

Functional Traits, Environmental Gradients and Community Assembly in a Temperate Forest

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Abstract

A central goal of ecology is to understand the processes that influence community assembly, which has important implications for the maintenance of biodiversity. Habitat filtering is a key process that may provide insight into community assembly, and indicates that a given habitat selects for individuals with similar survival strategies. Plant functional traits can be measured and used to study various processes of community assembly. While plant functional traits have been studied extensively as a way to learn more about community assembly, there are gaps in our knowledge of (1) how traits vary across multiple environmental gradients and (2) how trait-environment relationships vary across different functional groups (e.g. canopy vs. understory species). In this study, we examined relationships between community weighted means (CWMs) of five plant functional traits (leaf size, maximum DBH, seed mass, specific leaf area and wood density) across soil resource gradients (aluminum, nitrogen, phosphorus, pH and potassium) in a 12-ha oak-hickory forest dynamics plot at the Tyson Research Center, Missouri. If habitat filtering was important, we anticipated that trait values would be associated with environmental gradients. To test the hypothesis that CWM-soil relationships differ across functional groups, we performed separate analysis for all species combined, only canopy species, and only understory species. We found varying support for habitat filtering, as only some traits were strongly correlated with soil gradients. For all species combined, maximum DBH was strongly correlated with soil gradients, whereas wood density was weakly correlated. In addition, CWM-soil relationships between canopy and understory species indicated that these different functional groups assemble differently. In canopy species, leaf size was most strongly correlated with the soil gradients and seed mass had the weakest correlations. In understory species, maximum DBH had the strongest and SLA had the weakest correlation. Our results indicate that studying functional groups separately from each other can yield different results than studying them together, demonstrating how species respond differently to environmental gradients. Furthermore, this study reveals the relative importance of habitat filtering as a process of community assembly in this forest.

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Introduction

A central goal of ecology is to understand the processes that influence community assembly (McGill 2006; Kraft et al. 2008; HilleRisLambers et al. 2012; Katabuchi et al. 2012). The study of community assembly not only provides insight into the maintenance of biodiversity, but also into how biodiversity can be conserved in the face of environmental change (Lavergne et al. 2010). While the relative importance of stochastic (random) and deterministic (non-random) processes has been a topic of much debate, both processes have implications for community assembly (Grossman 1982; Chase and Myers 2011). If we account for plant functional traits and environmental gradients in studies of community assembly, we may be able to gain critical insight into how human changes to the environment will affect the diversity and composition of communities (McGill et al. 2006).

We use a trait-based approach to distinguish the stochastic and deterministic processes and further study how species may assemble in non-random ways. Plant functional traits provide important insights into mechanisms of community assembly (McGill et al. 2006; Kraft et al. 2008; Mayfield and Levine 2010; Paine et al. 2011; Katabuchi et al. 2012; Shipley et al. 2012). Reich et al. (2003) defines a plant functional trait as a characteristic that may notably impact the ability of an individual to survive in a given environment. Because taxonomic diversity is only one component of biodiversity, and species' names provide minimal information about the function of species (Swenson 2011), patterns of functional trait diversity may provide stronger inferences regarding community assembly than patterns of taxonomic diversity.

Two key processes involved in deterministic community assembly are habitat filtering and limiting similarity (MacArthur and Levins 1967; Weiher and Keddy 1995). Habitat filtering is predicted to result in local communities comprised of species with similar functional traits.

This is because the theory proposes that a given habitat selects for individuals with a similar strategy, meaning certain traits are better adapted to that habitat. In contrast, limiting similarity is predicted to result in a local community with differing functional traits. This would occur if functionally similar groupings of individuals compete more intensively with one another than functionally dissimilar species, allowing functionally different ones to coexist (Katabuchi et al. 2012). Studies using functional traits to test the strength of different processes of community assembly often find that habitat filtering plays a key role in the communities' formation (Paine et al. 2011; Shipley et al. 2012; Katabuchi et al. 2012). However, it is important to recognize that in many cases there is also evidence that in varying degrees, other processes (e.g. limiting similarity, dispersal limitation) play a role (Cornwell and Ackerly 2009; Katabuchi et al. 2012; Shipley et al. 2012).

Despite the importance of studying plant functional traits in community assembly, few researchers have taken up this challenge in tree communities in temperate forests; instead there has been an intense interest in high diversity tree communities in tropical forests (John et al. 2007; Kraft 2008; Paine et al. 2011; Paine et al. 2012; Shipley et al. 2012). Research on tree species diversity in temperate forests is far less common (Swenson 2012), but it is critical to understand how biodiversity operates in both tropical and temperate environments. This tropical bias has created gaps in our understanding of the relationship between plant functional traits and certain environmental factors.

