



Beyond mean functional traits: Influence of functional trait profiles on forest structure, production, and mortality across the eastern US



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ABSTRACT

Plant functional traits (PFTs) have increased in popularity in recent years to describe various ecosystems and biological phenomena while advancing general ecological principles. To date, few have investigated distributional attributes of individual PFTs and their relationship with key attributes and processes of forest ecosystems. The objective of this study was to quantify the distribution and contribution of various PFTs in determining forest structure, live tree production (volume and biomass), and tree mortality across the eastern US. In total, 16 metrics representing species specific gravity and their shade, flood, and drought tolerance were used to develop a PFT profile for over 23,000 permanent sample plots in the region. Spatial relationships were observed when analyzing not only the mean value of these traits but also measures of PFT complexity: the standard deviation, Shannon's index (a measure of PFT diversity), and Gini coefficient (a measure of PFT inequality). Results from nonparametric random forests models indicated that variables which formed the PFT profile contributed to explaining broad-scale patterns in the variability in forest structure (volume and biomass of overstory live trees, maximum stand density index, and tree seedling abundance; R^2 ranged from 0.09 to 0.78), production (volume [$R^2 = 0.16$] and biomass accretion [$R^2 = 0.11$]), and to a lesser degree, tree mortality. Despite the variability in the data employed and the variety of forest management regimes in these stands, this work demonstrates the utility of applying PFT profiles for understanding and predicting patterns of forest structure and production and their role in critical ecosystem processes such as carbon sequestration.

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1. Introduction

The ability to simultaneously manage forests for the sequestration of carbon (C) in addition to the other ecosystem services they provide, including wood products, has recently been highlighted as a scientific and public policy concern (Birdsey et al., 2006; Schwenk et al., 2012). Across the temperate forests of the eastern US, there may be opportunities to increase C stocks through appropriate management regimes, of which species composition may play a role (Woodall et al., 2011a). From an ecological perspective, species and functional trait diversity may regulate ecosystem productivity and other processes (Tilman, 1982; Johnson and Wardle, 2010; Wilfahrt et al., 2014) and are increasingly being used to aid predictions of ecosystem responses to global changes (Díaz and Cabido, 1997; Soudzilovskaia et al., 2013). Understanding the

relationships between species- and population-level functional traits and patterns of forest structure, composition, and associated dynamics could enhance our ability to manage forests for a variety of objectives, including (but not limited to) C sequestration, biodiversity, and wildlife habitat.

Despite the growing popularity of plant functional traits (PFTs) to describe ecological communities, few studies have investigated the diversity of these traits and their relationship with structure and production in forested ecosystems. In its broadest sense, a trait serves as a surrogate for representing the performance of an organism which can be related to growth, reproduction, and survival components (Violle et al., 2007). These may be considered either functional (e.g., leaf longevity; Wright, 2004), structural (e.g., wood density; Chave et al., 2009), or response traits (e.g., investment in leaf area; Díaz and Cabido, 1997). Specifically, such structural and response traits could possibly play a role in furthering our understanding of patterns of forest composition and structure. Although there are numerous approaches for calculating indices

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of PFTs (see Mouillot et al., 2013; their Table 1 and Fig. 1), specific traits may be useful in considering the use of PFTs in forest ecosystem management. For example, a species' tolerance to shade could be fundamental in understanding biomass allocation patterns (Walters et al., 1993), while structural traits such as wood density might aid in discerning ecological succession patterns (Wilfahrt et al., 2014). Refined understanding of PFTs across large scales may assist with quantifying the effect of future global change scenarios on disturbance regimes (Mouillot et al., 2013) and ecosystem processes (e.g., a species' tolerance to drought is essential to understanding drought-related tree mortality; van Mantgem et al., 2009; Allen et al., 2010). Similarly, quantifying the relationships between PFTs and productivity may help to refine ecosystem models that seek to accurately represent future forest structure and growth dynamics (Moorcroft et al., 2001).

To date, most studies examining the influence of tree community composition on forest structural conditions, productivity, and C sequestration have relied primarily on species-identity-based metrics, such as species richness or diversity, or average values of an individual trait such as shade tolerance. For example, Kirby and Potvin (2007) did not observe any relationships between species diversity and aboveground C stocking, whereas D'Amato et al. (2011) demonstrated important tradeoffs in aboveground C storage and species and structural diversity, highlighting the challenge that managing forests for both climate change mitigation and adaptation presents. Across eastern US forests, Woodall et al. (2011a) observed that species shade tolerance had no effect on the maximum amount of live aboveground C, however, mixtures of both shade tolerant and intolerant species could potentially maximize live aboveground C amounts for a given forest type. The strength of relationships between various measures of biodiversity and aboveground biomass are weakened in highly-stocked

stands and in stands with high site quality (Potter and Woodall, 2014), adding complexity to understanding diversity-structure interactions. Stand factors such as age in addition to geographic region have been related to mean values of PFTs (Wilfahrt et al., 2014) but much less is known on how the diversity of a PFT within a stand can be used in ecological applications. Based on these findings, examinations of species-identity-based metrics or functional traits based on a population-level mean attributes may be inadequate in capturing the true variability in trait characteristics that are inherent to a forest ecosystem and their relationship with ecosystem processes. Developing a functional trait profile for forests across the eastern US that employs PFTs common to forestry and ecological applications may aid in interpreting how these traits explain forest structure and production.

The overall goal of this study was to quantify the distribution and contribution of PFTs in determining forest structure, production, and mortality. Specific objectives of this study were to (1) assess the distribution of PFT profiles (i.e., the mean, standard deviation, diversity, and Gini coefficient) across the eastern US, and (2) quantify the relationship between PFT profiles and forest structure, live tree production (volume and biomass), and tree mortality.

