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Shifts in functional traits among tree communities across succession in eastern deciduous forests

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ABSTRACT

Throughout the eastern deciduous forest (EDF) region, disturbances, including fire, wind storms, and landslides, interweave with complex topography and vegetation history to produce a mosaic of forest types and ages. Forest composition and dynamics following disturbance can depend on the interaction of plant traits related to resource capture, regeneration, and growth with changes in the post-disturbance environment. Appropriate traits should vary predictably with the stand age of a forest community as this acts as a proxy for time since last disturbance. We used Forest Inventory and Analysis data to investigate the hypothesis that community level means of seed mass and wood density increase, and leaf nitrogen decreases, with age of eastern deciduous forests, reflecting a shift from light-seeded, fast-growing early successional vegetation to heavier-seeded, slower-growing vegetation. As hypothesized, seed mass and wood density were positively correlated with stand age; however, the relationship differed among ecoregions of the EDF. Northern forests in the Warm Continental Division showed lower seed mass and wood density values in young stands, with a stronger increase in these values as succession advanced relative to more southerly ecoregions. This could reflect slower succession, preponderance of light-seeded and low wood density early post-disturbance deciduous trees such as *Populus tremuloides* and *Betula papyrifera*, or presence of conifers in early successional stands. Leaf nitrogen showed no consistent relationship with stand age, suggesting no consistent relationship of photosynthetic rate or soil nitrogen content with tree composition over succession throughout the EDF. Instead, leaf nitrogen differed among the ecoregion divisions and showed a unimodal distribution with latitude, peaking near the middle latitudes of the Hot Continental and Prairie Divisions. Collectively, the results indicate functional trait shifts over succession throughout the EDF, in agreement with a shift from ruderal to more competitive or stress-tolerant strategies, but also point to differences in the strength and shape of that shift among ecoregions. Early post-disturbance forest harbors a unique combination of functional traits. Further, disturbance that creates a mosaic of forest stand ages is important for maximizing not just species diversity, but functional diversity as well.

1. Introduction

Disturbance has long been known to be an important process structuring plant communities (Pickett and White, 1985). Across the eastern deciduous forest (EDF) region, disturbances such as wind and fire variably increase light and soil resources, reduce standing biomass, and create a landscape mosaic of different successional stages (White et al., 2011). At the stand level, disturbances beyond a threshold of intensity or frequency can initiate or maintain early successional forest structure or composition (Romme et al., 1998; Frelich and Reich, 1999; White et al., 2011). Post-disturbance change in species composition, which often varies predictably over succession, is a result of different evolutionary strategies that are reflected in plant functional traits related to resource capture, regeneration, and growth (Campetella et al., 2011; Douma et al., 2012; Latzel et al., 2011; Navas et al., 2010; Raevel et al., 2012). The type of disturbances to today's eastern forests has shifted since European settlement from large, stand replacing disturbances to smaller-scale disturbances, resulting in aging forests and loss of early successional habitat within the region (White et al., 2011). The ongoing shift in disturbance regimes in EDF demands increased attention as to what constitutes early successional habitats and their importance in the landscape.

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The increasing availability of species' trait data allows for greater understanding of the distribution of plant traits in early post-disturbance forests, and how these traits change over succession. In turn, this provides insight into regeneration strategies, trophic dynamics, and conservation and management strategies for young forests and successional change. The concept of relating plant functional strategies to succession goes back at least as far as Grime's (1977) Competitive-Stress tolerant-Ruderal strategy categories. All three categories apply to our study: early successional tree species in EDF generally show certain ruderal characteristics of rapid growth and high dispersal abilities; mid to late successional species may be expected to have both competitive and stress tolerant characteristics such as traits conferring shade tolerance, slow growth with expansive canopies, and less investment in traits related to long-range seed dispersal. We used three traits to test how species functional strategies differ with time after disturbance across eight ecoregions of EDF: seed mass, wood density, and percent leaf nitrogen.

Variation in seed mass can be linked to tradeoffs in colonization and competition (Turnbull et al., 1999). Smaller, lighter seeds allow an individual to produce a greater number of seeds and usually do not require animal dispersal (Leishman et al., 2000). This is advantageous for disturbance dependent species by allowing for a bet hedging strategy of having the highest number of seeds in the highest number of places. At the other end of the seed-size spectrum, seedlings of large seeded species are generally more competitive and stress tolerant, particularly in low-light environments; this fits the strategy of late successional species, which often do not arrive at sites until canopies have largely closed (Clark and Ibanez, 2004). Seed mass also has a well-established, negative correlation with latitude in the northern hemisphere. Two possible explanations for this trend in EDF are: (1) larger seeds require longer periods of development, so shorter growing seasons in more northerly climates favor small seeds and (2) there are less vertebrate seed dispersers as latitude increases, lowering the dispersal ability of large seeded species (Moles et al., 2007).

