functional diversity (Chapman and McEwan, 2018b). We obtained information about dominant *soil types* from a 1 km resolution raster spatial layer (Fischer et al., 2008). We also derived a *soil moisture* index from the PSP data based on physiographic classes (US plots) or field estimates of soil moisture and drainage (Canadian plots). *Soil moisture* can be an important determinant of species occurrence and abundance, in particular, if water limitation exacerbates regionally under climate change (Fei et al., 2017).

2.4.5. Stewardship

Human activities have homogenized forest species composition worldwide, often negatively affecting FD (Hooper et al., 2005; Maeshiro et al., 2013). Due to large data gaps on management interventions across our study area, we estimated anthropogenic impacts on forests ("stewardship" in the following) indirectly. First, we obtained a raster layer with a 1 km resolution on the protection status of forests in our study area. This displayed six categories of management intensity ranging from strict nature reserves to protected areas with sustainable use of natural resources, as specified by the International Union for Conservation of Nature and Natural Resources (*IUCN category*) (CEC, 2010). Second, we retrieved the primary road network for North America at a 10 m resolution (Natural Earth, 2015), and computed the closest distance from roads (*road proximity*) to each PSP. *Road proximity* has been previously shown to be highly correlated with the global human influence on ecosystems, with longer distances from roads indicating more natural ecosystem conditions (Ibisch et al., 2016).

2.5. Data analysis

2.5.1. Functional similarity of tree species

First, we analyzed the functional distance of the selected eastern North American tree species. We defined non-continuous traits on an ordinal scale if they implied an order, and z-transformed continuous traits. As the trait matrix contained continuous and categorical variables, and some trait information was missing, we derived the similarity of species using a Gower distance matrix. We performed Agglomerative Hierarchical Clustering (AHC) with a Ward linkage method to quantify the overall distance among tree species in trait space and to categorize them into functionally similar groups. We tested for significant differences between clusters with a permutational multivariate analysis of variance (PERMANOVA).

2.5.2. Functional diversity hotspots

Next, we calculated the FD of each PSP in order to obtain the current trait diversity distribution and to identify FD cold- (low FD) and hotpots (high FD) across the study region. In particular, we used relative basal area per tree species in combination with the Gower distance matrix to obtain Hill numbers employing the hillR package (Li, 2018). Functional Hill numbers quantify the effective number of equally abundant and functionally equally distinct species (Chiu and Chao, 2014). Further, they enable the assessment of abundance effects by weighting species dominance by a q factor (Ohlmann et al., 2019). A q factor of 0 implies that no weight is given to species abundance, and thus equals functional richness. With increasing q more weight is given to abundant species, where q=1 equals the exponential Shannon entropy, and q=2 generalizes Rao's quadratic entropy.

Using the observed functional Hill numbers on the 48,426 PSPs, we derived the current trait diversity distribution across boreal and temperate forests of northeastern North America. By means of inverse distance weighting, we obtained a wall-to-wall estimate of FD for the total forest area of the study region (ca. 2.8 M Km^2). We performed the analysis for three q factors ({0,1,2}) to analyze the effect of species abundance on FD hotspots. Spatial interpolation accuracy was evaluated by deriving the Root Mean Square Error (RMSE) of predictions on the PSPs.

2.5.3. Drivers of spatial variation in functional diversity

We applied a robust ensemble modeling approach to identify the drivers of spatial variation in FD. We divided the data into 10 training datasets using 10 % of all PSPs, and 10 test datasets using the remaining 90 % of PSPs. Fitting each model with only 10 % of the original data reduced spatial autocorrelation. Additionally, we added PSP location coordinates (longitude and latitude) to account for the remaining spatial autocorrelation signal in the data (Dormann et al., 2007).

The model ensemble consisted of three non- or semi-parametric methods, including boosted regression trees (BRTs), random forests (RFs), and generalized additive models (GAMs). For each method, we used a different variable selection approach. For BRTs, we employed the dismo package (Hijmans et al., 2017) to conduct a backwards elimination based on variable importance.

Subsequently, we derived the RMSE of the test dataset for each candidate model, and selected the model with the lowest prediction error. For RFs, we used a minimal tree depth criterion to omit irrelevant variables using the randomForestSWR package (Ishwaran, 2019). For GAMs, we performed a forward selection of the eight most important predictors based on AICc using the FWDselect package (Sestelo et al., 2016). The different model selection methods account for a high variety in possible outcomes as well as computational efficiency. In comparison to GAMs, the BRT and RF model selection methods usually maintained a higher number of variables as they cope well with multicollinearity among explanatory variables (Dormann et al., 2013). Models were selected for the three Hill numbers of each training dataset, resulting in 30 models per method and 90 models in total.

We evaluated each model's goodness-of-fit using a pseudo-R^2 based on the correlation between predicted and observed data and tested for residual spatial autocorrelation with Moran's I. Moreover, models were cross-validated by comparing predictions with the observed FD of the test dataset using RMSE.

Relative variable importance measures were directly obtained from the BRT and RF models, and indirectly from the GAMs. In all models, variable importance was set to 0 if a variable was excluded in the variable selection process. For BRTs, importance was based on the number of times a variable is selected for splitting decision trees. This number was weighted by the squared improvement of the model as a result of each split, which ultimately was averaged over all trees (Elith et al., 2008). To measure variable importance of RFs, we used the increase in mean square error (MSE) when the observed values of an explanatory variable are randomly permuted (Breiman, 2001). Using GAMs, we derived the change in AICc by omitting each predictor individually from the final model. For each Hill number, we averaged the relative variable importance throughout all models (i.e., 30 models per Hill number).

Further, we tested if the effect of forest structure on FD was an indirect climate effect (i.e., whether the climate effect on FD was mediated by forest structure). To that end, we used the Lavaan package (Rosseel et al., 2020) to fit a structural equation model (SEM). Based on the variable importance of the model ensemble described above we selected the four strongest climatic drivers for each Hill number. Then we used all PSPs to derive the average standardized path coefficients between climate and forests structure, climate and FD, as well as forest structure and FD.

2.5.4. Sensitivity analysis

A sensitivity analysis of FD to changes of its drivers was performed to derive standardized effect sizes. We assessed the sensitivity of FD to changes in continuous forest structure, climate, and stewardship variables. In particular, we increased each variable individually by one standard deviation while all other variables were kept at their original values. We then derived the change in FD by comparing predictions of the modified dataset with those of the original dataset. Ultimately, we averaged changes in FD across the 30 models for each Hill number. Topography and soils were not tested as they are only subject to change over very long time frames, and as some variables were categorical.

