



Forest structure, not climate, is the primary driver of functional diversity in northeastern North America

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1 **Forest structure, not climate, is the primary driver of functional**
2 **diversity in northeastern North America**

3

4 Running title: Structure drives functional diversity

5

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28

29 **Abstract**

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

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

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

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

53

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

56

57

58 **1. Introduction**

59 Climate change is one of the greatest threats facing forest biodiversity (Bellard et al., 2012) and
60 the provisioning of ecosystem services (Schröter et al., 2005). Consequently, scientists are
61 investigating ecosystem traits (i.e., quantitative characteristics of organisms at the community
62 level (He et al., 2019)) that lend resilience to climate change (Barros et al., 2016; Enright et al.,
63 2014; Thom et al., 2019). One such measure is the functional diversity (FD) of plants coexisting
64 in communities, which potentially renders a “functional trait insurance” against future changes,
65 and is linked to the adaptive capacity of ecosystems (Aubin et al., 2016; Díaz et al., 2016; Stahl et
66 al., 2013). Although future forest ecosystem dynamics and functioning will likely strongly depend
67 on FD (Hisano et al., 2018), little is known about FD distributions, and their drivers.

68 FD is a measure of the diversity of functional traits that express morphological, physiological and
69 phenological features affecting growth, survival, and reproductive success of plants (Violle et al.,
70 2007). Thus, functional traits determine the tolerance ranges and competitive ability of plants
71 within their biotic and abiotic environment (Lavorel and Garnier, 2002). FD is fundamentally

72 linked to ecosystem functioning as species occupy different niches based on their traits (Goswami
73 et al., 2017). Consequently, FD is a proxy for drivers of ecosystem dynamics and resilience (Kéfi
74 et al., 2016), as well as the quantity and quality of services available for human well-being (Cadotte
75 et al., 2011).

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

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

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

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

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118 Ecosystem Productivity and hydrologic regulation, change with forest stand development
119 (Bormann and Likens, 1979; Franklin et al., 2002). For instance, an increase in structural
120 complexity during forest development (e.g., including heterogeneity in tree dimensions and gap
121 sizes) likely also causes an increase in FD by creating niches for a variety of species (Bauhus,
122 2009; Taylor et al., 2020). Canopy complexity of old forests supports species with very different
123 life history traits (e.g., mixes of shade-tolerant and shade-intolerant species), and disturbance
124 legacies (e.g., nurse trees and tip-up mounds) provide habitat for species with specialized traits
125 (Fahey et al., 2018). Also, changes in forest structure during stand development can alter litter
126 production and decomposition (Chen et al., 2017; O’Keefe and Naiman, 2006). Thus, edaphic
127 conditions may support regeneration of different species as forests age.

128 Direct and indirect (e.g., intensifying natural disturbance regimes) climate change effects on forest
129 ecosystems will alter nutrient and water cycles (Davis et al., 2019). Ecosystem responses (e.g.,
130 growth and competition) to these changes will depend on the functional traits of the species
131 community (Stahl et al., 2013). Temperatures may rise by more than 4°C in most parts of North
132 America by the end of the 21st century (Romero-Lankao et al., 2014). The boreal forest, which
133 constitutes the northernmost forest zone of North America, is critical to regulating global carbon
134 flux and climate (Pan et al., 2011). However, the inherently low biodiversity of the boreal biome
135 (Brooks et al., 2006) renders it vulnerable to changes in climate and disturbance regimes (Liang et
136 al., 2016; Paquette and Messier, 2011). Further, the boreal-temperate ecotone, linking the northern
137 boreal to the more southerly temperate forests of North America, may be particularly susceptible
138 to climate change as many constituent species are at their climatic range limits (Boulanger et al.,
139 2017; Evans and Brown, 2017). A shift in climate could drive rapid changes in composition

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

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

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

162

163

164 **2. Materials and methods**

165 **2.1. Study area**

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

180

181 **2.2 Community data**

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

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

191

192 **2.3 Functional trait data**

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

204 To derive functional traits, we searched the TRY Plant Trait Database (Kattge et al., 2020, 2011),
205 and performed an extensive literature review. The literature review did not follow a strict
206 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