Furthermore, most studies have not explicitly considered the fine scale soil gradients underlying patterns of functional diversity. In fact, while much research on discrete soil categories exists (Russo et al. 2005; Russo et al. 2008; Katabuchi et al. 2012) there has been an overall lack of studies accounting for the fact that communities assemble across environmental

gradients (McGill et al. 2006). By examining how multiple traits vary across soil resource gradients, we can begin to unravel the relationships between community assembly, plant functional traits and habitat filtering (Davies et al. 2005; McGill 2006).

We are able to further disentangle these relationships by studying how plant functional traits vary across different functional groups. The groups that we isolate are canopy and understory species. Understory species inherently receive less sunlight than canopy species, and may therefore be considered more shade tolerant than canopy species; canopy species are exposed to very different conditions than understory species when fully grown. There are important morphological and physiological differences between shade tolerant and shade intolerant species, so it is interesting to examine the corresponding plant functional traits separately (Valladares and Niinemets 2008).

Multiple traits are hypothesized to influence plant community assembly. Two key spectra exist, the “leaf economics spectrum” and the “wood economics spectrum,” along which relevant functional traits vary (Wright et al. 2004; Chave et al. 2009). Many of our traits are included on these spectra. Our first trait, leaf size, is impacted by variation in climate and geology, and is a good indicator of leaf energy and water balance (Cornelissen et al. 2003). In addition, specific leaf area (SLA; leaf area per unit leaf mass) tends to be positively correlated with the rate of photosynthesis but negatively correlated with leaf life spans (Wright et al. 2004; Swenson 2012). While there are valid reasons that SLA should be an indicator of certain aspects of plant behavior and performance, leaf economics spectrum traits, such as SLA, are some of the weakest predictors of growth and survival rates (Swenson 2012). Second, seed size influences seed dispersal distances, seedling growth rates, and seedling stress tolerance (Cornelissen et al. 2003). Larger seeded species may tolerate stress better than smaller-seeded species (Kitajima and

Myers 2008), though smaller seeded species produce a greater number of seeds m^{-2} of canopy outline year^{-1} (Moles and Westoby 2004). In tropical forests, seed mass is typically a very strong predictor of growth and survival rates, second only to wood density (Swenson 2012). Third, maximum DBH and wood density are both related to the “wood economics spectrum” (Chave et al. 2009). Maximum DBH is a measurement that can be used to represent maximum height, thereby giving us insight into the size of individuals (Kraft et al. 2008). Wood density is arguably one of the best indicators of growth and survival (Swenson 2012). It has been found to be negatively correlated with both growth and mortality rates (Chave et al. 2009; Wright et al. 2010; Swenson 2012). There are several proposed reasons for these correlations. For instance, dense wood is better able to resist stem breakage due to physical disturbance (Zimmerman et al. 1994; Swenson 2012). Furthermore, the more dense wood is, the less likely it is to be harmed by insects that may bore through the woody stem (Swenson 2012). Based on the “wood economics spectrum” (Chave et al. 2009), we expect wood-related traits to provide important insight into plant community assembly.

In this study, we examined trait-trait and trait-soil variable relationships in a temperate oak-hickory forest dynamics plot to achieve three primary objectives. First, we explored the importance of habitat filtering for community assembly. If habitat filtering is important, we hypothesize that plant functional trait values will be closely associated with the environmental soil gradients, because certain traits will be better suited for specific environments. Thus if there is a relatively strong association between the trait and soil gradient, we believe habitat filtering is a processes that may be contributing to the assembly of the communities we studied. Second, we examined whether some traits are filtered more or less than other traits in the gradients we considered. Finally, we tested if some soil gradients have a stronger influence on community

assembly. We expect to find low variance in a trait versus soil gradient graph if habitat filtering is taking place because in this case, specific localities should have similar trait values. We measured five traits – maximum diameter at breast height (maximum DBH), wood density, seed size, leaf size, and SLA – across 25 common woody species, including both canopy trees and understory shrubs (which makes up 99% of the number of stems in the FDP). We examined relationships between community weighted means (CWMs) of each trait and multiple soil resources (pH, nitrogen, phosphorus, aluminum and potassium) across local communities within the plot. We performed all analyses on CWMs from all species, from only canopy species, and finally from only understory species.