3. Results

3.1. Functional diversity hotspots in temperate forests and the ecotone

Our spatial analysis revealed several FD hotspots across the study region (Fig. 3). In particular, the temperate forests and the boreal-temperate ecotone east and northeast of the Great Lakes were high in FD. In contrast, the northeastern boreal forest and the boreal-temperate ecotone west of the Great Lakes were FD coldspots. FD was highest when different functional groups were mixed, in particular, coniferous and broadleaved tree species (Fig. S1). In contrast, a high diversity within each functional group, that is (i) early-seral northern hardwoods, (ii) mid- and late-seral northern hardwoods, (iii) central hardwoods, and (iv) conifers, could increase FD to a lesser degree. Trait diversity distributions were only marginally affected by species abundance. The correlation between all q factors was high, with values between r=0.863 (comparing q=0 and q=2) and r=0.986 (comparing q=1 and q=2). Across the study area, the effective number of tree species with a unique set of traits decreased with increasing q factor from 5.1 (q=0) to 3.9 (q=1), and 3.5 (q=2). The RMSE of spatial interpolations across all PSPs was 2.1 (q=0), 1.5 (q=1), and 1.4 (q=2).

3.2. High correlation between forest structure and functional diversity

While many of the explanatory variables were related to variation in FD, those associated with forest structure had the strongest effect (Fig. 4). Overall, all methods applied to analyze FD drivers performed similarly (Table 2). RF models had the highest goodness-of-fit (max. R^2 = 0.502), followed by BRT models (max. R^2 = 0.487) and GAMs (max. R^2 = 0.392). However, the RMSE of the test data were almost identical, indicating that RF and BRT models were overly complex and thus overfitted the training data to some degree. Residual spatial autocorrelation of all models was negligible.

Differences in q factors modified the relative importance and the rank of some explanatory variables (e.g., 6.9 % difference between q=0 and q=2 for *SD height*) (Table 3, Fig. S2), but only slightly changed the cumulative effect of each category. Forest structure was, by far, the most important variable group explaining variation in FD (69.3 % – 71.6 %), followed by climate (18.2 % – 20.4 %), topography (2.4 % – 2.8 %), soils (2.9 % – 3.3 %), and stewardship (0.3 % – 0.6 %) (Fig. 4, Table 3). The top three variables across all q factors were *basal area*, *stand density*, and *SD height*. Least important were *IUCN category* and *aspect*. In all cases, except *P seasonality* at q=2, all temperature variables were more important than precipitation variables for predicting FD. The structural equation model confirmed the positive effect of forest structure on FD. Moreover, the average standardized path coefficient between climate and forest structure were only between -0.004 and 0.008 indicating that the effect of forest structure on FD was not indirectly driven by climate (Fig. S3, Table S1).

The sensitivity analysis highlighted the strong, positive effect of forest structure on FD (Fig. 5). All increases of structural variables by one standard deviation had a positive impact on FD, independent from abundance weighting. However, a higher weight on abundant species generally reduced changes in the effective number of functionally different species. On average, the effect of *stand density* on FD (+0.58 to +0.22) was greater than *basal area* (+0.47 to +0.21), but had a wider 95 % confidence interval across model predictions. While an increase in tree height variability (*SD height*) also had a strong, positive impact on FD, dbh variability (*SD dbh*) increased FD only marginally. FD responses to increases in climate variables were diverse and idiosyncratic. Overall, temperature increases tended to positively affect FD whereas elevated precipitation had a negative impact. *Road proximity* did not have a discernible influence on FD.

4. Discussion

Our study constitutes one of the most detailed analysis of FD drivers in northeastern North America conducted to date. Temperate forests and the ecotone east of the Great Lakes were identified as FD hotspots. FD distributions were primarily driven by forest structure, not climate. Hence, our study provides only partial support for the stress-dominance hypothesis. The most abundant species explain most of the FD variation in the study region, supporting the mass-ratio hypothesis. Based on our study, management strategies can be derived requiring little to no knowledge in functional ecology to enhance the trait diversity insurance towards an uncertain future.

4.1. Environmental filtering is of secondary importance for functional diversity

We found distinct regional differences in the functional trait distribution, with lowest FD in the boreal-temperate ecotone west and the boreal forests northeast of the Great Lakes (Fig. 3). In contrast to our hypothesis, we identified forest structure, not climate, as the dominant regional-scale driver of FD (Fig. 4, Fig. 5, Fig. S2, Table 3). A path analysis did not indicate climate effects on FD were mediated by forest structure, providing additional evidence for a strong positive direct association between forest structure and FD (Fig. S3, Table S1). This result challenges our initial expectation that environmental filtering determines functional trait distributions in the study region. The stress-dominance hypothesis assumes that species assemblages in harsh environments are constrained by abiotic factors that are limiting ecological and evolutionary variation (Swenson and Enquist, 2007). As expected, FD was highest in parts of the temperate forests (Fig.

3).However, temperate forests south of the Great Lakes currently have only moderate FD, challenging the stress-dominance hypothesis.

Forest management and land-use history have strong impacts on forest structure and diversity, as well as on the resulting trajectories of long-term forest development (Duveneck et al., 2014; McLachlan et al., 2000). Forest management and land-use history differ considerably throughout the study region, which could explain the high FD of temperate and boreal-temperate regions dominated by northern hardwoods and the low FD of northeastern boreal forests (Fig. 3). Large portions of northern hardwood forests are either unmanaged or managed with low intensity, allowing them to develop (semi-)naturally since agricultural abandonment (Foster et al., 1998). In contrast, most eastern boreal forests have been intensively managed by even-aged silvicultural systems, leading to more homogenous forest structures as compared to historic baselines (Bergeron et al., 2017). The legacies of land-use on forest structure persist even after centuries (Foster et al., 1998). Also the moderate FD south of the Great Lakes might be explained by an intense land-use history that homogenized forest structure on regional scale (Schulte et al., 2007).