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

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

241

242 2.4.2. Climate

243 Climatic conditions influence species' geographic distributions, forest community composition,
244 and associated FD (Ordonez and Svenning, 2016; Thuiller et al., 2006). We derived baseline
245 climate normals (1970-2000 observation period) from WorldClim with a resolution of 1 km
246 (WorldClim, 2016). In addition to mean annual temperature (*T mean*) and annual precipitation (*P*
247 *sum*), we also differentiated between meteorological seasons. For instance, summer temperature
248 (*T summer*) has a strong impact on tree growth, while low temperatures during winter (*T winter*)

249 restrict seedling survival of many species. Hence, seasonal climatic effects on FD likely differ.
250 Moreover, we computed *seasonality* to account for climate variation during the year, as species
251 growing in continental regions are likely better adapted to wider temperature fluctuations than
252 those in maritime climates. Following O'Donnell and Ignizio (2012), *seasonality* was defined for
253 temperature as the standard deviation (SD), and for precipitation as the coefficient of variation
254 (CV) across all months of a year.

255

256 2.4.3. Topography

257 Topography may influence plant performance through its modulating effect on local
258 environmental conditions. All topographic variables were derived from a digital elevation model
259 (DEM) with a resolution of 25 m downloaded using the 'elevatr' package in R (Hollister and Shah,
260 2018). For computational efficiency, we aggregated the data to 1 km resolution. Based on the
261 disparities of DEM grid cells we derived *slope* and *aspect*, which influence the amount of radiation
262 reaching the forest. Moreover, we computed the Terrain Ruggedness Index (*TRI*), which is the
263 mean of the absolute differences between the value of a cell and the value of its eight surrounding
264 cells (in Meters) as well as the Topographic Position Index (*TPI*) which is the difference between
265 the value of a cell and the mean value of its eight surrounding cells (in Meters) (Wilson et al.,
266 2007). *TRI* informs about abrupt change, whereas *TPI* defines more general topographic changes.
267 Higher *TRI* and *TPI* indicate greater heterogeneity in environmental conditions, which may
268 influence levels of FD through greater niche differentiation.

269

270 2.4.4. Soils

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

283

284 2.4.5. Stewardship

285 Human activities have homogenized forest species composition worldwide, often negatively
286 affecting FD (Hooper et al., 2005; Maeshiro et al., 2013). Due to large data gaps on management
287 interventions across our study area, we estimated anthropogenic impacts on forests (“stewardship”
288 in the following) indirectly. First, we obtained a raster layer with a 1 km resolution on the
289 protection status of forests in our study area. This displayed six categories of management intensity
290 ranging from strict nature reserves to protected areas with sustainable use of natural resources, as
291 specified by the International Union for Conservation of Nature and Natural Resources (*IUCN*
292 *category*) (CEC, 2010). Second, we retrieved the primary road network for North America at a 10
293 m resolution (Natural Earth, 2015), and computed the closest distance from roads (*road proximity*)

294 to each PSP. *Road proximity* has been previously shown to be highly correlated with the global
295 human influence on ecosystems, with longer distances from roads indicating more natural
296 ecosystem conditions (Ibisch et al., 2016).

297

298 **2.5. Data analysis**

299 *2.5.1. Functional similarity of tree species*

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

308

309 *2.5.2. Functional diversity hotspots*

310 Next, we calculated the FD of each PSP in order to obtain the current trait diversity distribution
311 and to identify FD cold- (low FD) and hotspots (high FD) across the study region. In particular, we
312 used relative basal area per tree species in combination with the Gower distance matrix to obtain
313 Hill numbers employing the hillR package (Li, 2018). Functional Hill numbers quantify the
314 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 Km²). 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.

337 Subsequently, we derived the RMSE of the test dataset for each candidate model, and selected the
338 model with the lowest prediction error. For RFs, we used a minimal tree depth criterion to omit
339 irrelevant variables using the randomForestSWR package (Ishwaran, 2019). For GAMs, we
340 performed a forward selection of the eight most important predictors based on AICc using the
341 FWDselect package (Sestelo et al., 2016). The different model selection methods account for a
342 high variety in possible outcomes as well as computational efficiency. In comparison to GAMs,
343 the BRT and RF model selection methods usually maintained a higher number of variables as they
344 cope well with multicollinearity among explanatory variables (Dormann et al., 2013). Models were
345 selected for the three Hill numbers of each training dataset, resulting in 30 models per method and
346 90 models in total.

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

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

359 individually from the final model. For each Hill number, we averaged the relative variable
360 importance throughout all models (i.e., 30 models per Hill number).

