

# Environment and past land use together predict functional diversity in a temperate forest

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**Abstract.** Environment and human land use both shape forest composition. Abiotic conditions sift tree species from a regional pool via functional traits that influence species' suitability to the local environment. In addition, human land use can modify species distributions and change functional diversity of forests. However, it is unclear how environment and land use simultaneously shape functional diversity of tree communities. Land-use legacies are especially prominent in temperate forest landscapes that have been extensively modified by humans in the last few centuries. Across a 900-ha temperate deciduous forest in the northeastern United States, comprising a mosaic of different-aged stands due to past human land use, we used four key functional traits—maximum height, rooting depth, wood density, and seed mass—to examine how multiple environmental and land-use variables influenced species distributions and functional diversity. We sampled ~40,000 trees >8 cm DBH within 485 plots totaling 137 ha. Species within plots were more functionally similar than expected by chance when we estimated functional diversity using all traits together (multi-trait), and to a lesser degree, with each trait separately. Multi-trait functional diversity was most strongly correlated with distance from the perennial stream, elevation, slope, and forest age. Environmental and land-use predictors varied in their correlation with functional diversities of the four individual traits. Landscape-wide change in abundances of individual species also correlated with both environment and land-use variables, but magnitudes of trait–environment interactions were generally stronger than trait interactions with land use. These findings can be applied for restoration and assisted regeneration of human-modified temperate forests by using traits to predict which tree species would establish well in relation to land-use history, topography, and soil conditions.

**Key words:** community assembly; environment; functional diversity; land-use history; species distributions; temperate forest; traits.

## INTRODUCTION

Environmental conditions shape the composition and diversity of plant communities by regulating the establishment, growth, and survival of different plant species (Lebrija-Trejos et al. 2010, HilleRisLambers et al. 2012, Adler et al. 2013). Growth and survival depend on the ability of individuals to withstand biotic and abiotic stresses and to respond to variations in resource availability. Dealing with such stresses involve physiological and ecological trade-offs, resulting in species' life-history strategies (Uriarte et al. 2012, Philipson et al. 2014, Zhu et al. 2018), represented by functional traits that mediate performance and fitness at a site. Traits thus shape patterns of species occurrence and abundance (Westoby and Wright 2006, Wright et al. 2010, Adler et al. 2014), which in turn can influence ecosystem properties such as carbon storage and nutrient cycling (Díaz et al. 2007). Therefore, quantifying the relationships between functional traits and species distributions along environmental gradients can provide insights into mechanisms of community assembly

and ecosystem function and help predict responses of plant communities to natural or anthropogenic environmental change (Suding et al. 2008, Cornwell and Ackerly 2009, Weiher et al. 2011).

In northern temperate forests, topography influences tree species distributions by creating contrasting mesic (cool, moist) and xeric (warm, dry) conditions on adjacent slopes through differences in irradiance, temperature, and moisture availability (Whittaker 1960, Boerner 2006, Copeland and Harrison 2014, Murphy et al. 2015). Typically, higher irradiance on western and southern aspects makes soils drier and less productive compared with the cool and moist northeast facing slopes (McCune and Keon 2002). In addition, steeper slopes and ridge tops are usually drier than valleys, whereas areas close to large, perennial streams tend to be wetter and have higher moisture available for plants. Soil depth varies with topography, although soil characteristics can change independent of topography even over small to medium spatial scales (Farley and Fitter 1999). These local environmental gradients directly influence species composition and habitat associations of temperate trees (Whittaker 1960, Whittaker et al. 1973, Murphy et al. 2015), but the degree to which they shape local variation in diversity of functional traits (henceforth functional diversity) in temperate forests is less known.

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In addition to environmental factors, historic land use by humans, such as logging and agriculture, also impact present-day forest communities and their functional diversity (Thompson et al. 2002, Foster et al. 2003, Chazdon et al. 2010, Comita et al. 2010, Feng et al. 2014). Human activities can modify species' distributions and relative abundances by altering environmental conditions for plant growth (Weiher et al. 2011, Feng et al. 2014) or by altering the species pool that provides seed sources for recolonization (McEuen and Curran 2004). Consequently, functional diversity can vary with past human activities and proximity to current human land uses (Lohbeck et al. 2012, Bhaskar et al. 2014, Lasky et al. 2014, Wilfahrt et al. 2014). Although most extant temperate forests bear the legacy of past human activities, relatively few studies have assessed how human land-use legacies shape tree communities via functional traits (Verheyen et al. 2003, Bergès et al. 2017). Extensive reforestation advice is readily available (Davis et al. 2012), yet the degree to which these recommendations accord with natural forest regenerated on different sites is not always clear. Here we expressly test these perspectives.

Trait-mediated filtering through either abiotic constraints or competitive hierarchies (Funk et al. 2017) is typically evidenced by lower trait diversity relative to the null distribution for a given species richness (Cornwell and Ackerly 2009, Kraft and Ackerly 2010, Siefert et al. 2013). Examining how key traits, individually and together, respond to the effects of environmental gradients and past land uses can offer insights into species occurrences. Individual traits would reveal the relative strength of environmental filtering on different functions. The simultaneous response of multiple traits shows how species respond to the environment when taking into account multiple functions related to overall life-history strategy (Butterfield and Suding 2013). Thus, spatial variation in functional diversity of individual traits could reveal their relative importance for species distributions and indicate whether opposing assembly mechanisms are acting across a heterogeneous landscape (Swenson and Enquist 2009).

