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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

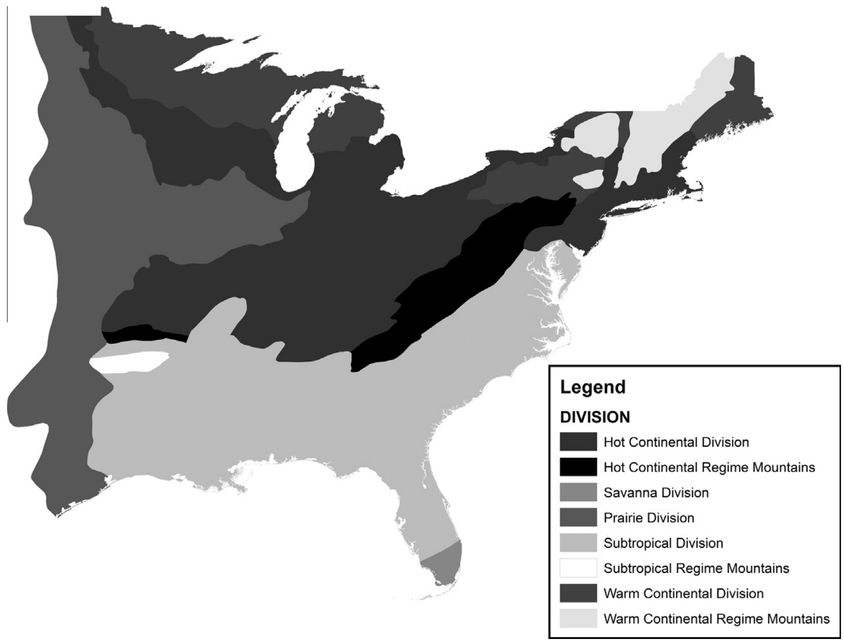

Fig. 1. Bailey's ecoregions. The eight divisions of Bailey's ecoregions used in the analyses.

and Weiser (2010), and supplemented from the literature (see Appendix A). The trait data provide species' means of wood density (dry mass divided by green mass in g/cm^3), seed mass (average mass of one seed in mg), and leaf nitrogen (percent nitrogen of dry matter). Trait scores for each plot are the abundance-weighted means for species present in that plot. A genus level mean was used when trees were identified only to genus, and plots containing species not in the trait database were excluded from analysis. Seed mass was log-transformed to normalize the overall species trait distribution. Stand age was truncated at 120 years due to the low number of older stands.

2.2. Analysis

Linear regression was used to examine plot trait scores relative to stand age; these regressions were calculated independently for each ecoregion. With ecoregions combined, multiple regression was used to examine how (1) latitude and stand age, and (2) ecoregion and stand age, predict plot trait scores. All models were compared using Akaike Information Criterion (AIC) and r^2 values. All analyses were run using R v. 2.15.3 (R Core Team, 2013). Figures were created using the ggplot2 package (Wickham, 2009). A map of seed mass scores for each plot within each successional category (early, intermediate, late) and each ecoregion was generated in ArcGIS (v. 10.1) to display the range of values within stand age categories and ecoregions.

3. Results

Seed mass was positively correlated with stand age in all eight ecoregions (Fig. 2). Stand age described 22% of the plot-to-plot variation in mean log seed mass for the Warm Continental Division (WCD), and over 10% for three other ecoregions (Table 1). In addition, the regression line intercept of log seed mass (mg) was 0.03 in the WCD, compared to the next lowest of 0.83 in the Warm Continental Mountain Region and the maximum of 1.66 in the Subtropical Division (Figs. 2 and 3). The WCD also had the second highest regression line slope, which suggests strongest increase in seed mass over succession in this ecoregion. Multiple regression showed that adding stand age to a linear model with either latitude or ecoregion as predictors improved the model fit for predicting seed mass, with ecoregion performing better than latitude (Table 2).