Besides forest management and land-use history, natural disturbances are an important driver of structural complexity (Halpin and Lorimer, 2016a). The spatial patterns of trait distribution identified here may, in part, be a result of different disturbance regimes. In particular, low-intermediate severity disturbances foster forest development towards structural complexity (Franklin et al., 2002; Meigs et al., 2017). Fine-scale gap dynamics induced by wind and biotic disturbance agents dominate temperate and boreal-temperate forests of northeastern North America (Kosiba et al., 2018). In contrast, large-scale disturbances induced by fire or spruce budworm *(Choristoneura fumiferana* Clem.) outbreaks in boreal forests can lead to a more homogenous stand structure (Bouchard et al., 2005; Smirnova et al., 2008). Unfortunately, meaningful management and disturbance indicators were not available in the heterogeneous databases we synthesized to analyze FD drivers. Future studies should investigate the effects of management and disturbance on FD in northeastern North America to test those hypothesized effects.

Our study indicates that climate change may have only modest impacts on FD for forests within the scope of this study (Fig. 4, Fig. 5). However, it is also likely that climate change will modify the structural development of forests (Silva Pedro et al., 2017) which may induce an indirect effect on FD. Yet we are not aware of any studies in northeastern North America addressing such an indirect climate change effect on FD. In addition, climate change increases disturbance activity (Seidl et al., 2017). Depending on disturbance size, frequency, and severity, future disturbances will have diverging impacts on forest development pathways and consequently on structural diversity (Donato et al., 2012; Meigs et al., 2017). For instance, an increase in small-scale disturbances may improve structural diversity, while large-scale disturbances reset forest succession starting with low structural complexity (Senf et al., 2020; Thom et al., 2017). In contrast, structural complexity is usually high in old-growth forests due to gap dynamics and other processes of stand development, leading to high niche complementarity (Franklin and Pelt, 2004; Halpin and Lorimer, 2016b). Old-growth characteristics include high basal area, spatial complexity in stand density and light environment, and high variation in tree sizes and ages (Tyrrell and Crow, 1994; Urbano and Keeton, 2017). Our analysis indicates that old-growth structures likely correlate positively with FD (Fig. 5). Thus, older forests may have a particularly high functional trait insurance towards future environmental changes.

Although our study constitutes one of the most detailed analysis of FD in northeastern North American forests conducted to date (Chapman and McEwan, 2018a; Duveneck and Scheller, 2015;

Ordonez and Svenning, 2016), it has limitations. The positive correlation between FD and stand structural complexity indicates that environmental filtering has only a weak effect on FD of adult tree communities. However, environmental filtering could constitute an important factor for the FD of tree regeneration, which is more sensitive to environmental conditions and changes (Stevens et al., 2015). Our analysis is based on historical records (inventory and trait collections) at a specific point in time. Time-series data is needed to analyze the relationship between FD and forest structure across stand development. Alternatively, this could be analyzed by means of process-based simulation modeling. Our trait data collection could be harnessed by simulation models to parameterize species responses to environmental conditions and to dynamically project future changes of FD or other ecosystem properties. Furthermore, we did not account for intraspecific trait variation in our analysis as data availability is currently limited to traits and species most commonly investigated (Kattge et al., 2020). Intraspecific trait variation can be considerable (Kumordzi et al., 2019). A global meta-analysis found that about 25% of the total trait variation within communities is explained by intraspecific trait variation (Siefert et al., 2015). For instance, leaf traits are highly variable within some species (Kleinschmit, 1993). Forest structure and stand development can alter traits, such as biomass allocation to different tree compartments (Van de Peer et al., 2017), and might, therefore, affect FD beyond the relationships we found between forest structure and FD. Moreover, the large geographic distribution of tree species considered in our analysis may imply high within-species variability driven by environmental gradients, whereas a recent study suggests that a large portion of intraspecific variation can be captured at local scales (Kumordzi et al., 2019). With increasing data availability, intraspecific variation should be more prominently included in future FD studies.

4.2. Functional diversity depends more on abundant than rare species

Our results remained robust across species abundance weightings (Hill numbers). We identified a decrease in the effective number of functionally diverging species with increasing q factor by up to 31% (Fig. 3). In addition, comparing different q factors, we found only minor divergences in FD drivers (Fig. 4, Fig. 5, Fig. S2) and distributions (Fig. 3). Independent from species abundance weightings the three most important variables were *basal area*, *stand density*, and *SD height*. Based on these results, we conclude that rare species only have a moderate impact on FD (Chiang et al., 2016). Instead, supporting the mass-ratio hypothesis (Grime, 1998), the most abundant species determine the bulk of FD in northeastern North America (see also Winfree et al. 2015). Based on this result we conclude that functional traits of northeastern species communities are redundant to some degree. While we derived a considerable functional trait database of 44 traits for 43 tree species, we acknowledge that this conclusion depends on the traits analyzed, and may differ for other trait subsets. Further, the choice of tree species is crucial to compare between Hill numbers. However, we assume little divergence from our results by including other tree species not considered here as other species were abundant on a small portion of the plots (20.1%) investigated, only.

4.3. Management strategies to enhance the insurance of functional trait diversity

The development of FD-based management strategies to enhance the diversity insurance of forests to global change is hindered by difficulty in conceptualizing such approaches. Our study suggests three broad strategies to increase FD, each requiring varying knowledge about functional ecology.

In decreasing order of complexity these are based on (i) individual species traits; (ii) functional groups; and (iii) forest structure as a surrogate for FD.

FD is fundamentally linked to processes ensuring future ecosystem functioning and services provisioning (de Bello et al., 2010; Faucon et al., 2017; Zhang et al., 2012). Our study has shown that northeastern boreal forest and the boreal-temperate ecotone west of the Great Lakes currently have the lowest trait diversity insurance (Fig. 3), and could thus be particularly susceptible to ecological surprises, including novel disturbance regimes (Elmqvist et al., 2003; Zurlini et al., 2013).

Management strategies to maintain or enhance FD are thus highly relevant for those ecosystems. Ideally, forest management strategies should consider three options for adapting forest ecosystems to future uncertainties: (i) improving resistance, (ii) increasing resilience, and (iii) fostering transition (Millar et al., 2007). Managing for FD can integrate elements of all three options.