For terrestrial woody plants, maximum height, seed mass, and wood density represent key dimensions of trade-offs in life-history strategies (Adler et al. 2014, Díaz et al. 2015). Maximum height represents the adult light niche (Westoby and Wright 2006). Seed mass reflects the ability of plants to disperse widely vs. tolerate stress during seedling establishment (Moles and Westoby 2004, Muller-Landau 2010). Wood density relates to shade-tolerance and the ability to resist mechanical damage, drought-induced embolism, and pathogens (Chave et al. 2009, Díaz et al. 2015), and species with higher wood density tend to have slower growth but higher survival (Visser et al. 2016). The minimum required soil depth for sapling survival for different species can regulate species distributions with topography-driven variation in soil depth and nutrient distributions.

To assess the influence of both environmental conditions and human land use on functional diversity, we used forest inventory data for nearly 40,000 trees collected across 900 ha of successional temperate mixed-mesophytic forest in the northeastern United States. We hypothesized that topographic effects in temperate forests should result in local communities that were functionally more similar than

expected by chance (Adler et al. 2013, Siefert et al. 2013). Furthermore, we expected lower functional diversity (multi-trait and individual trait) in areas of abiotic stress such as valleys and northern aspects with low irradiance, and drier areas like steeper slopes, higher elevations, and areas farther from perennial streams. Moreover, we expected areas of more recent (<80 yr) human land use to have lower functional diversity compared to areas with low or no human-use in recent decades (Thompson et al. 2002). Alternatively, functional diversity might decrease with successional age if colonization becomes infrequent or a limited set of traits are favored as canopy closure constrains light availability.

For individual traits, we expected species' relative abundances to correlate with environmental and land-use gradients (Murphy et al. 2015). Specifically, we expected higher abundances of denser-wooded, larger-seeded species in valleys and north-facing aspects where low irradiance would favor slower-growing species. We expected higher abundances of short-statured species in drier areas such as higher elevations, steeper slopes, and southern and western aspects. Species with low minimum rooting depth will be more abundant in higher elevations and steeper slopes where soil depth usually decreases and also do better in drier areas by meeting their resource needs from shallower soil layers. In response to land-use change, we expected higher abundances of larger-seeded, denser-wooded, and taller species in older forest and with less intensive land use. Degraded soils in younger forests could favor species that meet water and nutrient requirements at shallower soil depths.

## MATERIALS AND METHODS

### *Study site*

We conducted this study at the 900-ha Powdermill Nature Reserve (PNR), a temperate deciduous forest of mixed-mesophytic vegetation in the Allegheny plateau at the base of the Appalachian Mountains in southwestern Pennsylvania, USA (Westmoreland County; 40°09' S, 79°16' W). The PNR tree community is dominated by maple (*Acer* spp.) and other mesophytic species like tulip poplar (*Liriodendron tulipifera*), oaks (*Quercus* spp.), and hickories (*Carya* spp.). Annual precipitation is ~1,100 mm and average temperatures range from -20°C in January to 33°C in July (Murphy et al. 2015). Elevation and slope vary from 392–647 m and 0–24 degrees, respectively. The region was logged in the 19th century and used for agriculture in many parts until the mid-20th century. Northern parts of the reserve were surface mined for coal during 1930s and 1940s. Anthropogenic disturbances decreased after PNR was designated a nature reserve by the Carnegie Museum of Natural History in 1956 and forests have since regrown. PNR today comprises successional forests of different ages, as well as some fields and built-up land. Developed areas lie west of the reserve and the east adjoins state forest (Murphy et al. 2015).

### *Vegetation sampling*

Vegetation sampling was undertaken from 2006 to 2008; see Murphy et al. (2015) for details. Briefly, the 900-ha area was gridded into 647 sampling plots of 120 × 120 m each.

In each plot, we established nine circular subplots of radius 10 m (314 m<sup>2</sup> each) for vegetation surveys. One subplot was located at the center of the block and the other eight subplots were systematically placed adjacent to it. Trained field staff identified and measured all live and dead stems  $\geq 8$  cm diameter at breast height (DBH). Overall, nearly 40,000 individual trees were recorded over 183 ha. After discarding plots with no forest cover, we had 485 plots in the final analysis (137 ha).

#### Environmental variables

We described environmental gradients using topographic variables, depth to water table, soil properties, and distance to the main stream, Powdermill Run. GIS-derived topographic variables included elevation (m), slope (degree), aspect (NW, NE, SW, SE, E, W), and convexity (each focal plot's elevation minus the mean elevation of surrounding eight plots, i.e., larger values mean greater convexity [m]). For soils, we compiled data on soil bulk density (mg/m<sup>3</sup>), pH, cation exchange capacity (CEC, milliequivalents/100 g), available water capacity (AWC, %), and percentages of sand, silt, and clay from a publicly available database (Natural Resources Conservation Service 2013). We reduced dimensionality of soil variables using Principal Components Analysis followed by varimax rotation to maximize component loadings on individual axes. For further analyses, we used the first three axes, which explained 85% of variation in the soils data (Appendix S1: Table S1). Soil PCA1 represented texture and water availability: positive associations for silt, clay, and available water capacity and negative associations with sand and bulk density (Appendix S1: Fig. S1a). PCA2 loaded positively for soil oxygen and negatively for silt and CEC, suggesting differences in soil fertility; PCA3 loaded positively for bulk density and negatively for CEC and pH (Appendix S1: Table S1, Fig. S1b).

