

**FROM OLD FIELDS TO FORESTS: UNDERSTANDING PLANT SUCCESSIONAL
DYNAMICS THROUGH THE LENS OF FUNCTIONAL TRAITS**

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ABSTRACT

Peter Alan Wilfahrt: From old fields to forests: Understanding plant successional dynamics through the lens of functional traits
(Under the direction of Peter S. White)

Vegetative succession describes the turnover of plant species through time. This turnover enables coexistence of species temporally, but also spatially as different locations co-occur at different successional stages. Moreover, the suite of species that occupy different successional stages varies due to heterogeneous environments across both local and regional spatial scales. Understanding the processes that underlie succession as well as those that drive spatial variation in the species that comprise similar successional stages is a central goal in ecology. In order to understand these processes in this dissertation, I recast species into functional traits that connect species physiologies to their environments. Using a suite of traits thought to influence species success at various stages of succession, I examine functional trait changes through time in plant communities of the eastern US. Chapters 2 and 3 use an old field experiment to examine how soil nutrients and plant enemies influence temporal dynamics of early secondary succession by examining species-level trait responses (Chapter 2) and community-level trait responses (Chapter 3). Old fields are important and well-studied community types due to their frequency in the landscape and lend themselves well to experimental manipulation given the relatively rapid life cycles and small stature of their constituent herbaceous species. Chapters 4 and 5 use a continental-scale forest database to examine similar processes in trees, albeit at larger spatial and

temporal gradients. Chapter 4 uses a space-for-time substitute approach to ask how tree community traits change along a forest age gradient, while Chapter 5 asks how traits of tree seedling communities respond to forest disturbances using resampled plots. In Chapter 6, I synthesize my findings on trait responses to successional gradients in these two distinct successional stages. Overall, I found that seed mass, indicative of dispersal strategy, and investment in structural biomass (plant height and wood density) capture plant successional strategies. Leaf traits, however, did not consistently vary with succession or the manipulated environmental gradients in the old field experiment. Rather, leaf traits displayed large, unexplained variation across space, suggesting that they are responding to processes related to spatial heterogeneity independent of succession.

To my brother, Andrew C. Wilfahrt, I miss your implacable curiosity of the world and your fondness for the absurd every day.

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CHAPTER 1 : INTRODUCTION

Succession is the process of species turnover through time following a disturbance that removed a significant portion of biomass (Chase and Leibold 2003). Understanding the processes driving dynamics of successional plant communities is a long-standing interest in ecology (Clements 1904). Early studies examining shifts in composition through time were critical in advancing our understanding of ecological systems and the processes that structure them (Oosting 1942, Pickett et al. 1987). Exposing the underlying processes that occur during succession is critical to understanding how species coexist across space and through time (Pickett and White 1985). However, inferring mechanistic processes from composition alone is notoriously difficult, particularly in observational studies (Gotelli and Graves 1996). The increasing availability of functional trait data for plant species allows for stronger inferences and greater understanding of structuring processes (Lavorel and Garnier 2002, Spasojevic and Suding 2012). Functional traits connect species to their environment, as biotic and abiotic gradients create performance filters that act on a species' physiology in determining community membership (Webb et al. 2010). Traits detailing a species allocation of resources to leaves, height, and seed capture an array of species ecological tradeoff strategies that cause them to vary in fitness across heterogeneous environments (Westoby 1998). This dissertation examines successional dynamics through the lens of functional traits at two distinct stages of succession: early herbaceous communities and wooded forest communities.

The deciduous forest of eastern North America is a well-studied system for exploring the community dynamics during the process of succession (Braun 1950, Denslow 1980, Peet and

Christensen 1988). Widespread anthropogenic disturbance followed by extensive agricultural abandonment has resulted in a regional patchwork of vegetation at multiple stages of succession, from early herbaceous communities characterized by relatively rapid compositional turnover to forested communities composed of long lived woody species that have community dynamics that play out over decades to centuries (Pickett 1982). The different temporal dynamics and physical stature of these two distinct stages of succession have resulted in different scientific approaches to their study, with herbaceous systems lending themselves to experimental manipulation, while forested systems are often interpreted using long-term observational studies. Despite these differences, understanding the continuity of the system is important as the properties of the early successional communities, both abiotic and biotic, have ramifications for the establishment of subsequent woody communities (Oosting 1942, Wright and Fridley 2010).

The first portion of this dissertation examines succession during the herbaceous stage of post-agricultural abandonment. Isolating the mechanisms that structure communities requires experimental manipulation. The small stature, fast life-cycle, and often ephemeral nature of herbaceous communities such as early successional habitats make them appropriate habitats for such manipulation. As such, community succession mechanisms are emergent and well-studied at this level (HilleRisLambers et al. 2012). Even in the typically short time spans of experiments, important temporal dynamics may emerge from repeated sampling (Cardinale et al. 2007). I use trait data from an old field experiment that I implemented with Fletcher Halliday and Rob Heckman of Dr. Charles Mitchell's lab to examine mechanisms driving early successional turnover. We created an artificial disturbance in experimental plots by spraying herbicide on and removing existing vegetation, and then constructed artificial communities with different starting plant diversity levels, soil resource supply rates, and access by natural enemies. Following this,

we allowed natural colonization from the surrounding community to occur and measured plant community composition for four years. In doing so, we were able to examine how leaf-height-seed traits captured tradeoff axes by which species navigated environments that started at different successional stages and had variable top-down and bottom-up environmental conditions.

Chapter 2 examines how population trajectories of species relate to their functional traits. It specifically asks whether two ecological strategy tradeoffs, competition-colonization and growth-defense, exist in this system and how they relate to seed mass, vegetative height, and specific leaf area. These tradeoff axes are mechanisms thought to enable coexistence in plant assemblages, but it remains unclear how they relate to each other. This chapter also examines ten species in further detail by quantifying how they change in abundance in response to increased soil resource supply and diminished enemy access and whether changes in abundance corresponded to within-species variation in height or specific leaf area values.

Chapter 3 expands on Chapter 2 by scaling up to the community level. This chapter uses species trait data to examine how dominant processes related to colonization and competition changed along a temporal gradient in the experiment. It tests whether colonization dynamics are impacted by initial diversity, used here as a proxy for different successional status, how that influences the community-weighted trait means of invading species, and whether soil resource supply and enemy access further alter observed relationships. It further asks how observed trait patterns change two years later when herbaceous canopies have closed and competition is expected to be more intense. Additionally, the chapter examines how within-species variation shapes community trait patterns in response to these drivers.

The second portion of this dissertation examines similar dynamics as those studied in the herbaceous stage, but at the much broader spatial and temporal scale of forests. In forest ecosystems, both natural and anthropogenic disturbances are part of the dominant paradigm, which creates a landscape mosaic of forests in different stages of succession (Pickett and White 1985). The unpredictability of major disturbance and long temporal dynamics make the study of such systems inherently difficult to study. Space-for-time studies (Pickett 1989) are often used to quantify population and community dynamics that describe successional trajectories. Classically, species identity is an instrumental component of understanding forest succession (Denslow 1980), with tree species are often categorized as light dependent or shade tolerant to understand the underlying process of species turnover (Valladares and Niinemets 2008). This is convenient shorthand for describing a tradeoff across species from being able to rapidly colonize a site with increased resource abundance, or being a long-term competitor capable of eventually shading out the colonizing species. However, successional dynamics are more complex than this single tradeoff. The emergence of more readily available trait information for species enhances our ability to infer mechanisms that drive post-disturbance colonization and competition dynamics (Mouillot et al. 2013). Combined with long-term datasets or space-for-time substitutes, functional traits can greatly increase our understanding of forested systems.

Chapters 4 and 5 of this dissertation use the Forest Inventory and Analysis (FIA) database (“Forest Inventory and Analysis Database v.4.0” 2013), curated by the USDA along with tree species trait data to understand succession and disturbance in the eastern United States temperate forests. In chapter 4, I used estimated stand age data in the FIA database to arrange forest plots along a successional sequence across the eastern US. I calculated community weighted means of adult trees in each plot for three traits thought to be related to succession: seed mass, leaf

nitrogen, and wood density. The goal of this study was to quantify differences in trait patterns between early and late successional communities, determine whether patterns were significant across ecoregions of the eastern US, and make inferences about what this revealed of successional processes. Chapter 5 builds off of Chapter 4 by examining tree seedling recruitment in post-disturbance forests using an expanded set of functional traits, adding maximum height, shade tolerance, and drought tolerance. Using repeated sampling of FIA plots allowed me to overcome limitations of the space-for-time substitution approach while also capturing disturbance occurrences. Seedling recruitment is the first stage of post-disturbance forest recovery, so this is a narrow view of succession in that regard. I again examined variation in these patterns across ecoregions in the eastern US and regressed changes in traits with climate data in order to tease apart specific drivers of variation.

I conclude by synthesizing results from these two seemingly disparate stages of succession, old field and forest. In doing so, I examine similarities and differences in the mechanisms that enable species coexistence across space and time.

REFERENCES

- Braun, L. E. 1950. Deciduous forests of Eastern North America. Hafner, New York, NY.
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America* 104:18123–8.
- Chase, J. M., and M. A. Leibold. 2003. Ecological niches : linking classical and contemporary approaches. The University of Chicago Press, Chicago.
- Clements, F. 1904. The development and structure of vegetation. The Woodruff-Collins Printing Company, Lincoln, Nebraska.
- Denslow, J. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 21:18–21.
- Forest Inventory and Analysis Database v.4.0. 2013. . <http://apps.fs.fed.us/fiadb-downloads/datamart.html>.
- Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C.
- HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics* 43:227–248.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. *Trends in ecology & evolution* 28:167–77.
- Oosting, H. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist* 28:1–126.
- Peet, R., and N. Christensen. 1988. Changes in species diversity during secondary forest succession on the North Carolina Piedmont. Pages 233–245 *in* H. During, M. Werger, and J. Willems, editors. *Diversity and Pattern in Plant Communities*. SPB Academic Publishing, The Hague, The Netherlands.
- Pickett, S. 1982. Population patterns through twenty years of oldfield succession. *Vegetatio* 49:45–59.

- Pickett, S. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 in G. E. Likens, editor. *Long-Term Studies in Ecology: Approaches and Alternatives*. Springer, New York, NY.
- Pickett, S., S. Collins, and J. Armesto. 1987. Models, mechanisms and pathways of succession. *The Botanical Review* 53:335–371.
- Pickett, S., and P. S. White. 1985. *The Ecology of Natural Disturbances and Patch Dynamics*. Academic Press, New York, NY.
- Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *J. Ecol.* 100:652–661.
- Valladares, F., and Ü. Niinemets. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics* 39:237–257.
- Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology letters* 13:267–83.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and soil* 199:213–227.
- Wright, J. P., and J. D. Fridley. 2010. Biogeographic synthesis of secondary succession rates in eastern North America. *Journal of Biogeography* 37:1584–1596.

CHAPTER 2 : RECONCILING SPECIES POPULATION TRAJECTORIES WITH FUNCTIONAL TRADEOFF AXES IN AN EXPERIMENTAL OLD FIELD

Introduction

Ecological tradeoffs may manifest as variable population trajectories among species across heterogeneous environments and underlying these tradeoffs are functional traits which confer a species an advantage in acquiring or retaining resources in some environments, while potentially disadvantaging them in others (Webb et al. 2010). This results in species arrayed along multiple ecological tradeoff axes (Díaz et al. 2016). Community ecology seeks to understand how these species level tradeoffs scale up to allow assemblages of species to locally coexist. A plethora of community-level metrics exist to allow for such inferences, but often these metrics blur specific responses of species (Supp and Ernest 2014). Examining shifting species abundances in response to environmental drivers alongside relevant functional traits may elucidate niche differences between species that provide the foundation for community dynamics (McGill et al. 2006).

Herbaceous species often constitute the early stages of post-disturbance, successional habitats and their relatively rapid life cycles provide an opportunity to quantify population trajectories over short time periods (Tilman 1990, Meiners 2007, Lind et al. 2013). Prior to exclusion by closed woody canopies, early successional species respond to a variety of biotic and abiotic pressures including competition for limited soil nutrients and enemy pressure from herbivores and disease (Souza et al. 2016). In order to complete their life cycles and maintain

populations, species must either tolerate or avoid these pressures. Population dynamics of species across space and time may reveal their ecological strategies in regards to these co-occurring pressures. Tilman (1994) developed theoretical models of competition-colonization tradeoffs that detailed how species that compete for the same limiting resource can coexist by occupying different temporal niches. Species that peak early in abundance, deemed ‘colonizers’, rely on high resource environments of post-disturbance habitats before superior competitors arrived and draw resources down to a level which excludes colonizers. This tradeoff has been challenged on theoretical and conceptual grounds since competition is not strictly hierarchical between species; for instance a seedling of a superior light competitor cannot drawdown light availability to an adult individual of an inferior light competitor (Yu and Wilson 2001). Despite this, the theory has received empirical support in plant communities (Turnbull et al. 1999, Mouquet et al. 2004; though see Jakobsson and Eriksson 2003) and in microcosms of aquatic microfauna (Cadotte et al. 2006). The discrepancies in evidence and among conceptual underpinnings raise questions of how fully competition-colonization tradeoffs can describe species coexistence. Moreover, competition-colonization dynamics may exist in a system while being masked by stronger processes such as spatial heterogeneity which drives other species tradeoffs (Levine and Rees 2002). For instance, Lind et al. (2013) used population trajectories of herbaceous species from a global grassland study to detail that species exhibit tradeoffs along soil resource and enemy pressure axes. They found that species shifts in abundance in response to increased soil nutrient availability were generally positively correlated with abundance responses to removal of natural enemies, concluding that this indicated a general growth-defense tradeoff in herbaceous species. This means that species which invest in defense do so at the cost of decreased growth rates, as opposed to investing in defense in place of traits conferring interspecific competitive advantages.

Colonizers can potentially avoid a growth-defense tradeoff due to a lack of competition for resources in recently disturbed habitats (Chase and Leibold 2003), but could also be hindered by low soil resources (Bergholz et al. 2015) or herbivory (Olf and Ritchie 1998). The relationship between tradeoff axes such as competition-colonization and growth-defense remains unclear.

Examining population dynamics is attractive as one can make inferences into ecological tradeoffs without collecting trait data, which can be costly and time-consuming. Nonetheless, it remains unclear how these population trajectories map onto species trait data. Trait data can complement species abundance data by providing information on physiological aspects of a species that underlie the ecological tradeoffs controlling changes in abundance. How a species variously allocates resources to its leaves, stature, and seeds is indicative of its ecological strategy (Westoby 1998) and may be readily captured by measuring a species specific leaf area (SLA), maximum vegetative height, and seed mass respectively. Leaf and stature traits can impact a species abundance by controlling individuals' ability to accumulate biomass or by influencing frequency-dependent negative population growth which may reflect niche processes (Schroeder-Georgi et al. 2015). Seed mass is commonly used as a trait capturing competition-colonization tradeoffs, with low seed mass providing colonizers an increased likelihood to disperse to a recently disturbed community (Turnbull et al. 1999a, Levine and Rees 2002, Mouquet et al. 2004). Interspecific differences generally account for most of the variation in traits, but within-species variation often accounts for a non-negligible amount of variation within a species assemblage as well (Siefert et al. 2015). This within-species trait plasticity may itself be a fitness mechanism by allowing species to adjust traits toward some environmental optimum. These within-species responses to environmental conditions can be examined at the community level (Lepš et al. 2011, Siefert and Ritchie 2016, Chapter 3), or across species themselves

(Mitchell and Bakker 2016). Examining species-level trait plasticity may reveal patterns of within-species variation that is not apparent at the community level. For instance, it may be that the species that are able to vary their traits may gain a competitive advantage.

This study investigates how species population trajectories reveal ecological tradeoffs, and how a trait scheme of leaf, height, and seed traits captures these trajectories. Using a four year experimental herbaceous community, we ask whether species sort temporally in a manner consistent with competition-colonization theory, whether resource availability and enemy access drive additional tradeoff axes manifesting in population dynamics, and how these tradeoff axes relate to one another. Further, we ask whether these population tradeoff axes correlate with LHS traits consistent with how environmental conditions are expected to influence where species allocate resources to aboveground tissue across resource heterogeneity. Finally, we ask whether trait plasticity within species correlate with population responses under different environmental conditions.

Methods

Study system

This study was conducted in an herbaceous old field, Widener Farm, located within the Duke Forest in the Piedmont of North Carolina, USA. The site has been maintained as an old field since 1996, and prior to that was an agricultural field since the 1950s. Dominant vegetation is comprised of perennial grasses such as *Andropogon virginicus*, *Schedonorus arundinaceus*, and *Anthoxanthum odoratum*. The site receives an average of 1221mm of annual precipitation and has an average annual temperature of 15° C.

Experimental design

In order to test the effects of soil resource supply and enemy access on species population and trait dynamics, we used a randomized, complete block design with factorially crossed fertilization and pesticide treatments. These treatments were also crossed with a planting treatment that manipulated diversity, but we consider these treatments here only as far as they changed the initial abundances of several planted species. In 2011, we established 260, 1x1 m plots across 5 spatial blocks. These plots were denuded by applying glyphosate herbicide (Riverdale® Razor® Pro, Nufarm Americas Inc, Burr Ridge, IL), raked to remove dead aboveground biomass two weeks later, and then covered with landscape fabric to impede natural recolonization. One meter wide alleys between plots were left vegetated.

Diversity treatments were established by assigning plots to one of three treatment levels: monoculture, 5 species polycultures, and unplanted control. Six, perennial herbaceous species that already occurred at Widener Farm were selected and seedlings were grown in a greenhouse. The species included three grasses, *Andropogon virginicus*, *Setaria parviflora*, and *Tridens flavus*; two asters, *Packera anonyma* and *Solidago pinetorum*; and one mint, *Scutellaria integrifolia*. These species were germinated in a greenhouse, transplanted out to the field into the denuded plots, and given a year to establish before natural colonization occurred. More details on the planting treatment can be found in Chapter 3. Natural colonization occurred from the seed bank and surrounding alleys and communities, and no effort was made to maintain or advantage the planted species once natural colonization occurred. Control plots were denuded of aboveground vegetation at the same time and covered with landscape fabric, but did not receive any planting treatment. There were six possible polyculture species combinations, each excluding one of the six planted species, and six possible monocultures, creating 13 possible

initial community compositions. Because density was kept constant between monocultures and polycultures, polycultures started with lower abundances for any given planted species. These 13 compositions were fully replicated across the soil resource and enemy access treatments and across all five blocks.

Enemy access was manipulated by assigning plots to one of two treatment levels: control and pesticide application. Pesticide application involved spraying foliar fungicide (mancozeb, Dithane® DF, Dow AgroSciences, Indianapolis, IN) and insecticide (es-fenvalerate, Asana® XL, Dupont, Wilmington, DE) every two to three weeks during the growing season from July 2012 to September of 2015; the first application occurred after we removed the landscape fabric in July of 2012. Neither the fungicide nor insecticide had any non-target effects on plant growth of common Widener Farm species under greenhouse conditions.

Soil nutrient supply was manipulated by assigning plots to one of two treatment levels: control and fertilization. Fertilization involved yearly application of 10 g/ m² N as slow-release urea, 10 g/m² P as super triple phosphate, and 10 g/ m² K as potassium sulphate, each in slow release form to increase soil nutrient supply throughout the growing season. The first application occurred after we removed the landscape fabric in July of 2012 and in May of each subsequent year. In total, our study system comprised 260 plots (5 replicate blocks × 13 community compositions × 2 nutrient supply levels × 2 enemy access levels).

Plant surveys

Plots were surveyed for species presence and percent cover of all vascular plants at the end of the growing season for four years post-planting (2012-2015). Percent cover was measured within a centrally located 0.75 × 0.75 m subplot in each plot to avoid edge effects and used as a metric for species abundance. An additional survey conducted in June of 2014 (mid-growing

season) was used to inform trait data collection, but was not used to measure species population dynamics. For each survey, we searched within the subplot area for all rooted vascular plants (and also non-rooted vines) before jointly estimating the percent cover.

Trait data

Specific leaf area (SLA) was measured in July of 2014 immediately following the June cover survey. In each plot, we selected species in descending order of percent cover until 80% of the relative cover of that plot from the July 2014 survey was accounted for as per Pérez-Harguindeguy *et al.* (2013). Then, we selected ten leaves in each plot by cycling through its species list in descending order of cover. For instance, if six species accounted for >80% of the relative cover, two leaves were selected for the four most abundant species, and one leaf for the remaining two species. Thus, when a species accounted for a large portion of the relative cover of a plot, it would have high replication of sampling within that plot (max. five leaves per species per plot), while plots with high evenness would have less replication of any single species. Leaves within species were chosen randomly from within the plot, but an effort was made not to sample from the same ramet when a species was sampled multiple times. In total, 2590 leaves were sampled across the experiment; an average of 4.5 species were selected per plot. Species with multiple samples per plot were averaged within a plot.

We measured height data in September 2014 immediately following the cover survey in the same month. Similar to SLA, we selected species in descending order of percent cover until 80% of the relative cover was accounted for. Then the tallest individual, not including reproductive structures, was identified and we measured the distance between the ground and the tallest vegetative portion of the plant as it stood naturally. Because the variable of interest was a

species height potential in any given plot, replication of a species occurred only across plots. This resulted in 1124 individuals being measured with an average of 4.3 species per plot.

In order to examine species specific trait responses of height and SLA, we selected only species which had at least ten measurements for both traits in each of the following four treatment conditions: unfertilized, fertilized, unsprayed, sprayed. This resulted in ten species, including four of the species which were planted as part of the richness treatment (Table 2.1). We also used these ten species for species specific abundance responses to soil resource supply and enemy access treatments.

Seed mass data were acquired from Royal Botanic Gardens Kew (2016) for the most common species in the experiment. Where multiple masses were reported, we took the mean value from all sources reported; *S. integrifolia* and *S. pinetorum* were not present in the database, so we selected the value of their nearest phylogenetic neighbor (Table 2.1). Because these data were not collected locally, we were unable to estimate within-species variation, though several studies suggest that within species means of seed mass are not variable across environments (Violle et al. 2009, Kazakou et al. 2014). Seed mass values were log transformed at the species level to normalize the data as they ranged across four orders of magnitude.

Population trajectories

We used the repeated cover surveys to estimate population trajectories through time of the most frequent species in the experiment. We selected only species that occurred in at least 10% of the plots in at least one year and those which we had data on for at least one of the three traits. Finally, we omitted two tree species (*Pinus taeda* and *Liquidambar styraciflua*) which had begun to establish seedlings in our plots as tree species differ greatly in height in seed mass. This resulted in 30 species total, which accounted for 93-97% of the total cover in the four sampling

periods. Average time to maximum abundance in a plot was used as a proxy to estimate species colonization-competition strategy (*sensu* Meiners 2007). This was calculated for each species by identifying each plot a species was found in throughout the experiment and then, for each of those plots, identifying which survey year it had the highest percent cover in, and then averaging all plot values for that species. For planted species, we only considered the 140 plots where a species was not planted because we could not distinguish individuals that arrived via colonization from those that were planted. Time to maximum abundance was used in place of average time to colonization of a plot because many species likely established a persistent seed bank after 15 years of repeated disturbance from mowing in the field. Thus, the time lag to peak abundance is likely more representative of whether a species relies on post-disturbance resource environments due to diminished dispersal limitations in this system. For population trajectories related to enemy access and soil resource supply, we compared a species' abundance in the control and manipulated plots for each treatment by calculating the log of the average abundance in a treatment plot divided by the average abundance in its control plot; therefore positive values indicate higher abundance in the treatment plots and negative values indicate higher abundance in the control plots. For this calculation, we omitted plots that had received both the fertilization and spraying treatment, so that mean log ratio responses were restricted to the treatment of interest. This was conducted for the 2014 census data as this was when enemy and soil resource effects were most evident (see Chapter 3) and matches when trait data were collected.

Statistical analyses

Relationships among species' population trajectories and traits were analyzed with Pearson correlations, and relationships with a p-value of less than 0.05 were considered significant. Seed mass was log-transformed to meet assumptions of normality. General linear

mixed effect models were used to determine differences between species traits and abundance in September 2014 using the nlme package in R (Pinheiro et al. 2016). Three separate models predicted vegetative height, SLA, and abundance of the ten species with adequate trait data (described above). In each model, experimental treatments and species identity were used as fixed effects with interaction terms between species and treatments; the diversity treatment was included as a covariate to account for the data structure but we do not report results here. Random effects were plot nested within block. This approach allows testing for trait and abundance differences between species in response to treatments while accounting for structure in the data that may arise from unmeasured environmental gradients at the plot and block level that could influence species responses (Mitchell and Bakker 2014). We used a Tukey post-hoc test to examine species specific responses to treatments and adjusted for multiple comparisons. Abundance data was log transformed and plots where a species had never been recorded in any year were omitted, thus a species could be recorded absent only if it had previously been observed in a plot. This was done to avoid inflating ‘zeroes’ that were a result of failure to disperse to a site as opposed to a failure to establish in a site. For species that were planted as part of the diversity treatments, we used only those plots where they were planted in this analysis. This was done because we observed colonization into non-planted plots in later years of several of these species that was not evident early on, but generally these occurred with low abundance. Presumably this occurred as seed rain was increased from plots where they were planted, meaning these species colonized later on in the experiment under different environmental conditions.