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

367

368 2.5.4. *Sensitivity analysis*

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

377

378

379 3. Results

380 3.1. Functional diversity hotspots in temperate forests and the ecotone

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

393

394 3.2. High correlation between forest structure and functional diversity

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

402 Differences in q factors modified the relative importance and the rank of some explanatory
 403 variables (e.g., 6.9 % difference between q=0 and q=2 for *SD height*) (Table 3, Fig. S2), but only
 404 slightly changed the cumulative effect of each category. Forest structure was, by far, the most
 405 important variable group explaining variation in FD (69.3 % – 71.6 %), followed by climate (18.2
 406 % – 20.4 %), topography (2.4 % – 2.8 %), soils (2.9 % – 3.3 %), and stewardship (0.3 % – 0.6 %)
 407 (Fig. 4, Table 3). The top three variables across all q factors were *basal area*, *stand density*, and
 408 *SD height*. Least important were *IUCN category* and *aspect*. In all cases, except *P seasonality* at
 409 q=2, all temperature variables were more important than precipitation variables for predicting FD.
 410 The structural equation model confirmed the positive effect of forest structure on FD. Moreover,
 411 the average standardized path coefficient between climate and forest structure were only between
 412 -0.004 and 0.008 indicating that the effect of forest structure on FD was not indirectly driven by
 413 climate (Fig. S3, Table S1).

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

424

425

426 **4. Discussion**

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

435

436 **4.1. Environmental filtering is of secondary importance for functional diversity**

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

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

449 Forest management and land-use history have strong impacts on forest structure and diversity, as
450 well as on the resulting trajectories of long-term forest development (Duveneck et al., 2014;
451 McLachlan et al., 2000). Forest management and land-use history differ considerably throughout
452 the study region, which could explain the high FD of temperate and boreal-temperate regions
453 dominated by northern hardwoods and the low FD of northeastern boreal forests (Fig. 3). Large
454 portions of northern hardwood forests are either unmanaged or managed with low intensity,
455 allowing them to develop (semi-)naturally since agricultural abandonment (Foster et al., 1998). In
456 contrast, most eastern boreal forests have been intensively managed by even-aged silvicultural
457 systems, leading to more homogenous forest structures as compared to historic baselines (Bergeron
458 et al., 2017). The legacies of land-use on forest structure persist even after centuries (Foster et al.,
459 1998). Also the moderate FD south of the Great Lakes might be explained by an intense land-use
460 history that homogenized forest structure on regional scale (Schulte et al., 2007).

461 Besides forest management and land-use history, natural disturbances are an important driver of
462 structural complexity (Halpin and Lorimer, 2016a). The spatial patterns of trait distribution
463 identified here may, in part, be a result of different disturbance regimes. In particular, low-
464 intermediate severity disturbances foster forest development towards structural complexity
465 (Franklin et al., 2002; Meigs et al., 2017). Fine-scale gap dynamics induced by wind and biotic
466 disturbance agents dominate temperate and boreal-temperate forests of northeastern North
467 America (Kosiba et al., 2018). In contrast, large-scale disturbances induced by fire or spruce
468 budworm (*Choristoneura fumiferana* Clem.) outbreaks in boreal forests can lead to a more
469 homogenous stand structure (Bouchard et al., 2005; Smirnova et al., 2008). Unfortunately,

470 meaningful management and disturbance indicators were not available in the heterogeneous
471 databases we synthesized to analyze FD drivers. Future studies should investigate the effects of
472 management and disturbance on FD in northeastern North America to test those hypothesized
473 effects.

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

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

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

515

516 **4.2. Functional diversity depends more on abundant than rare species**

517 Our results remained robust across species abundance weightings (Hill numbers). We identified a
518 decrease in the effective number of functionally diverging species with increasing q factor by up
519 to 31% (Fig. 3). In addition, comparing different q factors, we found only minor divergences in
520 FD drivers (Fig. 4, Fig. 5, Fig. S2) and distributions (Fig. 3). Independent from species abundance
521 weightings the three most important variables were *basal area*, *stand density*, and *SD height*. Based
522 on these results, we conclude that rare species only have a moderate impact on FD (Chiang et al.,
523 2016). Instead, supporting the mass-ratio hypothesis (Grime, 1998), the most abundant species
524 determine the bulk of FD in northeastern North America (see also Winfree et al. 2015). Based on
525 this result we conclude that functional traits of northeastern species communities are redundant to
526 some degree. While we derived a considerable functional trait database of 44 traits for 43 tree
527 species, we acknowledge that this conclusion depends on the traits analyzed, and may differ for
528 other trait subsets. Further, the choice of tree species is crucial to compare between Hill numbers.
529 However, we assume little divergence from our results by including other tree species not
530 considered here as other species were abundant on a small portion of the plots (20.1%)
531 investigated, only.