2. Methods

2.1. Study region

Forests of the eastern US range from conifer and mixed conifer and hardwood types in the north to extensive areas of natural and planted pine and oak-hickory and oak-gum-cypress types in southern regions (Smith et al., 2009). The study area investigated here ranged eastward from the state of Minnesota to Maine in the north and from Louisiana and Florida in the south, spanning

Table 1
Description and summary of plant functional traits used in quantifying forest structure, production, and mortality across eastern US forests.

Variable	Description	Mean	Min	Max
<i>Structure</i>				
VOL	Volume in live trees (m ³ /ha)	123.37	0.00	998.48
BIO	Biomass in live trees (Mg/ha)	106.04	0.00	654.99
SDI _{MAX}	Maximum stand density index (Woodall et al., 2005)	1030.65	378.42	1448.71
SEED	Seedling abundance (1000 ha ⁻¹)	6.03	0.00	325.84
LAT	Latitude (°)	40.05	25.46	49.35
LONG	Longitude (°)	-84.12	-96.78	-67.01
DD5	Number of degree days greater than 5 °C	2858	663	6952
<i>Production</i>				
ΔVOL	Annual volume accretion (m ³ /ha/yr)	2.77	-125.00	106.29
ΔBIO	Annual biomass accretion (Mg/ha/yr)	2.11	-75.52	72.28
<i>Mortality</i>				
MORT	Annual mortality (m ³ /ha/yr)	1.29	0.00	66.55
<i>Functional traits</i>				
SG _{MEAN}	Mean of species specific gravity ^a	0.49	0.29	0.80
ShTol _{MEAN}	Mean of species shade tolerance ^b	2.93	0.87	5.01
FITol _{MEAN}	Mean of species flood tolerance	1.79	1.00	5.00
DrTol _{MEAN}	Mean of species drought tolerance	2.72	1.00	5.00
SG _{SD}	Standard deviation of species specific gravity	0.06	0.00	0.18
ShTol _{SD}	Standard deviation of species shade tolerance	0.73	0.00	2.19
FITol _{SD}	Standard deviation of species flood tolerance	0.55	0.00	2.25
DrTol _{SD}	Standard deviation of species drought tolerance	0.61	0.00	1.98
H _{SG}	Shannon's diversity index based on species specific gravity	0.99	0.00	1.99
H _{ShTol}	Shannon's diversity index based on species shade tolerance	1.04	0.00	2.04
H _{FITol}	Shannon's diversity index based on species flood tolerance	0.89	0.00	1.88
H _{DrTol}	Shannon's diversity index based on species drought tolerance	1.00	0.00	2.09
Gini _{SG}	Gini coefficient based on species specific gravity	0.06	0.00	0.17
Gini _{ShTol}	Gini coefficient based on species shade tolerance	0.12	0.00	0.37
Gini _{FITol}	Gini coefficient based on species flood tolerance	0.14	0.00	0.38
Gini _{DrTol}	Gini coefficient based on species drought tolerance	0.11	0.00	0.34

^a Specific gravity ranged from *Thuja occidentalis* L. (0.29) to *Quercus virginiana* Mill. (0.80).

^b Shade tolerance ranged from *Pinus palustris* Mill. (0.87) to *Abies balsamea* L. (5.01).