#### Forest age and land-use variables

We estimated land-use history and stand age using aerial images for 1939, 1957, 1967, 1993, and 2006. For each image, we used the standard national land-cover database classification system (Anderson et al. 1976) to assign 10 m radius subplots to forest, shrubland, planted/cultivated, developed, or barren (indicating strip mining). We assigned land-use history as follows: "forest" (had forest cover in all images, i.e., forested since at least 1939), "developed" (had built-up area in any image), "shrub" (classified as shrubland in any image), "mined" (barren in any image), "field" (cultivated in any image). The ~3% of subplots that had multiple historical land uses were assigned the most recent land use before forest regrowth occurred. We estimated stand age by subtracting from 2006 the most recent year that plots were classified as a non-forest, which may underestimate stand age as the exact date of transition to forest was not observed. We fixed stand age at 80+ yr for plots that were forested since 1939. Using this scheme, stand age ranged from 13 to 80+ yr (Appendix S1: Table S2). Only three plots had forests aged <13 yr (Appendix S1: Table S2), so we omitted these from our analysis. About 3% of subplots did not have the same age or land use in all nine plots, and the

most frequent (majority) category was used. From this classification, we calculated the proportion of forested subplots out of nine subplots per 120 × 120 m plot (hereafter forest proportion). Finally, we used GIS to calculate distances to nearest edge (boundary between forest and non-forest) for each of nine subplots and used median values for the plot as another proxy for human-impacts.

#### Functional traits

We used trait databases to get species-level values for seed mass (g), maximum height (m), wood density (g/cm<sup>3</sup>), and minimum soil depth required for good growth (cm; henceforth, minimum rooting depth; database *available online*).<sup>7</sup> Traits were moderately and significantly correlated with each other (Appendix S1: Table S3). Data were unavailable for three species in our study, so we assigned them mean trait values of congeneric species. We excluded gymnosperms and one unidentified *Rubus* sp., one *Robinia* sp., two *Crataegus* sp., two *Malus* sp., and *Hamamelis virginiana* because, being the only representatives of their genus, we could not compute mean trait values from congeneric species. In total, we compiled trait data for 61 of 68 species. The seven species without trait data occurred at low densities of fewer than five individuals per plot, and therefore their omission was unlikely to influence results. We excluded one plot with 17 *Crataegus* individuals (in an agricultural area). Further, we excluded conifers from our analysis because traits in conifers, particularly wood density, cannot be compared directly to angiosperms given the different water transport systems (tracheids vs. vessels). There were only four conifer individuals in the data. For comparability, we standardized all trait values by their mean and standard deviation (Mouchet et al. 2010). We log-transformed seed mass values before standardization.

#### Statistical analysis

**Functional diversity analysis using null models.**—We calculated two abundance-weighted indices of functional diversity using the picante package in R (Kembel et al. 2010): mean pairwise distance (MPW) and mean nearest neighbor distance (MNN; Swenson 2013) and standardized their effect sizes as  $SES = (\text{Observed} - \text{Mean}_{\text{random}}) / \text{SD}_{\text{random}}$ .  $\text{Mean}_{\text{random}}$  and  $\text{SD}_{\text{random}}$  are the mean and standard deviation from 999 null models generated by shuffling species in the trait dendrogram but maintaining observed species richness and relative abundances within plots. We refer to SES for MPW and MNN of traits as SESPW and SESNN where more negative (smaller) SES values suggest greater functional similarity of species within a plot. To determine whether observed values were significantly different from null expectations at the landscape-level, we conducted a sign test to examine whether the median of SES values for 485 plots was significantly less than zero.

**Environment, land use, and functional diversity.**—To assess whether functional diversity (multi-trait and for individual traits) increased or decreased in relation to different

<sup>7</sup> <https://plants.usda.gov/java/characteristics>

environmental and land-use variables within plots, we used generalized least squares (GLS; function `gls()`, package `nlme`; Pinheiro et al. 2007). Correlation between pairs of topographic variables was generally low (Appendix S1: Table S4), so we used them as separate predictors. The land-use variables forest proportion, dominant land use and dominant forest age were correlated, so we ran three separate models to test which of these three land-use variables best explained functional diversity patterns: all three models included all environmental variables. We standardized all continuous predictors by subtracting the mean and dividing by two standard deviations. Because land use can be correlated with topographic location, we tested for relationships between all land use and environmental variables. Only elevation was significantly correlated with land uses (Appendix S1: Table S5). Hence, we assessed whether potential multicollinearity affected model parameters by quantifying the variance inflation factor (VIF) per variable for all models. All variables had  $VIF < 3$  and were hence retained. To assess which land-use variable best explained variation in multi-trait and individual trait diversities, for each diversity index, we used AIC to compare models with forest proportion, dominant land use, and dominant forest age (Table 1). Additionally, areas closer to one another are likely to have similar functional diversity, land-use history, and/or forest age, so we modeled spatial autocorrelation as a function of spatial distance between sampling plots. These models had lower AIC than models without spatial autocorrelation. Models using linear autocorrelation functions consistently had lower AIC than models using Gaussian or exponential functions. Also, to account for the unbalanced study design, i.e., the majority of plots being “forest,” we modeled the variance structure as a function of forest age and land-use type.

*Trait influence on species relative abundances.*—To assess how traits explain species relative abundances along environmental and land-use gradients, we used a recently developed approach, CATS regression (community assembly via trait selection; Warton et al. 2015), which models species’ abundances across plots as a function of trait–environment interactions using a generalized linear mixed effect model (GLMM) with negative binomial errors (Eq. 1). Here, site

( $s_j$ ) as a random intercept,  $\ln(q_i)$  is a species-wise offset,  $\beta_0$  is the intercept,  $\beta_1$ ,  $\beta_2$ , and  $\beta_3$  are coefficient vectors for the effects of traits ( $x$ ), environment ( $z$ ), and trait–environment interactions per species  $i$  and site  $j$ .

$$\ln(\mu_{ij}) = s_j + \ln(q_i) + \beta_0 + x_i' \beta_1 + z_j' \beta_2 + (x_i \otimes z_j)' \beta_3 \quad (1)$$

This is equivalent to a log-linear model that estimates conditional effects of trait–environment interactions; the effect size is interpreted as how strongly a trait governs differences among species in their abundances along an environmental gradient (Warton et al. 2015). Since all predictors are standardized, the coefficient sizes of trait–environment interactions provide a measure of a trait’s importance, representing the amount by which one standard deviation change in the trait changes the slope between abundance and a given environmental or land-use variable. Due to collinearity among forest proportion, dominant land use, and dominant forest age, we assessed the interaction of traits and these three land-use variables in separate models; each model contained all environmental variables. We used a LASSO penalty to shrink non-significant parameters to zero (Warton et al. 2015).