Methods

Study site: The Tyson Research Center Forest Dynamics Plot (FDP)

The research for this project was conducted at Washington University in St. Louis's Tyson Research Center (TRC), located twenty five miles southwest of St. Louis (38° 31' N, 90° 33' W; Hampe 1984). The research center is comprised of 800 ha and Oak-Hickory forest is the dominant habitat type (<http://tyson.wustl.edu/trcbiology.php>).

At TRC there is an established 12-ha oak-hickory forest dynamics plot (FDP) that is organized into 20x20-m quadrats, contains more than 19,000 mapped stems (≥ 1 cm diameter at breast height (DBH)), and encompasses a variety of terrain types including bottomlands, ridge tops, and east, southwest, west and north facing slopes. In 1981 four hectares of the plot were established, and the first census was in 1981-1982 (Hampe 1984). There was a second census of the four hectares in 1989 (V. Sork and C. Hampe, unpublished data), and a third census of the full twelve hectares was carried out in 2011-2012 (J. Myers, unpublished data). The Center for Tropical Forest Science (CTFS) protocol was followed in the 2011-2012 census: all woody stems with a diameter at breast height (dbh) ≥ 1 cm were tagged, identified to species, mapped and recorded (Condit 1998). The soil of the 12-ha plot was sampled, and fifteen different soil variables were measured using protocols developed by John et al. (2007) for CTFS FDPs. The soil variables were measured across the plot using the 20x20-m quadrats as our unit of study, and the results were used to generate high-resolution soil maps (Fig. 1). The soils data was used to study variation in trait values across multiple soil resource gradients.

Functional Trait Sampling

We collected trait data from individuals located in the habitat in which they are most abundant. We measured leaf size, maximum DBH, seed mass, SLA and wood density for 25

species commonly found in the Tyson FDP (Table 2). Traits of 12 species were measured in 2011 through spring 2012 (Zanne and Oberle, unpublished data), whereas traits for the other 13 species were measured in summer and fall 2012. Maximum DBH was obtained from the Tyson FDP, and seed mass was obtained from the literature (Seed Information Database); we were unable to obtain seed mass values for three species (*Carya texana*, *Quercus marilandica* and *Rhamnus caroliniana*). For each species, we measured leaf size, SLA, and wood density from outer canopy branch samples with high light exposure (N = 5 individuals per species). For each branch sample, a wood segment approximately 2.5 cm in length was selected at the point where the terminal branch first became approximately 1 cm in diameter. To measure wood density we used the volume displacement method (Osazuwa-Peters and Zanne 2011); we removed all bark from the wood segment and if the pith was large enough to affect wood density measurements, we sliced the wood segment in half and removed the pith (wood density measurements were then applied to each half of the wood segment and added together). We attached the wood segment to a needle and thread, which allowed immersion of the wood sample into water without contributing additional volume. We then submerged it in a beaker of distilled water located on a balance such that the top of the wood segment was right below the meniscus. We calculated the mass of the water displaced, which equaled our fresh volume (assuming density of water is 1g/cm^3). We then dried the wood segment in an oven at 103°C for at least 72 hours, measured it, and calculated wood density using the dry mass and fresh volume (Table1). To measure leaf size and SLA, we selected three representative leaves with minimal herbivory from the branch (for compound species, three leaves were selected but leaflets are treated as the functional leaf unit so a variable number of leaflets were measured, based on how many were on each leaf). We scanned the leaves into the computer and used Image J (Schneider et al. 2012) to determine the

area of the leaves. We found the area of all leaves scanned, and divided it by the number of leaves scanned to obtain tree average leaf size. Next, we dried the leaves in an oven at 65° C for at least 48 hours and then found the dry mass. Mass and area were used to calculate SLA per tree (Table 1). Table 1 provides a brief explanation of each trait, and Table 2 provides detailed information on each species we sampled.

Data analysis: Traits means across species, and community weighted mean (CWM) traits and soil resource gradients