Results

Species displayed a broad range of responses in population trajectories and trait values suggesting a variety of life histories strategies. The three population trajectory metrics were not correlated with one another (Figure 2.1), suggesting that they represent different tradeoff axes. Traits were similarly uncorrelated with one another. Time to maximum abundance had significant, positive correlations with seed mass ($r = 0.36$) and maximum height ($r = 0.48$), and a significant, negative correlation with SLA ($r = -0.46$). Species abundance responses to spraying were negatively correlated with SLA ($r = -0.53$) but unrelated to seed mass or maximum height. Species abundance responses to soil resource supply were not significantly related to SLA or seed mass, and had a significant positive correlation with height ($r = 0.48$).

There were strong, among-species differences in abundance, max height, and SLA in 2014 (Table 2.1). While soil resource supply did not affect overall cover, it did have significant interactions with the species variable. Enemy exclusion significantly increased overall cover, and also interacted significantly with species. Tukey's post-hoc comparisons revealed that it was generally not the same species reacting to soil resource supply and enemy access, and three species did not differ in abundance across any of these treatments (Figure 2.2). This reinforces that species have unique life history strategies and the lack of a tradeoff axis connecting soil resource supply and enemy access in this experiment such as that found by Lind et al. (2013). An increase in height and decrease in SLA was observed in response to reduction in enemy access via spraying, and soil resource supply also led to an increase in height (Table 2.2). Both soil resource supply and enemy access treatments interacted with species in height responses, although Tukey post-hoc comparisons revealed only two species showed increased height in fertilized plots, and two different species increased in height in response to pesticide spraying

(Figure 2.3). Interestingly, *Scutellaria integrifolia* was one of the species that increased in height in fertilized plots, and *Lonicera japonica* increased in height following spraying, but they were two of three species that did not show changes in abundance in response to either treatment. However, it should also be noted that we used a conservative test statistic, so although they were not all statistically significant, 8 of the 10 species appeared to have increased height responses to both fertilization and spraying. SLA showed a significant interaction between soil resource supply and species identity, but not between enemy access and species identity. However, only one species, *Anthoxanthum odoratum*, showed a significant shift in SLA in sprayed plots, and this did not appear to impact its abundance (Figure 2.4).

Discussion

Species differed in their population dynamics across time and in response to enemy access and soil resource supply. All three LHS traits examined correlated with time to peak abundance, signifying that traits related to resource acquisition and allocation (height and SLA) and dispersal (seed mass) capture colonization-competition tradeoffs. Species population dynamics across time and in response to experimental treatments were unrelated to one another, suggesting that species have additional niche differentiation along the colonization-competition gradient. Species were idiosyncratic in their response to soil resource supply and enemy exclusion, both in terms of abundance and trait plasticity. The apparent lack of a synchronized response between which species had significant changes in abundance and which had significant trait responses suggest that although species may adjust to changing environments, trait plasticity itself was not a general mechanism by which species increased their abundance across treatments.

A shift from low to high seed mass represents a shift from low to high parental investment per seed, but also a shift from high to low fecundity (Leishman et al. 2000). This makes seed mass an attractive trait for investigating colonization-competition tradeoffs, as low seed mass enables higher dispersal from maternal individuals, while heavier seeded germinants may have increased capacity to persist in environments with low resource availability. As such seed mass is an often-used trait for investigating competition-colonization tradeoffs in plant communities (Turnbull et al. 1999, Levine and Rees 2002, Mouquet et al. 2004). We found a general pattern of low seed mass species peaking in abundance earlier than heavy species, but SLA and vegetative height were more strongly related to this population trajectory. Given that SLA, height, and seed mass were uncorrelated with one another, this suggests that multiple selection pressures are operating on species across time. Species that peaked in abundance early had a high SLA which is consistent with an ‘acquisitive’ strategy, where species are able to rapidly acquire resources at the expense of short lived leaves (Wright et al. 2004). Shorter species were also more likely to peak early, signifying that colonizers did not invest resources into structural biomass which may be adequate in low competition, post-disturbance habitats, but result in competitive exclusion as other, taller species arrive. Together, this suggests that early arriving species allocate resources towards maximal leaf surface area at the expense of height and leaf longevity. These are characteristics which are consistent with maximizing resource capture in low competition environments and potentially indicate increased resource availability for reproduction, but likely require short life cycles as they are outcompeted in later years. This is consistent with the low seed mass that also characterized early peaking species.

We did not find evidence for a growth-defense tradeoff (Lind et al. 2013) or an alternatively proposed and orthogonal competition-defense tradeoff (Viola et al. 2010) in this

system; instead species responses to the enemy access and soil resource supply treatments were uncorrelated with one another. This is surprising given that Lind et al. (2013) found growth-defense tradeoffs to be ubiquitous across a coordinated, global grassland experiment. Moreover, one of their sites which demonstrated this tradeoff was located in Widener Farm, adjacent to our experiment. However, two major differences exist between these studies. First, they did not remove extant vegetation meaning that communities started later in the successional sequence. While compositional outcomes along nitrogen gradients were independent of initial composition in a Minnesota grassland (Inouye and Tilman 1995), resetting communities to early stages of succession could result in the delayed emergence of observable community-level tradeoffs (Laliberte et al. 2012). Second, they examined the effects of vertebrate herbivores, while we suppressed invertebrate herbivores and fungal pathogens. Invertebrate herbivores may selectively disadvantage forbs (La Pierre et al. 2015). This is consistent with three of our four forb species increasing in abundance in sprayed plots, though we cannot disentangle the effects of invertebrate herbivores and fungal pathogens in this study. If this selectivity does not occur among vertebrate browsers, it could result in different emergent tradeoffs. Here, we observed distinctive population trajectories suggestive of multiple co-occurring tradeoff axes instead of a single axis capturing both bottom-up and top-down processes. Moreover, this was not a result of less common species driving the results, as the ten most common species in the experiment also had idiosyncratic abundance responses to soil resource supply and enemy access. Only one species, *Packera anonyma*, had significant responses to both treatments, and these responses were in opposite directions.

Soil resource supply and enemy access log ratio responses also correlated with different traits, height and SLA respectively, further indicating that different species are filtered by these

environmental conditions. These trait differences emerged primarily among species. Within-species height variation appeared to have similar responses to spraying and fertilization. Although only several species had significantly increased height values in response to either treatment, there was a general within-species increase of height with 8 of the 10 species analyzed appearing to have increased in height. Borer et al. (2014) proposed that enemy suppression and increased soil resources could both lead to decreased light availability as more plant biomass accumulates aboveground, and these potentially increased height values are consistent with this. *Lonicera japonica*, a climbing vine, was one of the species that had a significant increase in height in response to the spraying treatment. Because *L. japonica* requires other species for structural support, its increased height also supports a general increase in plot height. Height is a prevalent structuring trait for species fitness in this system, arraying species along a colonization-competition axis, a soil resource availability axis, and shows largely consistent within-species responses to soil resource supply and enemy access treatments.

Population trajectories in response to enemy access and soil resource supply were uncorrelated with the competition-colonization axis. Colonizers responded similarly to these treatments during early periods of succession as competitors did during later periods of succession. Thus, the species in our system that took advantage of early, low competition environments were still variable in their response to soil resource supply and enemy access in later years. Species which rely on disturbed patches may face more complex restrictions than solely unoccupied environments, including having competitive tradeoffs with other ‘colonizers’ (Turnbull et al. 2004). This also highlights that commonly used traits such as SLA and height may capture multiple tradeoff axes within species, despite the population trajectories being uncorrelated themselves.

The co-occurrence of multiple tradeoff axes interacting with each other during succession lays a foundation for species coexistence. If colonizers differ among each other in their capacity to drawdown resources and tolerate enemy damage, then they may coexist by stratifying across spatial gradients where these factors vary. When competition-colonization tradeoffs also exist, with varying patches of time since last disturbance, additional species can coexist. Ultimately, population trajectories and functional traits jointly reveal these ecological strategies, suggesting both approaches should be used in conjunction.

REFERENCES

- Bergholz, K., F. Jeltsch, L. Weiss, J. Pottek, K. Geißler, and M. Ristow. 2015. Fertilization affects the establishment ability of species differing in seed mass via direct nutrient addition and indirect competition effects. *Oikos* 124:1547–1554.
- Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, P. B. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, L. Biederman, D. Blumenthal, C. S. Brown, L. A. Brudvig, Y. M. Buckley, M. Cadotte, C. Chu, E. E. Cleland, M. J. Crawley, P. Daleo, E. I. Damschen, K. F. Davies, N. M. DeCrappeo, G. Du, J. Firn, Y. Hautier, R. W. Heckman, A. Hector, J. HilleRisLambers, O. Iribarne, J. A. Klein, J. M. H. Knops, K. J. La Pierre, A. D. B. Leakey, W. Li, A. S. MacDougall, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, B. Mortensen, L. R. O'Halloran, J. L. Orrock, J. Pascual, S. M. Prober, D. A. Pyke, A. C. Risch, M. Schuetz, M. D. Smith, C. J. Stevens, L. L. Sullivan, R. J. Williams, P. D. Wragg, J. P. Wright, and L. H. Yang. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508:517–20.
- Cadotte, M., D. Mai, S. Jantz, and M. Collins. 2006. On Testing the Competition-Colonization Trade-Off in a Multispecies Assemblage. *The American Naturalist* 168:704–709.
- Chase, J. M., and M. A. Leibold. 2003. Ecological niches : linking classical and contemporary approaches. The University of Chicago Press, Chicago.
- Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet'ev, H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function. *Nature* 529:167–171.
- Inouye, R. S., and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 years of nitrogen addition. *Ecology* 76:1872–1887.
- Jakobsson, A., and O. Eriksson. 2003. Trade-offs between dispersal and competitive ability: a comparative study of wind-dispersed Asteraceae forbs. *Evolutionary Ecology* 17:233–246.
- Kazakou, E., C. Violle, C. Roumet, M.-L. Navas, D. Vile, J. Kattge, and E. Garnier. 2014. Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science* 25:235–247.
- Laliberte, E., B. Shipley, D. A. Norton, and D. Scott. 2012. Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology* 100:662–677.
- Leishman, M. R., I. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pages 31–58 in M. Fenner, editor. *Seeds: The Ecology of Regeneration in Plant*

- Communities. Second edition. CAB International, New York, NY.
- Lepš, J., F. de Bello, P. Šmilauer, and J. Doležal. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography* 34:856–863.
- Levine, J. M., and M. Rees. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *American Naturalist* 160:452–67.
- Lind, E. M., E. Borer, E. Seabloom, P. Adler, J. D. Bakker, D. M. Blumenthal, M. Crawley, K. Davies, J. Firn, D. S. Gruner, W. S. Harpole, Y. Hautier, H. Hillebrand, J. Knops, B. Melbourne, B. Mortensen, A. C. Risch, M. Schuetz, C. Stevens, and P. D. Wragg. 2013. Life-history constraints in grassland plant species: a growth-defence trade-off is the norm. *Ecology letters* 16:513–21.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in ecology & evolution* 21:178–85.
- Meiners, S. J. 2007. Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88:1098–1104.
- Mitchell, R. M., and J. D. Bakker. 2014. Quantifying and comparing intraspecific functional trait variability: a case study with *Hypochaeris radicata*. *Functional Ecology* 28:258–269.
- Mitchell, R. M., and J. D. Bakker. 2016. Grass abundance shapes trait distributions of forbs in an experimental grassland. *Journal of Vegetation Science*.
- Mouquet, N., P. Leadley, J. Mériguet, and M. Loreau. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. *Oikos* 1:77–90.
- Olf, H., and M. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* 13:261–265.
- Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. Bret-Harte, W. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas, P. Reich, L. Poorter, I. Wright, P. Ray, L. Enrico, J. G. Pausas, A. de Vos, N. Buchmann, G. Funes, F. Quétier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter Steege, M. van der Heijden, L. Sack, B. Blonder, P. Poschlod, M. Valeritti, G. Conti, A. Staver, S. Aquino, and J. H. C. Cornelissen. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*.
- La Pierre, K. J., A. Joern, and M. D. Smith. 2015. Invertebrate, not small vertebrate, herbivory interacts with nutrient availability to impact tallgrass prairie community composition and forb biomass. *Oikos* 124:842–850.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2016. nlme: Linear and Nonlinear Mixed

- Effects Models. R package version. <http://CRAN.R-project.org/package=nlme>.
- Royal Botanic Gardens Kew. 2016. Seed Information Database (SID). Version 7.1. <http://data.kew.org/sid/>.
- Schroeder-Georgi, T., C. Wirth, K. Nadrowski, S. T. Meyer, L. Mommer, and A. Weigelt. 2015. From pots to plots: Hierarchical trait-based prediction of plant performance in a mesic grassland. *Journal of Ecology*. Blackwell Publishing Ltd.
- Siefert, A., and M. E. Ritchie. 2016. Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. *Oecologia*.
- Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, C. Baraloto, M. B. Carlucci, M. V. Cianciaruso, V. de L. Dantas, F. de Bello, L. D. S. Duarte, C. R. Fonseca, G. T. Freschet, S. Gaucherand, N. Gross, K. Hikosaka, B. Jackson, V. Jung, C. Kamiyama, M. Katabuchi, S. W. Kembel, E. Kichenin, N. J. B. Kraft, A. Lagerström, Y. Le Bagousse-Pinguet, Y. Li, N. Mason, J. Messier, T. Nakashizuka, J. M. Overton, D. A. Peltzer, I. M. Pérez-Ramos, V. D. Pillar, H. C. Prentice, S. Richardson, T. Sasaki, B. S. Schamp, C. Schöb, B. Shipley, M. Sundqvist, M. T. Sykes, M. Vandewalle, and D. A. Wardle. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18:1406–1419.
- Souza, L., T. J. Zelikova, and N. J. Sanders. 2016. Bottom-up and top-down effects on plant communities: nutrients limit productivity, but insects determine diversity and composition. *Oikos* 125:566–575.
- Supp, S. R., and S. K. M. Ernest. 2014. Species-level and community-level responses to disturbance: a cross-community analysis. *Ecology* 95:1717–1723.
- Tilman, D. 1990. Constraints and Tradeoffs: Toward a Predictive Theory of Competition and Succession. *Oikos* 58:3–15.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Turnbull, L., D. Coomes, A. Hector, and M. Rees. 2004. Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology*:97–109.
- Turnbull, L., M. Rees, and M. Crawley. 1999a. Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology* 87:899–912.
- Turnbull, L., M. Rees, and M. Crawley. 1999b. Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology*:899–912.
- Viola, D. V., E. a Mordecai, A. G. Jaramillo, S. a Sistla, L. K. Albertson, J. S. Gosnell, B. J. Cardinale, and J. M. Levine. 2010. Competition-defense tradeoffs and the maintenance of

- plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* 107:17217–22.
- Violle, C., H. Castro, J. Richarte, and M.-L. Navas. 2009. Intraspecific seed trait variations and competition: passive or adaptive response? *Functional Ecology* 23:612–620.
- Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology letters* 13:267–83.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and soil* 199:213–227.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–7.
- Yu, D. W., and H. B. Wilson. 2001. The competition-colonization trade-off is dead; long live the competition-colonization trade-off. *The American Naturalist* 158:49–63.

Table 2.1 - Species trait information. The ten species in the first section were used for the within-species trait analyses. Abbreviations correspond to those in Figures. 2-4.

Species	Abbr.	Family	Seed mass (mg / 1000)	Max height (cm)	Average SLA (cm ² /mg)
<i>Andropogon virginicus</i>	ANVI	Poaceae	0.30	36.3	0.296
<i>Anthoxanthum odoratum</i>	ANOD	Poaceae	0.55	49.5	0.196
<i>Holcus lanatus</i>	HOLA	Poaceae	0.30	35.3	0.264
<i>Lonicera japonica</i>	LOJA	Caprifoliaceae	2.2	48.2	0.168
<i>Packera anonyma</i>	PAAN	Asteraceae	0.23	28.9	0.099
<i>Schedonorus arundinaceus</i>	SCAR	Poaceae	2.4	65.8	0.159
<i>Scutellaria integrifolia</i>	SCIN	Lamiaceae	1.6 (<i>S. incana</i>)	48.7	0.167
<i>Solanum carolinense</i>	SOCA	Solanaceae	2.4	57.5	0.148
<i>Sorghum halapense</i>	SOHA	Poaceae	5.0	115.7	0.202
<i>Solidago pinetorum</i>	SOLI	Asteraceae	0.41 (<i>S. juncea</i>)	73.7	0.114
<i>Acalypha virginica</i>	-	Euphorbiaceae	0.61	-	-
<i>Apocynum cannabinum</i>	-	Apocynaceae	1.1	108.7	0.135
<i>Carex complanata</i>	-	Cyperaceae	2.1	47.4	0.151
<i>Chamaecrista nictitans</i>	-	Fabaceae	2.2	-	-
<i>Conyza canadensis</i>	-	Asteraceae	0.08	94.9	0.229
<i>Daucus carota</i>	-	Apiaceae	1.0	39.0	0.284
<i>Dichanthelium dichotomum</i>	-	Poaceae	0.08	38.0	0.218
<i>Digitaria sanguinalis</i>	-	Poaceae	0.51	47.6	-
<i>Erigeron annuus</i>	-	Asteraceae	0.03	88.2	0.183
<i>Eragrostis capilaris</i>	-	Poaceae	0.09	37.0	0.167
<i>Gamochaeta purpurea</i>	-	Asteraceae	0.037	-	-
<i>Lespedeza cuneata</i>	-	Fabaceae	1.6	101	0.154
<i>Oxalis dillenii</i>	-	Oxalidaceae	0.19	31.2	-
<i>Plantago lanceolata</i>	-	Plantaginaceae	1.3	33.5	0.168
<i>Poa pratensis</i>	-	Poaceae	0.30	-	-
<i>Rumex acetosella</i>	-	Polygonaceae	0.7	56.2	0.257
<i>Salvia lyrata</i>	-	Lamiaceae	1.2	24.0	0.231
<i>Schyzachyrium scoparium</i>	-	Poaceae	1.1	41.6	-
<i>Setaria parviflora</i>	-	Poaceae	1.6	38.7	-
<i>Tridens flavus</i>	-	Poaceae	1.0	48.0	0.207

Table 2.2 - Results of linear mixed models analyzing how soil resources and enemy access influenced abundance, height, and SLA responses of ten common species in the experiment. Random intercept terms were plots nested within block.

	df	F	P
Abundance			
Species	9 / 1336	987.1	<0.0001
Soil Resources	1 / 251	0.339	0.56
Enemy Access	1 / 251	8.57	<0.01
Soil x Species	9 / 1336	20.47	<0.0001
Enemy x Species	9 / 1336	10.95	<0.0001
Height			
Species	9 / 665	269.1	<0.0001
Soil Resources	1 / 251	28.0	<0.0001
Enemy Access	1 / 251	44.98	<0.0001
Soil x Species	9 / 665	2.74	<0.01
Enemy x Species	9 / 665	2.67	<0.01
SLA			
Species	9 / 674	349.9	<0.0001
Soil Resources	1 / 251	3.35	0.069
Enemy Access	1 / 251	15.77	<0.0001
Soil x Species	9 / 674	4.97	<0.0001
Enemy x Species	9 / 674	1.42	0.18

Figure 2.1 - Relationship among species of population trajectories and trait means. Pearson's r and p -values in the upper diagonal describe the correlation of the scatterplots in the lower diagonal, where each point represents a species. Time to max abundance is the average year a species peaked in abundance in all plots it ever occurred in. Enemy access and soil resource are the log ratio responses of species to the experimental treatments in 2014; positive values correspond to higher abundances relative to the control plots.

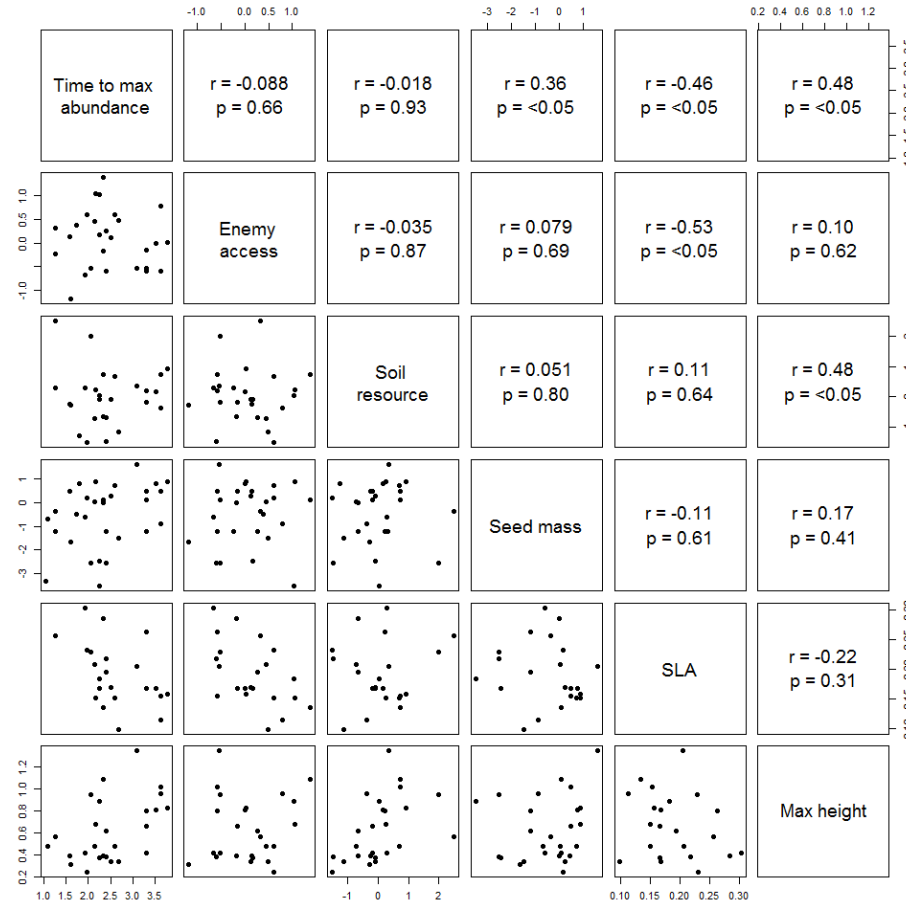


Figure 2.2 - Effects of soil resource supply and enemy access on species abundances in the third growing season of the experiment (2014). Boxplots represent model predictions of ANOVA models on individual species data; grey points show the raw data, jittered for clarity. Letters above the data indicate where treatments were significantly different from one another. Models only consider plots where the species was found; ANVI, PAAN, SCIN, and SOPI were part of the planting treatment and models for these species only consider plots where they were planted.

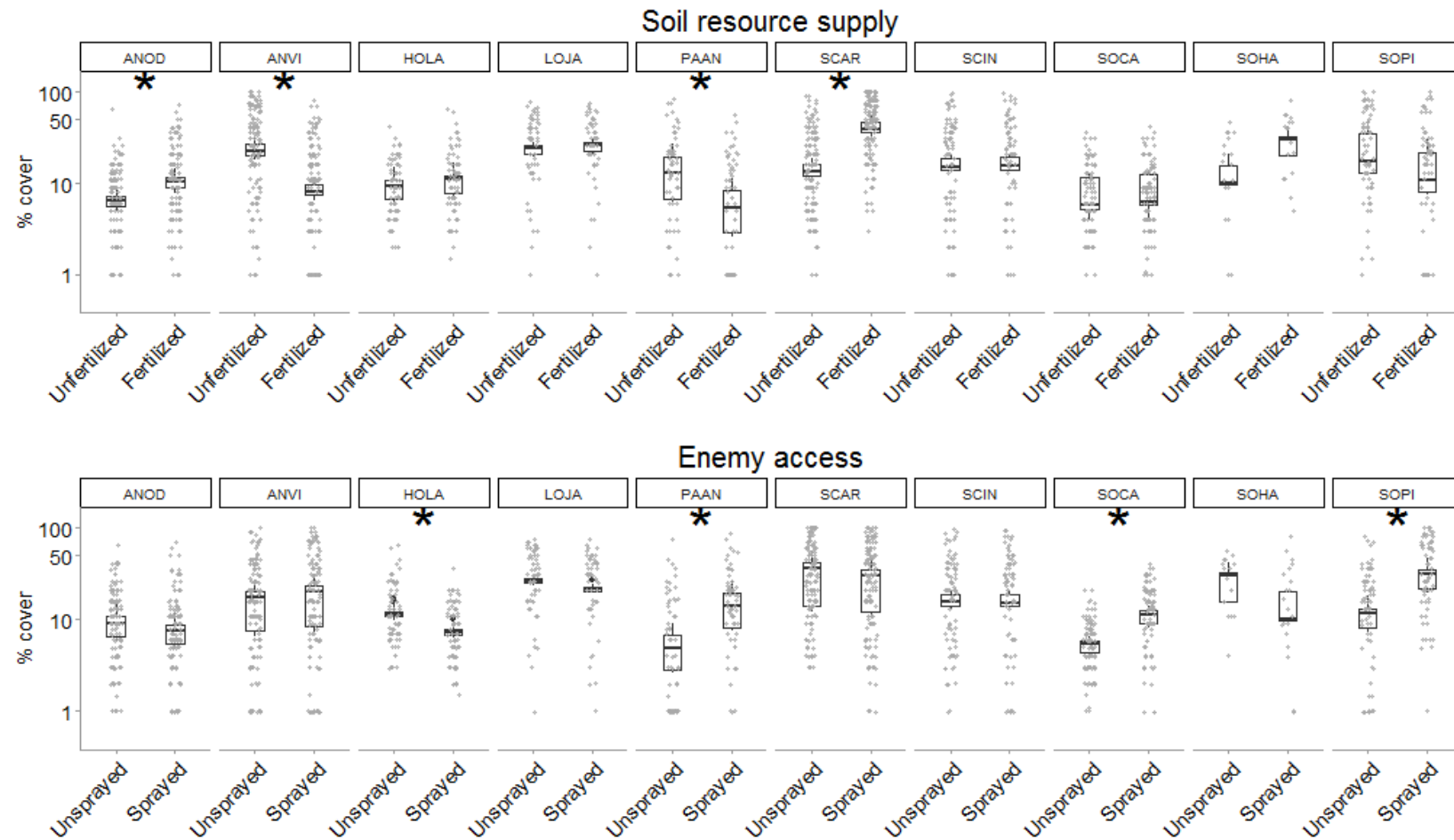


Figure 2.3 - Effects of soil resource supply and enemy access on species height in the third growing season of the experiment (2014). Boxplots represent model predictions of ANOVA models on individual species data; grey points show the raw data, jittered for clarity. Letters above the data indicate where treatments had significantly different height values from control plots. Trait data was only collected for a species where it was locally abundant.