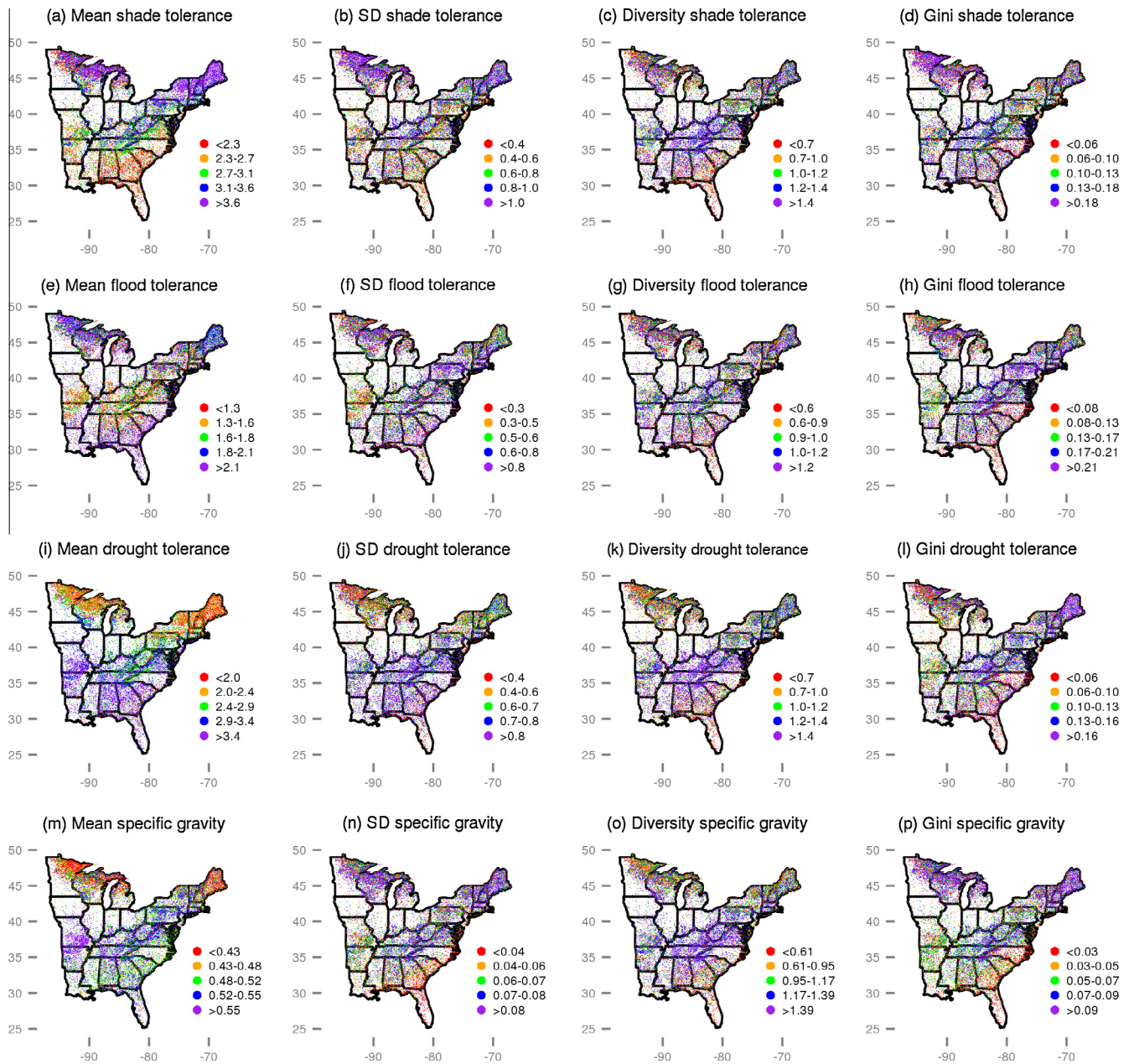


Fig. 1. Distribution of plant functional traits common to forestry and ecological applications from Niinemets and Valladares (2006) at approximate locations of forest inventory plots across the eastern US, 2003–2012. Legend group cutoffs represent the 0.2, 0.4, 0.6, and 0.8 percentiles of the data.

approximately 24° latitude (LAT) and 30° longitude (LONG; Fig. 1). Across the study area, mean annual temperatures ranged from -0.8 to 24.2 °C and precipitation from 47 to 216 cm (Rehfeldt, 2006; USDA Forest Service, 2013b). Data for the study region were classified into one of four classes of number of degree days (>5 °C; DD5) to serve as a surrogate of site productivity: low (663 to 1841), moderate-low (1842–2564), moderate-high (2565–3606), and high (3607–6952). One hundred and fifty-nine unique forest types were identified by the USDA Forest Service Forest Inventory and Analysis (FIA) program for the data collected across this region (USDA Forest Service, 2013a).

2.2. Data

The FIA program monitors forests by establishing permanent sample plots across the US using a three phase inventory

(Bechtold and Patterson, 2005). During the inventory's first phase (P1), sample plot locations are established at an intensity of approximately 1 plot per 2400 ha. If the plot lies partially or wholly within a forested area, field personnel visit the site and establish a phase two (P2) inventory plot. Standard P2 inventory plots consist of four 7.32-m fixed radius subplots for a total plot area of approximately 0.07 ha where standing tree and site attributes are measured. All live and standing dead trees with a diameter at breast height (DBH) of at least 12.7 cm are measured on these subplots. Within each subplot a 2.07-m microplot is established where live trees with a DBH between 2.5 and 12.7 cm are measured.

A total of 23,854 inventory plots were analyzed for a variety of characteristics related to forest structure, live tree production (volume and biomass accretion), and tree mortality. Initial plot measurements began around 2002 with a remeasurement occurring approximately five years later, the final of which took place in

2010. Bole volume was calculated for individual trees by first estimating gross volume using region-specific equations and then reducing this estimate through considering merchantable stem reductions to arrive at sound volume (Woodall et al., 2011b). Sound bole volume was converted to bole biomass using species-specific wood and bark density estimates (Miles and Smith, 2009; USDA Forest Service, 2013a). Total tree biomass was estimated via the component ratio method (Woodall et al., 2011b) which facilitated the calculation of tree component biomass as a ratio of bole biomass based on component proportions from Jenkins et al. (2003). Productivity (i.e., volume and biomass accretion) was computed at the plot level as the change in the stock from the two time periods. Mortality (as measured in volume) was computed by analyzing individual trees that were recorded as dead at their remeasurement but were alive at their initial measurement, then scaling to the plot level. Productivity and mortality were standardized on an annual basis.

2.3. Plant functional traits and complexity measures

Three PFTs of interest to forest managers, including shade (ShTol), flood (FITol; i.e., waterlogging), and drought tolerance (DrTol) were obtained from Niinemets and Valladares (2006) and applied to the FIA species list (see Appendix A; Supplementary Material). These tolerance indices ranged continuously from approximately one to five (low to high tolerance) and are based primarily on the scales presented in Baker (1949). In the event that a value for an FIA species was not found in Niinemets and Valladares (2006), tolerance values were either averaged across species in the same genus, or, a species with a similar phenotype was applied to the missing species. Out of the 215 species observed in this data across the eastern US, 60 did not have a tolerance values reported in Niinemets and Valladares (2006). Although this represented 28% of the species in the study, the total percentage of all observations without a tolerance value was 4%, signifying that tolerance measures were unavailable for uncommon species which were not generally abundant. After applying these species values to the entire FIA tree list, we calculated the mean and standard deviations (SD) of these tolerance scales across all trees for each FIA plot (e.g., ShTol_{MEAN} and ShTol_{SD}). We similarly calculated the mean and SD for wood specific gravity (SG) at each FIA plot (Miles and Smith, 2009; USDA Forest Service, 2013a).