532

533 **4.3. Management strategies to enhance the insurance of functional trait diversity**

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

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

539 FD is fundamentally linked to processes ensuring future ecosystem functioning and services
540 provisioning (de Bello et al., 2010; Faucon et al., 2017; Zhang et al., 2012). Our study has shown
541 that northeastern boreal forest and the boreal-temperate ecotone west of the Great Lakes currently
542 have the lowest trait diversity insurance (Fig. 3), and could thus be particularly susceptible to
543 ecological surprises, including novel disturbance regimes (Elmqvist et al., 2003; Zurlini et al.,
544 2013).

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

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

556 Resilience ensures a quick recovery of ecosystems and functional processes after disturbance or
557 the removal of a stressor, and facilitates the autonomous adaptation of ecosystems to novel
558 environmental conditions (Mori et al., 2013). A number of traits related to growth, recruitment,

559 and survival can improve resilience. For instance, resilient ecosystems can include species with
560 high resprouting ability after disturbance (e.g. *Populus* and *Prunus sp.*), fast juvenile growth (e.g.,
561 *Acer saccharum* and *Populus grandidentata*), serotiny (e.g., *Pinus banksiana*), and species that
562 maximize photosynthetic rates under different environmental conditions within a particular region
563 (Appendix S1).

564 Transition can be fostered through assisted migration (Williams and Dumroese, 2013). Assisted
565 migration of temperate species into boreal biomes would increase FD and accelerate species
566 turnover rates towards communities adapted to future climate conditions. However, decisions
567 about assisted migration must be case-specific, and there is considerable uncertainty which novel
568 species assemblages will improve ecosystem functioning and are desirable (Aerts and Honnay,
569 2011). For instance, it would be counterproductive to introduce temperate species in boreal forests,
570 if the management goal is to conserve boreal-obligate species (Murray et al., 2017).

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

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

592

593

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604

605

606 **Data availability**

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

609

610

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1028 Tables

1029 Table 1: Summary statistics of explanatory variables. Presented are means and ranges (in parentheses) of 21
 1030 continuous variables on 48,426 PSPs used for the analysis of functional trait diversity. For completeness, the table
 1031 also includes the four explanatory variables that were defined as categorical variables, with two of them being on an
 1032 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)

1033	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)
1034					

1035 Table 2: Model evaluation. Presented are Moran’s I statistic and the pseudo-R² of the training datasets as well as the
 1036 RMSE of the test data prediction. Means and standard deviations (in parentheses) of each model family and Hill
 1037 numbers (q factor) are shown. BRT=Boosted Regression Trees; RF=Random Forests; GAM=Generalized Additive
 1038 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)

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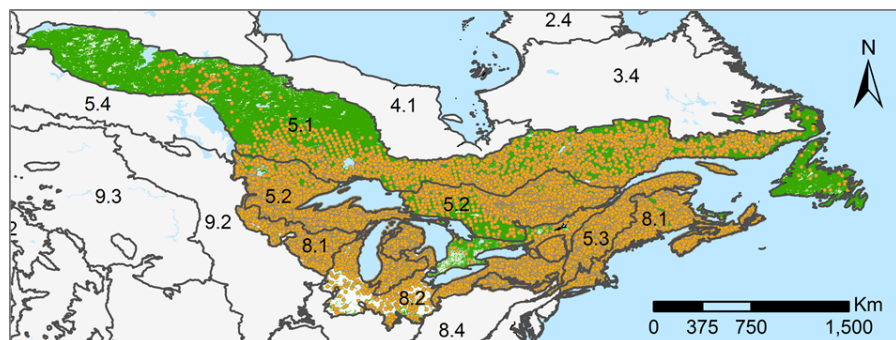
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Table 3: Relative variable importance for explaining variation in functional diversity. Relative importance indicates the relative contribution of each variable explaining FD (adding up to 100%). Values were averaged across 30 models for each Hill 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)