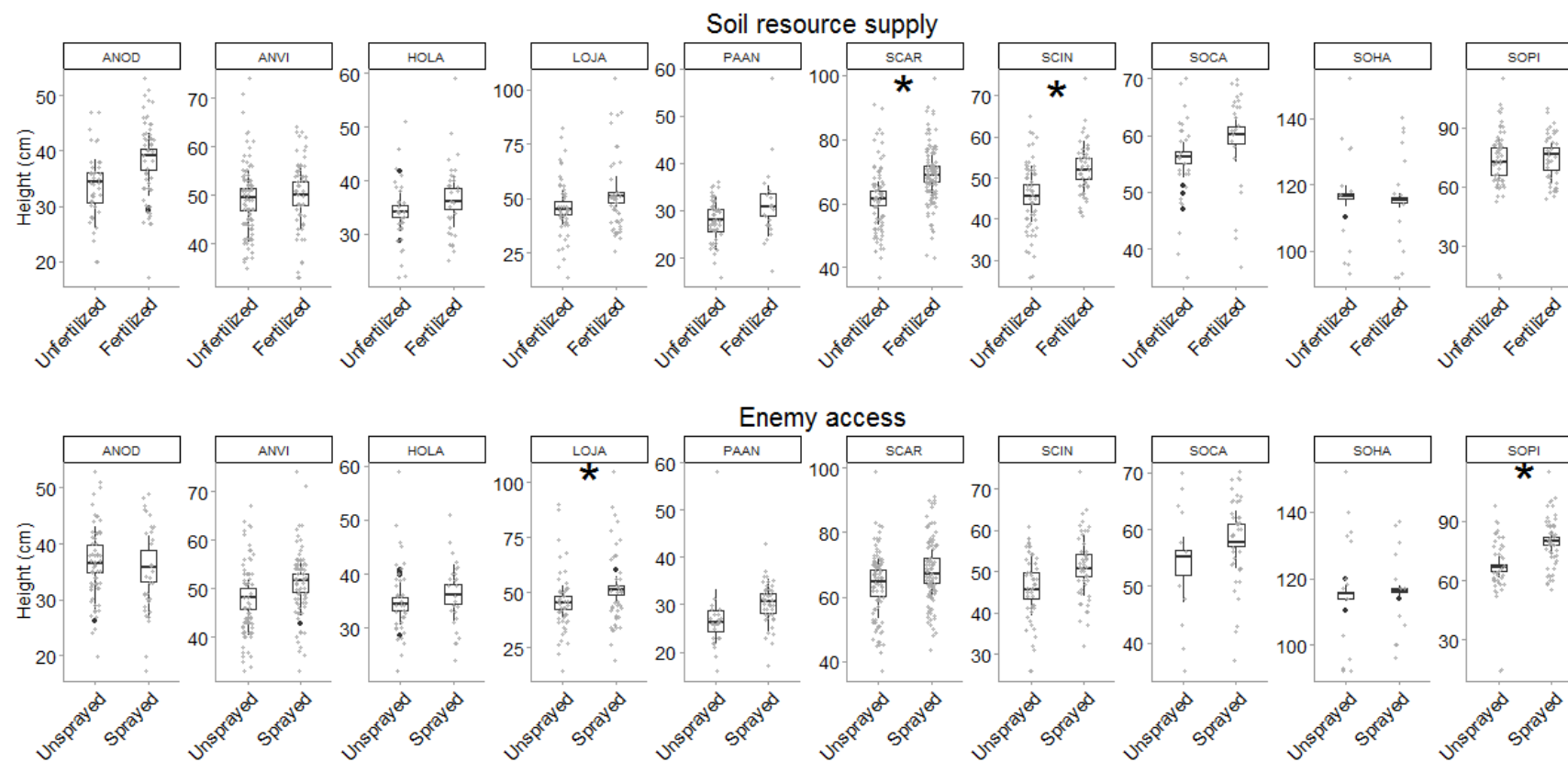
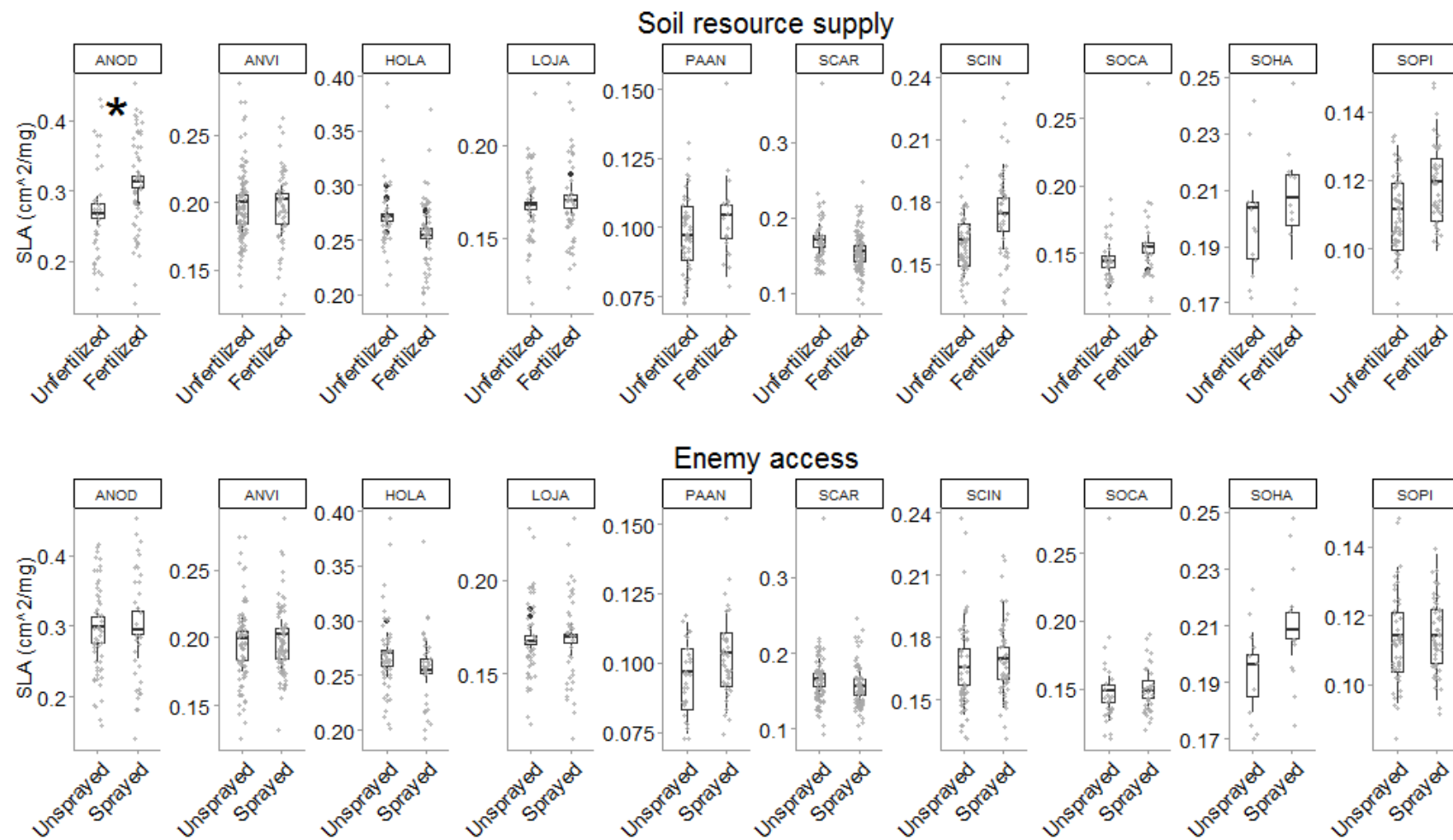


Figure 2.4 – Effects of soil resource supply and enemy access on species SLA in the third growing season of the experiment (2014). Boxplots represent model predictions of ANOVA models on individual species data; grey points show the raw data, jittered for clarity. Letters above the data indicate where treatments had significantly different SLA values from control plots. Trait data was only collected for a species where it was locally abundant.



CHAPTER 3 : EFFECTS OF INITIAL PLANT DIVERSITY, SOIL RESOURCE SUPPLY, AND ENEMY ACCESS ON COMMUNITY TRAIT PATTERNS DURING OLD FIELD SUCCESSION

Introduction

Succession drives community turnover through time, generally in response to change in the most limiting resource. For plant communities, diminishing ground-level light availability is often the most evident and rapid change in resource availability (Chase and Leibold 2003). This may result in competition-colonization tradeoffs among species, where good colonizers rely on recently disturbed, resource-rich habitats and good competitors arrive later but draw down resources and eventually competitively exclude colonizers (Tilman 1994). However, additional niche differences arising from bottom up soil resource supply or top down herbivory may alter the trajectory of community composition during succession by modifying colonizer and competitor success (Pacala and Rees 1998, Lind et al. 2013). Community-level plant functional traits reflect shifting ecological strategies of constituent species as their fitness changes in response to shifting successional resource environments (Webb et al. 2010). Westoby (1998) posited that tradeoff axes relating to colonization and competition are indicated by a species investment in leaf, height, and seed (LHS) traits. These tradeoffs may result in a species being a poor soil nutrient competitor but good light competitor (Dickson et al. 2014); having increased susceptibility to herbivory or disease but being capable of rapid growth (Throop and Lerdau 2004), or investing in a bet-hedging strategy enabling high dispersal of offspring, at the expense of high individual seedling mortality (Leishman et al. 2000). Investigating these processes in an

early successional system using the LHS framework reveals the relative strengths of structuring factors on plant communities across temporal gradients and environmental conditions.

Recently disturbed communities may see a species fail to establish despite being biologically suited because it either fails to disperse to that area, or it disperses but the germinule is unable to persist due to asymmetric competition from extant vegetation (Tilman 2004). This promotes a competition-colonization tradeoff among species that can be captured by measuring species seed mass (Turnbull et al. 1999, Mouquet et al. 2004). Species adopting a colonization strategy have high fecundity and low seed mass, allowing them to disperse to a greater number of sites. Species investing in a competition strategy have larger seeds but lower fecundity, with the advantage of increased parental investment per seed which may confer offspring with increased chances of survival when germinating underneath extant vegetation (Leishman et al. 2000). Following this, members of recently disturbed communities may exhibit lower average seed mass due to reduced competition from extant individuals favoring the ‘colonizer’ strategy. As communities undergo succession following disturbance, competition may increase as stronger competitors with larger seeds begin to colonize the community. Moreover, the severity of disturbance (i.e. amount of biomass removed) may leave communities at different stages of succession. Communities that have higher diversity levels in post disturbance communities may have higher resource drawdown and reduce the fitness of low seed mass species more immediately.

Competition for multiple limited soil nutrients acts as a stabilizing mechanism for coexistence, with a multitude of studies showing that fertilization leads to loss of species richness (Grime 1973, Rajaniemi et al. 2003, Suding et al. 2005, Harpole and Tilman 2007, Dickson and Foster 2011, Dickson et al. 2014). Evidence suggests that adding soil nutrients

shifts competition from belowground to aboveground, allowing species previously limited by a soil nutrient deficit to outcompete other species for light (Hautier et al. 2009, Borer et al. 2014). However, several studies have found that light reduction does not fully explain loss of diversity, suggesting that belowground competition is still occurring (Rajaniemi et al. 2003, Dickson and Foster 2011). Because light competition is highly asymmetric, vegetative height is a straightforward trait to measure to understand light competition (Westoby et al. 2002). To grow taller than its neighbors, an individual must invest in structural biomass, potentially at the cost of root or leaf biomass. As such, higher maximum height potential may be advantageous in habitats where light is more limiting than soil nutrients, while the cost of increased structural biomass may be disadvantageous where light is less limiting.

The presence of plant enemies, namely herbivores and pathogens, can reduce the biomass of plant photosynthetic organs and induce physiological changes within leaves (Agrawal 2001, Aldea et al. 2005). Thus, enemy pressure causes species to incur a cost due to either lost tissue or by diverting resource investment from growth and reproduction to mechanical or chemical defenses. In turn, enemy presence can alter community trait composition by filtering out individuals with suboptimal investment in defense mechanisms, which act on variation both between and within-species. If enemy presence is reduced, species that rely on rapid growth and replacement of lost tissue may have a competitive advantage over those that invest in defense. Specific leaf area (SLA) is a proxy for a species investment in defense versus growth (Cronin et al. 2010). Species with low SLA have a low leaf area to leaf mass ratio which generally correlates to high C:N ratios indicating increased allocation to defense against enemies. Therefore, species with low SLA may lose the advantage of indirect competition over high SLA species if enemy access to communities is reduced.

Maximum height, SLA, and seed mass are expected to relate most strongly to soil resource availability, enemy access, and post-disturbance community composition, respectively. However, these abiotic and biotic conditions may cause additional variation in each trait. Increased soil nutrients may favor species with higher SLA (Knops and Reinhart 2000, Laliberte et al. 2012) or cause within-species increases in SLA (Siefert and Ritchie 2016), indicating a shift toward increased growth rate (Laliberte et al. 2012). However, other studies have failed to find such a relationship (Wright and Sutton-Grier 2012, Kazakou et al. 2014). Seed mass may increase with soil nutrient supply indicating increased competitive pressure on seedlings due to low light availability (Manning et al. 2009), but seed mass may also decrease with increasing soil nutrient supply as low nutrient environments may also select for higher seed mass species (Bergholz et al. 2015). Reduction in enemy access may decrease light penetration to the ground as less aboveground tissue is lost (Borer et al. 2014), potentially causing communities to be increasingly represented by large seed mass species that can colonize in low light conditions, and potentially taller species if light drawdown occurs at multiple strata.

Communities may shift in trait means as trait optima change with environmental conditions, causing variation across space. This variation in trait means at the community level can arise from two sources: among-species variation resulting from turnover of species with different mean trait values and within-species variation (Jung et al. 2010). Globally, within-species variation has been estimated to account for on average 25% of the variation of within communities (Siefert et al. 2015). In one old-field experiment, fertilization effects on height arose almost entirely from within-species variation (Siefert and Ritchie 2016); while SLA appears to vary both among and within-species along nitrogen gradients (Knops and Reinhart 2000). Enemy presence may directly cause within-species variation in plant height by physically

removing photosynthetic organs which limits growth potential of individuals or if taller individuals are more apparent or easily accessed by enemies (Price 1991). While leaf chemistry has shown enemy induced changes (Agrawal 2001), within-species SLA responses to enemy presence is not well detailed. These studies highlight the need to consider within-species trait variation to understand community responses to environmental contexts.

Ultimately, post-disturbance community composition, soil resource supply, and enemy access simultaneously influence plant communities, and examining temporal trait responses within the same system can reveal the relative importance of these processes through time. In this study, we examine successional processes in a multifactor old field experiment manipulating initial plant diversity, soil resource supply, and enemy access and measuring the response of community LHS traits at two different periods. The first period occurred shortly after natural colonization began beneath experimental, planted communities and we expect colonization dynamics to be most evident in community trait values at this time. The second time point is two years later and we expect direct and indirect competition dynamics related to fertilization and enemy access to be most evident at this time. In doing so, we ask: **1)** Do initial plant diversity, soil resource supply, and enemy access influence community level trait patterns? **2)** Do the observed relationships vary through time? **3)** What role does within-species trait variation play in response to these factors?

Methods

Study area

This study was conducted at Widener Farm, an old field maintained as part of Duke Forest in the Piedmont of North Carolina, USA. Widener Farm was used for row crops from the

mid-1950s until 1996, and has since been maintained as an herbaceous community by annual mowing. The site receives an average of 1221mm of annual precipitation. It is dominated by perennial grasses such as *Andropogon virginicus*, *Schedonorus arundinaceus*, and *Anthoxanthum odoratum*, but also includes many subdominant grasses, forbs, and annual plants.

Experimental design

In order to test the effects of initial diversity, soil resource supply, and enemy access on community dynamics, we used a randomized, complete block design with factorially crossed treatments of the three variables of interest. In 2011, we established 260, 1x1 m plots across 5 spatial blocks. These plots were denuded by applying glyphosate herbicide (Riverdale® Razor® Pro, Nufarm Americas Inc, Burr Ridge, IL), raked to remove dead aboveground biomass two weeks later, and then covered with landscape fabric to impede natural recolonization. One meter wide alleys between plots were left vegetated.

Diversity treatments were established by assigning plots to one of three treatment levels: monoculture, 5 species polycultures, and unplanted control (herein referred to as blanks). Six, perennial herbaceous species that already occurred at Widener Farm were selected and seedlings were grown in a greenhouse. The species included three grasses (*Andropogon virginicus*, *Setaria parviflora*, and *Tridens flavus*), two Asteraceae (*Packera anonyma* and *Solidago pinetorum*), and one Lamiaceae (*Scutellaria integrifolia*). Eight to twelve weeks after planting in the greenhouse, species were transplanted into the field by cutting small holes into the landscape fabric, digging small holes, and planting 41 individuals per plot in a checkerboard fashion (9 rows alternating between 5 and 4 individuals). In polycultures, four species were randomly assigned to eight spaces, with one random species being assigned to nine spaces. Individuals were allowed to establish for 2011, and in 2012 we repeated this process to replace all dead individuals.

Originally, *Asclepias syriaca* was the sixth species, but due to poor germination and high field mortality, it was replaced in 2012 with *Setaria parviflora*. Following this replacement, *A. syriaca* was not observed within the experiment. In July of 2012, we weeded plots of all non-planted species and removed the landscape fabric without damaging planted individuals. Following this, natural colonization from the seed bank and surrounding alleys and communities was allowed to occur. Blank plots were denuded of aboveground vegetation at the same time and covered with landscape fabric, but did not receive any planting treatment. There were six possible polyculture species combinations, each excluding one of the six planted species, and six possible monocultures, creating 13 possible initial community compositions. These 13 compositions were factorially crossed with the soil resource and enemy access treatments and replicated once in each of five spatial blocks for a total of 260 plots.

Enemy access was manipulated by assigning plots to one of two treatment levels: control and pesticide application. Pesticide application involved spraying foliar fungicide (mancozeb, Dithane® DF, Dow AgroSciences, Indianapolis, IN) and insecticide (es-fenvalerate, Asana® XL, Dupont, Wilmington, DE) every two to three weeks during the growing season from July 2012 to September of 2015; the first application occurred after we removed the landscape fabric in July of 2012. Neither the fungicide nor insecticide had any non-target effects on plant growth of common Widener Farm species under greenhouse conditions.

Soil nutrient supply was manipulated by assigning plots to one of two treatment levels: control and fertilization. Fertilization involved yearly application of 10 g/ m² N as slow-release urea, 10 g/m² P as super triple phosphate, and 10 g/ m² K as potassium sulphate, each in slow release form to increase soil nutrient supply throughout the growing season. The first application occurred after we removed the landscape fabric in July of 2012 and in May of each subsequent

year. In total, our study system was comprised of 260 plots (5 replicate blocks \times 13 community compositions \times 2 nutrient supply levels \times 2 enemy access levels).

Plant community composition

I measured plant community composition from two sampling periods by visually estimating percent cover of all vascular plant species within a 0.75×0.75 m subplot in each plot, centrally located to avoid edge effects. The first survey was conducted in September 2012 two months after natural colonization began following removal of the landscape fabric. Percent cover for all vascular plant species, both planted and non-planted, was recorded. The second survey occurred two years later in September of 2014. An additional survey conducted in June of 2014 was used to inform trait data collection (described below), but was not used to calculate community composition. Each survey entailed three researchers searching within the subplot area for all rooted vascular plants (and also non-rooted vines) before jointly estimating the total percent cover of each species. Plots usually exceeded 100% cover due to canopy overlap between species.

Trait data

Specific leaf area (SLA) data were collected in July of 2014, immediately following the June cover survey. In each plot, we selected species in descending order of percent cover until 80% of the relative cover of that plot from the July 2014 survey was accounted for (Pérez-Harguindeguy et al. 2013). Then, we selected ten leaves in each plot by cycling through its species list in descending order of cover. For instance, if six species accounted for $>80\%$ of the relative cover, two leaves were selected for each of the four most abundant species, and one leaf for each of the remaining two species. Thus, when a species accounted for a large portion of the relative cover of a plot, it would have high replication of sampling within that plot (max. five

leaves per species per plot), while plots with high evenness would have less replication of any single species, but a better representative sample of the central tendency of SLA in that plot. Leaves within-species were chosen randomly from within the plot, but an effort was made not to sample from the same ramet when a species was sampled multiple times. In total, 2590 leaves were sampled across the experiment (on average 4.5 species were selected per plot).

We measured height in September 2014 immediately following the cover survey in the same month. Similar to SLA, we selected species in descending order of percent cover until 80% of the relative cover was accounted for. Then the tallest individual, not including reproductive structures, was identified and we measured the distance between the ground and the tallest vegetative portion of the plant as it stood naturally. Because the variable of interest was a species height potential in a given plot, we did not replicate species measurements within a plot. This resulted in 1124 individuals being measured with an average of 4.3 species per plot.

Seed mass data were acquired from Royal Botanic Gardens Kew (2016) for the most common species in the experiment. Where multiple weights were reported, we took the mean value from all sources reported; *Scutellaria integrifolia* and *Solidago pinetorum* were not present in the database, so we selected the value of their nearest phylogenetic neighbor (*Scutellaria incana* and *Solidago juncea*, respectively). Because these data were not collected locally, we were unable to estimate within-species variation. However, seed mass variability may not be important as several studies suggest that within-species means of seed mass are not variable across environments (Violle et al. 2009, Kazakou et al. 2014). Seed mass values were log transformed at the species level to normalize the data as they ranged across four orders of magnitude.

Community weighted means (CWM) were calculated using species means for each trait at two time points, September 2012 and September 2014. A CWM was calculated as:

$$CWM = \sum_{i=1}^{Nsp} p_i x_i$$

where Nsp is the number of species within a plot with a mean trait value in the dataset, p_i is the abundance of species, i , in the plot relative to the total abundance of Nsp, and x_i is the species trait values. SLA and height trait values took on two values for x_i : a specific mean representing the mean value of a species within each plot (i.e. within-species variation between plots) and a species level value calculated at the experiment level (i.e. no within-species variation between plots). For SLA, we used the experiment-wide mean for the species level value. For maximum height, we used the 90th quantile value of a species' experiment-wide measurements as maximum height represents a species genetic potential to allocate resources towards structural investments required for height. Therefore, the upper end of a species distribution is more representative of its height potential within the study system. Seed mass was only available as a species mean, so no plot specific value was calculated. Following Lepš et al. (2011), we refer to CWMs calculated using plot level species trait means as specific CWM and the CWMs calculated using experiment-wide species trait means as among-species CWM (i.e. only variation resulting from species turnover). Because specific CWMs incorporate variability arising from between and within-species variability, the difference between specific CWM and among-species CWM in each plot is the relative contribution of within-species variation. Only among-species CWMs were available for seed mass analyses.

Statistical analyses

All data were analyzed using the R programming environment version 3.2.2 (R Core Team 2015). At two time points, September 2012 and September 2014, we used ANOVAs to test

the effects of three categorical variables on among-species CWMs: initial species richness, soil resource supply, and enemy access. To account for spatial heterogeneity within the study, experimental blocks were included in all models as fixed effects. Differences between the three initial diversity levels were tested using a post-hoc Tukey HSD test in the lsmeans package (Lenth and Hervé 2015). In order to determine the relative strengths of the experimental treatments relative to one another and the block effects, we used variance partitioning to separate the total variation explained by the models into variation explained by individual effects within each model. Because we expected colonization to be the dominant process in the initial growing season, analyses of 2012 data used only non-planted species to calculate among-species CWMs for maximum height, SLA, and seed mass. This was done because the planted species had natural dispersal and establishment limitations overridden by the planting treatment, so should instead be viewed as sources of asymmetric competitive pressure on new colonists. We repeated this analysis in 2014 using only non-planted species for comparison, but because we expected effects of competition between all species, planted and non-planted, to have manifested, we also performed the analyses using all species.