## RESULTS

### Functional diversity and null models

Standardized effect size for multi-trait pairwise distances (SESPW) was significantly lower than null expectations in 64% of the plots, suggesting that co-occurring species belonged to similar functional groups (Fig. 1). No SESPW value was significantly higher than null. Multi-trait SESNN (nearest-neighbor distances) also tended to be lower than expected, but only 7% plots were statistically significant. For individual traits, percentage of significant plots for SESPW and SESNN varied among traits (Appendix S1: Table S6), with minimum rooting depth having the highest percentages (SESPW: 48%, SESNN: 25%), followed by seed mass (28%, 5%), wood density (16%, 2%), and maximum height (11%, 3%). Sign tests indicated that landscape trends for SESPW and SESNN values were significantly negative for all traits except SESNN of maximum height (Fig. 1).

### Environment, land use, and functional diversity

Both measures of functional diversity, SESPW and SESNN, showed qualitatively similar relationships with environment and land use (Table 2; Appendix S1: Table S7). Visual inspection of semivariograms showed no spatial autocorrelation in model residuals. We focus our discussion on SESPW since it is more appropriate to evaluate environment and land-use effects at the relatively large grain of  $120 \times 120$  m examined here and is comparable to other studies (Liu et al. 2013, Muscarella et al. 2016). SESNN is more relevant when examining patterns at smaller spatial scales where limiting similarity is likely to play out. Henceforth, functional diversity refers to SESPW. Multi-trait diversity was negatively correlated with distance to Powdermill Run (hereafter perennial stream) and elevation and positively correlated with slope (Fig. 2a). Functional diversity

TABLE 1. Akaike’s information criterion (AIC) values for models testing influence of environmental and land-use variables on landscape-scale variation in functional diversity.

Functional diversity	Models		
	Env + forest prop	Env + forest age	Env + land use
All traits	827.5	<b>826.2</b>	833.7
Maximum height	<b>873.7</b>	873.6	873.6
Rooting depth	<b>921.3</b>	923.3	926.4
Seed mass	888.7	891.7	<b>884.1</b>
Wood density	260.1	<b>254.6</b>	268.9

*Notes:* All models contained all environmental variables (Env), distance to edge, and distance to road. Relationships of functional diversity with forest proportion (prop), forest age, and historical land use were tested in separate models and compared using the Akaike information criterion (AIC). Boldface type indicates the model with the lowest AIC value in each row.