1048 **Figures and figure legends**

1049



1050

1051 Fig. 1: Map of the study region and locations of the 48,426 permanent sample plots (PSPs) gathered
 1052 for this study. The green background denotes the forest cover (ca. 2.8 M km²). The study region
 1053 encompasses the ecoregions 5.1 (Softwood Shield), 5.2 (Mixed Wood Shield), 5.3 (Atlantic
 1054 Highlands), 8.1 (Mixed Wood Plains), and 8.2 (Central USA Plains). Ecoregion 5.1 represents
 1055 boreal forests, 5.2 and 5.3 constitute the boreal-temperate ecotone, and 8.1 and 8.2 are temperate
 1056 forests. Ecoregions are based on EPA (2016).

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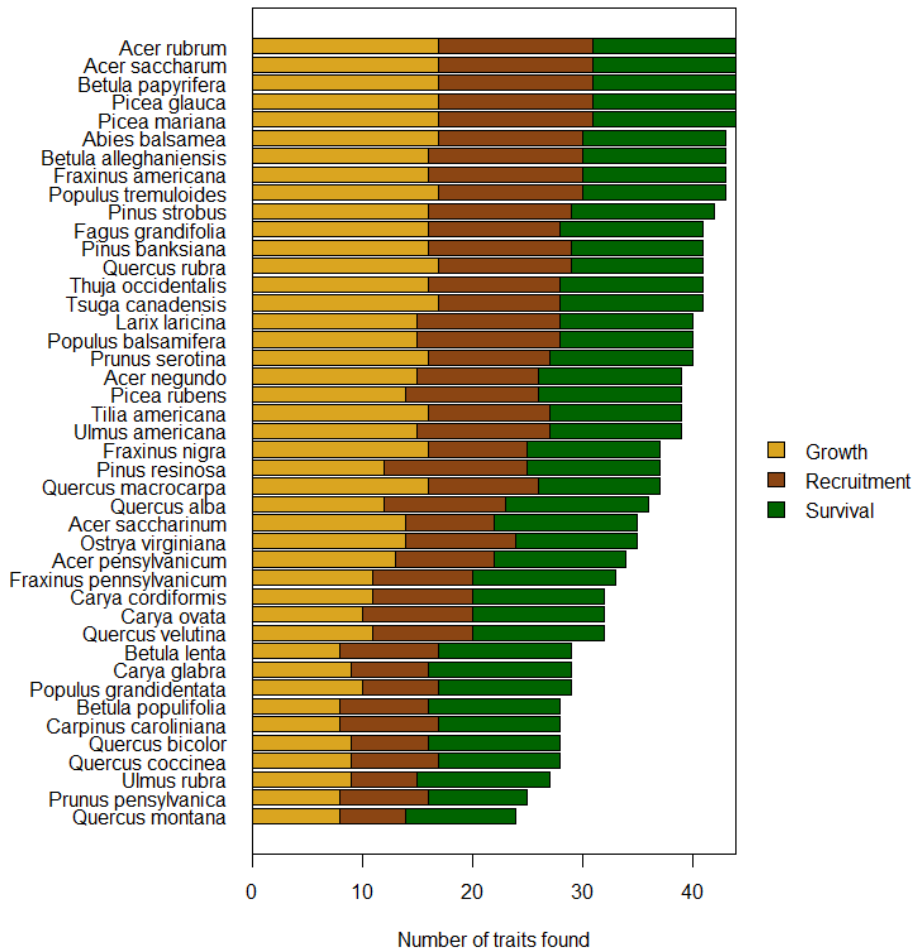
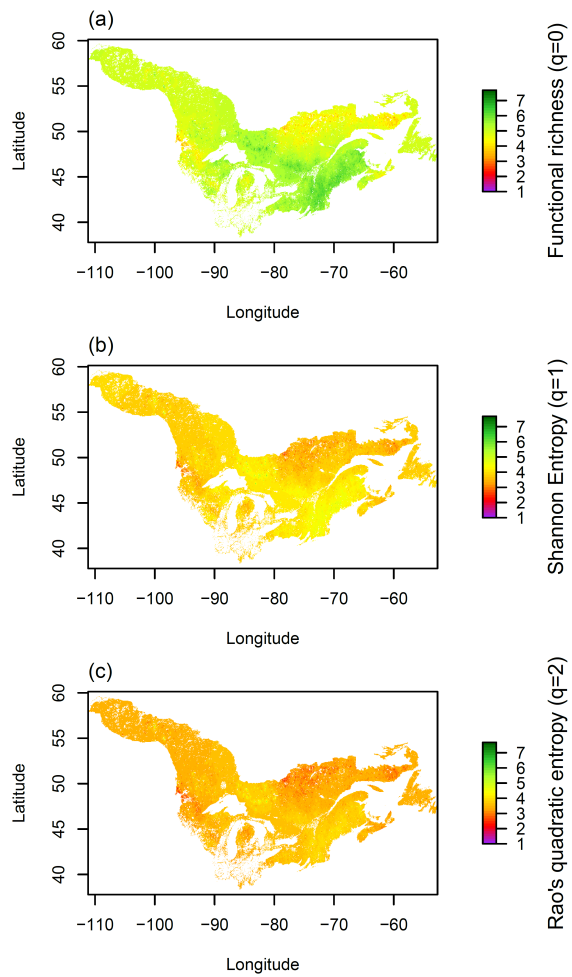