Wood density was positively correlated with stand age in seven of the eight ecoregions; only the Savannah Division lacked a significant relationship (Fig. 2). WCD again displayed the highest correlation between wood density and stand age (r^2 = 0.17; Table 1); no other ecoregion had an r^2 greater than 0.10, and five of the eight were less than 0.05. WCD also had the lowest regression line intercept and highest slope. Multiple regression showed that adding stand age to a linear model with either latitude or ecoregion as predictors improved the model fit for predicting wood density, although the model with latitude performed better than that with ecoregion (Table 2).

Leaf nitrogen was negatively correlated with stand age in four ecoregions, positively correlated in three ecoregions, and displayed no significant relationship in the Warm Continental Division Mountains (Fig. 2). The Savannah Division had the strongest relationship (r^2 = 0.11; Table 1), though this appears to be driven by a small number of early successional plots with high nitrogen values and should be interpreted cautiously. The Hot Continental Regime Mountains was the only other ecoregion with an r^2 higher than 0.05. The regression intercept varied among ecoregions, indicating regional differences in percent leaf nitrogen, but these differences appear independent of stand age. Multiple regression showed that ecoregion was a stronger predictor than latitude for leaf nitrogen (Table 2). Although adding stand age improved model fit according to AIC, the improvement in r^2 was negligible. Leaf nitrogen was observed to have the highest intercept in mid-latitude ecoregions (Table 1); including a quadratic term for latitude in the post hoc multiple regressions improved model fit substantially, but ecoregion remained a stronger fit (Table 2).

4. Discussion

4.1. Seed mass

Seed mass increased with stand age in all EDF ecoregions, supporting our hypothesis. The strongest correlation was observed in