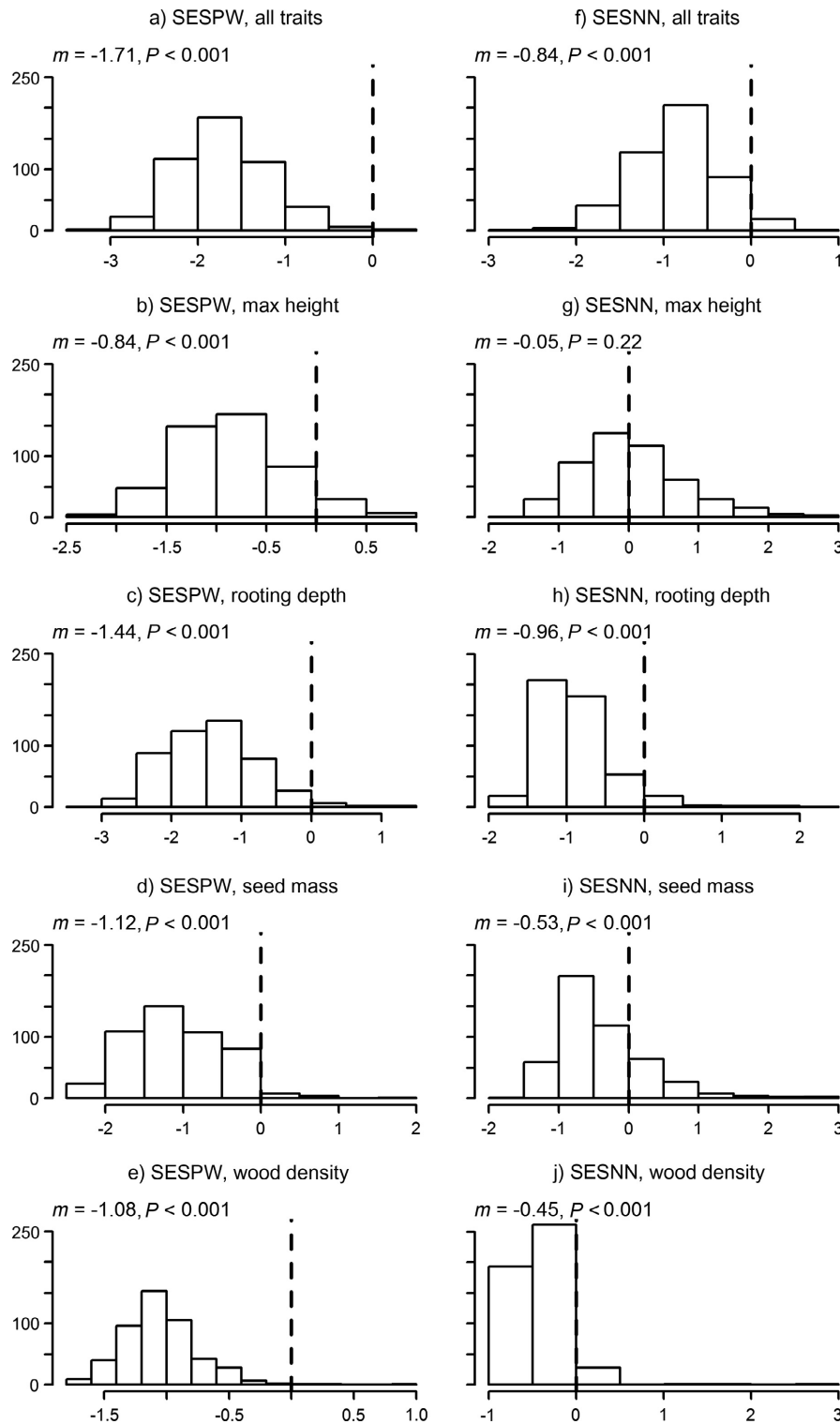


FIG. 1. From 485 plots (137 ha) in a 900-ha temperate mixed-mesophytic forest, distribution of standardized effect sizes of (a–e) pairwise distances (SESPW) and (f–j) nearest-neighbor distances (SESNN). SES were calculated by subtracting observed values of pairwise distances and nearest neighbor distances for all and individual traits from mean expected functional diversity and its standard deviation estimated from null values generated for 999 random communities. Dashed line indicates no difference from expected functional diversity of null models. Also provided are results of sign-median tests to assess landscape-wide patterns in SESPW and SESNN (index “*m*” indicates estimated median values of functional diversity indices).

of maximum height decreased farther from perennial stream and with convexity (Fig. 2c). Diversity of minimum rooting depth was best correlated with elevation and aspect,

decreasing with elevation and being higher on northeast aspects. Seed mass diversity increased with elevation and on west and southwest aspects (Fig. 2g). For wood density,

TABLE 2. Coefficient estimates from generalized least squares models to examine correlation of functional diversity with environment and land use.

Parameter	All traits	Maximum height	Rooting depth	Seed mass	Wood density
Intercept	−1.70 (0.11)	−0.77 (0.08)	−1.39 (0.12)	−1.17 (0.09)	−0.94 (0.07)
Environmental predictors					
Distance to stream	<b>−0.07 (0.03)</b>	<b>−0.06 (0.03)</b>	<b>−0.13 (0.03)</b>	0.05 (0.03)	−0.01 (0.02)
Elevation	<b>−0.07 (0.03)</b>	0.03 (0.03)	<b>−0.22 (0.03)</b>	<b>0.15 (0.03)</b>	0.00 (0.02)
Slope	<b>0.09 (0.03)</b>	0.02 (0.03)	<b>0.12 (0.03)</b>	−0.05 (0.03)	<b>0.09 (0.02)</b>
Convexity	0.02 (0.03)	<b>−0.06 (0.03)</b>	<b>0.12 (0.03)</b>	0.03 (0.03)	−0.02 (0.02)
Depth to water table	0.03 (0.03)	−0.05 (0.03)	<b>0.15 (0.04)</b>	−0.02 (0.04)	0.01 (0.02)
AspectNE	0.00 (0.10)	−0.14 (0.10)	<b>0.24 (0.11)</b>	−0.05 (0.10)	0.05 (0.05)
AspectNW	0.09 (0.09)	−0.08 (0.10)	0.19 (0.10)	0.11 (0.10)	0.07 (0.05)
AspectSE	−0.10 (0.18)	−0.29 (0.19)	0.07 (0.20)	0.10 (0.19)	0.05 (0.10)
AspectSW	0.03 (0.12)	−0.01 (0.12)	−0.02 (0.13)	<b>0.29 (0.12)</b>	−0.03 (0.06)
AspectW	0.02 (0.09)	−0.06 (0.10)	0.04 (0.11)	<b>0.21 (0.10)</b>	0.02 (0.05)
Soil.PCA1	0.01 (0.01)	−0.01 (0.02)	0.02 (0.02)	0.02 (0.02)	0.00 (0.01)
Soil.PCA2	0.02 (0.02)	−0.03 (0.03)	<b>0.07 (0.02)</b>	−0.03 (0.03)	0.01 (0.01)
Soil.PCA3	0.00 (0.03)	−0.04 (0.03)	0.00 (0.02)	−0.01 (0.03)	<b>−0.04 (0.01)</b>
Land-use predictors					
Distance to edge	0.04 (0.03)	−0.03 (0.03)	0.00 (0.04)	<b>0.09 (0.03)</b>	0.02 (0.02)
Distance to road	0.00 (0.03)	−0.01 (0.03)	0.01 (0.04)	0.00 (0.03)	0.03 (0.02)
Forest proportion	—	—	<b>−0.21 (0.09)</b>	—	—
Historical land use: field	—	<b>0.19 (0.10)</b>	—	<b>−0.42 (0.10)</b>	—
Historical land use: shrub	—	<b>−0.38 (0.18)</b>	—	0.11 (0.19)	—
Historical land use: developed	—	0.31 (0.21)	—	−0.14 (0.21)	—
Historical land use: mined	—	−0.09 (0.18)	—	0.19 (0.18)	—
Forest age: 49	<b>−0.38 (0.20)</b>	—	—	—	<b>−0.21 (0.11)</b>
Forest age: 67	<b>−0.34 (0.14)</b>	—	—	—	<b>−0.28 (0.08)</b>
Forest age: 80+	<b>−0.27 (0.10)</b>	—	—	—	<b>−0.21 (0.06)</b>

Notes: Separate models were run for all traits and individual traits. Coefficient estimates (with SE in parentheses) are presented from the top-ranked model (lowest AIC) among the separate models used to estimate effects of correlated land-use variables: forest proportion, forest age, and historical land use. Statistically significant parameters are shown in boldface type ( $P < 0.05$ ). Cells with dashes indicate the variables excluded from the model in the corresponding column.

steeper slopes had higher diversity and dense soils supported lower diversity (Fig. 2i).