Resistant ecosystems are able to withstand stress and disturbances with little change in functioning. Resistance can be improved by mixing species with traits that are expected to increase tree survival after perturbations (Griess et al., 2012). Our study indicates that species mixtures in northeastern North America lending resistance capacity include species with a high tolerance to drought (e.g., *Pinus banksiana*, *Carya* and *Quercus sp.*), fire (e.g., *Carya ovata*, *Populus balsamifera*, and *Populus tremuloides*), wind (e.g., *Fraxinus americana*, *Quercus coccinea*, and *Carya sp*.), and biotic disturbance (e.g., *Larix laricina*, *Pinus strobus*, and *Quercus alba*) (Appendix S1).

Resilience ensures a quick recovery of ecosystems and functional processes after disturbance or the removal of a stressor, and facilitates the autonomous adaptation of ecosystems to novel environmental conditions (Mori et al., 2013). A number of traits related to growth, recruitment, and survival can improve resilience. For instance, resilient ecosystems can include species with high resprouting ability after disturbance (e.g. *Populus* and *Prunus sp*.), fast juvenile growth (e.g., *Acer saccharum* and *Populus grandidenta*), serotiny (e.g., *Pinus banksiana*), and species that maximize photosynthetic rates under different environmental conditions within a particular region (Appendix S1).

Transition can be fostered through assisted migration (Williams and Dumroese, 2013). Assisted migration of temperate species into boreal biomes would increase FD and accelerate species turnover rates towards communities adapted to future climate conditions. However, decisions about assisted migration must be case-specific, and there is considerable uncertainty which novel species assemblages will improve ecosystem functioning and are desirable (Aerts and Honnay, 2011). For instance, it would be counterproductive to introduce temperate species in boreal forests, if the management goal is to conserve boreal-obligate species (Murray et al., 2017).

These very detailed and case-specific recommendations to adapt forest ecosystems based on individual species traits are challenging to apply in a local context, and require detailed knowledge about functional traits. Based on our study, a more general approach to increase FD is to mix species of different functional groups (Fig. S1). This includes mixing species associated with different seral stages as well as northern and central hardwoods. A particularly strong positive effect on FD can be expected when coniferous and broadleaved species are mixed. For instance, a variety of intermediate treatments (i.e. thinnings) and regeneration harvesting systems (e.g. multi-aged and uneven-aged) can be adapted to improve the composition of species categorized into these different functional groups (Keeton et al. 2018). Enrichment planting (including assisted migration) could further enhance FD where necessary.

An approach to enhance FD without requiring knowledge of functional ecology is to manage for structural diversity. Our study indicates that forest structure drives FD through the creation of various niches for species co-existence. Adaptive management could thus focus on structural complexity as a surrogate, to some extent, for FD. This might employ a range of silvicultural approaches, such as irregular (multi-aged) shelterwood systems, variable density thinning, variable retention harvesting, and modified group selection or gap-based approaches with permanent retention of legacy trees, designed to emulate aspects of stand structural complexity associated with natural disturbances (Franklin et al., 2007; Kern et al., 2017; North and Keeton, 2008). As a number of silvicultural approaches are suitable to promote FD, conflicts with other management objectives can be minimized. Thus, fostering FD could constitute a key strategy to safeguard desired forest ecosystem services in an uncertain future.

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Data availability

Functional trait data gathered for this study can be retrieved from the Excel spreadsheet in the supplement, and will be accessible via the TRY Plant Trait Database (https://try-db.org).

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Tables

Table 1: Summary statistics of explanatory variables. Presented are means and ranges (in parentheses) of 21 continuous variables on 48,426 PSPs used for the analysis of functional trait diversity. For completeness, the table also includes the four explanatory variables that were defined as categorical variables, with two of them being on an ordinal scale. cat.: categorical; dim: dimensionless; NA: not applicable.

Category	Attribute	Description	Unit	Value
Forest structure	Basal area	Basal area of live trees	$m^2\ ha^{-1}$	19.7 (0; 100)
	SD dbh	Standard deviation of diameter at breast height	cm	6.9 (0; 51.2)
	SD height	Standard deviation of tree height	m	3.0 (0; 12.1)
	Stand density	Stand density of live trees	$n\ ha^{-1}$	698 (15; 17125)
Climate	T mean	Annual mean temperature	°C	4.3 (-4.3; 12.7)
	T winter	Winter temperature (DJF)	°C	-10.7 (-24.0; 0.6)
	T spring	Spring temperature (MAM)	°C	3.4 (-6.3; 12.4)
	T summer	Summer temperature (JJA)	°C	17.3 (10.6; 23.7)
	T autumn	Autumn temperature (SON)	°C	6.4 (-2.1; 13.7)
	T seasonality	Standard deviation of annual temperature	°C	11.0 (7.2; 15.5)
	P sum	Annual precipitation sum	mm	958 (453; 1814)
	P winter	Winter precipitation (DJF)	mm	111 (24; 346)
	P spring	Spring precipitation (MAM)	mm	220 (78; 455)
	P summer	Summer precipitation (JJA)	mm	295 (200; 461)
	P autumn	Autumn precipitation (SON)	mm	262 (116; 531)
	P seasonality	Coefficient of variation of annual precipitation	mm	29 (5; 70)
Topography	Aspect	Orientation of the slope in N, E, S or W direction	cat.	NA
	Elevation	Height above sea level	m	336 (1; 1283)
	Slope	Inclination of the ground surface	degrees	0.9 (0.0; 13.6)
	TPI	Topographic Position Index, expresses the difference between the value of a cell and the mean value of its eight surrounding cells	dim.	0.8 (-188.0; 197.5)
	TRI	Terrain Ruggedness Index, expresses the mean of the absolute difference between the value of a cell and the value of its eight surrounding cells	dim.	17.0 (0.0; 209.3)

Soils	Moisture	Soil moisture in three classes: xeric, mesic, hydric	ordinal	NA
	Soil type	Dominant soil types differentiated into 28 classes	cat.	NA
Stewardship	IUCN category	Protection status according to the IUCN definition in nine classes	ordinal	NA
	Road proximity	Forest plot distance from the closest main road	km	10.6 (0.0; 177.1)

Table 2: Model evaluation. Presented are Moran's I statistic and the pseudo-R^2 of the training datasets as well as the RMSE of the test data prediction. Means and standard deviations (in parentheses) of each model family and Hill numbers (q factor) are shown. BRT=Boosted Regression Trees; RF=Random Forests; GAM=Generalized Additive Models.