Complexity, typically defined as the degree of heterogeneity in the distribution of biomass or individuals across different tree sizes or species (e.g., D'Amato et al., 2011), was instead defined in the context of PFTs by considering the distribution of SG and tolerance indices. Shannon's diversity index (H; Staudhammer and LeMay, 2001) was calculated for the three tolerance classes and SG. Tolerance classes were summed across classes of 0.5 units while SG was summed across classes of 0.05 units. This resulted in approximately the same number of classes for both SG and tolerance values (on average, the number of classes in each FIA plot was 3.9, 4.2, 3.4, and 3.9 for SG, ShTol, FITol, and DrTol, respectively). Here, large H values indicate a greater number of PFT classes:

$$H_{ij} = -\sum_{i=1}^S \frac{n_{ij}}{N} \ln \left(\frac{n_{ij}}{N} \right) \quad (1)$$

where S is the total number of classes in each plot, N is the total number of trees in each plot, n_i is the number of trees in each class i , and j is the PFT of interest. Functional trait equality was similarly calculated using the Gini coefficient (Glasser, 1962). This value ranged from zero (perfect trait equality) to one (maximum trait inequality) and was calculated by sorting the tree list of each FIA plot ascendingly by the PFT of interest:

$$Gini_{ij} = \frac{\sum_{i=1}^n (2i - n - 1)PFT_{ij}}{n^2 \mu} \quad (2)$$

where n is the number of trees in each plot, PFT_i is the value for the trait associated with tree i , μ is the mean PFT value in the plot, and j is the PFT of interest. Ultimately, 16 variables were calculated that represented functional trait complexity for the FIA plots (i.e., the mean, SD, H, and Gini for each of the variables SG, ShTol, FITol, and DrTol; Table 1). Data from the initial plot measurement were used to calculate the PFT profile and forest structure variables, while production and mortality variables were calculated using information from both the remeasurement and initial conditions.

2.4. Analysis of traits and complexity measures

We assessed the direction (positive or negative) and strength of the relationships between measures of functional trait complexity and forest structure, production, and mortality using Spearman correlation coefficients. To compare trends in the PFT profiles developed with those based on mean values presented in Niinemets and Valladares (2006), we employed generalized additive regression models. Correspondence analysis (CA; Ter Braak, 1986) was used as a multivariate statistical approach to graphically display PFTs using ordination followed by trait vectors. The CA method is based on Chi-squared distances where correlations are weighted within an ordination axis. Although there are some drawbacks to the CA method, including compression of distances near the end of axes and distortions of second and later axes (McCune and Grace, 2002), the method may be more efficient with large datasets (e.g., $n > 25,000$) when compared to more quantitatively-demanding multivariate analyses such as nonmetric multidimensional scaling. To identify the direction and strength of trait vectors using the PFT information, we fit vectors onto the ordination using 1000 permutations. Ordinations and trait vectors were carried out using the 'vegan' package in R (Oksanen et al., 2013).

2.5. Modeling

We used nonparametric random forests (RF; Breimen, 2001) in R (Liaw and Wiener, 2002) to test the ability of functional trait complexity measures to explain forest structure, production, and mortality. The RF method ranked the relative influence that each trait had on forest structure measurements. This method involved building a set of regression trees based on bootstrapped samples of the trait data that were compiled.

Measures of forest structure included the volume and biomass of live trees (VOL, BIO), seedling abundance (SEED), and maximum stand density index (SDI_{MAX}). The SDI_{MAX}, defined as the maximum number of trees per hectare that can exist for a given average tree size under the conditions of self-thinning (Long, 1996), was calculated using the average specific gravity of all trees on each FIA plot (Woodall et al., 2005). Hence, SDI_{MAX} (a unit-less value) was employed as a measure of the maximum stocking potential of each plot. Measures of tree dynamics included volume (Δ VOL) and biomass accretion (Δ BIO) and annual mortality (MORT; Table 1). In the RF method, classification trees are taken as independently-sampled bootstraps of the data (Breimen, 2001). For ecological data, RF models can offer high classification accuracy and provide a method for assessing the relative importance of predictor variables (Cutler et al., 2007). Although RF models can be robust against overfitting (Breimen, 2001), we used an approach outlined in Weiskittel et al. (2011a) to balance model parsimony with the risk of overfitting. To determine the optimal number of variables to use from the host of functional trait information, we performed

the RF model iteratively, each time dropping the least influential variable as reflected in the RF variable importance score. After plotting the number of variables used in each RF against R^2 and root mean square error (RMSE) fit statistics, we chose the model which produced the minimum number of variables where the slope of the fit statistic began to reach its asymptote. We defined this as the optimal model. We sampled 250 regression trees for each iteration of the RF model.

For the parsimonious RF model, input variables were altered to perform a sensitivity analysis. We modified inputs by $\pm 25\%$ to assess the influence of moderate changes to variables on forest structure and production. We then compared these new predictions to the mean predicted value for BIO, VOL, and Δ VOL and Δ BIO to compute the percent change in prediction that resulted from altering one input variable while holding the others fixed.