Land-use variables differed as to which trait diversity they predicted best, but in general effect sizes of land-use variables were greater than environmental variables (Table 2). Multi-trait diversity was significantly correlated with forest age, being lower in forests older than 39 yr. Maximum height diversity decreased in areas historically shrubland but increased in previously cultivated lands. Diversity in minimum rooting depth decreased with increasing forest proportion within plots. As expected, functional diversity of seed mass increased farther from forest edges (Fig. 2d) and historically farmed areas had markedly lower seed mass diversity (Table 2). Forest age was the best predictor of diversity in wood density, which decreased in older forest (Fig. 2e).

#### *Traits and species' relative abundances*

As expected, traits varied in their magnitude and direction of interactions with environmental variables (Fig. 3; Appendix S1: Table S8; all non-significant interactions are shrunk to zero using the LASSO penalty). Taller species were less abundant with greater convexity (i.e., flatter areas) and more abundant on steeper slopes. As expected, abundance of deeper-rooted species increased in plots with greater depth to water table and in drier soils and decreased at higher elevations. Smaller-seeded species were less abundant in drier soils, areas farther from perennial

stream, where the water table was deeper, on higher elevations and on steeper slopes. Further, northern aspects and low-lying (less convex/valley) plots, receiving less irradiance, had higher abundances of smaller-seeded species, whereas abundance of larger-seeded species increased on west and southwest aspects (Fig. 3). Denser-wooded species were more abundant in more convex areas, farther from the stream, with deeper water table, and in denser soils (Soil PCA3) but less abundant on higher elevations and steeper slopes.

Traits also varied in their interactions with land-use variables (Fig. 3; Appendix S1: Table S8). Species' distributions with respect to maximum height only weakly correlated with land use (Fig. 3). Abundance of shallow-rooted species increased in plots with more forest, older forest, and forest farther from roads and edges. Plots historically farmed (field) had higher abundances of deep-rooted species. Larger-seeded species decreased in areas once farmed (field) and in younger forest, and strongly increased with greater forest proportion and in forests aged 80+ yr (Fig. 3). Species with lower wood density increased in plots with more forest, older forest, and with historical land uses "developed" and "forest." Abundance of denser-wooded species increased in plots that were mined.

#### DISCUSSION

Across a temperate forest in the northeastern United States, we found that functional diversity of tree communities varied