Model	Moran's I statistic	Pseudo-R^2	RMSE
BRT q=0	0.010 (0.013)	0.487 (0.024)	2.2 (0.0)
BRT q=1	0.005 (0.014)	0.394 (0.024)	1.7 (0.0)
BRT q=2	0.002 (0.015)	0.340 (0.017)	1.6 (0.0)
RF q=0	0.021 (0.012)	0.506 (0.015)	2.2 (0.0)
RF q=1	0.005 (0.015)	0.439 (0.020)	1.7 (0.0)
RF q=2	-0.002 (0.016)	0.399 (0.010)	1.6 (0.0)
GAM q=0	0.022 (0.014)	0.392 (0.018)	2.2 (0.0)
GAM q=1	0.011 (0.017)	0.301 (0.021)	1.7 (0.0)
GAM q=2	0.003 (0.018)	0.252 (0.019)	1.6 (0.0)

Table 3: Relative variable importance for explaining variation in functional diversity. Relative importance indicates the relative contribution of each variable explaining FD (adding up to 100%). Values were averaged across 30 models for each Hill number (q factor), i.e., ten BRT, RF, and GAMs, respectively. Standard deviations are shown in parentheses.

Category	Attribute	Relative importance (%)		
		q=0	q=1	q=2
Forest structure	Basal area	31.8 (17.8)	27.1 (12.4)	27.4 (10.3)
	SD dbh	2.8 (2.3)	3.4 (2.9)	4.0 (3.0)
	SD height	13.8 (8.8)	19.2 (11.8)	20.7 (12.9)
	Stand density	23.2 (15.7)	19.6 (5.6)	19.4 (6.5)
Climate	T mean	2.7 (3.9)	1.6 (1.9)	1.3 (1.7)
	T winter	2.1 (4.5)	2.6 (5.4)	2.1 (2.6)
	T spring	2.4 (2.1)	3.4 (3.9)	2.5 (2.4)
	T summer	5.7 (5.3)	3.8 (3.7)	3.4 (2.7)
	T autumn	1.7 (1.7)	3.4 (4.8)	1.9 (2.5)
	T seasonality	1.7 (1.7)	1.7 (1.8)	1.5 (1.4)
	P sum	0.3 (0.5)	0.3 (0.6)	0.6 (0.9)
	P winter	0.2 (0.6)	0.5 (0.9)	1.0 (2.0)
	P spring	0.2 (0.4)	0.4 (0.7)	0.6 (0.7)
	P summer	1.1 (1.5)	1.2 (1.3)	0.9 (1.1)
	P autumn	0.6 (0.8)	0.8 (0.9)	0.9 (1.1)
	P seasonality	0.5 (0.7)	0.7 (1.2)	1.6 (2.7)
Topography	Aspect	0 (0.1)	0.1 (0.2)	0.1 (0.3)
	Elevation	0.2 (0.5)	0.2 (0.5)	0.3 (0.5)
	Slope	0.4 (0.5)	0.9 (1.2)	0.8 (1.1)
	TPI	0.2 (0.5)	0.1 (0.3)	0.3 (0.4)
	TRI	2 (2.2)	1.3 (1.4)	1.1 (1.3)
Soils	Moisture	0.1 (0.3)	0.2 (0.4)	0.3 (0.7)
	Soil type	2.8 (2.5)	2.7 (3.2)	2.9 (4.3)
Stewardship	IUCN category	0.0 (0.0)	0.0 (0.1)	0.0 (0.0)
	Road proximity	0.3 (0.5)	0.3 (0.5)	0.6 (0.7)
Coordinates	Latitude	1.9 (3.3)	2.8 (3.1)	2.2 (2.6)
	Longitude	1.2 (1)	1.8 (2.1)	1.7 (1.8)

Figures and figure legends

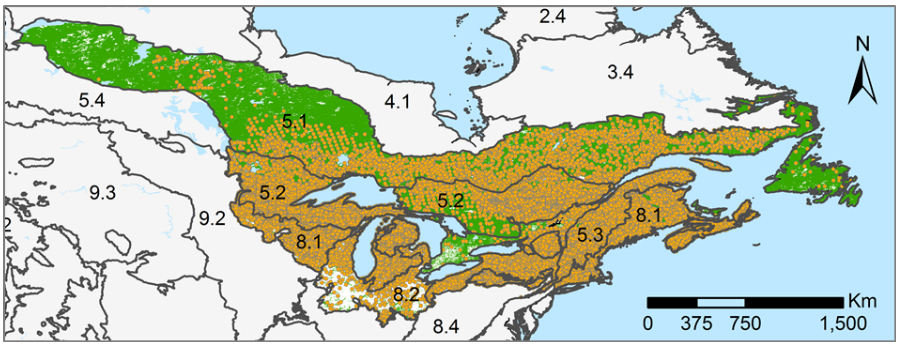


Fig. 1: Map of the study region and locations of the 48,426 permanent sample plots (PSPs) gathered for this study. The green background denotes the forest cover (ca. 2.8 M km²). The study region encompasses the ecoregions 5.1 (Softwood Shield), 5.2 (Mixed Wood Shield), 5.3 (Atlantic Highlands), 8.1 (Mixed Wood Plains), and 8.2 (Central USA Plains). Ecoregion 5.1 represents boreal forests, 5.2 and 5.3 constitute the boreal-temperate ecotone, and 8.1 and 8.2 are temperate forests. Ecoregions are based on EPA (2016).

