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

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A B S T R A C T

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.

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
Structure				
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
Production				
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
Mortality				
MORT	Annual mortality (m^3/ha/yr)	1.29	0.00	66.55
Functional traits				
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
$FlTol_{MEAN}$	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
$FlTol_{SD}$	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_{FlTol}	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
$Gini_{FlTol}$	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).