The contributions of among-species and within-species variation to specific CWMs could only be determined for 2014 SLA and height trait data, which is when they were collected. To test the relative contributions of among-species and within-species trait variation in 2014, we followed the approach employed by Lepš et al. (2011). This approach involves conducting ANOVAs on the three component CWMs: specific, among-species, and within-species, in response to the environmental treatments. The effect of each predictor from each ANOVA can be decomposed to their component sum of squares (SS). These decompositions can then be applied across the three models such that, $SS_{\text{specific}} = SS_{\text{among-species}} + SS_{\text{within-species}} + SS_{\text{cov}}$, where

SS_{cov} represents the covariation between among-species and within-species variation. SS_{cov} will be positive where treatments have the same effect on among-species and within-species variation, but can also take on negative values if the directionality differs between the two sources of variation.

Results

Soil resource supply and enemy access did not influence non-planted community trait dynamics in 2012 (Figure 3.1, Table 3.1). Higher initial plant diversity led to higher seed mass of non-planted species in monocultures and polycultures relative to blank plots, while monocultures and polycultures did not differ statistically ($P < 0.001$, $P < 0.0001$, $P = 0.09$, respectively; Figure 3.1, Table 3.4). Higher initial plant diversity led to higher maximum height of non-planted species in polycultures relative to blank plots and monoculture ($P < 0.05$, $P < 0.01$, respectively), while monocultures and blanks did not differ significantly ($P = 0.58$; Figure 3.1, Table 3.4). Non-planted SLA was not influenced by initial plant diversity (Figure 3.1, Table 3.1). This highlights that post-disturbance community assembly is shaped by established vegetation and not soil resource supply or enemy access.

Initial plant diversity had similar effects in 2014 on non-planted seed mass and height CWMs (Figure 3.2, Table 3.2), but these effects were weaker, and only polycultures showed significant differences from the other planting treatments (Table 3.4); non-planted SLA did not vary with initial plant diversity. When planted species were included, the observed effect on seed mass and height was no longer evident (Figure 3.3, Table 3.3), but polycultures had lower SLA than blanks or monocultures indicating a persistent priority effect (Table 3.4). Soil resource supply had a strong effect on seed mass and maximum height, with fertilized plots having

significantly higher CWMs for both in non-planted CWMs (Figure 3.2, Table 3.2), and when all species were included (Figure 3.3, Table 3.3). There was no observed effect on SLA. Sprayed plots had significantly lower SLA among non-planted species, but did not impact seed mass or height (Figure 3.2, Table 3.2). When all species were included, spraying still reduced community SLA but explained more variation indicating a stronger effect size (Figure 3.3, Table 3.3). Spraying also reduced community seed mass with all plants included, but had no effect on height via among-species variation.

Intraspecific variation

Among-species variation accounted for 44% of the total variation of maximum height observed among plots, and within-species variation accounted for another 36%, with the remaining 20% being accounted for covariation between the two (Table 3.5). Initial plant diversity did not explain a significant amount of variation ($P = 0.63$). Soil resource significantly influenced maximum height ($P < 0.001$) via both among-species ($P < 0.001$) and within-species variation ($P < 0.001$). Enemy access had a significant, positive effect on maximum height ($P < 0.001$), but this was driven by within-species variation ($P < 0.001$) and not among-species variation ($P = 0.48$), explaining why it was not evident in the previous analyses. Overall, the experimental treatments explained 15.6% of the observed variation in height, and the blocking variable explained an additional 25%, potentially indicating a pronounced role of one or more unmeasured environmental gradients controlling species height across the experimental area.

Among-species variation accounted for 40.3% of the total observed variation of SLA, within-species variation explained 63.1%, and there was a small amount (-3.4%) of negative covariation between the two (Table 3.5). Initial plant diversity had a significant, negative effect on SLA via among-species variation ($P < 0.0001$), but had no effect on specific variation ($P =$

0.10) due to negative covariance between among-species and within-species variation. This indicates that higher planting diversity had higher abundances of lower SLA species, but some species tended to have individuals with higher SLA than their species mean. Soil resource supply did not affect species SLA ($P = 0.41$). Enemy access led to decreased SLA in sprayed plots ($P < 0.0001$), and this was driven by among-species ($P < 0.0001$) and not within-species variation ($P = 0.29$). The experimental blocks explained a significant portion of the observed variation of both among-species ($P < 0.0001$) and within-species variation ($P < 0.0001$), but negative covariance led to less total variation being explained than the sum of its part ($P < 0.0001$). Overall, a large portion of variation (81.3%) was unexplained by the treatments or the blocks, indicating that SLA does not strongly affect species fitness in this system relative to manipulated environmental variables.

Discussion

Overall, we found evidence for linkages between seed mass and initial planting diversity, maximum height and soil resource supply, and SLA and enemy access. This indicates that multiple tradeoffs occurred among plant assemblages during succession, which drove community heterogeneity across the experiment. Additional trait-treatment linkages (e.g. seed mass and soil resource supply) were also found indicating that a suite of traits determine species fitness relative to their biotic and abiotic environment (Kraft et al. 2015). Within-species variation also responded to the treatments; in fact, the maximum height response to enemy access was only apparent from explicitly considering within-species trait variation. Collectively, this demonstrates that co-occurring processes contribute to successional states across time and species trait information lends process to the observed patterns of change.

In the 2012 sampling period, soil resource supply and enemy access did not influence community trait composition of non-planted species, while the initial planting treatment affected both seed mass and maximum height of non-planted species. Blank plots, or those without initial aboveground competition, were comprised of lower seed mass species relative to planted plots, while the difference between monocultures and polycultures was only marginally significant. This implies that it was not the species richness of the planting treatment, but rather the presence of any established vegetation that drove the response. This, along with the lack of response to soil resource supply and enemy access, suggests that light availability is the most strongly limiting resource at this early stage of succession. Interestingly, the selection that initial planting diversity exerted on the height of species differed between polycultures and monocultures, but not monocultures and the blank plots. Maximum height was calculated in 2012 using species means from 2014, and, therefore, does not represent actual height of the individuals present, but rather the height potential of the species present. This suggests that there was a threshold value of diversity that must be reached before increased height potential confers a significant advantage to early establishment. This could potentially be due to a sampling effect, where polycultures are more likely than monocultures to have a planted species with disproportionate effects on colonization dynamics. It does indicate that height and seed mass were driven by different niche processes during the colonization phase.

The effects of initial planting treatment were still evident amongst non-planted species in 2014 with polycultures having higher seed mass and height means, though monocultures no longer differed significantly from blank plots for seed mass. This reflects that early colonization events continue to persist into future years, highlighting that priority effects in post-disturbance herbaceous systems may have lasting impacts on community composition. The convergence of

seed mass values in blank plots and monocultures may reflect high species turnover early in the open blank plots resulting in a rapid drawdown of light penetration (Chase and Leibold 2003) and becoming more environmentally similar to monocultures two years later. When planted species were included, significant trait differences between planting treatments disappeared. This may indicate that our planting treatments overrode colonization limitations of our planted species, allowing species that would have been filtered in the colonization phase to establish and persist by eliminating early competition. However, SLA was also only observed to decrease with increasing initial planting diversity when planted species were included. As all planted species were present in the field prior to the start of the experiment, this suggests that low SLA species may be poor colonizers, but able competitors when dispersal limitations are overcome.

Increased soil resource supply did not affect traits during the colonization phase, but had strong, positive effects on seed mass and maximum height for all species in 2014. This is consistent with the expectation of reduced soil nutrient limitation promoting increased light competition (Hautier et al. 2009). The increase in seed mass in fertilized plots could occur due to a rapid initial drawdown in light availability, followed by increased colonization by large-seeded species whose seedlings could tolerate low light communities. Therefore, the results support previous studies that suggest seedlings are more limited by light drawdown from extant vegetation (Manning et al. 2009), than they are limited by soil nutrients (Bergholz et al. 2015). This is further supported by the absence of a soil resource supply effect in 2012. If seedling establishment was limited by soil nutrients, then increased seed mass would be expected in unfertilized plots to increase germinant survival rates. The absence of an SLA response to soil resources could be due to insufficient time for filtering based on soil nutrient supply rates (Laliberte et al. 2012). This could occur if there is an initial upward shift in SLA as colonists are

replaced with competitors, irrespective of whether competition is predominant belowground or aboveground.

The lack of trait effects in 2012 was unsurprising, given that indirect competitive effects arising from top-down regulation may take multiple years to manifest at the community level (Allan et al. 2010, Allan and Crawley 2011, Souza et al. 2016). However, enemy access had unexpected effects on trait values in 2014. The decrease in community SLA in sprayed plots is the opposite effect of what would be anticipated by a competition-defense tradeoff. A competition-defense tradeoff posits that species investing in defense mechanisms are prone to competitive exclusion if top-down pressure is removed. While this tradeoff is not a general paradigm of herbaceous communities (Viola et al. 2010, Lind et al. 2013), it is still peculiar that decreased enemy presence would benefit low SLA species. This could occur in this experiment if SLA does not confer species in this species pool resistance to insect herbivores or fungal pathogens, which the spraying treatment targeted. Alternative advantages of low SLA could be deterrence of vertebrate herbivores or increased tolerance to unmeasured abiotic stressors such as drought (Jung et al. 2010). The effect was even stronger when planted species were included. The two planted aster species, *Packera anonyma* and *Solidago pinetorum*, both had relatively low SLA values, and also were among the lowest in seed mass of common species in the experiment. Together, this could explain decreased community seed mass in sprayed plots. If these two species are both enemy limited and have low parental investment per juvenile individual, then they may be limited in their ability to establish. Higher susceptibility to pathogens among species with rapid life cycles, which low seed mass may indicate, has been observed in other taxonomic groups (Johnson et al. 2012). For both planted and non-planted species, we generally observed a positive response to spraying among forbs, but either no

response or a negative response among grasses (see Chapter 2). Many of our forb species, including *P. anonyma* and *S. pinetorum*, had SLA values on the lower end of the spectrum. If forb species are indeed more regulated by enemies, this could explain the decrease in SLA in sprayed plots.

The significance of within-species trait variation varied between treatments and traits. No treatment affected within-species variation of SLA. However, more of the observed trait variation across blocks was due to within-species than among-species variation, and they covaried negatively suggesting that while among-species variation across blocks caused SLA differences, within-species variation mitigated the observed total SLA variation across blocks. Larger within-species than among-species variation was also observed in the unexplained residual variation of SLA. In sprayed plots, we observed increased within-species height, but not among-species height. This contrasts to other studies which have suggested that plant enemies may preferentially target fast-growing species (Coley et al. 1985, Stamp 2003), as it indicates that insect herbivory and fungal pathogens do not filter communities based on a species' potential height. Rather, enemy reduction may increase within-species height directly by decreasing loss of leaves, which fix photosynthate that enables increased growth (Aldea et al. 2005), decreased susceptibility of taller individuals that are more apparent to enemies (Cunningham and Floyd 2006), or indirectly as less aboveground biomass is removed which decreases light availability and may cause species to invest more in structural biomass to access light (Borer et al. 2014). Within-species variation also contributed to increased vegetative height in the fertilized plots. This indicates that species shift resources to aboveground growth as soil nutrient limitations are removed

Each process examined in this study of early succession drove variation in multiple trait axes, indicating that communities experience multiple filters which select for optimal trait values in their constituent species. The five spatial blocks had significant effects on most traits measured in this study, which indicates additional unmeasured environmental drivers of communities. For SLA and height, the blocks often explained a larger percentage of the observed variation than the experimental treatments. This was not true of seed mass, further indicating that it captures disturbance responsiveness in this system, which was equal across blocks by design. The large residual unexplained variation in seed mass may not be surprising given Widener Farm's anthropogenic history. Fifteen years of mowing prior to the start of the experiment likely created a filter for species unable to maintain populations in a system with repeated disturbances and may also have selected for species that can develop a persistent seed bank. Given this, experimental manipulations may have a limited species pool, and therefore a limited spectrum of trait variation, to act upon. Moreover, our experiment was designed to encourage natural colonization by leaving intact vegetation in the alleys, providing an immediate seed source. This could potentially hasten the shift from light seeded colonizers to heavy seeded, taller competitors.

Significant shifts in traits were observed over the two year timespan between sampling periods, providing evidence for both a shift from colonization to competition dominated communities. Additionally, soil resource supply and enemy access created different niche axes which created different trait optima in later successional communities. Initial community diversity still impacted community trait values in 2014, though the effect appeared to weaken relative to the colonization phase. Previous research has shown that initial community composition did not impact the compositional outcomes along nitrogen gradients (Inouye and

Tilman 1995), and it may take considerably longer to see convergence in trait values within the experiment (Laliberte et al. 2012). Nonetheless, the two year period detailed in this study was long enough to show a pronounced shift from colonization constraints to competitive niche differences as the dominant successional process.

REFERENCES

- Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* 294:321–6.
- Aldea, M., J. G. Hamilton, J. P. Resti, A. R. Zangerl, M. R. Berenbaum, and E. H. DeLucia. 2005. Indirect effects of insect herbivory on leaf gas exchange in soybean. *Plant, Cell and Environment* 28:402–411.
- Allan, E., and M. J. Crawley. 2011. Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. *Ecology letters* 14:1246–53.
- Allan, E., J. van Ruijven, and M. J. Crawley. 2010. Foliar fungal pathogens and grassland biodiversity. *Ecology* 91:2572–82.
- Bergholz, K., F. Jeltsch, L. Weiss, J. Pottek, K. Geißler, and M. Ristow. 2015. Fertilization affects the establishment ability of species differing in seed mass via direct nutrient addition and indirect competition effects. *Oikos* 124:1547–1554.
- Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, P. B. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, L. Biederman, D. Blumenthal, C. S. Brown, L. A. Brudvig, Y. M. Buckley, M. Cadotte, C. Chu, E. E. Cleland, M. J. Crawley, P. Daleo, E. I. Damschen, K. F. Davies, N. M. DeCrappeo, G. Du, J. Firn, Y. Hautier, R. W. Heckman, A. Hector, J. HilleRisLambers, O. Iribarne, J. A. Klein, J. M. H. Knops, K. J. La Pierre, A. D. B. Leakey, W. Li, A. S. MacDougall, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, B. Mortensen, L. R. O’Halloran, J. L. Orrock, J. Pascual, S. M. Prober, D. A. Pyke, A. C. Risch, M. Schuetz, M. D. Smith, C. J. Stevens, L. L. Sullivan, R. J. Williams, P. D. Wragg, J. P. Wright, and L. H. Yang. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508:517–20.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches : linking classical and contemporary approaches*. The University of Chicago Press, Chicago.
- Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource Availability and Plant Antiherbivore Defense. *Science* 230:895–899.
- Cronin, J. P., M. E. Welsh, M. G. Dekkers, S. T. Abercrombie, and C. E. Mitchell. 2010. Host physiological phenotype explains pathogen reservoir potential. *Ecology letters* 13:1221–32.
- Cunningham, S. A., and R. B. Floyd. 2006. *Toona ciliata* that suffer frequent height-reducing herbivore damage by a shoot-boring moth (*Hypsipyla robusta*) are taller. *Forest Ecology and Management* 225:400–403.
- Dickson, T. L., and B. L. Foster. 2011. Fertilization decreases plant biodiversity even when light is not limiting. *Ecology letters* 14:380–8.
- Dickson, T., G. Mittelbach, H. Reynolds, and K. Gross. 2014. Height and clonality traits determine plant community responses to fertilization. *Ecology* 95:2443–2452.
- Grime, J. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.

- Harpole, W. S., and D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446:791–793.
- Hautier, Y., P. A. Niklaus, and A. Hector. 2009. Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636–8.
- Inouye, R. S., and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology* 76:1872–1887.
- Johnson, P. T. J., J. R. Rohr, J. T. Hoverman, E. Kellermanns, J. Bowerman, and K. B. Lunde. 2012. Living fast and dying of infection: host life history drives interspecific variation in infection and disease risk. *Ecology letters* 15:235–42.
- Jung, V., C. Violle, C. Mondy, L. Hoffmann, and S. Muller. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98:1134–1140.
- Kazakou, E., C. Violle, C. Roumet, M.-L. Navas, D. Vile, J. Kattge, and E. Garnier. 2014. Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science* 25:235–247.
- Knops, J. M. H., and K. Reinhart. 2000. Specific Leaf Area Along a Nitrogen Fertilization Gradient. *The American Midland Naturalist* 144:265–272.
- Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America* 112:797–802.
- Laliberte, E., B. Shipley, D. A. Norton, and D. Scott. 2012. Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology* 100:662–677.
- Leishman, M. R., I. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pages 31–58 in M. Fenner, editor. *Seeds: The Ecology of Regeneration in Plant Communities*. Second edition. CAB International, New York, NY.
- Lenth, R., and M. Hervé. 2015. *lsmeans: Least-Squares Means*.
- Lepš, J., F. de Bello, P. Šmilauer, and J. Doležal. 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography* 34:856–863.
- Lind, E. M., E. Borer, E. Seabloom, P. Adler, J. D. Bakker, D. M. Blumenthal, M. Crawley, K. Davies, J. Firn, D. S. Gruner, W. S. Harpole, Y. Hautier, H. Hillebrand, J. Knops, B. Melbourne, B. Mortensen, A. C. Risch, M. Schuetz, C. Stevens, and P. D. Wragg. 2013. Life-history constraints in grassland plant species: a growth-defence trade-off is the norm. *Ecology letters* 16:513–21.
- Manning, P., K. Houston, and T. Evans. 2009. Shifts in seed size across experimental nitrogen enrichment and plant density gradients. *Basic and Applied Ecology* 10:300–308.

- Mouquet, N., P. Leadley, J. Méridet, and M. Loreau. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. *Oikos* 1:77–90.
- Pacala, S. W., and M. Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *The American Naturalist* 152:729–737.
- Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. Bret-Harte, W. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas, P. Reich, L. Poorter, I. Wright, P. Ray, L. Enrico, J. G. Pausas, A. de Vos, N. Buchmann, G. Funes, F. Quétier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter Steege, M. van der Heijden, L. Sack, B. Blonder, P. Poschlod, M. Valertti, G. Conti, A. Staver, S. Aquino, and J. H. C. Cornelissen. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*.
- Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62:244–251.
- R Core Team. 2015. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Rajaniemi, T. K., V. J. Allison, and D. E. Goldberg. 2003. Root competition can cause a decline in diversity with increased productivity. *Journal of Ecology* 91:407–416.
- Royal Botanic Gardens Kew. 2016. Seed Information Database (SID). Version 7.1. <http://data.kew.org/sid/>.
- Siefert, A., and M. E. Ritchie. 2016. Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. *Oecologia*.
- Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, C. Baraloto, M. B. Carlucci, M. V. Cianciaruso, V. de L. Dantas, F. de Bello, L. D. S. Duarte, C. R. Fonseca, G. T. Freschet, S. Gaucherand, N. Gross, K. Hikosaka, B. Jackson, V. Jung, C. Kamiyama, M. Katabuchi, S. W. Kembel, E. Kichenin, N. J. B. Kraft, A. Lagerström, Y. Le Bagousse-Pinguet, Y. Li, N. Mason, J. Messier, T. Nakashizuka, J. M. Overton, D. A. Peltzer, I. M. Pérez-Ramos, V. D. Pillar, H. C. Prentice, S. Richardson, T. Sasaki, B. S. Schamp, C. Schöb, B. Shipley, M. Sundqvist, M. T. Sykes, M. Vandewalle, and D. A. Wardle. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18:1406–1419.
- Souza, L., T. J. Zelikova, and N. J. Sanders. 2016. Bottom-up and top-down effects on plant communities: nutrients limit productivity, but insects determine diversity and composition. *Oikos* 125:566–575.
- Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. *The Quarterly review of biology* 78:23–55.
- Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America* 102:4387–92.

- Throop, H. L., and M. T. Lerdau. 2004. Effects of Nitrogen Deposition on Insect Herbivory: Implications for Community and Ecosystem Processes. *Ecosystems* 7:109–133.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 101:10854–61.
- Turnbull, L., M. Rees, and M. Crawley. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology*:899–912.
- Viola, D. V., E. a Mordecai, A. G. Jaramillo, S. a Sistla, L. K. Albertson, J. S. Gosnell, B. J. Cardinale, and J. M. Levine. 2010. Competition-defense tradeoffs and the maintenance of plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* 107:17217–22.
- Violle, C., H. Castro, J. Richarte, and M.-L. Navas. 2009. Intraspecific seed trait variations and competition: passive or adaptive response? *Functional Ecology* 23:612–620.
- Webb, C. T., J. a Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology letters* 13:267–83.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and soil* 199:213–227.
- Westoby, M., D. S. Falster, A. T. Moles, P. A. Veski, and I. J. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33:125–159.
- Wright, J. P., and A. Sutton-Grier. 2012. Does the leaf economic spectrum hold within local species pools across varying environmental conditions? *Functional Ecology* 26:1390–1398.

Figure 3.1 – Treatment effects on CWM traits of non-planted species in 2012. Boxplots show the distribution of the model predictions. Gray points are the raw data. Shared letters indicate no significant differences between treatment levels.

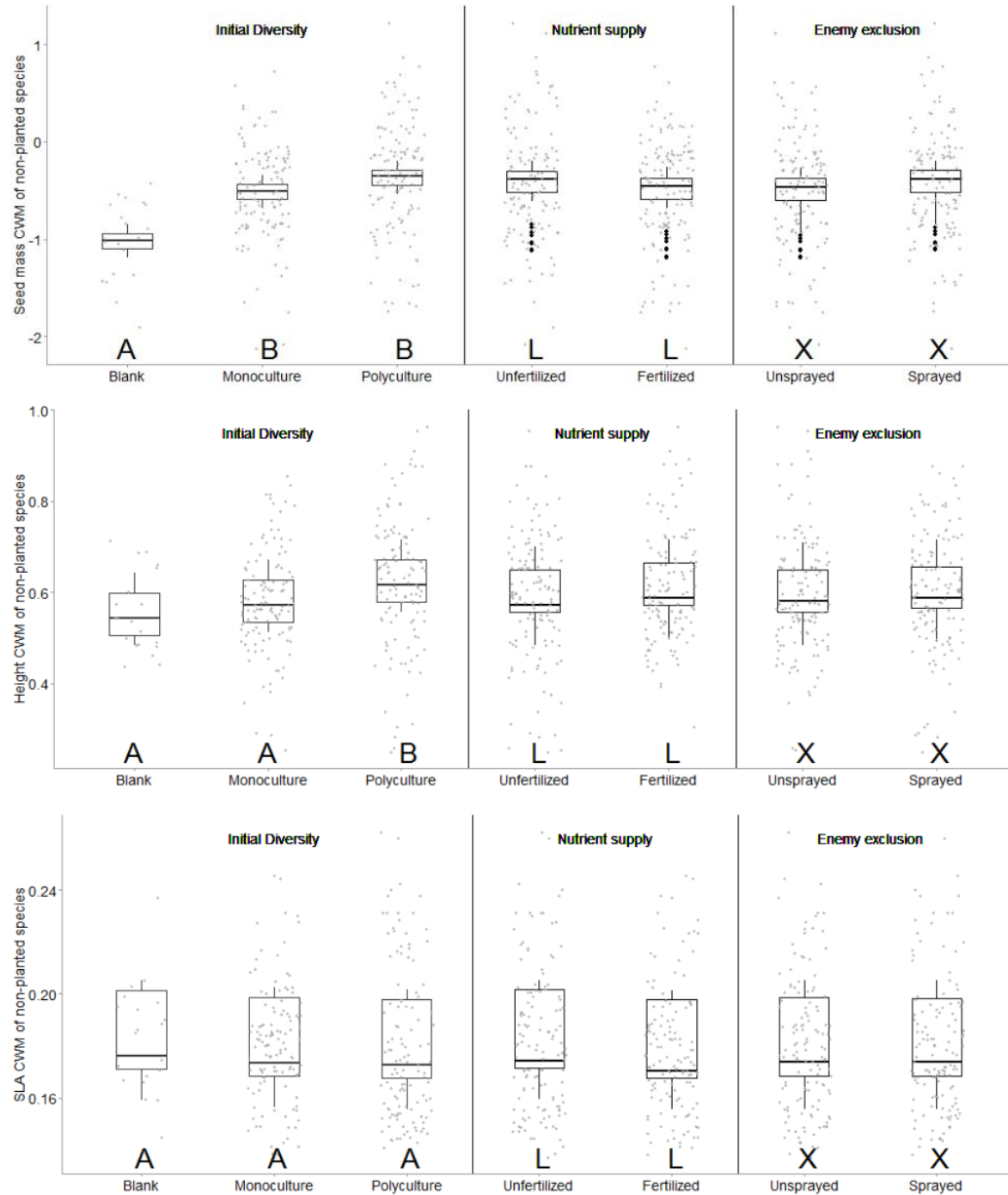


Figure 3.2– Treatment effects on CWM traits of non-planted species in 2014. Boxplots show the distribution of the model predictions. Gray points are the raw data. Shared letters indicate no significant differences between treatment levels.