3. Results

There were several apparent trends when visualizing the spatial distribution PFT profiles across the eastern US (Fig. 1). Both the mean and SD of shade tolerance were highest (>3.6) in the Northeast and upper Midwest regions and lowest (<2.7) in the Atlantic and Gulf Coastal Plains across the southeastern US. Tolerance to flooding was generally low across all FIA plots (mean of 1.79 on a 1–5 scale; Table 1; Niinemets and Valladares, 2006), however, greatest values (>2.1) were observed in the upper Midwest and southeastern Coastal Plain regions. Stands that exhibited the greatest tolerance to drought generally displayed the lowest tolerance to shade, and vice versa (Fig. 1). Drought tolerance was highest (>3.4) in the Coastal Plains and lowest (<2.0) in the Northeast and upper Midwest. Measurements that quantified the SD and diversity of tolerance scales were less distinguishable among regions compared to observing mean values. There was a trend of greatest SD and diversity in the tree tolerance scales examined across the Appalachian Mountain chain, principally in the states of Kentucky, Tennessee, and Virginia. Gini coefficients (measurements of PFT inequality) for the four traits of interest tended to be lowest across the Atlantic Coastal Plain and highest across northern states (Fig. 1). Spearman rank correlation coefficients were generally strongest between mean and SD values of PFTs and LAT, LONG, and DD5, confirming many of the spatial trends observed. For example, the correlation between $ShTol_{MEAN}$ and LAT (-0.489) and $DrTol_{MEAN}$ and DD5 (0.679) were some of the

strongest observed. Correlations were less in magnitude for other measures of PFT diversity with LAT, LONG, and DD5 (Table 2).

Scatterplots indicated significant negative relationships between $ShTol_{MEAN}$ and $DrTol_{MEAN}$ and with $DrTol_{MEAN}$ and $FitTol_{MEAN}$ (Spearman rank correlation coefficients of -0.51 and -0.41 , respectively), with a nonsignificant relationship between $ShTol_{MEAN}$ and $FitTol_{MEAN}$ (Fig. 2). A slight positive relationship was observed for variables that described the SD of tolerance scales (correlation ranged from 0.17 to 0.35), with relationships generally stronger for stands that displayed low SDs of tolerance variables. Correlations among measures reflecting the diversity of tolerance values were all in excess of 0.64. The Gini coefficient of the three tolerance scales mimicked trends in SD, i.e., relationships were stronger for stands that displayed a low Gini of tolerance variables, with correlations ranging from 0.34 to 0.48 (Fig. 2). For these correlations, it should be noted that statistically significant results may emerge despite marginal biological effects, a reflection of our large sample size.

The degree of correlation between metrics of PFT diversity and forest structure and dynamics varied depending on the variable of interest (Table 2). Spearman rank correlations for PFTs were stronger for BIO than for VOL and were all positive with the exception of $FitTol_{MEAN}$ and $DrTol_{MEAN}$. For SDI_{MAX} and seedling abundance, strongest negative correlations were observed for $DrTol_{MEAN}$ (-0.528 and -0.120 , respectively) and strongest positive correlations were observed for $FitTol_{MEAN}$ and $ShTol_{MEAN}$ (0.287 and 0.189, respectively). Correlations between PFTs and production and mortality were generally low (range from -0.117 to 0.179).

Differences in PFTs were illustrated by the broad distribution of points in ordination space by corresponding classes of site productivity (Fig. 3). The variation in PFTs was explained by axis 1 (35.5%) and 2 (22.5%) with total inertia = 0.1183. Patterns in fitted trait vectors reflected a distribution of plots along axis 1 ranging from stands with a higher degree of variability in PFTs in the negative portion to those with lower levels in the positive portion of the axis. Axis 2 primarily reflected broad trends in average PFTs with higher mean flood and shade tolerance in the negative portion and plots with higher mean drought tolerance and specific gravity in the positive portion. The R^2 values for vectors ranged from 0.21 to 0.87 depending on the PFT with all PFTs significantly correlated based on the random permutations drawn from the data (Appendix B; Supplementary Material).

Results from the RF regression indicated increasing R^2 and decreasing RMSE as additional variables were considered in the

Table 2

Spearman rank correlations between plant functional traits and forest structure, production, and mortality across the eastern US^a. Correlations significant at $p < 0.05$ are italic; correlations >0.250 and significant at $p < 0.05$ are italic bold.

Functional traits	Structure							Production		Mortality
	VOL	BIO	SDI_{MAX}	SEED	LAT	LONG	DD5	Δ VOL	Δ BIO	MORT
SG_{MEAN}	0.160	0.307	-1.000	-0.024	-0.489	0.010	0.449	-0.009	0.037	-0.004
$ShTol_{MEAN}$	0.305	0.318	-0.017	0.189	0.344	0.302	-0.454	-0.117	-0.115	0.061
$FitTol_{MEAN}$	-0.058	-0.092	0.287	-0.097	0.073	-0.032	-0.024	-0.096	-0.089	0.071
$DrTol_{MEAN}$	-0.067	-0.023	-0.528	-0.120	-0.636	-0.145	0.679	0.174	0.179	-0.070
SG_{SD}	0.195	0.193	0.015	0.135	0.128	0.063	-0.147	-0.021	-0.043	0.079
$ShTol_{SD}$	0.072	0.045	0.207	0.174	0.264	0.003	-0.267	-0.070	-0.085	0.096
$FitTol_{SD}$	0.215	0.227	-0.005	-0.024	-0.071	0.169	0.051	0.065	0.062	0.090
$DrTol_{SD}$	0.196	0.218	0.217	-0.035	-0.402	0.123	0.376	0.131	0.118	0.074
H_{SG}	0.305	0.345	-0.260	0.043	-0.199	0.062	0.185	0.046	0.028	0.124
H_{ShTol}	0.270	0.296	-0.173	0.135	-0.107	0.069	0.083	0.037	0.017	0.148
H_{FitTol}	0.210	0.231	-0.136	0.105	-0.117	0.041	0.113	0.027	0.020	0.142
H_{DrTol}	0.314	0.354	-0.284	0.089	-0.284	0.147	0.229	0.086	0.067	0.138
$Gini_{SG}$	0.188	0.160	0.194	0.167	0.220	0.052	-0.228	-0.020	-0.051	0.106
$Gini_{ShTol}$	0.022	0.000	0.150	0.127	0.099	-0.124	-0.057	-0.024	-0.042	0.100
$Gini_{FitTol}$	0.257	0.289	-0.171	0.100	-0.043	0.162	0.008	0.077	0.073	0.085
$Gini_{DrTol}$	0.276	0.276	0.041	0.078	-0.033	0.249	-0.026	0.052	0.033	0.134

^a Variable descriptions can be found in Table 1.