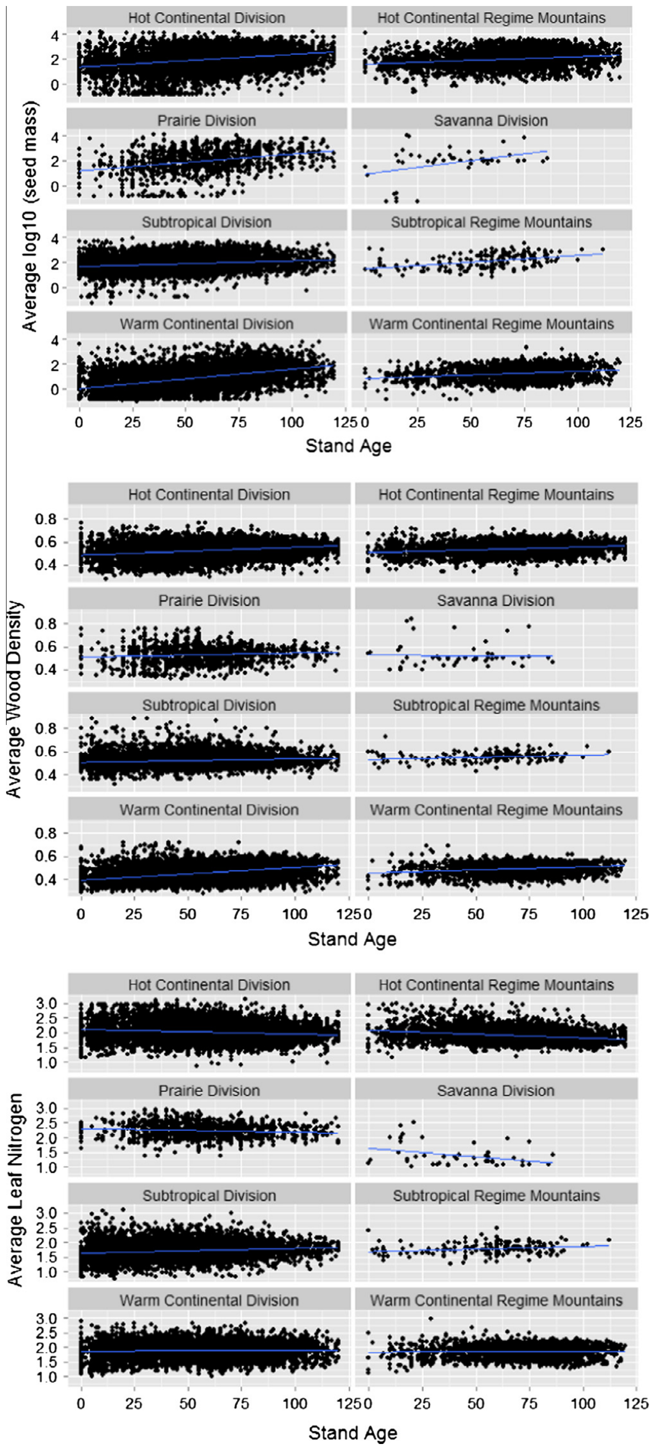

Fig. 2. Plot trait scores versus stand age by ecoregion – each point represents the abundance weighted trait mean of all species within a plot.

the Warm Continental Division (WCD), which extends from northern Minnesota eastward to northern Michigan and covers northern sections of New England. The low regression intercept value and high slope drive the higher correlation in this ecoregion. This implies that early successional plots of WCD contain species with lower seed mass relative to other ecoregions rather than higher seed mass species occupying late successional plots. Typical early successional species in this zone include *Populus tremuloides* and *Betula papyrifera*, which are among the smallest seeded species in the dataset. Smaller seeded species represent a shift toward increased numbers of seeds produced at the expense of seedling survival. Additionally, smaller seeds are more likely to rely on chance processes such as wind or water dispersal, which could be either an advantage or disadvantage depending on the availability of animal dispersers. This allows for a greater number of seeds in a greater number of areas, which would benefit disturbance dependent species. Additionally, smaller seeds are more easily worked into the soil, allowing longer persistence (Leishman et al., 2000) and perhaps greater survival following fire due to increased insulation.

The trend of increasing seed mass with time since disturbance may become weaker as one moves south over EDF ecoregions for several reasons. First, succession is observed to occur more rapidly as one moves south (Wright and Fridley, 2010); this may be due in part to large seeded species, such as those in the *Fagaceae* family, establishing more quickly in younger plots. Second, very light seeded species may have low seedling establishment or be outcompeted by more shade tolerant seedlings of larger-seeded species in the denser vegetation of early post-disturbance southern forests. Typical early successional species at lower latitudes include *Liriodendron tulipifera*, *Acer rubrum*, *Pinus taeda*, and *Diospyros virginiana* which occur in the mid to upper range of seed mass. Several of these are animal dispersed and *A. rubrum* has modifications for wind dispersal which increase its seed mass. Thus, seed mass and dispersal strategies in lower latitudes may be more equal across successional communities. In addition, Subtropical Division plots may include longleaf pine communities which have a more consistent species composition of *Pinus palustris* and *Quercus virginiana* across successional stages, obscuring potential trends in seed mass over time. Weaker relationships between seed mass and stand age in the Warm and Hot Mountain Regimes may also be attributable to heavier seeded early successional species such as *Prunus pensylvanica* and *Acer negundo*, persistent conifer presence in late successional plots, and earlier establishment of heavy seeded species such as *Quercus montana* and *Tilia americana*.

4.2. Wood density

The Warm Continental Division showed the strongest positive relationship between stand age and wood density. All other regions displayed either a weak correlation or no correlation. As with seed mass, the relationship between wood density and stand age in WCD has a low intercept and higher slope. The shorter growing season at higher latitudes may favor colonizing species that can gain diameter, and therefore height, rapidly. Although high wood density species may be able to persist from year to year as saplings, severe disturbances that reset successional age can prevent their reestablishment as trees for some time. At lower latitudes, with longer growing seasons, the time required for a high wood density species requires to reach the sub-canopy or canopy may become short enough to obscure differences over stand age.