Fig. 2: Number of traits found per species. Traits relevant for growth, regeneration and survival are distinguished by color. The maximum number of traits is 44 for each of the 43 tree species (i.e., 1892 traits in total). The total number of traits found was 1570, i.e., 83.0% (see Appendix S1 for details).

1064



1065

1066 Fig. 3: Observed functional diversity distribution across northeastern North America. Scales
1067 denote the effective number of tree species with different functional traits weighted by different q
1068 factors. Distributions are based on 44 traits of 43 species on 48,426 PSPs. We used inverse distance
1069 weighting to derive wall-to-wall estimates of the trait distribution. Three different q factors were

1070 considered to derive Hill numbers to illustrate the effect of species abundance on FD. (a)
1071 Functional richness, (b) exponential Shannon entropy, and (c) Rao's quadratic entropy.
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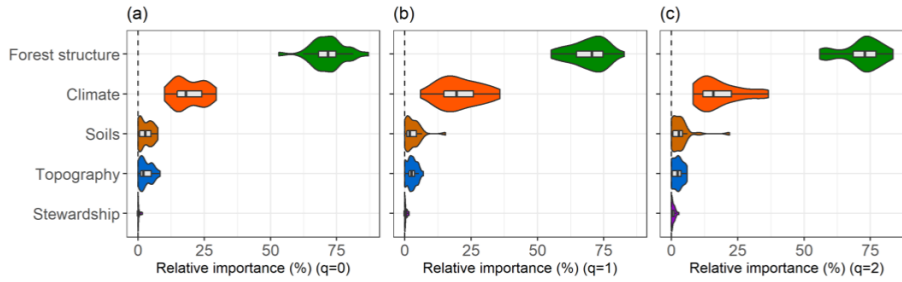
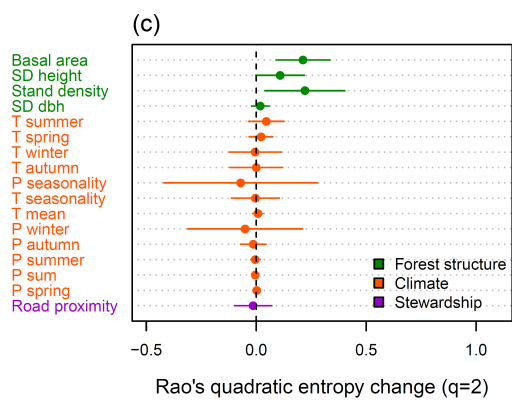
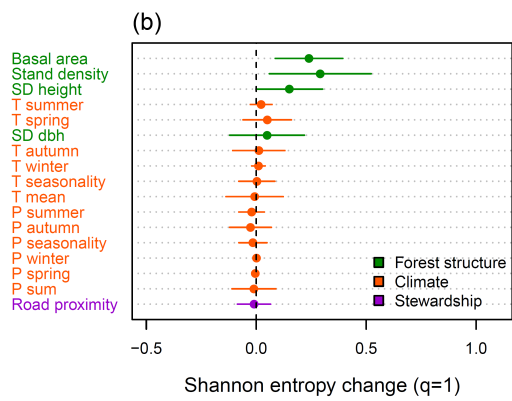
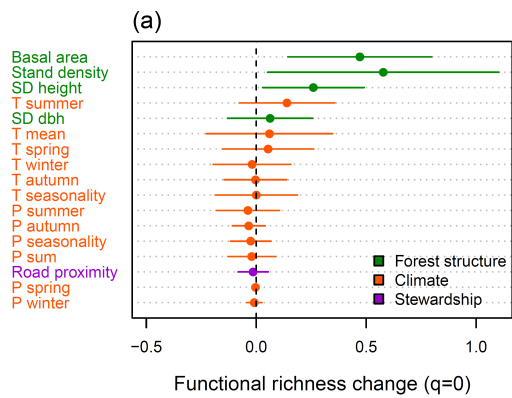