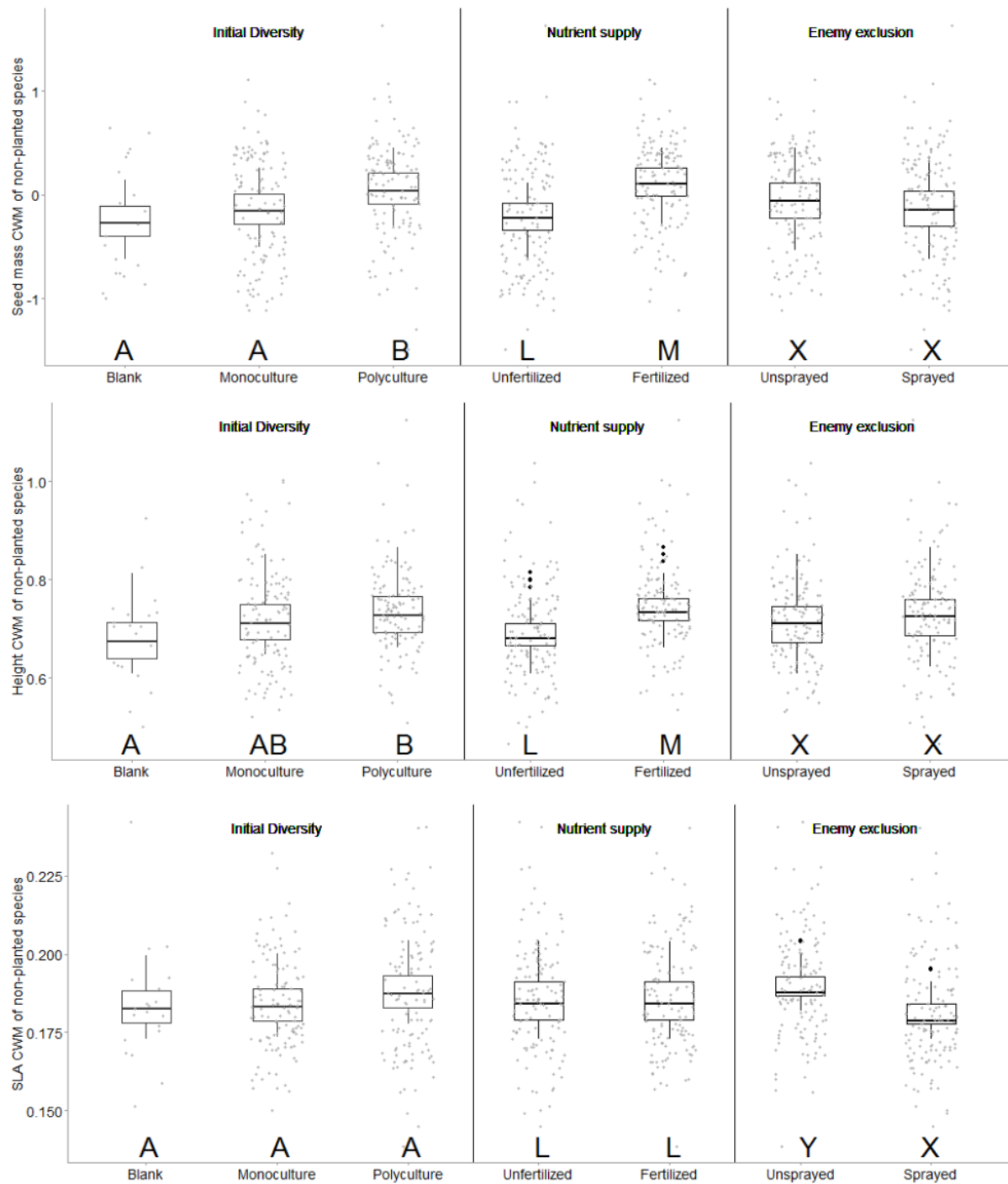
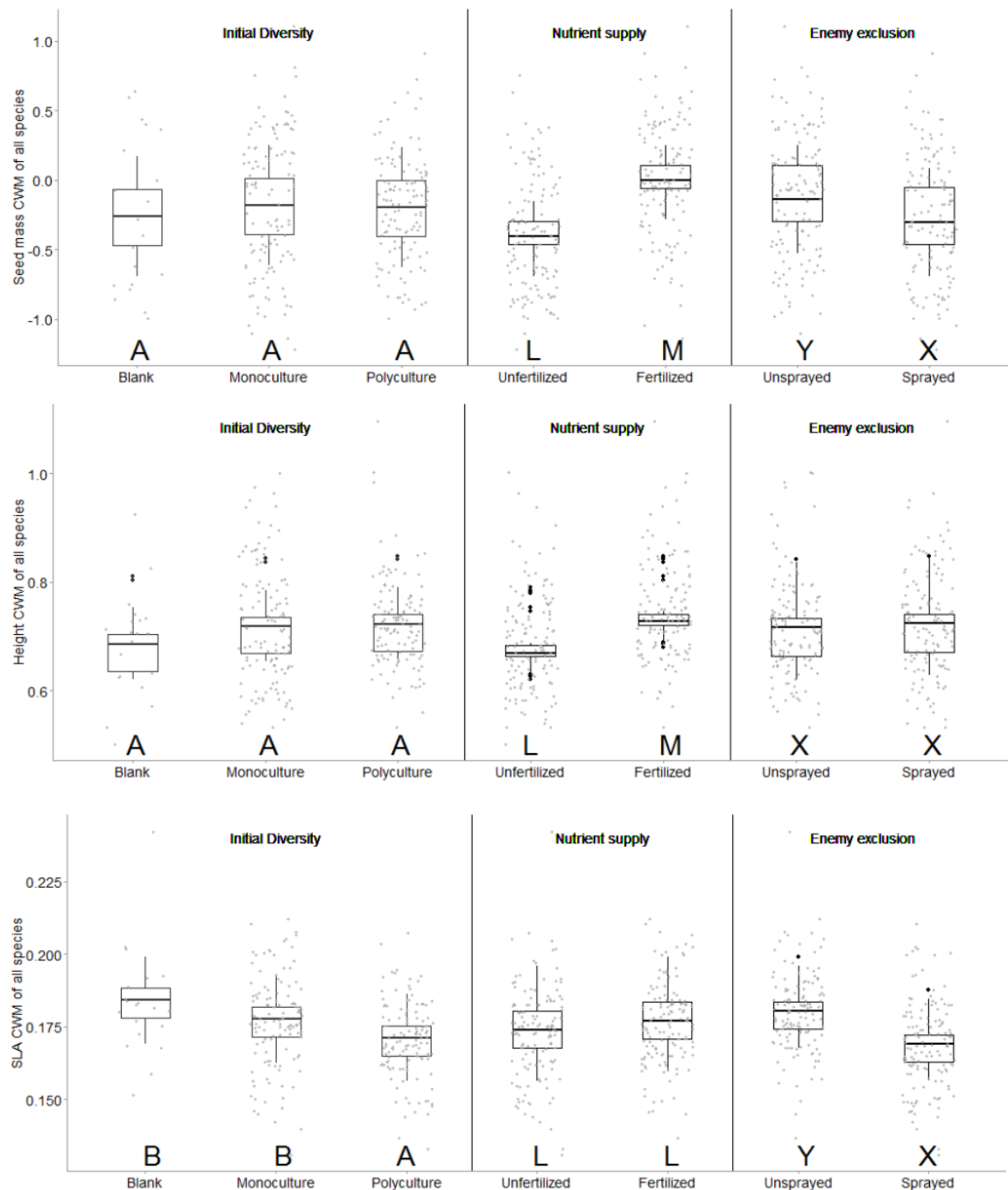


Figure 3.3 – Treatment effects on CWM traits of all species (planted and non-planted) in 2014. Boxplots show the distribution of the model predictions. Gray points are the raw data. Shared letters indicate no significant differences between treatment levels.



Tables

Table 3.1 – Results of ANOVA for non-planted species in 2012.

	df	MS	F	P	Adj. R ²
Seed mass (non-planted)					0.09
Initial Diversity	2	3.79	13.0	<0.0001	0.08
Soil Resources	1	0.31	1.05	0.31	0.00
Enemy Access	1	0.40	1.37	0.24	0.00
Block	4	0.44	1.51	0.20	0.01
Error	251	0.29			
Height (non-planted)					0.18
Initial Diversity	2	0.084	6.08	<0.01	0.03
Soil Resources	1	0.016	1.16	0.28	0.00
Enemy Access	1	0.003	0.23	0.63	0.00
Block	4	0.178	12.92	<0.0001	0.15
Error	251	0.014			
SLA (non-planted)					0.42
Initial Diversity	2	0.0001	0.26	0.77	0.00
Soil Resources	1	0.0010	2.52	0.11	0.00
Enemy Access	1	0.0000	0.003	0.96	0.00
Block	4	0.0186	48.02	<0.0001	0.42
Error	251	0.0004			

Table 3.2 – Results of two-way ANOVA for non-planted species in 2014.

	df	MS	F	P	Adj. R ²
Seed mass (non-planted)					0.20
Initial Diversity	2	1.56	7.4	<0.001	0.04
Soil Resources	1	7.18	33.94	<0.0001	0.10
Enemy Access	1	0.45	2.10	0.15	0.00
Block	4	1.23	5.83	<0.001	0.06
Error	251	0.21			
Height (non-planted)					0.32
Initial Diversity	2	0.026	3.73	<0.05	0.01
Soil Resources	1	0.17	25.46	<0.0001	0.06
Enemy Access	1	0.013	1.92	0.17	0.00
Block	4	0.16	23.65	<0.0001	0.24
Error	251	0.007			
SLA (non-planted)					0.17
Initial Diversity	2	0.0006	2.07	0.77	0.01
Soil Resources	1	0.0000	0.003	0.11	0.00
Enemy Access	1	0.0052	19.75	<0.0001	0.06
Block	4	0.0025	9.55	<0.0001	0.11
Error	251	0.0003			

Table 3.3 - Results of two-way ANOVA for all species in 2014.

	df	MS	F	P	Adj. R ²
Seed mass (all)					0.27
Initial Diversity	2	0.06	0.37	0.69	0.00
Soil Resources	1	10.64	70.94	<0.0001	0.20
Enemy Access	1	1.78	11.85	<0.001	0.03
Block	4	0.73	4.89	<0.001	0.04
Error	251	0.15			
Height (all)					0.32
Initial Diversity	2	0.012	1.85	0.16	0.00
Soil Resources	1	0.22	34.43	<0.0001	0.09
Enemy Access	1	0.003	0.49	0.48	0.00
Block	4	0.14	22.25	<0.0001	0.22
Error	251	0.006			
SLA (all)					0.29
Initial Diversity	2	0.0021	11.99	<0.0001	0.06
Soil Resources	1	0.0006	3.62	0.06	0.01
Enemy Access	1	0.0085	49.11	<0.0001	0.13
Block	4	0.0016	9.25	<0.0001	0.09
Error	251	0.0002			

Table 3.4 – Results of multiple comparisons for diversity treatments and trait responses. Bolded values are significant at the $P < 0.05$ level. Values indicate estimated effect of the first planting treatment relative to the second for among-species CWMs and values inside parentheses indicate the associated t-statistic.

Non-planted 2012	Seed Mass	Height	SLA
Blank – Monoculture	-0.51 (-3.91)	-0.028 (-1.00)	0.0027 (0.57)
Blank – Polyculture	-0.66 (-5.04)	-0.073 (-2.58)	0.0034 (0.72)
Monoculture - Polyculture	-0.15 (-2.12)	-0.045 (-2.95)	0.0007 (0.28)

Non-planted 2014	Seed Mass	Height	SLA
Blank – Monoculture	-0.12 (-1.04)	-0.037 (-1.87)	-0.001 (-0.193)
Blank – Polyculture	-0.31 (-2.79)	-0.053 (-2.63)	-0.005 (-1.21)
Monoculture - Polyculture	-0.20 (-3.29)	-0.015 (1.43)	-0.004 (-1.90)

All species 2014	Seed Mass	Height	SLA
Blank – Monoculture	-0.08 (-0.68)	-0.033 (-1.68)	0.007 (2.06)
Blank – Polyculture	-0.06 (-0.79)	-0.037 (-1.92)	0.013 (4.05)
Monoculture - Polyculture	0.02 (0.37)	-.004 (-0.45)	0.006 (3.73)

Table 3.5 – Variance partitioning of between and within-species community weighted means of height and SLA in 2014. Bolded values indicate significant differences between treatment levels, except for covariation which could not be tested

	Maximum Height				Specific Leaf Area			
	Among-species	Within-species	Covariation	Total	Among-species	Within-species	Covariation	Total
Initial Diversity	0.4	0.4	-0.1	0.2	2.6	0.4	-1.6	1.5
Soil Resources	4.0	1.2	4.4	9.7	0.4	0.2	0.7	1.4
Enemy Access	0.1	4.8	1.1	5.9	5.4	0.2	2.2	7.9
Block	10.4	6.9	7.7	25.0	4.1	10.1	-6.2	8.0
Residuals	29.3	22.3	7.5	59.2	27.7	52.0	1.5	81.3
Total	44.3	35.7	20.0	100	40.3	63.1	-3.4	100

CHAPTER 4 : FUNCTIONAL SHIFTS IN TREE COMMUNITIES ACROSS SUCCESSION IN EASTERN DECIDUOUS FORESTS

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 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 ecological 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; Raavel et al. 2012). The type of disturbances experienced by today's eastern forests have 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.

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 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 largest number of seeds in the largest 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 fewer 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). Previous studies have shown a weak, positive relationship between leaf nitrogen and latitude (Reich and Oleksyn 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.

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. These ecoregions 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.

Methods

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 FIA 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 classification (USDA Forest Service 2004) based on plot latitude and longitude (Figure 4.1). 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 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. Plots with stand age over 120 years were omitted to avoid a low number of older plots driving the results.

Statistical 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.

Results

Seed mass was positively correlated with stand age in all eight ecoregions (Figure 4.2). 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 4.1). 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 (Figures 4.2, 4.3). 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 4.2).

Wood density was positively correlated with stand age in seven of the eight ecoregions; only the Savannah Division lacked a significant relationship (Figure 4.2). WCD again displayed the highest correlation between wood density and stand age ($r^2=0.17$; Table 4.1); 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 4.2).

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 (Figure 4.2). The Savannah Division had the strongest relationship ($r^2 = 0.11$; Table 4.1), 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 4.2). 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 4.1); including a quadratic term for latitude in the post-hoc multiple regressions improved model fit substantially, but ecoregion remained a stronger fit (Table 4.2).

Discussion

Seed mass increased with stand age in all EDF ecoregions, supporting our hypothesis. The strongest correlation was observed in 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 indicate that the higher correlation in this ecoregion is driven by a higher proportion of early successional plots with low seed mass species rather than higher seed mass in 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. Additionally, although conifer dominated plots were excluded from the analysis, many early successional plots could have a strong presence of *Pinus* and *Abies* species, which are lower in the seed mass spectrum. Smaller seeded species represent a shift toward increased numbers of seeds produced at the expense of seedling viability. 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*, *Pinus taeda*, and *Diospyros virginiana* which occur in the mid to upper range of seed mass. Several of these are animal dispersed and *P. taeda* relies on wind dispersal.

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* species 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*.

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 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.

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 also contradicts Grime's classic CSR model, which predicts that disturbance adapted species acquire resources relatively rapidly for fast growth and early reproduction. It is possible, however, 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.

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. Ordonez (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. Higher leaf nitrogen plots in this ecoregion appears to be driven by high leaf nitrogen species both early (e.g. *P. pensylvanica*) and late (e.g. *Acer saccharum*, *Tilia americana*) in succession.

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. 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 that early, post-disturbance forests harbor a unique combination of functional traits related to plant dispersal and growth. Further, a shift in plant traits over succession indicates that disturbance creates a mosaic of forest stand ages which is important for maximizing not just species diversity, but functional diversity as well.

REFERENCES

- Bailey, R.G., 1995. Description of the ecoregions of the United States. USDA Forest Service. Online at: <http://www.fs.fed.us/land/ecosysmgmt/index.html>. Accessed July, 2013.
- Bailey, R.G., 2004. Ecoregions of the United States. USDA Forest Service. Online at: <http://www.fs.fed.us/rm/ecoregions/products/map-ecoregions-united-states/>. Accessed July, 2013.
- Campetella, G., Botta-Dukát, Z., Wellstein, C., Canullo, R., Gatto, S., Chelli, S., Mucina, L., Bartha, S., 2011. Patterns of plant trait–environment relationships along a forest succession chronosequence. *Agriculture, Ecosystems and Environment* 145, 38-48.
- Chave, J., D. Coomes, S. Jansen, S. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Clark, J.S., Ibanez, I., 2004. Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs*, 415.
- Denslow, J.S., 1980. Gap partitioning among tropical rain-forest trees. *Biotropica* 12(supplement), 47-55.
- Douma, J.C., de Haan, M.W.A., Aerts, R., Witte, J.-P.M., van Bodegom, P.M., 2012. Succession-induced trait shifts across a wide range of NW European ecosystems are driven by light and modulated by initial abiotic conditions. *Journal of Ecology* 100, 366-380.
- Falster, D.S., Westoby, M., 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology* 93, 521-535.
- Frelich, L.E., Reich, P.B., 1999. Forest dynamics across three century-length disturbance regimes in the Illinois Ozark Hills. *American Midland Naturalist* 162, 418-449.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111, 1169-1194.
- Latzel, V., Klimešová, J., Doležal, J., Pyšek, P., Tackenberg, O., Prach, K., 2011. The Association of Dispersal and Persistence Traits of Plants with Different Stages of Succession in Central European Man-Made Habitats. *Folia Geobotanica* 46, 289-302.
- Leishman, M.R., Wright, I.J., Moles, A.T., Westoby, M., 2000. Chapter 2 The Evolutionary Ecology of Seed Size. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd Ed. CAB International

- Moles, A.T., Ackerly, D.D., Tweddle, J.C., Dickie, J.B., Smith, R., Leishman, M.R., Mayfield, M.M., Pitman, A., Wood, J.T., Westoby, M., 2007. Global patterns in seed size. *Global Ecology and Biogeography* 16, 109-116.
- Navas, M.L., Roumet, C., Bellmann, A., Laurent, G., Garnier, E., 2010. Suites of plant traits in species from different stages of a Mediterranean secondary succession. *Plant Biology* (Stuttgart, Germany) 12, 183-196.
- Ordoñez, J.C., Bodegom, P.M.v., Witte, J.-P.M., Wright, I.J., Reich, P.B., Aerts, R., 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography* 18, 137-149.
- Pickett, S.T.A., White, P.S., 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- USDA Forest Service Forest Inventory and Analysis Program, 2013. FIA DataMart v. 5.1. In.
- USDA Forest Service Forest Inventory and Analysis Program. 2013. *The Forest Inventory and Analysis Database: Database Description and User's Manual Version 5.1.6 Phase 2*. July, 2013.
- R Core Team (2013). *R: A language and environment for statistical computing* v. 2.15.3. R Foundation for Statistical Computing.
- Raavel, V., Violle, C., Munoz, F. 2012. Mechanisms of ecological succession: insights from plant functional strategies. *Oikos* 121, 1761-1770.
- Reich, P.B., Ellsworth, D.S., Uhl, C., 1995. Leaf Carbon and Nutrient Assimilation and Conservation in Species of Differing Successional Status in an Oligotrophic Amazonian Forest. *Functional Ecology* 9, 65-76.
- Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *PNAS* 101, 11001-11006.
- Romme, W.H., Everham, E.H., Frelich, L.E., Moritz, M.A., Sparks, R.E., 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems* 1, 524-534.
- Swenson, N.G., Enquist, B.J., 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community wide variation across latitude and elevation. *American Journal of Botany* 94, 451-459.
- Swenson, N.G., Weiser, M.D., 2010. Plant geography upon the basis of functional traits: an example from eastern North American trees. *Ecology* 91, 2234-2241.

- Turnbull, L.A., Rees, M., Crawley, M.J., 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology* 87, 899-912.
- White, P. S., Collins, B., Wein, G., 2011. Natural disturbances and early successional habitats. In: Greenberg, C.H., Collins, B.S., Thompson, F.R. III, eds. *Managing Forest Ecosystems V. 21: Sustaining young forest communities*. Springer, New York. 27-40
- Wickham H. 2009. *GGplot2: elegant graphics for data analysis*. Springer New York.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z. *et al.* (2004). The world-wide leaf economics spectrum. *Nature*, 428, 821–827.
- Wright, J.P., Fridley, J.D., 2010. Biogeographic synthesis of secondary succession rates in eastern North America. *Journal of Biogeography* 37, 1584-1596.

Table 4.1 - 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.

Seed mass							
Ecoregion	r^2	Intercept	Slope	Std. Err.	p-value	t value	Number of plots
Hot Continental Division	0.095	1.34	0.010	2.7E-4	<0.0001	38.6	14091
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							
Ecoregion	r^2	Intercept	Slope	Std. Err.	p-value	t value	Number of plots
Hot Continental Division	0.066	0.49	6.7E-4	2.1E-5	<0.0001	31.6	14091
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							
Ecoregion	r^2	Intercept	Slope	Std. Err.	p-value	t value	Number of plots
Hot Continental Division	0.016	2.11	-0.0015	1.0E-4	<0.0001	-14.9	14091
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

Table 4.2 – Linear and multiple regressions by trait scores – Linear and multiple regressions predicting trait scores. AIC and r² were used to inform model selection. Models best fitting the data in the most parsimonious manner are in italics.

Seed mass						
Model	r ²	AIC	Std. Error	p-value	F-statistic	df
Latitude	0.22	89981	0.754	<0.0001	10861.7	1 / 39567
Ecoregion	0.20	87612	0.732	<0.0001	1998.1	7 / 39561
Latitude + Stand age	0.32	84475	0.704	<0.0001	9196.4	2 / 39566
<i>Ecoregion + Stand age</i>	0.34	83228	0.693	<0.0001	2533.0	8 / 39560
Wood density						
Model	r ²	AIC	Std. Error	p-value	F-statistic	df
Latitude	0.19	-109905	0.0603	<0.0001	9137.1	1 / 39567
Ecoregion	0.20	-110301	0.0600	<0.0001	1382.5	7 / 39561
<i>Latitude + Stand age</i>	0.28	-114400	0.0570	<0.0001	7519.8	2 / 39566
Ecoregion + Stand age	0.26	-113305	0.0578	<0.0001	1695.4	8 / 39560
Leaf Nitrogen						
Model	r ²	AIC	Std. Error	p-value	F-statistic	df
Latitude	0.067	10705	0.277	<0.0001	2843.6	1 / 39567
Latitude (quadratic)	0.19	5113	0.258	<0.0001	4641.9	2 / 39566
<i>Ecoregion</i>	0.22	3870	0.254	<0.0001	1550.6	7 / 39561
Latitude + stand age	0.068	10676	0.276	<0.0001	1438.0	2 / 39566
Ecoregion + stand age	0.22	3852	0.254	<0.0001	1359.9	8 / 39560
Latitude (quadratic) + stand age	0.19	5010	0.258	<0.0001	3136.8	3 / 39565

Figure 4.1 – Bailey's ecoregions. The eight divisions of Bailey's ecoregions used in the analyses

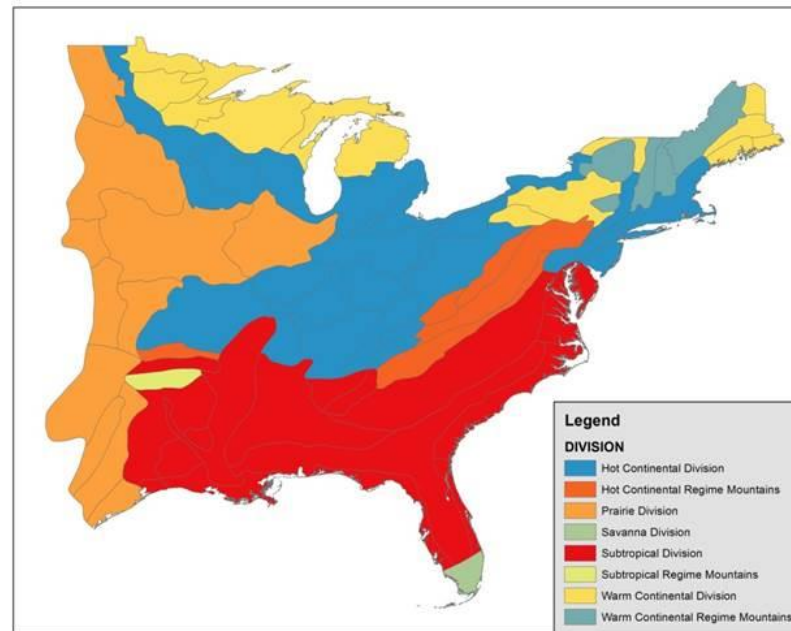


Figure 4.2– Plot trait scores versus stand age by ecoregion – Each point represents the abundance weighted trait mean of all species within a plot