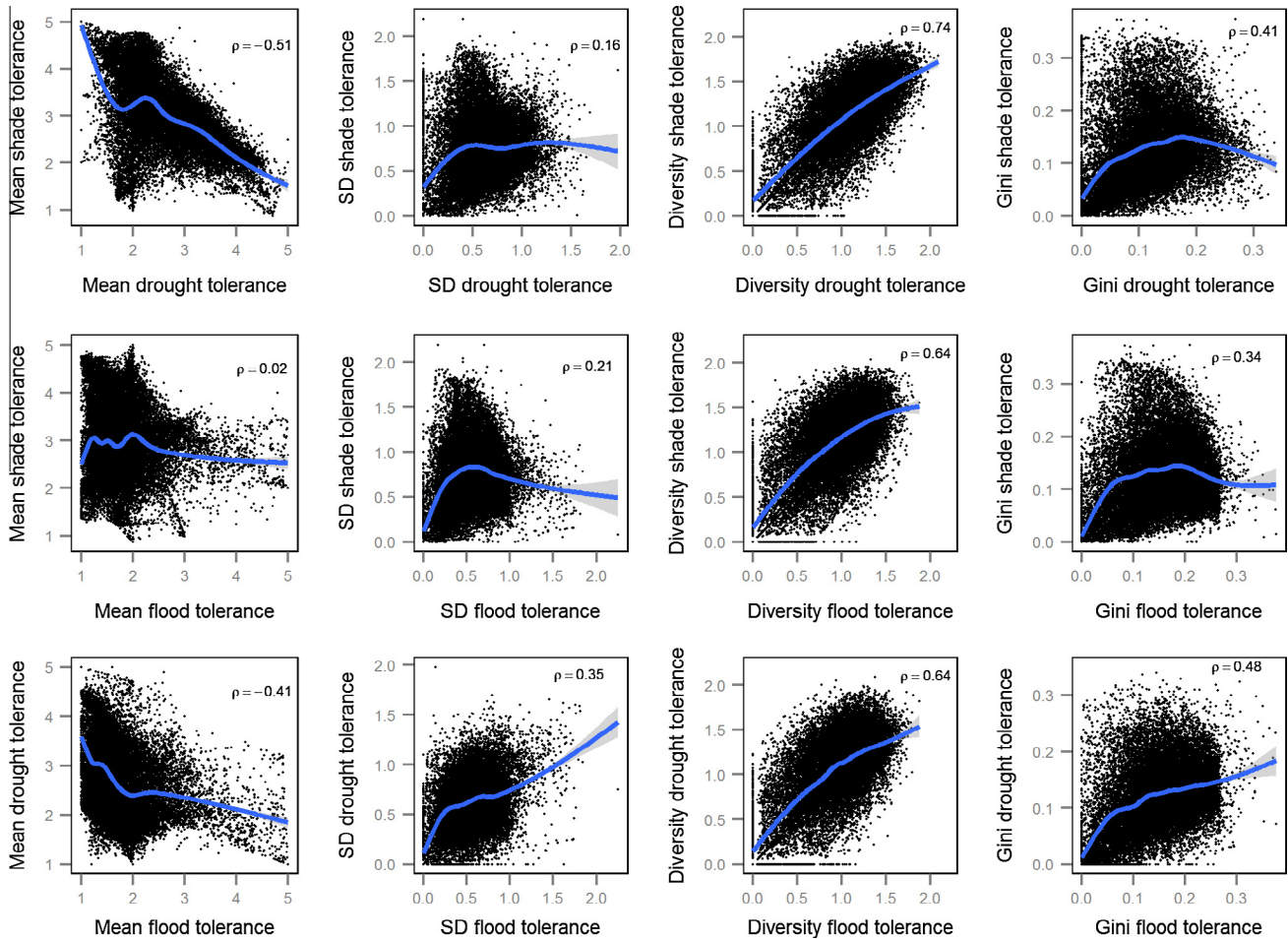


Fig. 2. Scatterplots of mean, standard deviation (SD), diversity and Gini coefficient of plant functional traits from Niinemets and Valladares (2006) across the eastern US. Smoothed line is a generalized additive model regression with 95% confidence bounds in gray, and Spearman correlation reported in upper right.

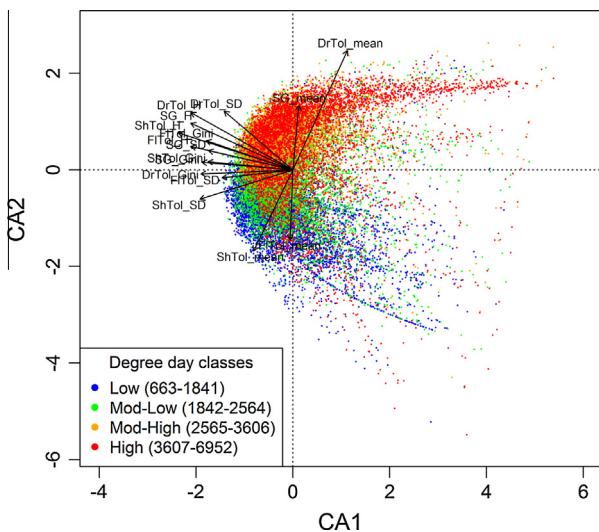


Fig. 3. Ordination results from correspondence analysis and vectors representing plant functional traits. Traits listed are significantly correlated ($p < 0.05$) with axis 1 or 2 where correlations are weighted within an ordination axis. Results are plotted across various forest productivity classes, as measured in total cumulative degree days.