Fig. 4: Relative importance of forest structure, climate, soils, topography, and stewardship for functional diversity. Violins show the density distribution of variable importance summarized for each category (see Table 3 for individual variable importance). A boxplot presenting the median (vertical line), interquartile ranges (grey box), and ranges (i.e., whiskers showing the $1.5 \times$ 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 ($q=2$).



1082 Fig. 5: Sensitivity analysis of functional diversity driver effects. Presented are mean effects and
1083 95% confidence intervals. The three panels weight the species abundance effect on the drivers of
1084 functional diversity differently: (a) functional richness, (b) exponential Shannon entropy, and (c)
1085 Rao's quadratic entropy. Changes in functional diversity were predicted by increasing each
1086 continuous variable by one standard deviation individually while retaining the original values of
1087 the PSPs for all other variables. Predictions for each panel were aggregated from 30 models (i.e.,
1088 ten BRT, RF, and GAMs) respectively. Effects of explanatory variables are ordered according to
1089 their relative importance (see Table 3 and Fig. S2).

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1092 **Supplementary material**

1093 Appendix S1: Individual traits for each species and references (see additional Excel spreadsheet
1094 provided).

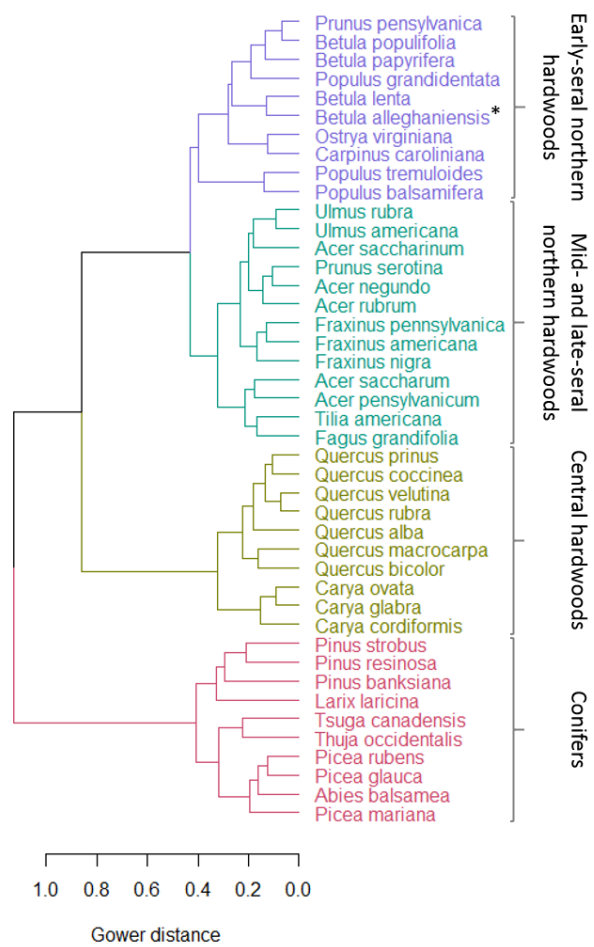
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Table S1: Standardized path coefficients among FD, forest structure and the four most important climatic drivers of FD (see Fig 5 and Fig. S1). Coefficients are based on structural equation modeling (SEM) of 48,426 inventory plots. q=0: Functional 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