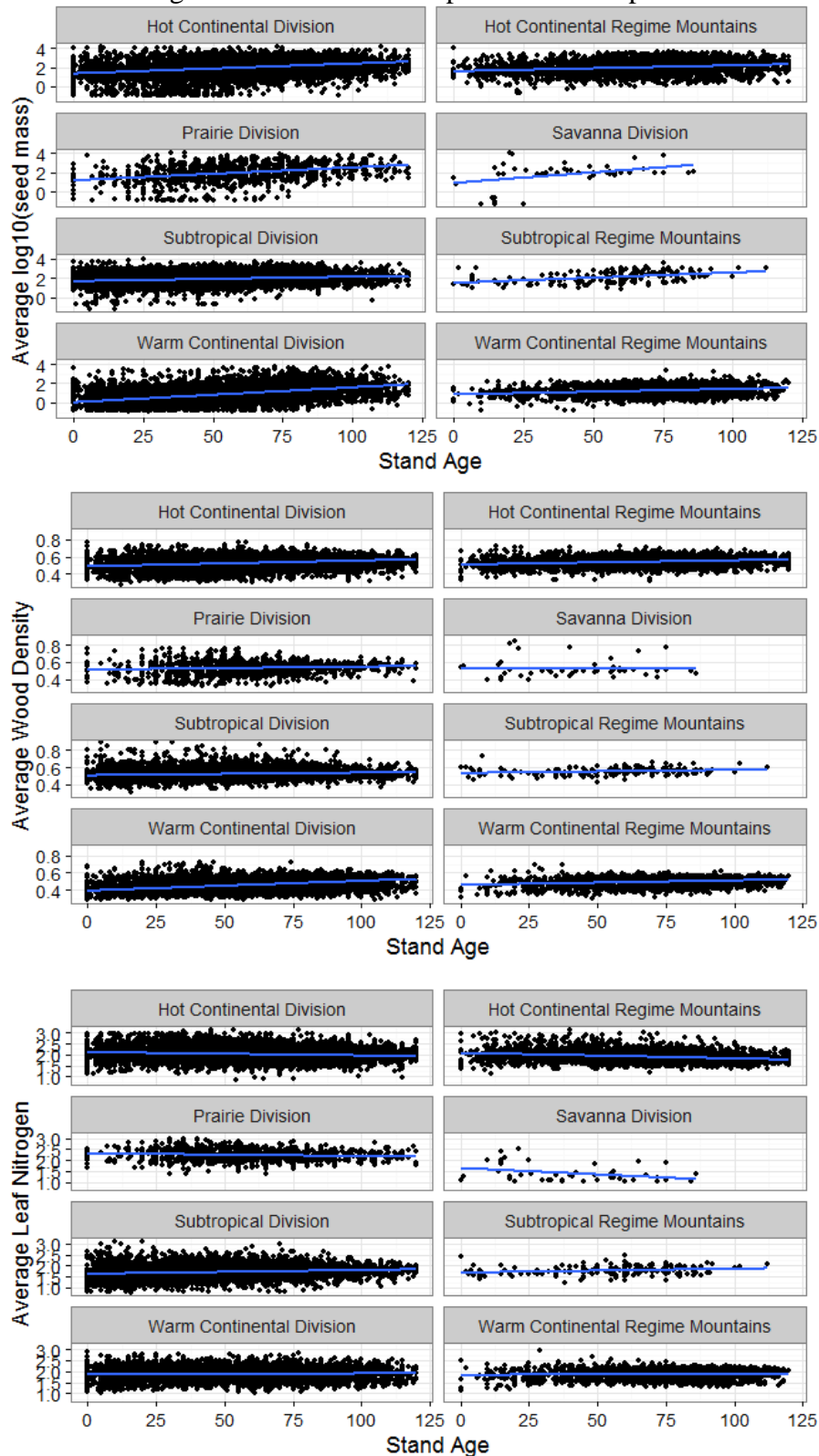
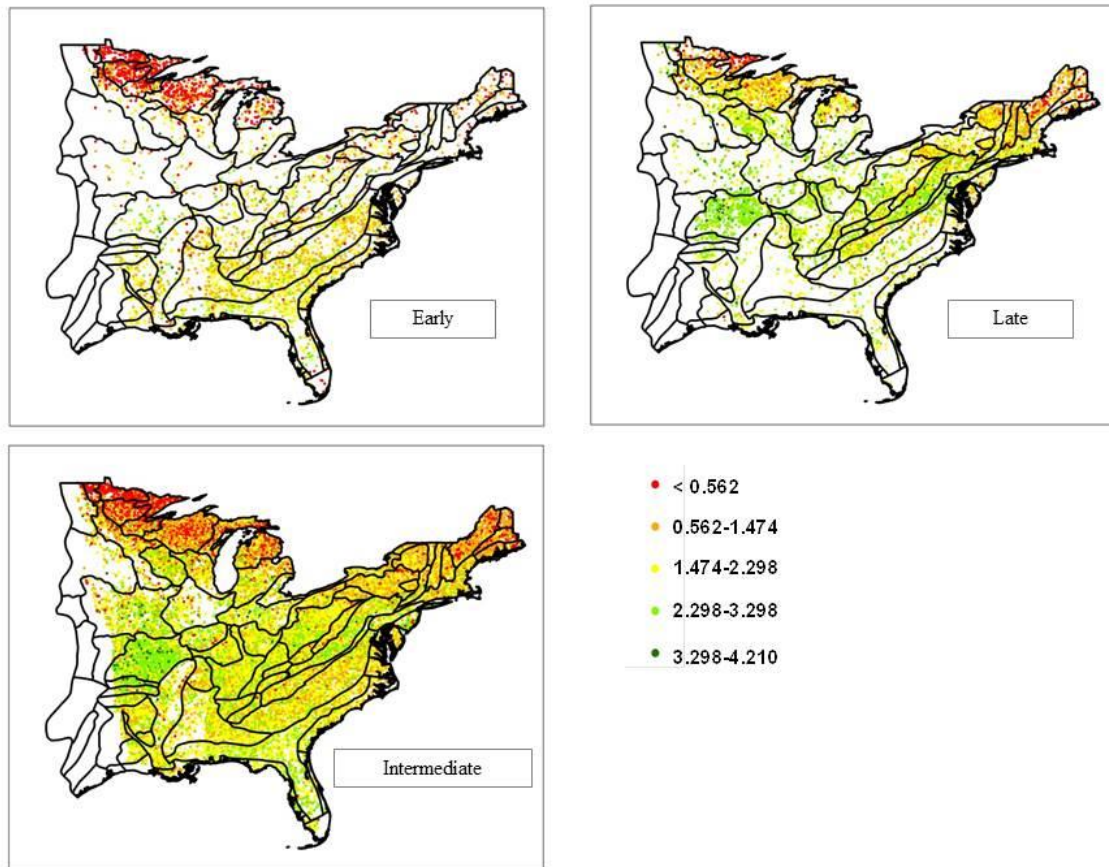


Figure 4.3 - Geographic distribution of seed mass across different successional stages. Average per-plot seed mass (mg) in early (<20yr), middle (21-80) and late (>80) successional forests. Dark lines are Bailey's ecoregions (USDS Forest Service 2004).



CHAPTER 5 : REGIONAL RECRUITMENT PROCESSES IN POST-DISTURBANCE TEMPERATE FORESTS: FUNCTIONAL TRAITS REVEAL CONTINENTAL-SCALE VARIABILITY

Introduction

Disturbances are ubiquitous across ecological systems and promote species coexistence by altering resource availability across space and time (Pickett and White 1985). Gaining a clearer understanding of the underlying mechanisms controlling species' responses to disturbance is therefore critical to understanding large-scale spatial and temporal diversity patterns. Broadly, disturbances temporarily increase resource availability due to mortality of individuals that were previously prominent in resource drawdown. This increased resource availability allows disturbance-dependent species to colonize and establish in areas previously dominated by species tolerant of low resource availability (Bazzaz 1979, Niinemets and Valladares 2006). As landscapes develop a patchwork of recently disturbed and undisturbed areas, species sort across the landscape due to ecological tradeoffs. Often, tradeoff axes are expressed phenotypically by measurable functional trait characteristics (Webb et al. 2010). By recasting functional groups in terms of functional trait characteristics, more mechanistic inferences can be made on the processes underlying community responses to disturbance (Lavorel and Garnier 2002). Moreover, while a set of fundamental traits may separate disturbance-dependent species from others, environmental gradients and biogeographic history may constrain or cause additional trait variation between species in how they respond to disturbance or its absence (Díaz et al. 1999). Classifying and monitoring the functional traits that

are responsive to disturbance in different climatic and edaphic conditions should therefore clarify the mechanisms controlling species' temporal niches across physiographic regions.

In mature forest communities, light is generally the predominant limiting resource as mature trees form a closed canopy, reducing light at the ground level by as much as 99% (Canham et al. 1994). Such highly asymmetric light competition limits the performance of seedlings and saplings, and forest disturbances that remove tree biomass may therefore promote species diversity across landscapes by increasing access to light and promoting the recruitment of disturbance-dependent species (White et al. 2011). Because of this, disturbance is often viewed as a process that resets communities to earlier successional states (White et al. 2011, King and Schlossberg 2014). Examining successional gradients through a functional trait lens using chronosequence approaches has gained increasing attention. In eastern deciduous forests of the US, community seed mass and wood density of adult trees increase with stand age in northerly regions, but are independent of stand age in southerly regions (Wilfahrt et al. 2014). In tropical forests, early successional communities favor species with stress tolerant traits as open canopies cause drought conditions that select for resource conservation traits (Buzzard et al. 2015), while in wet forests, where water is not limiting, young forests favor species with traits that enable rapid resource acquisition (Lohbeck et al. 2013, Craven et al. 2015). Increased light availability may also lower species recruitment success in temperate forests if light leads to changes in soil properties such as decreased soil moisture, indirectly creating harsh abiotic conditions that exceed the direct benefit a seedling gains from increased light availability (Ibáñez and McCarthy-Neumann 2014). This highlights that while functional traits of tree communities respond to changing light availability along successional gradients, there are further sources of trait variation contingent on other abiotic conditions.

Despite recent attention to successional-gradient trait patterns, few studies have explicitly evaluated post-disturbance forest communities in the context of traits. Those that have focus on extant adult tree individuals (Schamp and Aarssen 2009, Wonkka et al. 2013, Giehl and Jarenkow 2015, Wilfahrt et al. 2016), which likely reveal traits that confer tolerance to disturbance as opposed to those that promote recruitment after a disturbance event. As such, the trait composition of juvenile individuals in post-disturbance communities may be more indicative of future community composition of older trees (Pacala et al. 1996, Umaña et al. 2015). Six functional traits thought to inform post-disturbance recruitment are seed mass, wood density, leaf nitrogen content, maximum height, shade tolerance, and drought tolerance. These traits are proxies for ecological tradeoff axes such as dispersal strategy (seed mass; Leishman et al. 2000), stress tolerance (drought tolerance, shade tolerance, wood density; Niinemets and Valladares 2006, Chave et al. 2009), resource capture (maximum height, shade tolerance, leaf nitrogen; Wright et al. 2004, Falster and Westoby 2005, Niinemets and Valladares 2006), and growth potential (wood density, maximum height; Falster and Westoby 2005, Chave et al. 2009). In addition to capturing post-disturbance recruitment dynamics, these axes indicate seedling fitness at different stages of forest succession due to differing resource environments. Post-disturbance communities should favor good dispersers and resource competitors when climatic conditions are favorable, where undisturbed forests in later stages of succession should increasingly favor traits that confer tolerance to low light conditions and resource conservatism (Rees et al. 2001).

A commonality across various forms of forest disturbance is the reduction in aboveground biomass (Lorimer 1980, Peet 1981). Properties of disturbance in relation to biomass loss will also impact trait responses. As the severity of disturbance increases and more

biomass is lost, the magnitude of trait responses should increase as more of the seedling community is affected and the canopy gap takes longer to close (Runkle 1985). The amount of aboveground biomass in the system is a structural character of successional stage (Lichstein et al. 2009) and may thus be viewed as a proxy for time since last disturbance. Therefore, communities with high initial biomass should generally indicate mid- to late-successional stands with seedling communities adapted to low light conditions, resulting in higher potential to see larger trait shifts in seedling communities following disturbance. Conversely, stands that are undisturbed may experience the most rapid trait turnover in earlier successional communities (i.e. low initial biomass) due to a rapidly changing resource environment (Reich et al. 1995).

This study makes use of a continental-scale tree database with repeated surveys of permanent plots in the eastern temperate forests (ETF) of the US to reveal patterns of tree functional traits in response to forest disturbances. This removes uncertainty arising from chronosequence approaches that cannot control for site contingencies and allows for examination across large geographic gradients. Previous studies of disturbance-trait relationships have been conducted predominantly in the tropics, and it is unclear how conclusions from those studies apply to temperate systems, given differences in biogeographic histories (Wiens and Donoghue 2004), dominant assembly processes (Myers et al. 2013), and functional diversity constraints imposed by climate (Swenson et al. 2012).

In this paper, I ask three questions. **1)** Do fundamental trait shifts occur in post-disturbance seedling communities across ETF and how do they compare to seedling community trait shifts in undisturbed communities? **2)** Do disturbance properties such as severity and time since last disturbance affect observed trait shifts? **3)** Do patterns of trait shifts in response to

disturbance vary across ecological provinces within the study system and do climatic gradients correlate with these patterns?

Methods

Forest Inventory and Analysis plot data

I used the US Forest Service Forest Inventory and Analysis database to analyze seedling trait shifts in resampled permanent forest plots. Seedlings are defined within the database as all individuals taller than 30.48cm (15.24cm for gymnosperms) to individuals with a diameter at breast height of less than 2.54cm. All plots used had no record of logging since their establishment, were categorized as forested, and used the phase two sampling design which includes seedling microplots (2.07m radius, just off center of each subplot); subplots (7.32m radius, separated by 36.6m from other subplots) without seedling data for two sampling periods were omitted from analysis (“Forest Inventory and Analysis Database v.4.0” 2013). Plots were separated into their four constituent subplots for the purposes of the analysis so as to maximize the likelihood that observed changes in tree biomass at the subplot level were linked to changes in the nested seedling microplots by being recorded in the same area. A subplot was categorized as either ‘disturbed’ if it had experienced a net loss in basal area of saplings (2.54cm to 12.7cm DBH; sampled in microplot) and adult trees (>12.7cm DBH; sampled in subplot) in between sampling periods, and otherwise ‘undisturbed’. Subplots were sampled from all forest biogeographic provinces of the eastern US, while omitting the subtropical provinces of the prairie park region and the everglades (Figure 5.1). This resulted in 111,146 subplots, with 88,164 classified as undisturbed, and 22,982 classified as disturbed. 75% of all subplots (84,477 subplots) were resampled five years after the first sampling date, and the remaining subplots

were resampled 1 to 15 years after the first sampling date (> 95% of subplots were resampled within 8 years).

Trait data

Trait data herein represents species-level means of the six continuous quantitative traits: seed mass, wood density, leaf nitrogen content, maximum height, shade tolerance, and drought tolerance. The four physiological traits were compiled from literature sources and publically available trait databases (for further information and access to trait data, see Coyle et al. (2014) for leaf nitrogen content, seed mass, and wood density; and Swenson and Weiser (2010) for maximum height data). The drought and shade tolerance indices are continuous metrics ranging from 1 (intolerant) to 5 (tolerant) and were provided in Russell et al. (2014; adapted from Niinemets and Valladares 2006). Missing species data were estimated using genus-level means from the dataset. Seed mass was log transformed as it spanned five orders of magnitude. All traits were centered on zero and standardized to have a standard deviation of 1 at the species level in order to make effect sizes comparable between traits.

Seedling counts by species were used to create regional weighted means (RWM) based on ecological subsections (herein referred to as regions, which are subsections of the aforementioned provinces) of eastern US forests as described by McNab et al. (2005). RWMs were computed for disturbed and undisturbed subplots by aggregating the seedling count for each species in each subplot of that region and disturbance status and calculating it such that:

$$RWM = \sum_{i=1}^{Nsp} p_i x_i$$

where p_i is the relative abundance of species i , and x_i is the species trait mean of species i .

Analyses use either the RWMs from the initial sampling periods, or the change in RWM for the six traits between sampling periods. RWMs are analogous to commonly calculated community

weighted means, but I distinguish RWM here as they are calculated at a regional spatial scale. Using RWMs reduces the potential for sampling error that may result from the small spatial grain of seedling observation ($\sim 13.5\text{m}^2$) by aggregating multiple observations made across the region, providing a more accurate estimate of the central tendency of trait shifts within environmentally distinct regions. Regions that did not have at least one observation for both ‘disturbed’ and ‘undisturbed’ were omitted from RWM analysis, resulting in a total of 412 regions.

Sensitivity analyses

The aggregation of subplots masked plot level variables, such as percent basal area change, that may be predictive of trait shifts. I used sensitivity analyses to investigate two possible subplot-level predictors. The first predictor is the magnitude of change of basal area, used as a proxy for disturbance severity. A small decrease in subplot basal area is more likely to occur away from the seedling microplot and any canopy gap that formed may close rapidly. Both of these effects may dampen observed disturbance response. On the other hand, a small increase in basal area could potentially mask a disturbance, if the increase in basal area of surviving trees exceeds the lost basal area of dead trees. The second predictor is the initial basal area of a subplot which is used as proxy for time since last disturbance. Higher basal area subplots are more likely to have more developed canopies and these subplots are more likely to have filtered out seedlings of early successional species, which in turn should magnify the effects of post-disturbance trait shifts. Therefore, excluding ‘disturbed’ subplots with low initial basal area should result in increased effect sizes of RWM trait shifts. Conversely in ‘undisturbed’ subplots, the most species turnover may occur in early successional subplots with small amounts of basal

area as the canopy shifts from open to closed. Therefore, excluding subplots with high initial basal should result in increased effect sizes of RWM trait shifts in undisturbed conditions.

To evaluate the impact of disturbance severity, disturbance subplots with the smallest basal area losses were omitted. Two cutoffs were used for this: removal of subplots in the bottom 10th and 25th percentile of study-wide basal area loss. Similarly, undisturbed subplots with the smallest basal area gains were omitted (again at the 10th and 25th percentile level). Then, RWMs were recalculated with these reduced datasets. To understand the effect of time since last disturbance, disturbed subplots had subplots with the lowest initial basal areas omitted at the 10th and 25th percentile level. Conversely, undisturbed subplots had subplots with the *highest* initial basal area excluded at the 10th and 25th percentile level. Then, RWMs were recalculated with the reduced datasets. Because these reduced datasets resulted in fewer subplots used, some regions ceased to have any plot data for one of the two disturbance categories. In such cases, that region was omitted from the analysis for *both* disturbed and undisturbed subplots. Furthermore, since RWM analysis was performed over community level data to reduce uncertainty resulting from small spatial grain of observation, a sensitivity analysis was performed to determine whether regions with few observations influenced the results. To test this, I performed a sensitivity analysis that removed regions that relied on fewer than 10 and 25 subplots in *either* disturbance category from the full dataset and recalculated RWMs.

Climate and province data

In order to look for geographic trends in trait response to disturbance, I use two regional climate variables, mean annual precipitation (MAP) and mean annual temperature (MAT), and a hierarchical level of nesting from the McNab et al. (2005) ecoregion descriptions, herein referred to as province (Figure 5.1). Climate data were derived from the online PRISM data set (PRISM

Climate Group 2015) and represent regional means by intersecting 2.5 arcminute raster data with regional spatial polygons using the raster package in R (Hijmans 2015). Both variables were centered on zero and standardized to prevent issues of collinearity between intercepts and slopes in the statistical models. Provinces were used as grouping variables for their constituent regions in order to capture geographic trait tendencies. While climate is likely to be a large part of provincial differences, including provinces in models also captures lurking variables such as large scale edaphic properties, biogeographic history, and non-measured environmental gradients. Due to a low number of constituent regions in montane provinces, they were incorporated into their analogous non-montane provinces to ensure model convergence.

Statistical Analysis

All analyses were performed using Bayesian analysis in the JAGS program, through the rjags package (Plummer 2015) in the R programming environment (R Core Team 2015). In order to test for system-wide trait shifts (i.e. not accounting for disturbance or provincial properties), single-level models were fit to a multivariate response of the six traits' change through time (RWM:y), such that:

$$y_i \sim MVN(\mu_i, \tau)$$

$$\tau \sim IW(Q, S + 1)$$

where y_i is an $S \times 1$ matrix ($S = \#$ of traits) for each region i , MVN indicates a multivariate normal distribution, μ_i is an $S \times 1$ vector of trait means, and τ is an $S \times S$ covariance matrix. The multivariate response approach allows the model to account for trait responses that are driven by covariance between the trait values by reducing the effective sample size as covariance increases. The covariance matrix is an inverse Wishart (IW) distribution with an uninformative prior defined by an $S \times S$ covariance matrix, Q , and degrees of freedom $S + 1$.

The process model for estimating response μ_i was defined as:

$$\mu_i = \beta_0 * x_{0i} + \beta_1 * x_{1i}$$

where x_0 is an $n \times 1$ design matrix, with a 0 for disturbed subplots/ecoregions, 1 for undisturbed subplots/ecoregions, and x_1 switches the 0s and 1s in x_0 . This approach was taken instead of using an intercept model with a single design matrix for disturbed subplots in order to quantify the effects of each disturbance status (disturbed/undisturbed) relative to 0 (no change in trait mean) as opposed to relative to one another. An uninformative multivariate normal prior distribution was used for the betas. In order to account for disturbance properties and sampling effort, this process was repeated for the three sensitivity analyses accounting for community level basal area change, community level initial basal area, and number of subplots per region. This required recalculating RWMs for each region for the two community level variables and reducing the original dataset for the number of subplots per region.

In order to account for geographic variation in trait shifts, a second level was added to the original model. This level represented ecological provinces as described by McNab et al. (2005). For both conditions, the regression coefficients, β_0 and β_1 , in the single level model were allowed to vary between province, j , again modeled by a multivariate normal process:

$$\beta_j \sim MVN(\alpha_j, \sigma)$$

Similar to the single level model, hyperparameters α_j and σ had uninformative multivariate normal and inverse Wishart priors, respectively. This approach allowed for different responses across provinces for both conditions, as opposed to including a single random effect term which would only allow for regional variation undistinguished by disturbance status.

The influence of climate was tested by running separate single level multiple regression models predicting three multivariate response variables: RWMs of all traits of seedling subplots

from their initial sampling period, RWM shifts of all traits in disturbed subplots, and RWM shifts of all traits in undisturbed subplots. Each model estimated parameter values for intercepts and linear and quadratic terms for both climate variables. An uninformative multivariate normal prior distribution was used for the parameter estimates, and the error term was a covariance matrix with an uninformative inverse Wishart prior. R-squared values were calculated based on estimated parameters from model output to assess the predictive power of climate variables.

All models used uninformative prior distributions. Posterior distributions were estimated for all parameters using Markov chain Monte Carlo (MCMC) Gibbs sampling with 3 chains, for 10,000 iterations with a 1,000 iteration burn-in. All chains were examined to visually confirm convergence. Parameters whose 95% credibility intervals did not cross zero were deemed statistically significant.

Results

Across the ETF, five of the six RWM traits studied demonstrated shifts significantly different from zero in response to disturbance (Figure 5.2). Four of the six traits demonstrated shifts significantly different from zero in undisturbed subplots, and all four were opposite in sign to the observed disturbance effect (increased shade tolerance, seed mass and wood density; decreased maximum height). Leaf nitrogen content is the only trait without an observable shift in either condition, and drought tolerance only showed a shift in disturbed subplots. Due to standardizing the trait scores at the species level, the effect sizes of these responses are relative to the total trait variation in the 217 species observed in the dataset. Disturbed subplots generally showed larger effect sizes than the undisturbed subplots.

Disturbance Properties

The sensitivity analysis to basal area change revealed that removal of low severity disturbances resulted in the effect sizes of trait shifts moving further from zero for all traits except for leaf nitrogen; only shade tolerance, seed mass, and wood density had significantly different parameter estimates (Figure 5.3). Undisturbed trait shifts were not sensitive to basal area change, having similar effect sizes at all sensitivity levels for all traits. The sensitivity analysis to initial basal area revealed that as low starting values of basal area were removed from the analysis of disturbed subplots, the effect sizes of all significant trait shifts moved further away from zero (except maximum height), though only shade tolerance and seed mass had significantly different parameter estimates (Figure 5.4). As subplots with high initial basal area were removed from the analysis of undisturbed subplots, RWM shifts for all traits remained relatively constant. In the sensitivity analysis for minimum number of subplots per region, both disturbed and undisturbed RWM shifts remained constant as minimum number of subplots per region increased, or the effect size moved further away from zero (Figure 5.5). Only shade tolerance showed a significantly different parameter estimate in the disturbed condition.

Provincial variation

The hierarchical provincial model revealed high variation of regional shifts in RWMs in disturbed and undisturbed subplots (Table 5.1). Leaf nitrogen content did not respond to disturbance in any province, but did show increases in undisturbed conditions of two provinces: the central interior/Ozark broadleaf forests and temperate prairie parklands. Seed mass decreased in disturbed conditions in 4 of the 9 provinces, and most strongly in the northern Laurentian mixed forests. Seed mass increased in undisturbed conditions in 6 of the 9 provinces. Wood density decreased following disturbance in 5 of the 9 provinces, and increased in undisturbed

condition for only the two most northern provinces. Maximum height increased in response to disturbance in 4 of the 9 provinces, but decreased in response to disturbance in the Laurentian mixed forest province; while it showed decreases in undisturbed conditions in 6 of the 9 provinces. Shade tolerance decreased in response to disturbance in 7 of the 9 provinces, and increased in undisturbed conditions in 6 of the 9 provinces. Drought tolerance increased in disturbed conditions in 3 of the 9 provinces, while also showing an increase in undisturbed conditions of the northeastern/Adirondack mixed forest province. All provinces showed a significant response to disturbed and undisturbed conditions in at least one trait, and every province had a unique set of trait responses to disturbance.