Moving south from the WCD, the trend of increasing wood density with stand age is still weakly evident in the mid-latitude ecoregions, Hot Continental Division and Hot Continental Regime Mountains, but interestingly is completely absent in the Prairie Division. Historically higher fire frequency in this region could have selected against lighter wood densities, which may be more prone to girdling from fire. Fire adaptation could also lead to increasing seed mass with stand age for the Prairie Division as older stands may have been without fire long enough to select for larger seeded species. Overall, however, the stronger relationship between latitude and wood density suggests temperature and growing season are the main drivers of wood density in early post-disturbance forests.

Table 1
Plot trait scores versus stand age by ecoregion – linear models for trait scores versus stand age for all eight ecoregions. Models are best interpreted using r^2 as low p-values are driven by the large number of plots used in most ecoregions.

Ecoregion	r^2	Intercept	Slope	Std. Err.	p-value	t value	Number of plots
Seed mass							
Hot Continental Division	0.095	1.34	0.010	2.7E−4	<0.0001	38.6	14,091
Hot Continental Mountains	0.048	1.58	0.006	4.3E−4	<0.0001	14.0	3868
Prairie Division	0.11	1.20	0.013	9.6E−4	<0.0001	13.9	1564
Savanna Division	0.15	0.93	0.022	7.4E−3	<0.01	2.91	49
Subtropical Division	0.041	1.66	0.005	2.4E−4	<0.0001	19.3	8578
Subtropical Mountains	0.18	1.48	0.011	1.7E−3	<0.0001	14.3	183
Warm Continental Division	0.22	0.03	0.016	3.1E−4	<0.0001	50.5	9033
Warm Continental Mountains	0.053	0.83	0.006	5.2E−4	<0.0001	11.1	2203
Wood density							
Hot Continental Division	0.066	0.49	6.7E−4	2.1E−5	<0.0001	31.6	14,091
Hot Continental Mountains	0.053	0.51	4.9E−4	3.3E−5	<0.0001	14.7	3868
Prairie Division	0.011	0.51	3.5E−4	8.5E−5	<0.0001	4.08	1564
Savanna Division	1.4E−4	0.53	−5.7E−5	7.1E−4	0.94	−0.081	49
Subtropical Division	0.025	0.51	3.2E−4	2.1E−5	<0.0001	14.8	8578
Subtropical Mountains	0.045	0.53	3.7E−4	1.3E−4	<0.0001	2.92	183
Warm Continental Division	0.17	0.39	1.1E−3	2.6E−5	<0.0001	43.2	9033
Warm Continental Mountains	0.047	0.46	5.3E−4	5.1E−5	<0.0001	10.5	2203
Leaf Nitrogen							
Hot Continental Division	0.016	2.11	−0.0015	1.0E−4	<0.0001	−14.9	14,091
Hot Continental Mountains	0.062	2.08	−0.0025	1.6E−4	<0.0001	−15.9	3868
Prairie Division	0.014	2.31	−0.0013	2.8E−4	<0.0001	−4.63	1564
Savanna Division	0.11	1.64	−0.0058	0.0024	<0.05	−2.46	49
Subtropical Division	0.028	1.63	0.0017	1.1E−4	<0.0001	15.6	8578
Subtropical Mountains	0.042	1.67	0.0018	6.2E−4	<0.01	2.82	183
Warm Continental Division	0.0011	1.87	3.0E−4	9.7E−5	<0.01	3.13	9033
Warm Continental Mountains	7.5E−4	1.84	2.7E−4	2.1E−4	0.20	1.29	2203