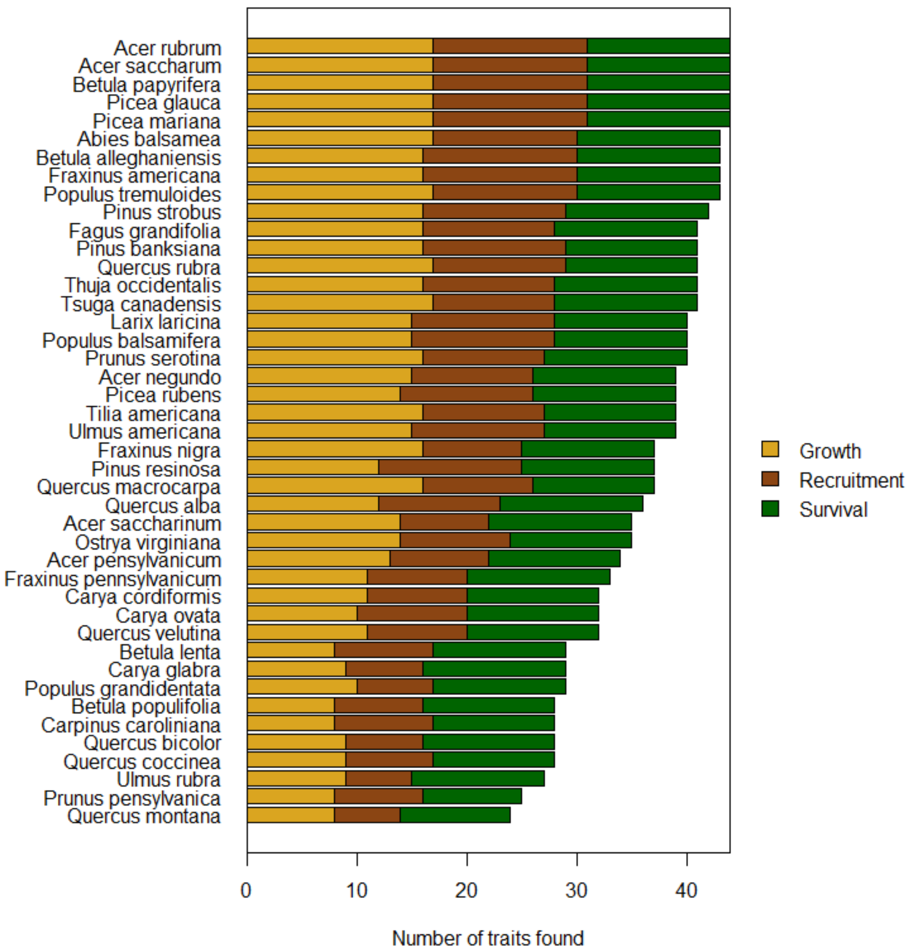


Fig. 2: Number of traits found per species. Traits relevant for growth, regeneration and survival are distinguished by color. The maximum number of traits is 44 for each of the 43 tree species (i.e., 1892 traits in total). The total number of traits found was 1570, i.e., 83.0% (see Appendix S1 for details).

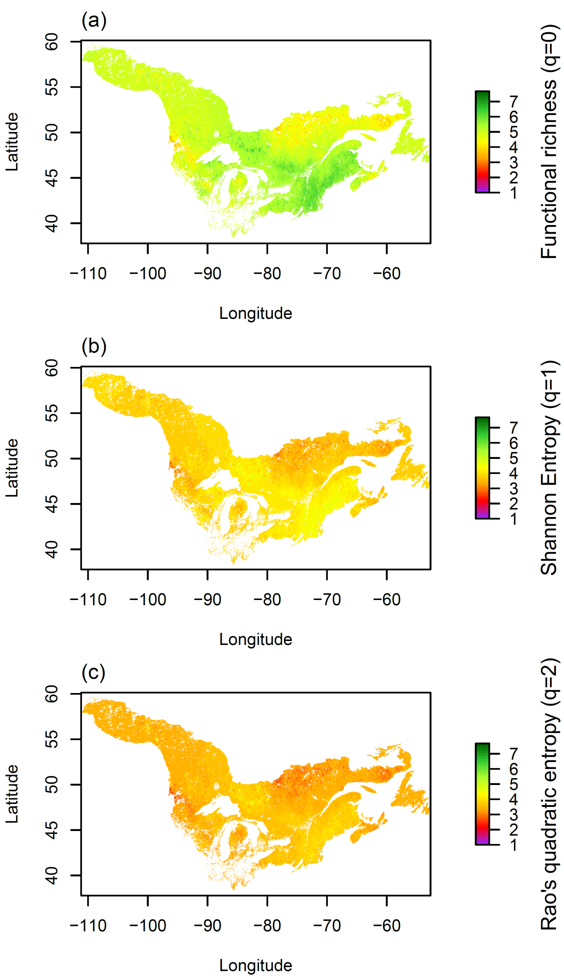


Fig. 3: Observed functional diversity distribution across northeastern North America. Scales denote the effective number of tree species with different functional traits weighted by different q factors. Distributions are based on 44 traits of 43 species on 48,426 PSPs. We used inverse distance weighting to derive wall-to-wall estimates of the trait distribution. Three different q factors were

considered to derive Hill numbers to illustrate the effect of species abundance on FD. (a) Functional richness, (b) exponential Shannon entropy, and (c) Rao's quadratic entropy.

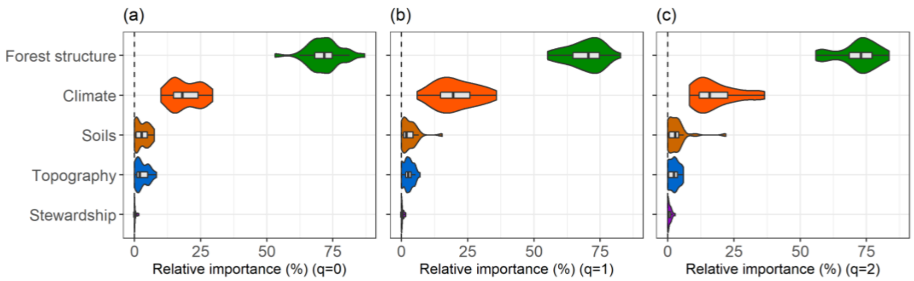


Fig. 4: Relative importance of forest structure, climate, soils, topography, and stewardship for functional diversity. Violins show the density distribution of variable importance summarized for each category (see Table 3 for individual variable importance). A boxplot presenting the median (vertical line), interquartile ranges (grey box), and ranges (i.e., whiskers showing the 1.5 × interquartile range) are displayed in the center of each violin. The three panels weight the species abundance effect on the drivers of functional diversity differently: (a) Functional richness (q=0), (b) exponential Shannon entropy (q=1), and (c) Rao's quadratic entropy (q=2).