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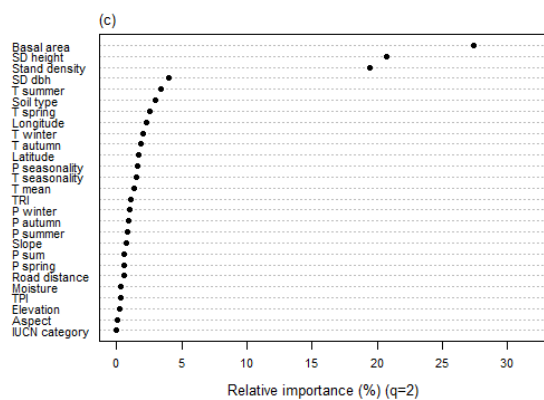
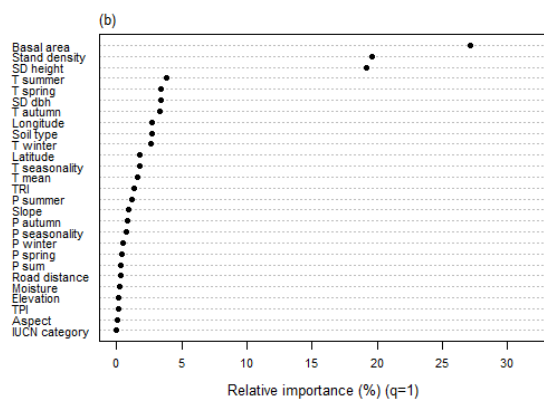
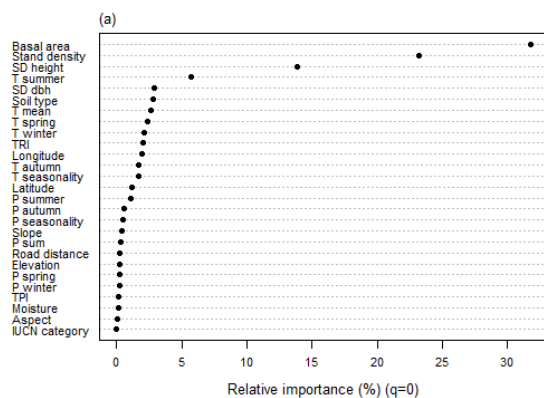


1101

1102 Fig. S1: Agglomerative Hierarchical Clustering (AHC) with a Ward linkage method of the
1103 functional trait similarity of 43 northeastern North American tree species. We identified four
1104 distinct functional groups for the 43 species investigated. We categorized these groups into: (i)
1105 early-seral northern hardwoods; (ii) mid- and late-seral northern hardwoods; (iii) central
1106 hardwoods; and (iv) conifers. This categorization applied to all species of each cluster, except
1107 *Betula alleghaniensis* which has many traits in common with early-seral northern hardwoods, but
1108 is considered a mid-late seral species. While both northern hardwood clusters were functionally
1109 most similar, the functional distance increased markedly to central hardwoods, and conifers were
1110 furthest apart from all of the other clusters. A subsequent PERMANOVA supported the AHC
1111 results. The test revealed that differences in the average trait composition of the groups were highly
1112 significant ($p < 0.001$).

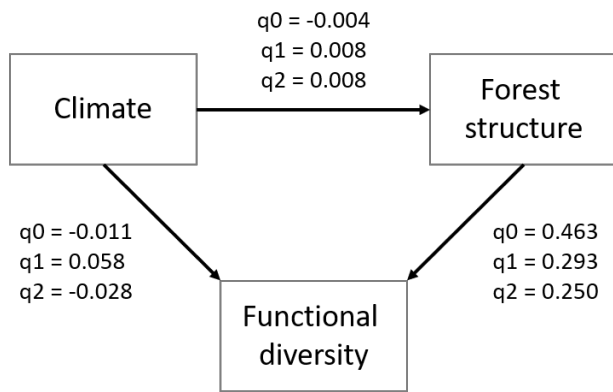
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1116 Fig. S2: Relative variable importance for functional diversity. The three panels weight the species
1117 abundance effect on the drivers of functional diversity differently: (a) Functional richness ($q=0$),
1118 (b) exponential Shannon entropy ($q=1$), and (c) Rao's quadratic entropy ($q=2$). Each panel presents
1119 the average relative variable importance across 30 models, i.e., ten BRT, RF, and GAMs,
1120 respectively.

1121



1122

1123 Fig. S3: Structural equation model (SEM) analyzing the indirect effect of climate on FD mediated
 1124 via forest structure. Presented are the average standardized path coefficients among the four most
 1125 important climatic drivers of FD (see Fig. S1), forest structure, and FD based on 48,426 inventory
 1126 plots. q=0: Functional richness; q=1: exponential Shannon entropy; q=2 Rao's quadratic entropy

1127