model. To generate a parsimonious model, a five-variable model was chosen because the decrease in R^2 was minimal and RMSE

appeared to stabilize after dropping variables (see Appendix C; Supplementary Material). Values for R^2 ranged from 0.00 to 0.78. Traits that exhibited the strongest spatial patterns, e.g., the mean values of the PFTs (Fig. 1), tended to be strong predictors of forest structure, as measured by their importance scores (Table 3). Variables representing the Gini coefficient of traits similarly contributed to explaining the variation of forest structure attributes. The means of SG and DrTol ranked high in terms of their importance scores for variables representing forest structure/production.

Analysis of the five-variable RF regression indicated that VOL was most sensitive to changes in ShTol_{MEAN} followed by Gini_{DrTol} and BIO was most sensitive to changes in ShTol_{MEAN} followed by SG_{MEAN} (Fig. 4). In terms of production, Δ BIO was more sensitive to changes in input parameters than Δ VOL. Changes of a $\pm 25\%$ magnitude in ShTol_{MEAN} and SG_{MEAN} resulted in a 56% and 34% difference in the prediction of Δ BIO, respectively. Volume accretion was most sensitive to changes in DrTol_{MEAN} (-23%) and ShTol_{MEAN} (-21%).

4. Discussion

Researchers and forest land managers in any given region are generally well-acquainted with the functional traits that are characteristic of their species of interest, such as their shade tolerance. Similarly, the structural characteristics of forests across the eastern US are routinely measured through forest inventories. Building on this information, a PFT profile can be quantified and implemented

Table 3Summary of variables used in random forests and their importance scores (%IncMSE) for predicting forest structure, production, and mortality across the eastern US^a.

VOL		BIO		SDI _{MAX} ^b		SEED	
Variable	%IncMSE	Variable	%IncMSE	Variable	%IncMSE	Variable	%IncMSE
ShTol _{MEAN}	78.2	ShTol _{MEAN}	97.8	DrTol _{MEAN}	114.7	ShTol _{MEAN}	22.9
SG _{MEAN}	71.7	SG _{MEAN}	84.4	ShTol _{MEAN}	96.8	ShTol _{SD}	18.7
FITol _{MEAN}	58.1	Gini _{SG}	69.7	Gini _{DrTol}	88.0	H _{ShTol}	16.8
Gini _{DrTol}	52.5	ShTol _{SD}	58.5	FITol _{MEAN}	75.4	FITol _{MEAN}	16.1
Gini _{ShTol}	49.9	FITol _{MEAN}	58.2	Gini _{ShTol}	67.3	DrTol _{MEAN}	13.4
R ²	0.22	R ²	0.30	R ²	0.78	R ²	0.09
RMSE	77.03	RMSE	55.24	RMSE	65.51	RMSE	6989.05
ΔVOL		ΔBIO		MORT			
Variable	%IncMSE	Variable	%IncMSE	Variable	%IncMSE		
ShTol _{MEAN}	41.9	SG _{MEAN}	33.2	SG _{MEAN}	24.7		
SG _{MEAN}	40.7	DrTol _{MEAN}	32.1	DrTol _{MEAN}	23.7		
DrTol _{MEAN}	37.4	FITol _{SD}	31.3	H _{FITol}	19.5		
ShTol _{SD}	29.5	FITol _{MEAN}	30.3	DrTol _{SD}	17.6		
H _{FITol}	19.5	ShTol _{MEAN}	28.4	H _{SG}	12.2		
R ²	0.16	R ²	0.11	R ²	0.00		
RMSE	4.63	RMSE	3.51	RMSE	2.71		

^a Variable descriptions can be found in Table 1. Overall fit statistics are also provided: R² and root mean square error (RMSE).

^b Measures of SG were withheld from estimating SDI_{MAX} given the use of SG in determining this value (Woodall et al., 2005).

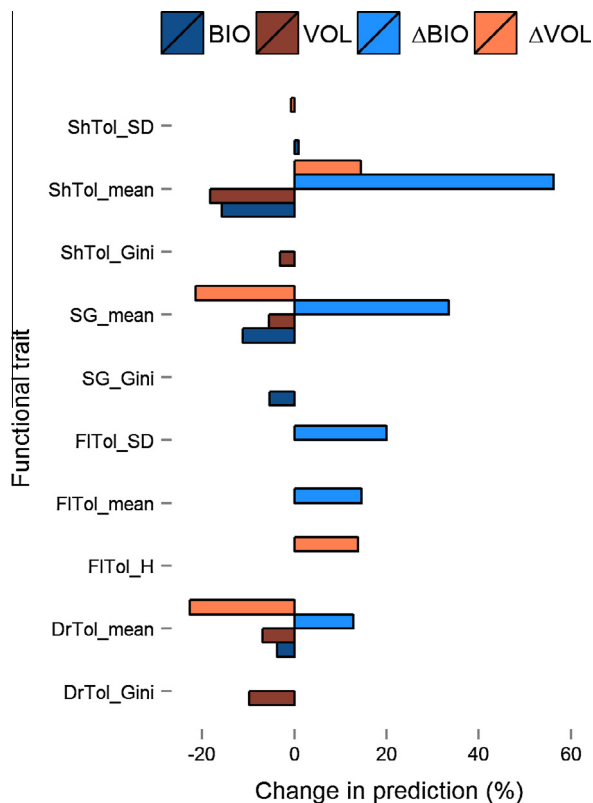


Fig. 4. Results of sensitivity analysis assuming a $\pm 25\%$ change in variables obtained from the five-variable random forests model.