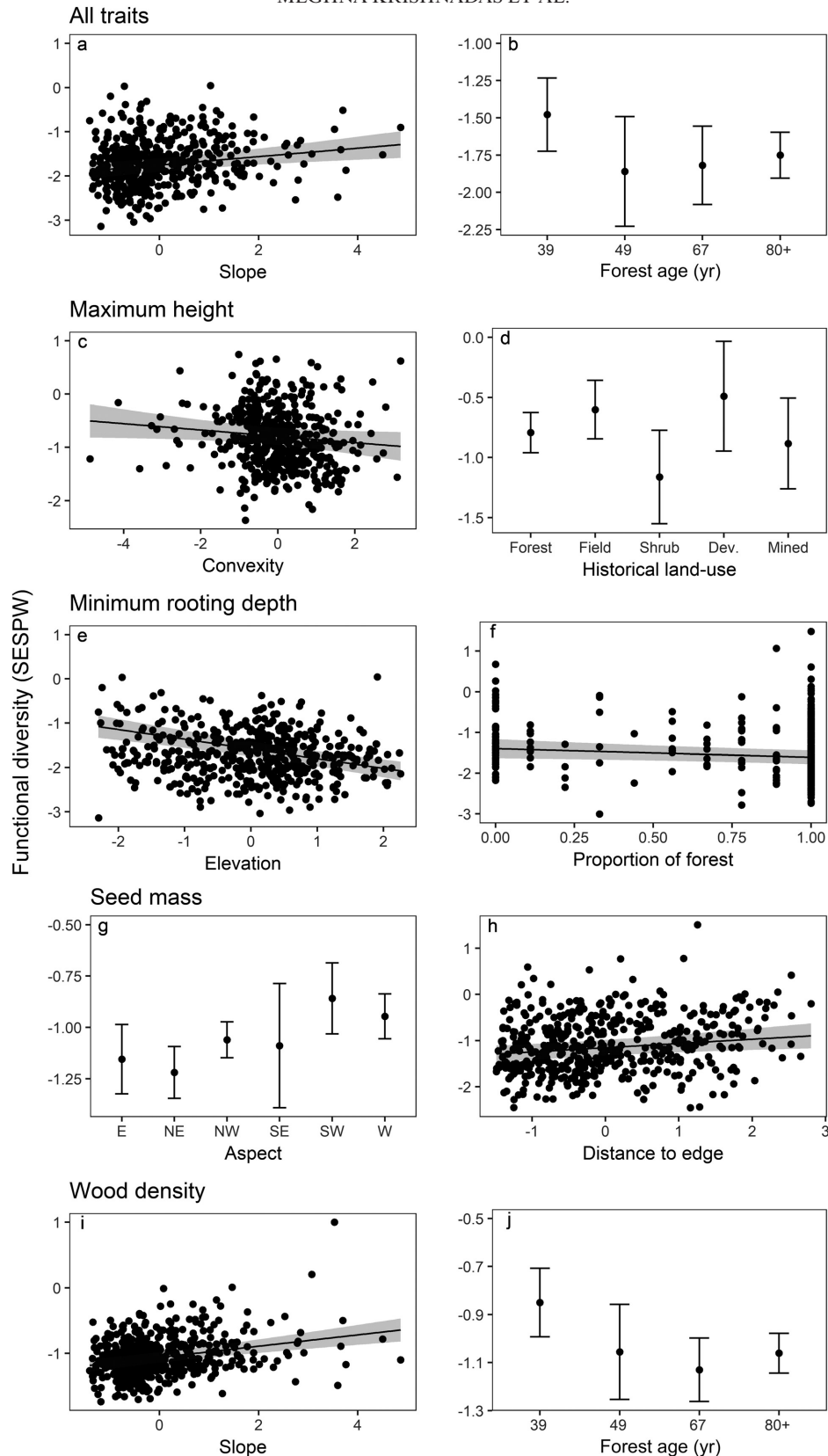


FIG. 2. Correlation of functional diversity (standardized effect size of pairwise distances, SESPW) with top (i.e., largest magnitude of effect) environmental and land-use variables across 485 plots, estimated using generalized least squares. Slope was measured in degrees; convexity, elevation and distance to forest edge was measured in meters. Correlations are shown between top two predictors for SESPW of (a, b) all traits (c, d) maximum height (e, f) minimum rooting depth (g, h) seed mass and (i, j) wood density. Shaded bands and error bars represent 95% confidence intervals. Each point represents a  $120 \times 120$  m block within which trees were sampled. Smaller values correspond with lower functional diversity after controlling for species richness. Dev. stands for developed areas.

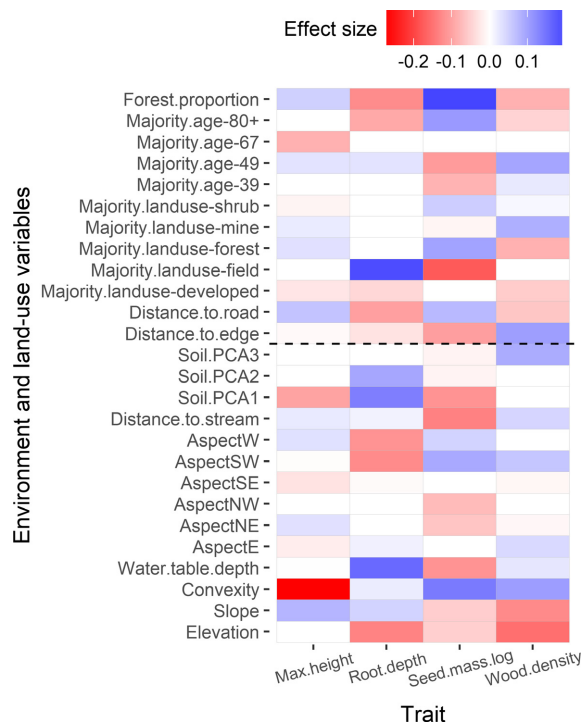


FIG. 3. Coefficients of trait interactions with environmental and disturbance variables in influencing species relative abundances across the landscape, estimated using community assembly via trait selection (CATS) regression with LASSO penalty. Due to collinearities, between forest age, forest proportion, and historical land use, we estimated their effects in separate models and the effect sizes shown for trait-environment interactions are from the top model based on log likelihood (environment + historical land use). With the LASSO penalty, non-significant effects have been shrunk to zero. Dashed line separates environmental and land-use predictors.

with both land use and environmental gradients. Co-occurring species converged in functional strategies, suggesting that habitat filtering and/or competitive exclusion of species contributed to community assembly. For individual traits, variation in functional diversity correlated with both environment and land use, and predictors differed in the strengths of their correlation with traits. Species abundances were regulated by trait interactions with environmental and topographic factors that typically represent gradients in water availability. Historical mining and farming, distance to edge, and forest proportion also regulated species distributions.

#### Functional diversity in a temperate forest

We found that local assemblages were more functionally similar than expected by chance, suggesting that the local environment mediated community assembly (Funk et al. 2017). Notably, for multi-trait and individual trait diversity, more plots exhibited higher local similarity of broad functional groups (SESPW) than close functional groups (SESNN; Appendix S1: Table S6). Thus, species were sifted from the larger pool based on broad functional suitability to local conditions, but functionally close species (i.e., nearest neighbors) were only slightly more likely to co-occur than expected by chance. Niche-differentiation due to shared resources or natural enemies could reduce the possibility of

functionally close species coexisting within plots (Webb et al. 2006, Johnson et al. 2012, Piao et al. 2013). However, the lack of clear overdispersion in functional diversity, particularly for SESNN, suggests that habitat filtering might override limiting similarity here (Funk et al. 2017). Alternatively, competition could favor species with similar traits (Mayfield and Levine 2010), understanding which require experimental manipulations or dynamic data on interspecific competition (Kunstler et al. 2012, Funk et al. 2017).

Differences in observed functional diversity from null expectations were less apparent for individual traits than multi-trait diversity (Fig. 1), and individual traits were clustered to different extents. Strong clustering in minimum rooting depth suggests that access to water or soil resources influenced species distributions. Clustering of seed mass and wood density, associated with regeneration and growth–mortality trade-offs, respectively (Adler et al. 2014), could reflect increases in small-seeded, fast-growing species in a successional landscape (Laurance et al. 2006, Chazdon et al. 2010, Feng et al. 2014). Environmental stress is one reason for functional convergence (Coyle et al. 2014). Indeed, we found that convergence in plant strategies depended on local environmental context: highly underdispersed traits, such as wood density and rooting depth, became less constrained in conditions such as steeper slopes or lower elevations.