Climate

All RWMs from the initial sampling period showed significant relationships with both MAP and MAT (Table 5.2), except for maximum height with MAT. Five of the six traits had significant quadratic terms with both climate variables and R^2 values ranging from 0.43 to 0.67; maximum height had a positive linear relationship with MAP and an R^2 value of 0.09. When RWM shifts following disturbance were regressed with quadratic models, only leaf nitrogen showed a quadratic relationship with MAT (Table 5.2). Given the lack of disturbance response in leaf nitrogen and the weakness of this relationship ($R^2 = 0.02$), this may be a spurious effect. Wood density RWM shifts had a quadratic term with a downward opening parabola centered close to zero indicating that wood density decreases following disturbance in areas of low and high MAP, but not in regions of average MAP, though this relationship was very weak ($R^2 = 0.04$). Seed mass demonstrated a positive, linear response to precipitation, with negative RWM shifts more common at lower precipitation values, though this relationship was very weak ($R^2 = 0.04$). RWM shifts in undisturbed subplots demonstrated more significant relationships than

disturbed subplots, but still had low R^2 values (Table 5.2). Negative linear relationships were found between maximum height and both MAP and MAT ($R^2 = 0.05$). Quadratic relationships were found between seed mass, wood density, and drought tolerance and MAP ($R^2 = 0.09, 0.07, 0.04$, respectively); and leaf nitrogen content and shade tolerance and MAT ($R^2 = 0.07, 0.09$, respectively).

Discussion

The general expectation was that disturbance should favor good dispersers (low seed mass) and good resource competitors (high maximum height, high leaf nitrogen), traits which may come at the expense of decreased stress tolerance (low shade tolerance, low wood density), although open post-disturbance communities may favor drought tolerant species under water deficit conditions (Lohbeck et al. 2013, Buzzard et al. 2015). Disturbance resulted in study-wide trait shifts in seedling communities consistent with these expectations, with the exception of leaf nitrogen. This result is reinforced as four of the five traits responsive to disturbance also showed trait shifts in the opposite direction when basal area increased between sampling periods. This is consistent with the notions that disturbance ‘resets’ the process of succession, species sort along successional gradients, and this sorting occurs due to underlying ecological tradeoff axes captured by the traits used in this study. The magnification of observed trait shifts in response to increasing disturbance severity and time since last disturbance indicates that aboveground biomass indirectly impacts seedling trait dynamics, with increased light availability being a likely mediating influence given the strong response of shade tolerance. RWM trait values correlate with regional climatic patterns (consistent with previous findings; Swenson & Weiser 2010), while disturbance responses largely operate independently of climate despite varying

across ecological provinces. Collectively, this indicates that climate may influence successional patterns of trait variation, but more immediate disturbance responses are largely independent of these two climatic variables. Instead, implicit changes in seedling resource availability due to changes in adult biomass has a clear effect on trait shifts, with provincial variation further structuring these patterns by muting or further magnifying observed effects. Examining this variation within each trait highlights potential factors driving variable recruitment processes across the study area.

Significance of Individual Trait Responses

The strong response of shade tolerance in both disturbed and undisturbed conditions reinforces that light availability is a critical environmental gradient driving tree species composition during disturbance-succession dynamics. This is demonstrated by its large effect size relative to the other traits, its strong response to selecting subplots with higher basal area loss or higher initial basal area, and the near ubiquitous response across ETF provinces. The two provinces that did not display shade tolerance responses, the Lower Mississippi Riverine Forest and Temperate Prairie Parkland, are characterized by open landscapes where tree communities tend to cluster around rivers and streams (McNab et al. 2005), potentially allowing shade intolerant species to persist in the seedling layer of mature stands due to large edge effects increasing light penetration to the understory. Overall, this reinforces the value of characterizing tree species by shade tolerance indices for predicting disturbance response in forest systems. Nonetheless, shade tolerance is a surrogate for a broader range of a species' physiological traits and may have complex interactions with other limiting biotic and abiotic pressures (Valladares and Niinemets 2008, Sendall et al. 2015). This highlights the need for a broader array of traits to understand disturbance responses.

The significant shifts in four of the five other traits are suggestive that light or other resource gradients influence tree species recruitment dynamics beyond a stress tolerance tradeoff axis. These responses were more spatially idiosyncratic than shade tolerance, indicating that abiotic and biotic drivers differ in relative strengths across ecological provinces. Seed mass, an indicator of a species' dispersal strategy, showed a general increase in undisturbed subplots and a decrease in disturbed subplots. However, it had significant shifts in *both* disturbed and undisturbed subplots in only the two most northern provinces and the outer coastal plain mixed forest, though the effect sizes were smaller in the latter. Wood density also showed significant responses to both disturbance and succession in the two most northern provinces, and only disturbance responses in two other northerly provinces and the outer coastal plain. Collectively, the seed mass and wood density results are consistent with trait patterns of stand age previously demonstrated by Wilfahrt et al. (2014), indicating that these traits capture a successional gradient as community weighted means of adult trees for both traits increase in older-aged forest stands. However, the increase in these two traits occurs predominantly in northern provinces of the eastern US. Northerly ETF provinces and the outer coastal plain are both conifer-dominated areas (Delcourt and Delcourt 1988). As conifers tend to have lower wood density and seed mass values relative to angiosperms (though in both cases the *lowest* values are angiosperms in ETF; see appendix of Coyle *et al.* 2014), this could reflect hardwood encroachment in later successional forests. Seed mass generally decreases with latitude for all plant types, with multiple hypotheses potentially explaining this pattern (Moles et al. 2007). Among these are an increased reliance on abiotic dispersal at higher latitudes and shorter growing seasons limiting development time of seed crops. This would mean that disturbance-dependent species in lower latitudes would be free of two potential filters promoting decreased seed mass. Decreased wood

density following disturbance in these same regions could also reflect shorter growing seasons driving gap-dependent species to maximize growth toward the canopy more rapidly, though this is not captured by the temperature gradient analysis. Wood density and seed mass were the only two traits besides shade tolerance to show significantly stronger responses to higher severity disturbances, and seed mass showed stronger responses to disturbance subplots with higher initial basal area. Increases in both wood density (Kunstler et al. 2016) and seed mass (Clark et al. 2004) indicate a shift from species selected for colonization to species selected for competition, consistent with expectations of selection along successional gradients.

Maximum height responses were inconsistent across provinces and often weaker than other traits. Decreases in maximum height in undisturbed subplots were often synchronous with increases in seed mass, while in disturbed subplots increases in height tended to occur in southerly regions where both seed mass and wood density showed no effect. This may result from an observed trade-off between cold hardiness and height potential (Loehle 1998), whereby the cost of investing in cold resistance for northerly tree species reduces their competitive ability in southerly ranges. Early successional species in northern provinces would be not only limited by this tradeoff, but could face less competitive pressure from extant trees post-disturbance. While the province-level results appear to partially support this notion, it is not reflected in the temperature analysis. The general regional asynchrony in significant height and wood density responses suggests that any species level trade-off between maximum height and wood density does not scale up to community level disturbance responses in ETF.

The lack of leaf nitrogen response is consistent with previous studies on succession in ETF (Wilfahrt et al. 2014) and tropical forests (Reich et al. 1995, Falster and Westoby 2005). The two provinces with positive leaf nitrogen shifts in undisturbed subplots are on the western

edge of the study area where agricultural nitrogen inputs are high. However, atmospheric nitrogen deposition is generally high, though spatially heterogeneous, across all of the ETF (Gilliam 2006). Coyle et al. (2014) found that community-level mean leaf nitrogen had an increasing, but saturating relationship with soil fertility in North and South Carolina tree communities. Collectively, this indicates that edaphic conditions, not disturbance or climatic conditions filter species based on leaf nitrogen. As temperate forests are historically nitrogen limited (Anderson-Teixeira et al. 2015), monitoring community-level disturbance responses relative to nitrogen deposition patterns may be an important tool in predicting future forest composition changes.

Drought tolerance showed similar levels of increase following disturbance in all provinces, though only three were significant, and one province had a significant increase in undisturbed subplots. Drought tolerance increases would be expected if open canopies cause drought-like conditions on the forest floor (Lohbeck et al. 2013). However, Berdanier & Clark (2016) showed that following severe and prolonged drought, drought intolerant species experienced decreased growth rates for an extended time period prior to eventual mortality. If species' fecundities are also suppressed during these periods, then seedling community responses in drought tolerance may be observed prior to biomass loss from disturbance due to seed rain being skewed toward drought tolerant species. It also means that drought tolerance shifts may be more sensitive to periodic drought patterns not captured by MAP and MAT. The outer coastal plain province for example, where a significant post-disturbance drought tolerance increase was observed, has experienced increased drought events in recent years and has interacted with a diminished disturbance regime to reduce understory species richness (Palmquist et al. 2014).

This could potentially reduce competitive pressure on seedlings allowing drought tolerance to be a more viable strategy.

This research highlights that continental-scale disturbance-trait relationships exist, but these relationships are provincially contingent. The results are consistent with previous studies detailing the ecological interpretation of the traits used here, and are further reinforced by increased responsiveness to severity and time since disturbance, as well as the observed responses in undisturbed plots. Future studies would benefit from controlling for several aspects that may mask disturbance responses. First, seedling data stratified into new recruits and resprouts may increase effect sizes of trait shifts. Resprouting is a common trait in angiosperms of the ETF and adult individuals damaged in a disturbance may mask recruitment trends if they resprout and are included in seedling censuses (Bond and Midgley 2001). Further, different disturbance types (e.g. fire versus ice storm) variably impact forest understories where seedling communities exist (McIntyre et al. 1999, White et al. 2011). Certain disturbances may have high survivorship of pre-disturbance seedlings that would continue to contribute to a RWM post-disturbance, thereby masking the trait signal of new recruits. Finally, intraspecific variation may account for over 25% of trait variation within and among communities (Siefert et al. 2015) and ontogenetic trait shifts are prominent in trees, particularly in juveniles (Spasojevic et al. 2014, Lasky et al. 2015). This within species variation may enable species to alter their ecological strategy across environmental gradients such as light availability. However, large spatial scale studies such as this one likely have a minimal impact from intraspecific variation as regional gradients drive large interspecific variation (Auger and Shipley 2013). These sources of variation may have reduced observed effect sizes in this study, but did not mask overall disturbance and successional trait patterns.

In this study, I expand on well-documented taxonomic responses to canopy disturbances and succession in ETF by exposing functional trait syndromes that lend process to these observed patterns. Analysis of multiple traits and two spatial scales provides evidence for additional mechanisms beyond shade intolerance controlling species recruitment in response to disturbance and succession. The independence of disturbance responses from climatic gradients diverges from previous studies in tropical forests, indicating that biogeographic history or edaphic properties may be more important in driving the observed provincial variation in trait responses across temperate forests. Ultimately, I demonstrate that different suites of traits determine species recruitment in post-disturbance resource environments across ecological provinces of temperate forests.

REFERENCES

- Anderson-Teixeira, K. J., S. J. Davies, A. C. Bennett, E. B. Gonzalez-Akre, H. C. Muller-Landau, S. J. Wright, K. Abu Salim, A. M. Almeyda Zambrano, A. Alonso, J. L. Baltzer, Y. Basset, N. A. Bourg, E. N. Broadbent, W. Y. Brockelman, S. Bunyavejchewin, D. F. R. P. Burslem, N. Butt, M. Cao, D. Cardenas, G. B. Chuyong, K. Clay, S. Cordell, H. S. Dattaraja, X. Deng, M. Detto, X. Du, A. Duque, D. L. Erikson, C. E. N. Ewango, G. A. Fischer, C. Fletcher, R. B. Foster, C. P. Giardina, G. S. Gilbert, N. Gunatilleke, S. Gunatilleke, Z. Hao, W. W. Hargrove, T. B. Hart, B. C. H. Hau, F. He, F. M. Hoffman, R. W. Howe, S. P. Hubbell, F. M. Inman-Narahari, P. A. Jansen, M. Jiang, D. J. Johnson, M. Kanzaki, A. R. Kassim, D. Kenfack, S. Kibet, M. F. Kinnaird, L. Korte, K. Kral, J. Kumar, A. J. Larson, Y. Li, X. Li, S. Liu, S. K. Y. Lum, J. A. Lutz, K. Ma, D. M. Maddalena, J.-R. Makana, Y. Malhi, T. Marthews, R. Mat Serudin, S. M. McMahon, W. J. McShea, H. R. Memiaghe, X. Mi, T. Mizuno, M. Morecroft, J. A. Myers, V. Novotny, A. A. de Oliveira, P. S. Ong, D. A. Orwig, R. Ostertag, J. den Ouden, G. G. Parker, R. P. Phillips, L. Sack, M. N. Sainge, W. Sang, K. Sri-Ngernyuang, R. Sukumar, I.-F. Sun, W. Sungpalee, H. S. Suresh, S. Tan, S. C. Thomas, D. W. Thomas, J. Thompson, B. L. Turner, M. Uriarte, R. Valencia, M. I. Vallejo, A. Vicentini, T. Vrška, X. Wang, X. Wang, G. Weiblen, A. Wolf, H. Xu, S. Yap, and J. Zimmerman. 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global change biology* 21:528–549.
- Auger, S., and B. Shipley. 2013. Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science* 24:419–428.
- Bazzaz, F. A. 1979. *The Physiological Ecology of Plant Succession*.
- Berdanier, A. B., and J. S. Clark. 2016. Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests. *Ecological Applications* 26:17–23.
- Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants : the persistence niche. *Trends in ecology & evolution* 16:45–51.
- Buzzard, V., C. M. Hulshof, T. Birt, C. Violle, and B. J. Enquist. 2015. Re-growing a tropical dry forest: functional plant trait composition and community assembly during succession. *Functional Ecology*.
- Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* 24:337–349.

- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology letters* 12:351–66.
- Clark, J. S., S. LaDeau, and I. Ibanez. 2004. Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs* 74:415–442.
- Coyle, J. R., F. W. Halliday, B. E. Lopez, K. A. Palmquist, P. A. Wilfahrt, and A. H. Hurlbert. 2014. Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. *Ecography* 37:814–826.
- Craven, D., J. S. Hall, G. P. Berlyn, M. S. Ashton, and M. van Breugel. 2015. Changing gears during succession: shifting functional strategies in young tropical secondary forests. *Oecologia* 179:293–305.
- Delcourt, H., and P. Delcourt. 1988. Eastern Deciduous Forests. Pages 357–395 in M. Barbour and W. Billings, editors. *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, UK.
- Díaz, S., M. Cabido, M. Zak, E. Martínez Carretero, and J. Aranibar. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science* 10:651–660.
- Falster, D., and M. Westoby. 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology* 93:521–535.
- Forest Inventory and Analysis Database v.4.0. 2013. . <http://apps.fs.fed.us/fiadb-downloads/datamart.html>.
- Giehl, E. L. H., and J. A. Jarenkow. 2015. Disturbance and stress gradients result in distinct taxonomic, functional and phylogenetic diversity patterns in a subtropical riparian tree community. *Journal of Vegetation Science* 26:889–901.
- Gilliam, F. S. 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology* 94:1176–1191.
- Hijmans, R. J. 2015. raster: Geographic Data Analysis and Modeling.

- Ibáñez, I., and S. McCarthy-Neumann. 2014. Integrated assessment of the direct and indirect effects of resource gradients on tree species recruitment. *Ecology* 95:364–375.
- King, D. I., and S. Schlossberg. 2014. Synthesis of the conservation value of the early-successional stage in forests of eastern North America. *Forest Ecology and Management* 324:186–195.
- Kunstler, G., D. Falster, D. A. Coomes, F. Hui, R. M. Kooyman, D. C. Laughlin, L. Poorter, M. Vanderwel, G. Vieilledent, S. J. Wright, M. Aiba, C. Baraloto, J. Caspersen, J. H. C. Cornelissen, S. Gourlet-Fleury, M. Hanewinkel, B. Herault, J. Kattge, H. Kurokawa, Y. Onoda, J. Peñuelas, H. Poorter, M. Uriarte, S. Richardson, P. Ruiz-Benito, I.-F. Sun, G. Ståhl, N. G. Swenson, J. Thompson, B. Westerlund, C. Wirth, M. A. Zavala, H. Zeng, J. K. Zimmerman, N. E. Zimmermann, and M. Westoby. 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529:204–207.
- Lasky, J. R., B. Bachelot, R. Muscarella, N. Schwartz, J. Forero-Montaña, C. J. Nytych, N. G. Swenson, J. Thompson, J. K. Zimmerman, and M. Uriarte. 2015. Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology* 96:2157–2169.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- Leishman, M. R., I. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pages 31–58 in M. Fenner, editor. *Seeds: The Ecology of Regeneration in Plant Communities*. Second edition. CAB International, New York, NY.
- Lichstein, J. W., C. Wirth, H. S. Horn, and S. W. Pacala. 2009. Biomass Chronosequences of United States Forests: Implications for Carbon Storage and Forest Management. Pages 301–341 in C. Wirth, G. Gleixner, and M. Heimann, editors. *Old-Growth Forests: Function, Fate and Value*. Springer Berlin Heidelberg.
- Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography* 25:735–742.
- Lohbeck, M., L. Poorter, E. Lebrija-Trejos, M. Martinez-Ramos, J. Meave, H. Paz, E. Perez-Garcia, I. Romero-Peraz, A. Tauro, and F. Bongers. 2013. Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology* 94:1211–1216.
- Lorimer, C. G. 1980. Age Structure and Disturbance History of a Southern Appalachian Virgin Forest. *Ecology* 61:1169–1184.

- McIntyre, S., S. Lavorel, J. Landsberg, and T. D. A. Forbes. 1999. Disturbance response in vegetation - towards a global perspective on functional traits. *Journal of Vegetation Science* 10:621–630.
- McNab, W. H., D. T. Cleland, J. A. Feeouf, J. E. Keys, Jr., G. . Nowacki, and C. A. Carpenter. 2005. Description of ecological subregions: sections of the conterminous United States. Washington, D.C.
- Moles, A. T., D. D. Ackerly, J. C. Tweddle, J. B. Dickie, R. Smith, M. R. Leishman, M. M. Mayfield, A. Pitman, J. T. Wood, and M. Westoby. 2007. Global patterns in seed size. *Global Ecology and Biogeography* 16:109–116.
- Myers, J. A., J. M. Chase, I. Jimenez, P. M. Jorgensen, A. Araujo-murakami, N. Paniagua-Zambrana, and R. Seidel. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters* 16:151–157.
- Niinemets, Ü., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* 76:521–547.
- Pacala, S. W., C. D. Canham, J. Saponara, J. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest Models Defined by Field Measurements : Estimation , Error Analysis and Dynamics. *Ecological Monographs* 66:1–43.
- Palmquist, K. A., R. K. Peet, and A. S. Weakley. 2014. Changes in plant species richness following reduced fire frequency and drought in one of the most species-rich savannas in North America. *Journal of Vegetation Science* 25:1426–1437.
- Peet, R. K. 1981. Changes in biomass and production during secondary forest succession. Pages 324–338 *in* D. West, H. Shugart, and D. Botkin, editors. *Forest succession: Concept and applications*. Springer-Verlag, New York, NY.
- Pickett, S., and P. S. White. 1985. *The Ecology of Natural Disturbances and Patch Dynamics*. Academic Press, New York, NY.
- Plummer, M. 2015. rjags: Bayesian Graphical Models using MCMC.
- PRISM Climate Group. 2015. Oregon State University. <http://prism.oregonstate.edu>.

- R Core Team. 2015. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Rees, M., R. Condit, M. Crawley, S. Pacala, and D. Tilman. 2001. Long-term studies of vegetation dynamics. *Science* (New York, N.Y.) 293:650–5.
- Reich, P., D. Ellsworth, and C. Uhl. 1995. Leaf carbon and nutrient assimilation and conservation in species of differing successional status in an oligotrophic Amazonian forest. *Functional Ecology* 9:65–76.
- Runkle, J. R. 1985. Disturbance Regimes in Temperate Forests. Pages 17–33 *in* S. Pickett and P. S. White, editors. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, NY.
- Russell, M. B., C. W. Woodall, A. W. D’Amato, G. M. Domke, and S. S. Saatchi. 2014. Beyond mean functional traits: Influence of functional trait profiles on forest structure, production, and mortality across the eastern US. *Forest Ecology and Management* 328:1–9.
- Schamp, B. S., and L. W. Aarssen. 2009. The assembly of forest communities according to maximum species height along resource and disturbance gradients. *Oikos* 118:564–572.
- Sendall, K. M., C. H. Lusk, and P. B. Reich. 2015. Trade-offs in juvenile growth potential vs. shade tolerance among subtropical rain forest trees on soils of contrasting fertility. *Functional Ecology*.
- Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, C. Baraloto, M. B. Carlucci, M. V. Cianciaruso, V. de L. Dantas, F. de Bello, L. D. S. Duarte, C. R. Fonseca, G. T. Freschet, S. Gaucherand, N. Gross, K. Hikosaka, B. Jackson, V. Jung, C. Kamiyama, M. Katabuchi, S. W. Kembel, E. Kichenin, N. J. B. Kraft, A. Lagerström, Y. Le Bagousse-Pinguet, Y. Li, N. Mason, J. Messier, T. Nakashizuka, J. M. Overton, D. A. Peltzer, I. M. Pérez-Ramos, V. D. Pillar, H. C. Prentice, S. Richardson, T. Sasaki, B. S. Schamp, C. Schöb, B. Shipley, M. Sundqvist, M. T. Sykes, M. Vandewalle, and D. A. Wardle. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18:1406–1419.
- Spasojevic, M. J., E. A. Yablon, B. Oberle, and J. A. Myers. 2014. Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* 5:1–20.
- Swenson, N. G., B. J. Enquist, J. Pither, A. J. Kerkhoff, B. Boyle, M. D. Weiser, J. J. Elser, W.

- F. Fagan, J. Forero-Montaña, N. Fyllas, N. J. B. Kraft, J. K. Lake, A. T. Moles, S. Patiño, O. L. Phillips, C. A. Price, P. B. Reich, C. A. Quesada, J. C. Stegen, R. Valencia, I. J. Wright, S. J. Wright, S. Andelman, P. M. Jørgensen, T. E. Lacher Jr, A. Monteagudo, M. P. Núñez-Vargas, R. Vasquez-Martínez, and K. M. Nolting. 2012. The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography* 21:798–808.
- Swenson, N. G., and M. D. Weiser. 2010. Plant geography upon the basis of functional traits: an example from eastern North American trees. *Ecology* 91:2234–41.
- Umaña, M. N., C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2015. Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. *Ecology letters* 18:1329–37.
- Valladares, F., and Ü. Niinemets. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics* 39:237–257.
- Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology letters* 13:267–83.
- White, P. S., B. Collins, and G. R. Wein. 2011. Natural Disturbances and Early Successional Habitats. Pages 27–40 *in* C. Greenberg, B. Collins, and F. Thompson III, editors. *Sustaining Young Forest Communities*. Springer Netherlands, Dordrecht.
- Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography , ecology and species richness. *Trends in ecology & evolution* 19:639–644.
- Wilfahrt, P. A., B. Collins, and P. S. White. 2014. Shifts in functional traits among tree communities across succession in eastern deciduous forests. *Forest Ecology and Management* 324:179–185.
- Wilfahrt, P. A., P. S. White, B. S. Collins, and J. P. Tuttle. 2016. Disturbance, Productivity, and Tree Characteristics in the Central Hardwoods Region. Pages 295–317 *in* H. C. Greenberg and S. B. Collins, editors. *Natural Disturbances and Historic Range of Variation*. Springer International Publishing, Cham.
- Wonkka, C. L., C. W. Lafon, C. M. Hutton, and A. J. Joslin. 2013. A CSR classification of tree life history strategies and implications for ice storm damage. *Oikos* 122:209–222.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–7.

Table 5.1– Province specific trait responses. Bolded values indicate parameter estimates whose 95% credibility intervals do not include zero.

Table 5.2

Province	Status	LNC	Seed	Density	Height	Shade	Drought	# of regions
Northeastern and Adirondack-Mixed Forest	Disturbed	0.012	-0.040	-0.030	0.016	-0.099	0.025	48
	Undisturbed	0.002	0.122	0.007	-0.219	0.048	0.032	
Laurentian Mixed Forest	Disturbed	0.012	-0.127	-0.067	-0.054	-0.211	0.019	58
	Undisturbed	-0.002	0.038	0.023	-0.026	0.068	0.007	
Eastern US and Central Appalachian Broadleaf Forest	Disturbed	0.000	-0.013	-0.025	0.035	-0.056	0.029	58
	Undisturbed	0.014	0.026	0.018	-0.026	0.048	0.001	
Midwest Broadleaf Forest	Disturbed	-0.002	-0.018	-0.031	0.027	-0.068	0.030	44
	Undisturbed	0.018	0.033	0.016	-0.029	0.046	0.006	
Central Interior and Ozark Broadleaf Forest	Disturbed	0.015	-0.034	-0.025	0.027	-0.087	0.026	50
	Undisturbed	0.040	0.019	0.018	-0.025	0.020	0.004	
Southeastern US and Ouachita Mountains Mixed Forest	Disturbed	-0.006	-0.002	-0.021	0.046	-0.053	0.034	61
	Undisturbed	0.017	0.023	0.019	-0.027	0.042	0.003	
Outer Coastal Plain Mixed Forest	Disturbed	-0.004	-0.033	-0.033	0.015	-0.078	0.032	55
	Undisturbed	0.003	0.033	0.018	-0.033	0.059	0.003	
Lower Mississippi Riverine Forest	Disturbed	0.013	0.024	-0.008	0.071	-0.023	0.024	14
	Undisturbed	0.014	0.032	0.018	-0.028	0.046	0.004	
Temperate Prairie Parkland	Disturbed	0.013	-0.005	-0.024	0.048	-0.055	0.023	24
	Undisturbed	0.034	0.024	0.014	-0.021	0.023	0.002	

Table 5.2 – Estimated parameter values from a multiple regression model with linear and quadratic terms for both precipitation and temperature. Bolded values indicate parameter estimates whose 95% credibility intervals do not include zero. R^2 values were calculated based on model estimates.