to aid in assessing biodiversity benchmarks, understanding forest ecosystem dynamics, and as shown here, may help to explain variation in forest structure and changes in volume and biomass accretion. Moreover, describing the broad scale patterns and tradeoffs associated with response traits such as drought and shade tolerance are useful in anticipating future impacts of changing precipitation regimes and the regions where these effects might be greatest (Melillo et al., 2014). The spatial distribution and variability of the PFT profiles developed here no doubt reflect current and past forest management practices and highlight the

importance of accounting for regional vulnerabilities that may emerge if management practices inadvertently promote homogeneity at broad spatial scales. Finally, these PFT profiles can improve our understanding of processes related to forest structure and dynamics.

Results from the spatial analysis of these PFTs across regional scales generally aligns with what Niinemets and Valladares (2006) observed at species scales, namely that no regions simultaneously exhibited high tolerance to shade, flood, and drought collectively (as measured using mean values). The tradeoffs observed between tolerance to shade and drought (i.e., areas of high shade tolerance displayed low drought tolerance) is likely a reflection of a plant's investment strategy capturing light versus avoiding drought (Niinemets and Valladares, 2006). From a biomass allocation perspective, species that can survive shade are likely to display large leaf area with preferred partitioning of carbon to foliage, whereas species attempting to avoid drought may allocate a greater proportion of biomass belowground (Hertel et al., 2013). As the difference between BIO and VOL is inherently wood density, it is expected there would be stronger correlations between the PFTs and BIO given that biomass is not purely structure but an integrated metric that brings together both structure and traits. Despite these tradeoffs, mean values for these tolerance scales were important predictors of structure and production (Table 3). Differences in the sensitivity between ΔVOL and ΔBIO when examining changes in predictions from altering shade and drought tolerance in the RF model (Fig. 4) could indicate biomass allocation tradeoffs, namely because merchantable volume considers only the stemwood portion while biomass considers all woody components. The sensitivity of the RF regression to H_{FITol} (in the case of ΔVOL), FITol_{SD} (in the case of ΔBIO), and Gini_{DrTol} (in the case of VOL) indicates that variability in PFTs are apparent and may influence the distribution of forest structure and production attributes across the temperate forests of the eastern US.

Results from the eastern US indicated negative correlations between shade and drought tolerance and drought and flood tolerance (Fig. 2) which was similarly observed by Niinemets and Valladares (2006). Further analysis beyond solely the means of the data permitted us to explore additional relationships among the traits of interest. For example, although mean values may not be correlated for various tolerance metrics (e.g., between ShTol_{MEAN} and FITol_{MEAN}; Niinemets and Valladares, 2006), what information can be gleaned from assessing alternate measures from their PFT profile? For the SD, diversity, and Gini coefficient, we observed

significant positive relationships between ShTol and FITol, but observed no trends when investigating means alone. These measures were similarly important in the RF model, indicating that incorporating the complete trait profile may help to explain large-scale patterns in forest structure and production. Similarly, stands with higher ShTol_{MEAN} had greater mortality rates (Table 2), whereas relationships between DrTol_{MEAN} and mortality were negative. This suggests that sites with greater variability in ShTol may exhibit lower mortality risk, potentially reflecting differences in susceptibility to mortality agents or stressors across the shade tolerance spectrum. Future work investigating this mortality-shade tolerance tradeoff may be further ameliorated by examining the temporal trends in forest stand dynamics. For example, mortality may be low during early stages of stand development (e.g., stand initiation; Oliver and Larson, 1996) while increasing during later stages. Concomitant with these transitions is an increasing presence of shade tolerant species while shade intolerants likely die as light becomes a limiting resource. Such data sources like FIA may help to inform assessments of these dynamics in the future.

To our knowledge, information depicting this variability and diversity of plant traits has not been incorporated into ecosystem models and/or dynamic global vegetation models that employ plant trait data. In a management context, if an adaptive framework for forest management is considered to provide a range of stand development pathways (e.g., Puettmann et al., 2009), metrics related to the PFT profile and their associated relationships with stand processes such as production and mortality could prove useful for anticipating the outcomes of management regimes aimed at increasing forest ecosystem complexity.

Although the RF models had substantial unexplained variability in terms of describing mortality, traditional ecosystem models often employ a myriad of independent variables that relate to initial stand conditions (e.g., basal area), climate information, and productivity potential (e.g., site index). Given that most forest growth models struggle to predict mortality because of its rare and highly episodic nature (Weiskittel et al., 2011b), this analysis similarly found difficulties in relating observed mortality in the FIA inventory to the PFT profile. Logical next steps will be to assess the degree to which PFT profiles aid in ecosystem models by reducing prediction uncertainty above and beyond what is provided by currently employed forest variables. Similarly, additional metrics may aid modelers in refining diversity measurements across large geographic scales (e.g., the Hill transformation of Shannon's diversity presented in Jost, 2006). Additional research questions can subsequently be examined, such as what is the appropriate scale (i.e., individual tree to landscape levels) to incorporate PFT metrics? As the use of remotely-sensed information becomes more commonplace to answer questions at regional and/or continental scales (e.g., assessing forest C stocks; Saatchi et al., 2011), understanding the relationships between forest structure and a profile of PFT information will be crucial as these new technologies emerge.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.05.014>.

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