#### Environment and functional assembly

Functional diversity patterns together with trait–environment interactions indicated that community composition was partly shaped by optimal trait values in relation to environmental and land-use conditions. For example, areas farther from the stream and with greater depth to water table had higher abundances of species requiring greater soil depth, suggesting deeper roots as a more optimal strategy in drier areas. However, diversity of rooting depth decreased farther from the stream and increased with water table depth, hinting at different assembly mechanisms. Distance to stream likely constrained species due to lower water availability whereas species responded to deeper water tables by diversifying resource-access strategies (Coyle et al. 2014). Shallower rooting depths and lower functional diversity seen at higher elevations could occur with lower soil depth at higher elevations.

Water stress can also favor shorter-statured, dense-wooded species (Tyree 2003, Chave et al. 2009, Hoffmann et al. 2011). Indeed, we found that shorter, dense-wooded species increased in areas farther from the stream and areas with deeper water tables also had species with denser wood (Fig. 3). However, while maximum height diversity decreased farther from the stream, suggesting potential stress (Tyree 2003), diversity of wood density was unrelated to potential differences in water availability (Table 2). These patterns are consistent with Coyle et al.'s (2014) findings: across the entire eastern United States, diversity of wood density was uncorrelated with water availability even though mean wood density increased with water deficit.

Aspect was the strongest environmental correlate of seed mass diversity. Western and southern aspects had greater seed mass diversity, and higher diversity was associated with



an increase in larger-seeded species on southwestern aspects. Smaller-seeded species were more abundant in areas farther from stream and with greater depth to water table, potentially drier areas. The variation in mean seed size with environmental gradients could be due to the relative functional advantage of small vs. large seeds in the prevalent local stress during recruitment (Leishman and Westoby 2000, Moles and Westoby 2004). Typically, larger-seeded species are more shade tolerant (Leishman and Westoby 1994, Baraloto and Forget 2007, Bruun and ten Brink 2008, Muller-Landau 2010), but smaller-seeded species may better withstand desiccation (Pritchard et al. 2004, Daws et al. 2006). Higher abundances of smaller-seeded species in drier areas suggest water as a limiting factor during early establishment here.

#### *Land use and functional assembly*

Different land-use factors acted upon different functional aspects of species (Table 2). Lower diversity of wood density in older forest suggests restrictions on growth–survival trade-offs as forests age. However, denser-wooded species were more abundant in younger forest (39 and 49 yr) compared to the oldest forest (80+ yr), which is contrary to previously observed patterns (Bhaskar et al. 2014, Wilfahrt et al. 2014). These patterns could be driven by the increase in dense-wooded species we observed in previously mined areas, which had younger forest dominated by dense-wooded *Carya* and *Quercus* (Murphy et al. 2015), perhaps due to their tolerance of compacted or acidic soils of mined/farmed lands. Because wood density correlates with carbon storage in forests (Chave et al. 2006), using these dense-wooded species to restore mined and farmed areas can help augment carbon storage.

We found evidence for selection towards optimal trait values in relation to land use. Previous agriculture (fields) had lower abundances of large-seeded species and lower seed diversity, perhaps due to reduced dispersal or increased seed predation (Zimmerman et al. 2000, Meiners et al. 2002, LoGiudice and Meiners 2003). Larger-seeded species also increased in older forest, reflecting the trade-off between early colonization by small seeds early vs. establishment of large seeds later in succession (Coomes and Grubb 2003). Species that required shallow soils increased in plots with more forest cover and in older forest, but areas with less forest had greater diversity of rooting depth, indicating diversified resource-access strategies in forest patches with more disturbance. Fields had species requiring greater soil depth, suggesting an advantage to accessing resources in the deeper layers for soils that are compacted or degraded with agriculture. These results suggest that assisted regeneration of larger-seeded species and initial planting of species that thrive in deeper soils could help restoration of farmed lands.

Land use can itself be correlated with environmental variables and species distributions could be due to topographic locations of forests rather than forest age and extent alone (Foster et al. 2003). At our study site, higher elevations had older forest and greater forest extent (Appendix S1: Table S5). Hence, in older forest, the increase in species that can survive in shallower soils could be due to older forest being at higher elevations where soils are less deep than

lower elevations. However, no other environmental variable significantly correlated with land use, suggesting that land use independently affected functional diversity and trait-based species distributions.

#### CONCLUSION: ENVIRONMENT, LAND USE, AND FUNCTIONAL DIVERSITY

Because functional diversity can affect ecosystem function, understanding functional changes in human-modified forests have attracted interest (Lohbeck et al. 2012, Bhaskar et al. 2014, Lasky et al. 2014, Wilfahrt et al. 2014). We found that human land use can affect functional diversity and species distributions as much as local environmental conditions. However, species suitability to a location can be driven in opposing directions through different traits, resulting in multiple axes of community assembly (Ackerly and Cornwell 2007). These opposing axes are not unexpected, given that environmental filters on traits depend on the ecological role of the trait, e.g., resource use or stress tolerance (Coyle et al. 2014). Thus, the role of functional diversity for ecosystem function might be best assessed in relation to individual traits rather than multi-trait diversity (Butterfield and Suding 2013).

Furthermore, reforestation efforts frequently use fast-growing species such as pines. This work shows that a better choice might be fast-growing hardwoods such as tulip poplar or maples that more closely approximate natural forest habitat across much of the northeast landscape. Additionally, augmenting these pioneers with slow growing species (e.g., *Carya* and *Quercus*) might more quickly establish appropriate communities if species are chosen according to their functional fit to the site. Understanding which traits predict species recovery in relation to different abiotic factors and land uses such as mining or farming can help restore tree diversity and desired ecosystem functions in human-modified forests (Davis et al. 2012, Laughlin 2014).

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