Data	Trait	Intercept	Precipitation	Temperature	Prec x Prec	Temp x Temp	R^2
RWM of Initial Sampling Period	LNC	0.254	-0.145	0.011	0.046	-0.283	0.52
	Seed mass	0.066	-0.014	0.223	-0.042	-0.079	0.56
	Wood density	0.022	-0.043	0.230	-0.032	-0.071	0.43
	Max height	0.217	0.046	0.025	-0.016	-0.023	0.09
	Shade tolerance	0.499	0.253	-0.531	-0.095	0.083	0.59
	Drought tolerance	0.074	-0.207	0.526	0.030	-0.214	0.67
Disturbed Trait Shifts	LNC	-0.002	-0.016	-0.007	-0.016	0.022	0.02
	Seed mass	-0.015	0.034	0.001	-0.006	-0.014	0.04
	Wood density	-0.021	0.024	-0.008	-0.027	0.015	0.04
	Max height	0.050	0.011	0.016	-0.012	-0.019	0.03
	Shade tolerance	-0.056	0.012	0.027	-0.019	-0.015	0.04
	Drought tolerance	0.044	0.029	0.000	-0.012	-0.005	0.02
Undisturbed Trait Shifts	LNC	0.041	-0.020	0.033	-0.003	-0.024	0.07
	Seed mass	0.002	-0.021	0.004	0.023	0.004	0.09
	Wood density	-0.012	-0.008	0.003	0.028	0.001	0.07
	Max height	-0.020	0.022	-0.041	-0.009	0.002	0.05
	Shade tolerance	0.004	-0.004	-0.023	0.010	0.033	0.09
	Drought tolerance	-0.015	-0.012	0.005	0.028	-0.011	0.04

Figure 5.1 – Biogeographic provinces from McNab et al (2005). Diagonal lines indicate montane provinces which were binned with their constituent non-montane provinces. **211** – Adirondack (patterned) and Northeastern Mixed Forest. **212** – Laurentian Mixed Forest. **221** – Central Appalachian (patterned) and Eastern US Broadleaf Forest. **222** – Midwest Broadleaf Forest. **223** – Ozark (patterned) and Central Interior Broadleaf Forest. **231** – Ouachita Mountain (Patterned) and Southeastern US Mixed Forest (continues west of province 234). **232** – Outer Coastal Plain Mixed Forest (continues west of province 234). **234** – Lower Mississippi Riverine Forest. **251** – Temperate Prairie Parkland.

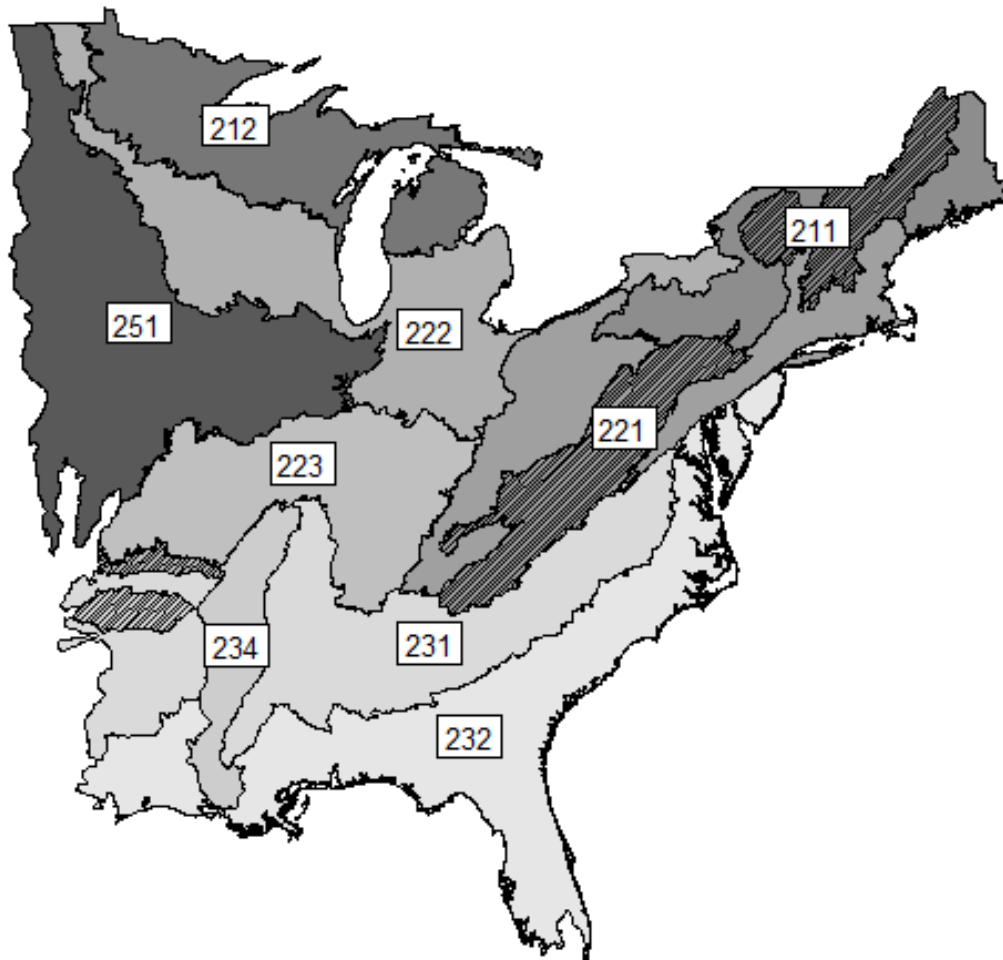


Figure 5.2 – Effect of basal area change, binned as ‘undisturbed’ (basal area increase) and ‘disturbed’ (decrease), on the six traits across the entire study area. Circles represent mean parameter estimates and bars cover the 95% credibility interval from the Bayesian models. Greyed out points’ credibility intervals cross zero.

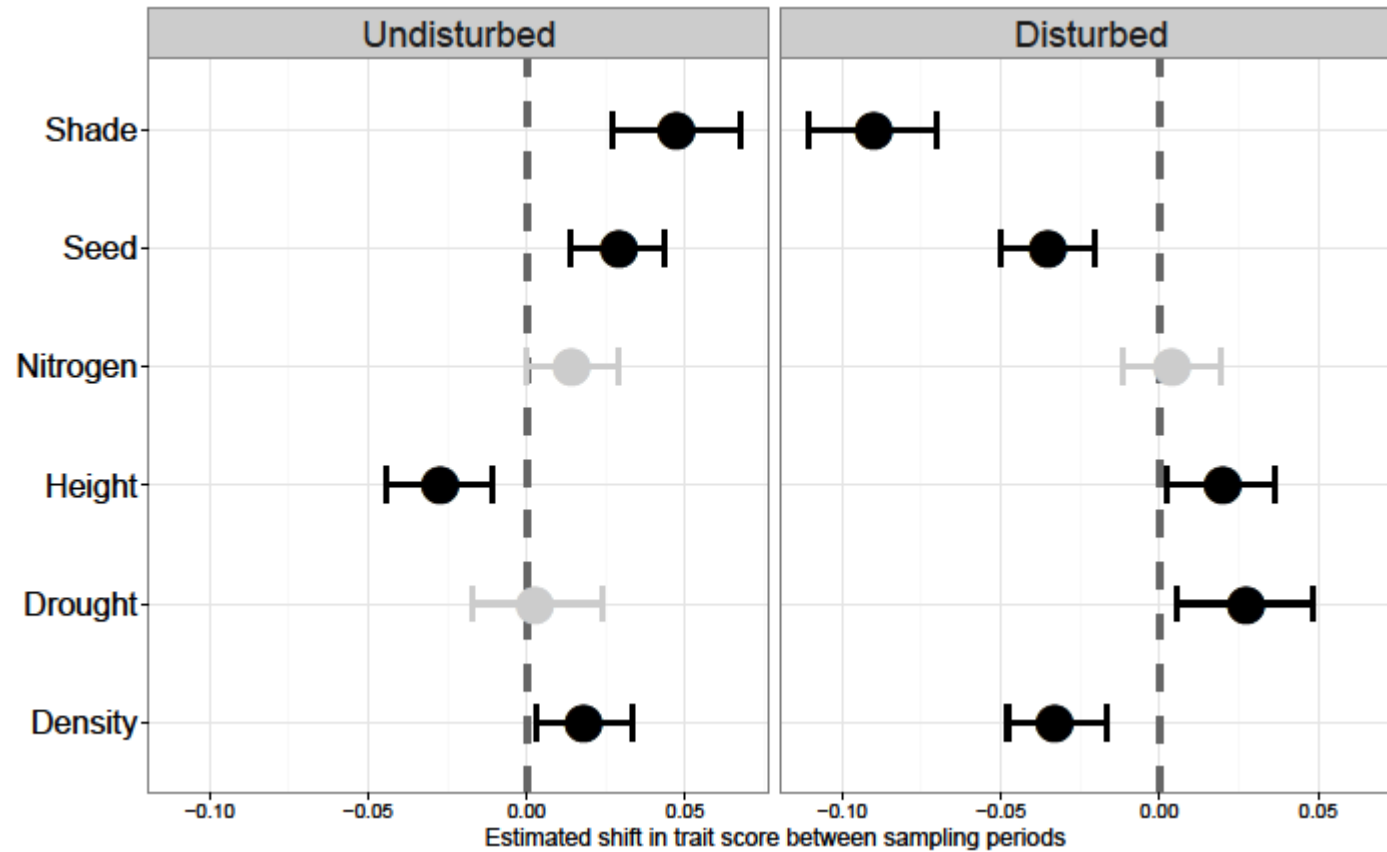


Figure 5.3 – Sensitivity analyses of the amount of basal area change observed. Bars with circular midpoints represent all subplots used, triangles represent excluding subplots in the lower 10th quantile of absolute basal area change squares represent subplot exclusion at the 25th quantile. Bars represent 95% credibility intervals of the respective model. Greyed out points' credibility intervals cross zero.

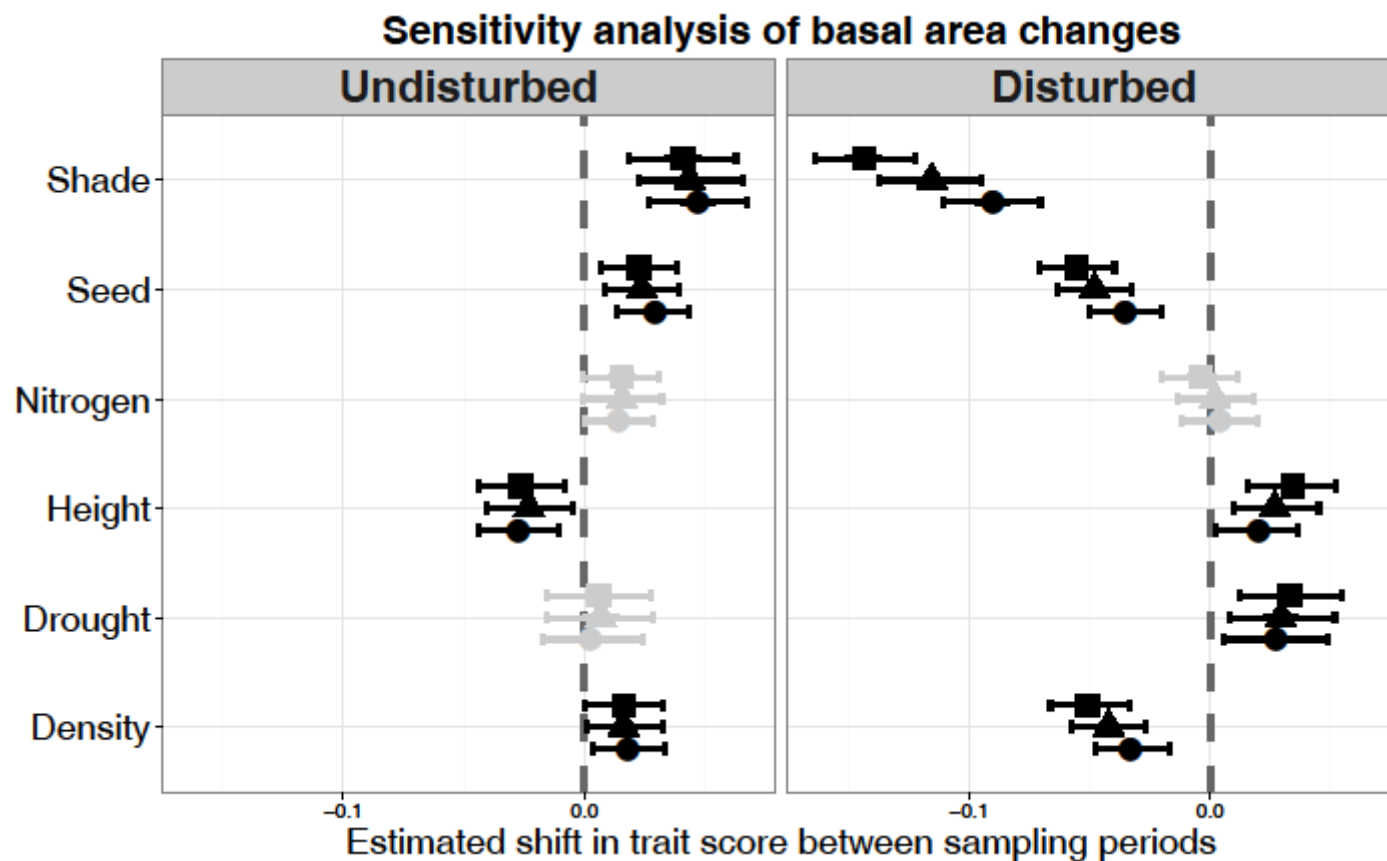


Figure 5.4 – Sensitivity analyses of the initial basal area. Bars with circular midpoints represent all subplots used, triangles represent excluding subplots in the lower 10th quantile of initial basal area for disturbed subplots and upper 10th quantile of initial basal area for undisturbed subplots. Squares represent subplot exclusion at the 25th quantile level. Bars represent 95% credibility intervals of the respective model. Greyed out points' credibility intervals cross zero.

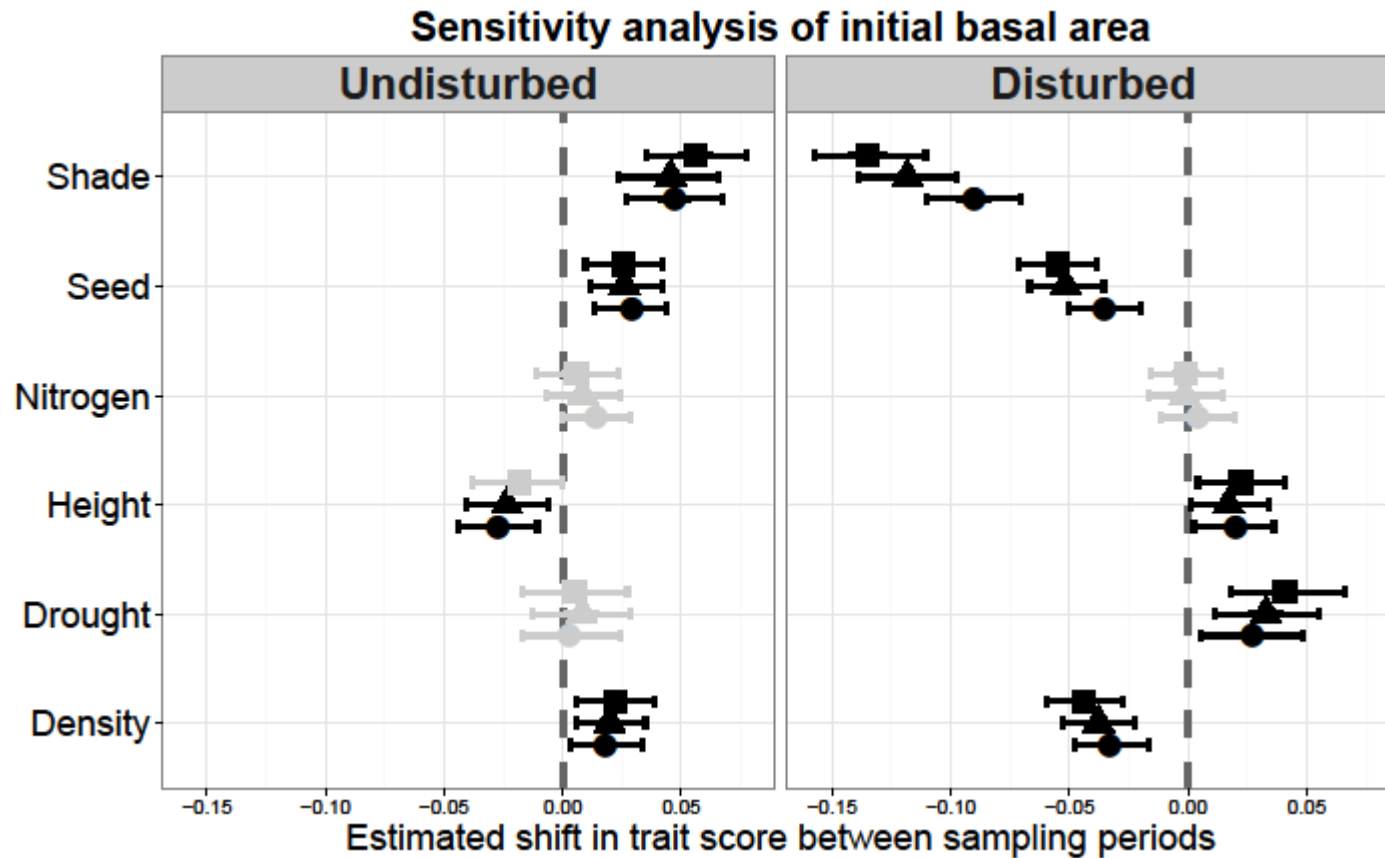
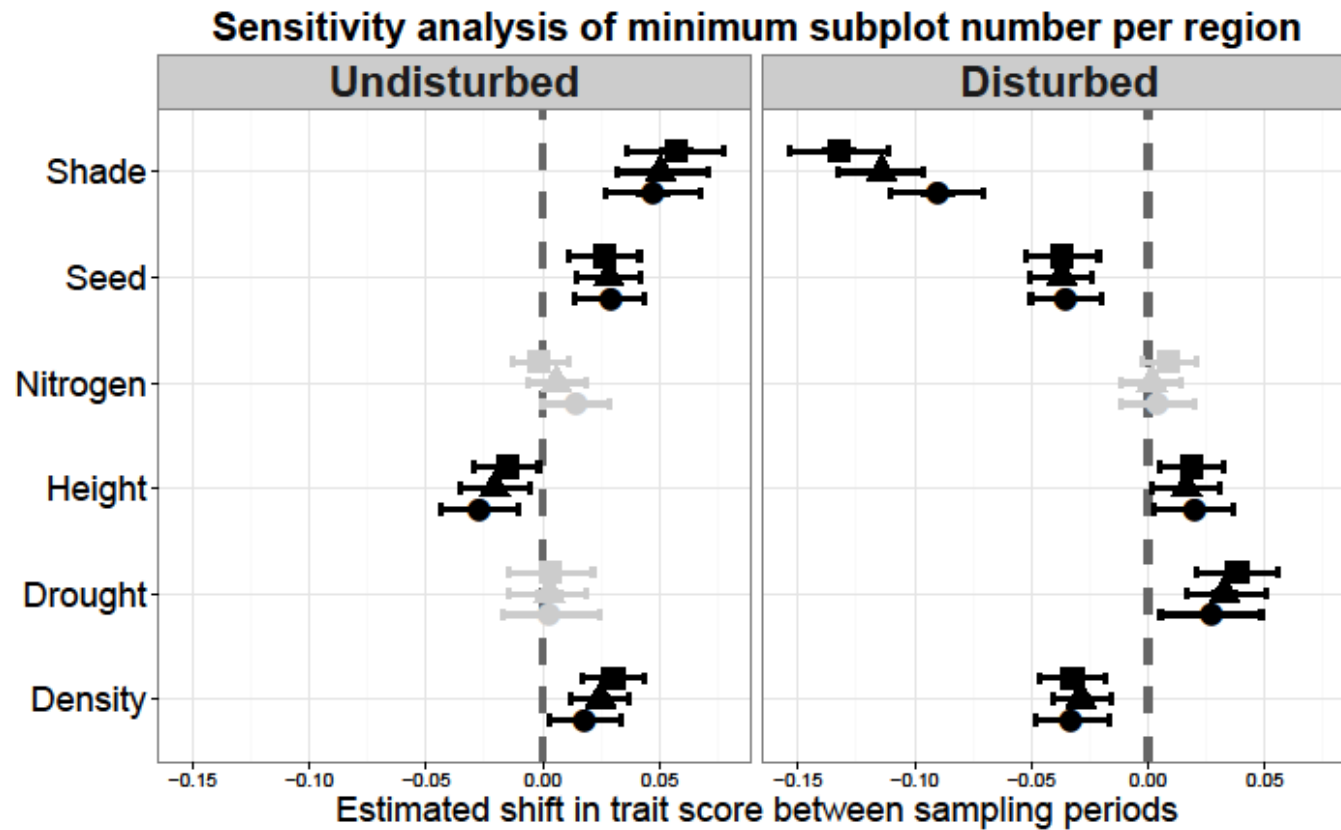


Figure 5.5 – Sensitivity analyses of the minimum number of subplots per region. Bars with circular midpoints represent all subplots used, triangles represent excluding regions with less than 10 representative subplots for either disturbance status, squares represent subplot exclusion at the 25 minimum subplot level. Bars represent 95% credibility intervals of the respective model. Greyed out points' credibility intervals cross zero.



CHAPTER 6 : CONCLUSION

Understanding the processes that drive succession aids in elucidating one of community ecology's central goals: understanding what maintains species coexistence across time and space. I have demonstrated in this dissertation that successional sequences constrain species based on their functional traits due to changing interspecific competition across time, but these general relationships additionally vary across different climatic, edaphic, and biotic conditions. Thus, succession is not a linear path to a climax community, but rather a series of possible species assemblages influenced by multiple environmental constraints and ecological tradeoff axes.

One of the central connections to emerge from studying old fields and forest in the eastern US is the importance of seed mass as a structuring trait during succession. Chapter 2 showed that seed mass correlated positively with when species maximized their abundance, and Chapter 3 showed that initial plot conditions filtered colonizing species based on seed mass. Similarly, seed mass emerged as a highly responsive trait to stand age and disturbance in forest communities as detailed in Chapter 4 and Chapter 5. Collectively, this indicates the importance of the colonization process for both herbaceous and tree species, since small seeded species sacrifice survival rates of offspring in favor of maximizing dispersal. Traits relating to stature were also important in both systems, although wood density responded more strongly than maximum height to disturbance in Chapter 5. This may result from differences in the temporal scale of turnover in these systems, as herbaceous dominants are less likely to invest in traits that confer shade tolerance since they can more rapidly access the canopy and shade out inferior

competitors, while tree species dominants often have to endure long periods of low light conditions before reaching the canopy. Nonetheless, both of these traits relate to species investment in structural biomass and change in consistent manners during succession. Leaf traits were the least informative in both of these systems. Leaf nitrogen was unresponsive to stand age and disturbance in Chapters 4 and 5. SLA did correlate with time to maximum abundance in Chapter 2 and responded to reduced enemy access in Chapter 3, but a large portion of its variation was unexplained relative to height and seed mass. However, both systems appeared to have unmeasured gradients that explained these leaf traits, ecoregions and latitude in the forested system, and experimental blocks.

Ultimately, I have demonstrated the utility of functional traits in explaining succession and disturbance processes in eastern temperate forests, a system where they are under used. Given the wide regional variability that was observed in Chapters 4 and 5, a clear next step is to identify these sources of variation at finer scales of inquiry. Conversely, while experimental manipulation can more reliably provide attribution to sources of trait variation, a next step in the old field experiment is in understanding how our results extrapolate to other systems. Exploring how population trajectories and LHS traits in other systems can reveal the generalizability of the results presented here. Future work would also benefit from including additional traits. While the LHS scheme is attractive for its simplicity, it ignores several broad suites of traits that may shed light on species' relationships to succession. Traits capturing resource allocation to root growth and form as well as traits detailing species phenology would aid in our understanding of the successional systems studied in this dissertation. Additionally, multiple traits detailing leaf structural and chemical composition (e.g. SLA, leaf dry matter content, leaf nitrogen content, carbon to nitrogen ratios) may be more informative than individual traits alone, despite their

tendency to be highly correlated. Finally, while height and wood density certainly inform competitiveness for light and growth rate, certain species may compete for light by increasing their lateral spread as opposed to their height. Nonetheless, the LHS scheme does capture significant portions of variation among and within species across successional gradients.

Overall, the work presented in this dissertation provides evidence that two disparate vegetation systems have similar ecological tradeoff axes influencing community composition across successional gradients. Understanding trait patterns expands on a wealth of previous work in these systems detailing taxonomic responses to variation in successional gradients, and lends process to observed patterns. As trait information continues to become increasingly available, we can expand our knowledge of these ecological tradeoffs and how they influence species coexistence.