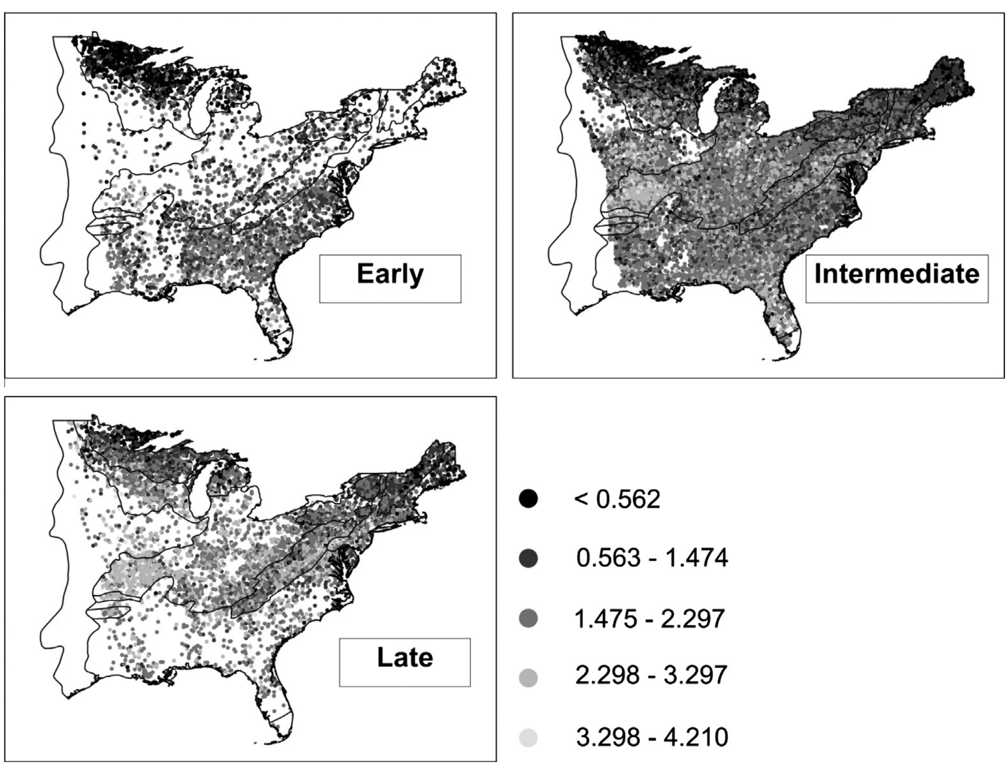

Fig. 3. Geographic distribution of seed mass across different successional stages. Average per-plot seed mass (mg) in early (<20 y), middle (21–80) and late (>80) successional forests. Dark lines are Bailey's ecoregions (USDA Forest Service, 2004).

4.3. Leaf nitrogen

The absence of a relationship between stand age and leaf nitrogen mirrors results of similar studies in tropical forests (Reich et al., 1995; Falster and Westoby, 2005) and does not support our hypothesis that the EDF's more nitrogen limited soil might increasingly constrain leaf nitrogen content and photosynthetic capacity over time. This result appears to contradict Grime's classic CSR model, which predicts that disturbance adapted species acquire resources relatively rapidly for fast growth and early

Table 2
Linear and multiple regressions by trait scores – linear and multiple regressions predicting trait scores. AIC and r^2 were used to inform model selection. Models best fitting the data in the most parsimonious manner are in italics.

Model	r^2	AIC	Std. Error	p-value	F-statistic	df
Seed mass						
Latitude	0.22	89,981	0.754	<0.0001	10861.7	1/39,567
Ecoregion	0.20	87,612	0.732	<0.0001	1998.1	7/39,561
Latitude + stand age	0.32	84,475	0.704	<0.0001	9196.4	2/39,566
Ecoregion + stand age	0.34	83,228	0.693	<0.0001	2533.0	8/39,560
Wood density						
Latitude	0.19	−109905	0.0603	<0.0001	9137.1	1/39,567
Ecoregion	0.20	−110301	0.0600	<0.0001	1382.5	7/39,561
Latitude + stand age	0.28	−114400	0.0570	<0.0001	7519.8	2/39,566
Ecoregion + stand age	0.26	−113305	0.0578	<0.0001	1695.4	8/39,560
Leaf nitrogen						
Latitude	0.067	10,705	0.277	<0.0001	2843.6	1/39,567
Latitude (quadratic)	0.19	5113	0.258	<0.0001	4641.9	2/39,566
Ecoregion	0.22	3870	0.254	<0.0001	1550.6	7/39,561
Latitude + stand age	0.068	10,676	0.276	<0.0001	1438.0	2/39,566
Ecoregion + stand age	0.22	3852	0.254	<0.0001	1359.9	8/39,560
Latitude (quadratic) + stand age	0.19	5010	0.258	<0.0001	3136.8	3/39,565