Wood density also represents a tradeoff between fast growth and stress tolerance or competition (Swenson and Enquist, 2007). Lower wood density correlates with higher annual growth, but also increases the risk of cavitation, breakage, and susceptibility to fire (Chave et al., 2009). Although the relationship may be confounded by conifers, which are adapted to avoid cavitation risks at lower wood densities, later successional stands would be predicted to have a greater proportion of species with high wood density, as this greater stress tolerance also allows for greater maximum height (Swenson and Enquist, 2007). Wood density also has been shown to be negatively correlated with latitude and elevation.

Leaf nitrogen represents a similar tradeoff between faster growth through increased photosynthetic capacity and ability to tolerate stressful conditions such as herbivory (Wright et al., 2004). Over time, early post-disturbance stands would be predicted to have high percentages of leaf nitrogen, reflecting a colonization strategy of fast growth and rapid allocation of resources, while later successional stands would be predicted to have lower percent leaf nitrogen that reflects greater allocation to stem growth (competition) and lower photosynthetic rates (shade tolerance). Previous studies have failed to find a relationship between leaf nitrogen content and succession in tropical forests (Reich et al., 1995; Falster and Westoby, 2005). However, we know of no similar studies conducted in EDF, where nitrogen is more often a limiting nutrient. This limitation may result in shifting nitrogen allocation strategies more prominently in species of temperate forest compared to those in tropical forests.

Leaf nitrogen has been shown to have a weak, positive relationship with latitude (Reich and Oleksyn, 2004). This relationship is likely confounded by foliar leaf nitrogen being responsive to the increased, but spatially heterogeneous, anthropogenic nitrogen deposition of the last century (Gilliam, 2006). Although most studies of the effect of nitrogen deposition on plants have focused on herbaceous species, it has been observed to increase growth in fast-growing tree species, stunt growth in other trees with ectomycorrhizal fungal associations, and have no observed effect on other tree species (Pardo et al., 2011). This combination of factors could obscure our hypothesized patterns of leaf nitrogen.

Global latitudinal trends in plant functional traits suggest successional trends in eastern deciduous forest could vary over its distinct ecoregions (USDA Forest Service, 2004). Notably, EDF grades from west to east from midwestern prairies, through deciduous forest of the central US, the Appalachian Mountains and Piedmont, to coastal plain evergreen and mixed deciduous temperate forest. From north to south, it ranges from northern mixed conifer and hardwood forests of the Laurentian region to pine and mixed hardwood forests of the southern coastal plain. Here, we focus on hardwood forests; however, it is important to note that conifers can occur in high abundances in association with hardwood species at all stages of succession within the EDF. Conifers typically have low values on the spectrum of all three traits regardless of whether they are considered early- or late-successional species and we therefore have no *a priori* reason to assume their presence would affect our results. The ecoregions of the EDF also vary in climate, soils, disturbance patterns, and biogeographic history; these factors can combine to create unique trait compositions in all successional stages (Swenson and Weiser, 2010).

We used Forest Inventory and Analysis data (FIA; USDA Forest Service, 2013a) to investigate the relationship between age of eastern deciduous forests and the selected plant traits (seed mass, density, leaf nitrogen) to test the hypotheses that seed mass and wood density increase with stand age, while percent leaf nitrogen decreases with stand age. We also hypothesized that, as shown in previous research, seed mass and wood density would decrease, and leaf nitrogen increase with latitude.

2. Methods

2.1. Plot data

We used 39,569 plots from the Forest Inventory and Analysis (FIA) database (accessed June, 2013) to examine the variation in plant traits over succession. Plots were distributed from Minnesota to Louisiana eastward, and represented eastern deciduous forest; only plots with at least one dominant deciduous species or clade were used. Only the most recent sampling of a plot was used, and we removed plots that did not conform to the standard FIA sampling protocol or were missing variables needed in the analysis. We also removed all plots classified as wetlands, those showing evidence of artificial regeneration, and those with subplots in non-forested area or of variable stand age.

We used plot stand age, which is approximated in the field based on height and diameter of the dominant age class (USDA Forest Service, 2013b), as a proxy for successional stage; plots were categorized as early (0–20 year stand age), intermediate (21–80 year) or late (81 year or older). Each plot also was assigned to one of eight ecoregions within Bailey's ecoregion map (USDA Forest Service, 2004) based on plot latitude and longitude (Fig. 1). Although plots have their coordinates fuzzed to protect the plot location, the degree of fuzzing (typically within 0.5 miles) is unlikely to cause significant shifts in the ecoregion designation. Although the Prairie Division extends to the Gulf of Mexico, plots from this ecoregion in our dataset were found no further south than Missouri. Abundance was calculated for each species in each plot based on stem counts. Trait data were acquired from Swenson