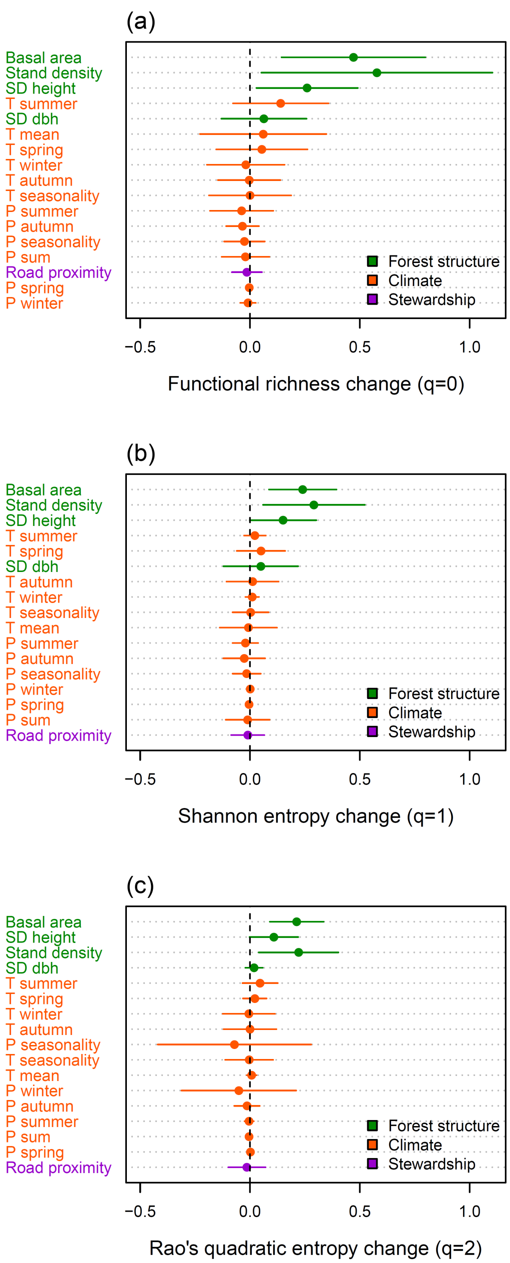

(a)
Basal area
Stand density
SD height
T summer
SD dbh
T mean
T spring
T winter
T autumn
T seasonality
P summer
P autumn
P seasonality
P sum
Road proximity
P spring
P winter
Forest structure
Climate
Stewardship
−0.5
0.0
0.5
1.0
Functional richness change (q=0)
(b)
Basal area
Stand density
SD height
T summer
T spring
SD dbh
T autumn
T winter
T seasonality
T mean
P summer
P autumn
P seasonality
P winter
P spring
P sum
Road proximity
Forest structure
Climate
Stewardship
−0.5
0.0
0.5
1.0
Shannon entropy change (q=1)
(c)
Basal area
SD height
Stand density
SD dbh
T summer
T spring
T winter
T autumn
P seasonality
T seasonality
T mean
P winter
P autumn
P summer
P sum
P spring
Road proximity
Forest structure
Climate
Stewardship
−0.5
0.0
0.5
1.0
Rao's quadratic entropy change (q=2)

Fig. 5: Sensitivity analysis of functional diversity driver effects. Presented are mean effects and 95% confidence intervals. The three panels weight the species abundance effect on the drivers of functional diversity differently: (a) functional richness, (b) exponential Shannon entropy, and (c) Rao's quadratic entropy. Changes in functional diversity were predicted by increasing each continuous variable by one standard deviation individually while retaining the original values of the PSPs for all other variables. Predictions for each panel were aggregated from 30 models (i.e., ten BRT, RF, and GAMs) respectively. Effects of explanatory variables are ordered according to their relative importance (see Table 3 and Fig. S2).

Supplementary material

Appendix S1: Individual traits for each species and references (see additional Excel spreadsheet provided).

Table S1: Standardized path coefficients among FD, forest structure and the four most important climatic drivers of FD (see Fig 5 and Fig. S1). Coefficients are based on structural equation modeling (SEM) of 48,426 inventory plots. q=0: Functional richness; q=1: exponential Shannon entropy; q=2 Rao's quadratic entropy.

Response variable	Covariate	q=0	q=1	q=2
FD	Basal area	0.668	0.223	0.129
	Stand density	0.499	0.441	0.434
	SD height	0.502	0.345	0.280
	SD dbh	0.183	0.164	0.157
	T mean	-0.757	NA	NA
	T winter	0.490	0.257	0.207
	T spring	0.475	0.276	0.240
	T summer	0.224	0.049	0.035
	T autumn	NA	-0.351	-0.326
Basal area	T mean	0.846	NA	NA
	T winter	-0.221	0.134	0.134
	T spring	-0.706	-0.544	-0.544
	T summer	-0.029	0.140	0.140
	T autumn	NA	0.204	0.204
Stand density	T mean	0.877	NA	NA
	T winter	-0.283	-0.045	-0.045
	T spring	-1.097	-0.881	-0.881
	T summer	0.046	0.144	0.144
	T autumn	NA	0.360	0.360
SD height	T mean	1.065	NA	NA
	T winter	-0.517	-0.009	-0.009
	T spring	-0.076	0.106	0.106
	T summer	-0.251	-0.001	-0.001
	T autumn	NA	0.186	0.186
SD dbh	T mean	0.977	NA	NA
	T winter	-0.468	0.004	0.004