reproduction, though there are several more attractive explanations for the absence of the expected pattern. First, leaf nitrogen may not be an appropriate trait for measuring resource capture in tree species. It is additionally possible that a pattern of higher leaf nitrogen in the earliest periods of succession could be masked over a 120 year timespan (Reich et al., 1995), or that species level traits do not account for intraspecific plasticity that may differentiate communities. Finally, spatial heterogeneity in nitrogen deposition may influence composition and species abundance at multiple stages of succession, thereby masking expected temporal patterns (Gilliam, 2006; Pardo et al., 2011).

The hump shaped distribution of leaf nitrogen across latitude in EDF was driven by mid-latitude ecoregions (HCD, HCRM, and PD) having higher average leaf nitrogen values and may reflect higher soil fertility in these regions. Ordoñez et al. (2009) demonstrated that leaf nitrogen content correlates with several metrics of soil fertility. However, the high leaf nitrogen values of the Hot Continental Mountains Regime, which follows the Appalachians from Pennsylvania down to northern Alabama and is characterized by highly weathered, nutrient poor Ultisols contradict this relationship (Bailey, 1995). An alternative explanation is that these regions are more affected by nitrogen deposition, which in turn influences the tree community. This is partially supported by Clark et al. (2013), who showed that nitrogen deposition in the eastern US has exceeded critical nitrogen loads for long enough to have already had a substantial impact on the herbaceous communities of much of the region. Superficially, the most impacted regions in terms of the effect on biodiversity (Clark et al., 2013) appear to align with our ecoregions with the highest plot level nitrogen values. There remains a paucity of research, however, on how nitrogen deposition affects tree communities. Our results indicate that there may be promise in merging a community level functional trait approach with plot level nitrogen deposition and soil data for greater understanding of the issue.

4.4. Conclusion

The pattern of increasing seed mass and wood density with stand age supports a ruderal/colonization – competition/stress tradeoff, or shift from light-seeded, fast-growing trees to heavier-seeded, slower-growing species over succession. However, we also found evidence for an interactive effect of geography and stand age in relation to functional ecology of tree species. Seed mass was most geographically consistent in responding to stand age, though the relationship was stronger at higher latitudes. Wood density was strongly influenced by stand age only at northern latitudes, and was not related to age in regions with higher historic fire frequency or at lower latitudes. Although leaf nitrogen was strongly tied to ecoregion, the lack of a relationship with stand age is perplexing given the importance of leaf physiology to herbivory defense, resource acquisition, and allocation. The relationship is likely confounded by nitrogen deposition, and future investigation of the relationship of other leaf traits, such as C:N, photosynthetic capacity, or specific leaf area, with stand age, especially in the southern EDF, where we did not detect strong successional trait differences could yield more compelling results.

This demonstration of variation in traits across EDF and succession has important conservation and management implications. In combination with species composition, functional differences provide a more complete picture of forest diversity and structure. Further, functional traits provide linkages among ecosystem components; for example, seed size impacts dispersers, while wood density and leaf traits can affect decomposition, nutrient cycling, and herbivory. Our analysis indicates early post-disturbance forest harbors a unique combination of functional traits related to plant dispersal and growth. Further, a shift in plant traits over succession indicates disturbance that creates a mosaic of forest stand ages is important for maximizing not just species diversity, but functional diversity as well.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.01.018.

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