T spring	0.054	0.219	0.219
T summer	-0.286	-0.054	-0.054
T autumn	NA	0.165	0.164

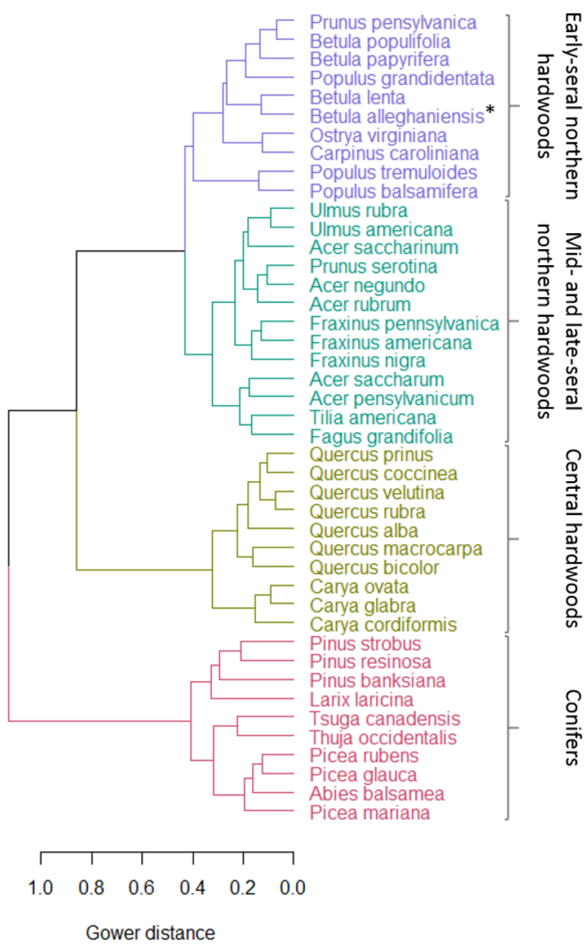
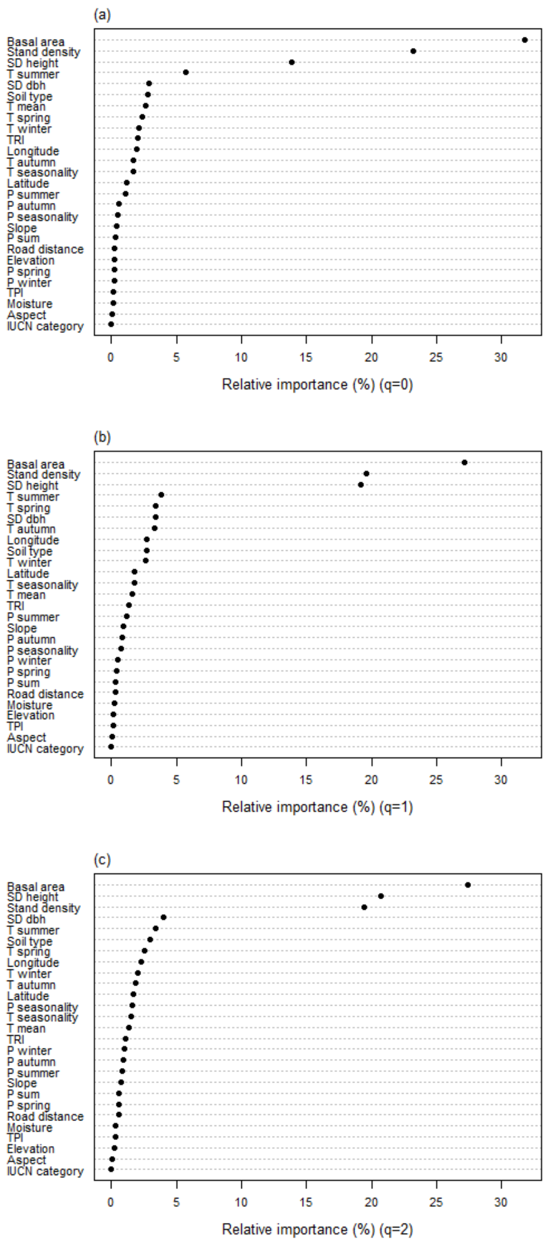


Fig. S1: Agglomerative Hierarchical Clustering (AHC) with a Ward linkage method of the functional trait similarity of 43 northeastern North American tree species. We identified four distinct functional groups for the 43 species investigated. We categorized these groups into: (i) early-seral northern hardwoods; (ii) mid- and late-seral northern hardwoods; (iii) central hardwoods; and (iv) conifers. This categorization applied to all species of each cluster, except *Betula alleghaniensis* which has many traits in common with early-seral northern hardwoods, but is considered a mid-late seral species. While both northern hardwood clusters were functionally most similar, the functional distance increased markedly to central hardwoods, and conifers were furthest apart from all of the other clusters. A subsequent PERMANOVA supported the AHC results. The test revealed that differences in the average trait composition of the groups were highly significant ($p < 0.001$).



(a)
Basal area
Stand density
SD height
T summer
SD dbh
Soil type
T mean
T spring
T winter
TRI
Longitude
T autumn
T seasonality
Latitude
P summer
P autumn
P seasonality
Slope
P sum
Road distance
Elevation
P spring
P winter
TPI
Moisture
Aspect
IUCN category
0 5 10 15 20 25 30
Relative importance (%) (q=0)
(b)
Basal area
Stand density
SD height
T summer
T spring
SD dbh
T autumn
Longitude
Soil type
T winter
Latitude
T seasonality
T mean
TRI
P summer
Slope
P autumn
P seasonality
P winter
P spring
P sum
Road distance
Moisture
Elevation
TPI
Aspect
IUCN category
0 5 10 15 20 25 30
Relative importance (%) (q=1)
(c)
Basal area
SD height
Stand density
SD dbh
T summer
Soil type
T spring
Longitude
T winter
T autumn
Latitude
P seasonality
T seasonality
T mean
TRI
P winter
P autumn
P summer
Slope
P sum
P spring
Road distance
Moisture
TPI
Elevation
Aspect
IUCN category
0 5 10 15 20 25 30
Relative importance (%) (q=2)

Fig. S2: Relative variable importance for functional diversity. The three panels weight the species abundance effect on the drivers of functional diversity differently: (a) Functional richness (q=0), (b) exponential Shannon entropy (q=1), and (c) Rao's quadratic entropy (q=2). Each panel presents the average relative variable importance across 30 models, i.e., ten BRT, RF, and GAMs, respectively.

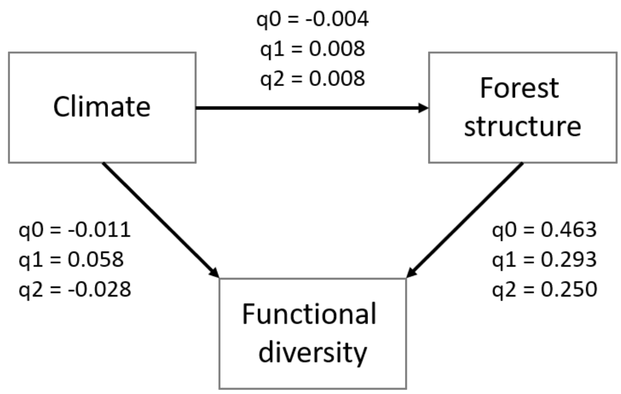


Fig. S3: Structural equation model (SEM) analyzing the indirect effect of climate on FD mediated via forest structure. Presented are the average standardized path coefficients among the four most important climatic drivers of FD (see Fig. S1), forest structure, and FD based on 48,426 inventory plots. q=0: Functional richness; q=1: exponential Shannon entropy; q=2 Rao's quadratic entropy