First we calculated the mean value for each trait across all species. These values were used to look at differences in trait values among the species (Fig. 2). Next we used CWMs because these are measurements that account for trait values as well as abundance. The CWMs we calculated represent the mean value of a trait weighted by the quantity of the individuals with that trait in each 20x20-m quadrat (Lavorel et al. 2007). We used 20 X 20-m quadrats because this size quadrat generally avoids crossing major habitat types while providing enough species and individuals that interactions are important (Kraft et al. 2008; Katabuchi et al. 2012). Since species in the Tyson FDP tend to cluster based on habitat type, the species (and therefore trait values for each species) are not distributed evenly across the Tyson FDP. If we calculated mean trait values (as opposed to CWMs) for each quadrat, we would not have been able to account for differences in species abundance across the quadrats. CWMs were calculated for all species combined, for canopy species only, and for understory species only. For our statistical analyses, we used the ‘FD’ package (Laliberté and Legendre 2010; Laliberté and Shipley 2011) in the software R (version 2.14.2; R Development Core Team 2012). We also have estimates of fifteen different soil variables for each 20x20-m quadrat. We excluded highly correlated variables (Pearson $r > 0.80$). This yielded five soil variables: 1) pH, 2) nitrogen mineralization rate, 3)

phosphorus, 4) aluminum and 5) potassium. We used a linear regression to determine whether traits were correlated with each other trait, and whether each trait was correlated with each environmental variable. This analysis was done using CWMs from all species combined, with CWMs from only canopy species, and with CWMs from only understory species.

Results

Our results indicate substantial variability in traits across the different species; we found variation in a given trait across all species, and variation in how much each trait varied as compared to the other traits (Fig. 2). We also found important differences between canopy and understory species. In the following sections, we study CWMs for all species, and then canopy and understory species separately.

Trait-environment relationships – CWMs from all species combined

(1) *Relative importance of habitat filtering:* We found strong but variable correlations between CWMs and soil gradients (Table 6). We found strong negative relationships (e.g. $|r| > 0.50$) between leaf size and pH, and between maximum DBH and potassium, phosphorus and pH. The only strong positive correlation was between maximum DBH and nitrogen. This indicates that a high percentage of variation in these plant traits is explained by the corresponding soil gradients. With the exception of wood density and nitrogen, all CWM-soil relationships were significant ($p \leq 0.05$).

(2) *Which traits are filtered least and most:* Across all traits, leaf size and maximum DBH were most strongly correlated with soil gradients. Wood density was most weakly correlated with soil gradients (Table 6).

(3) *Which soil gradients filter the least and most:* Across all soil gradients, pH was most strongly correlated with the traits, and nitrogen was most weakly correlated with the traits (Table 6).

Trait-environment relationships – CWMs from canopy species

(1) *Relative importance of habitat filtering:* Using CWMs from only canopy species, we found the same number of strong correlations between CWMs and soil gradients as when using CWMs from all species combined. However, the strong correlations occurred between different traits

and soil gradients (Table 6 and Table 7). We found strong negative relationships (e.g. $|r| > 0.50$) between leaf size and pH and potassium, and between wood density and pH. We found strong positive relationships between leaf size and aluminum and nitrogen. Thus, a high percentage of variation in these plant traits is explained by the corresponding soil gradients. All relationships were significant ($p \leq 0.05$) except for the relationships between maximum DBH and phosphorus, and between seed mass and phosphorus.

(2) *Which traits are filtered least and most:* Across all traits, leaf size and wood density were most strongly correlated with soil gradients. Seed mass was most weakly correlated with soil gradients (Table 7).

(3) *Which soil gradients filter the least and most:* Across all soil gradients, pH was most strongly correlated with the traits, and phosphorus was most weakly correlated with the traits (Table 7).

Trait-environment relationships – CWMs from understory species

(1) *Relative importance of habitat filtering:* Using CWMs from only understory species yielded fewer strong correlations between CWMs and soil gradients than using CWMs from only canopy species or all species combined (Table 6, Table 7 and Table 8). Regardless, there are still strong correlations between some CWMs and soil gradients (Table 8). We found strong negative relationships ($|r| > 0.50$) between maximum DBH and pH and potassium. We found strong positive relationships between maximum DBH and nitrogen, and between wood density and pH. Accordingly, there is a high percentage of variation in these plant traits explained by the corresponding soil gradients. Our analysis yielded significant relationships between the traits and gradients ($p \leq 0.05$), excluding relationships between leaf size and potassium, and between SLA and all gradients besides aluminum.

(2) *Which traits are filtered least and most:* Across all traits, maximum DBH and wood density were most strongly correlated with soil gradients. SLA was most weakly correlated with soil gradients (Table 8).

(3) *Which soil gradients filter the most:* Across all soil gradients, pH was most strongly correlated with the traits, and phosphorus was most weakly correlated with the traits (Table 8).

Discussion

By examining plant functional traits and their relationships to environmental gradients, this study has shed light onto several fundamental aspects of community assembly. First, consistent with habitat filtering, we found significant and strong associations between certain traits and environmental soil gradients, a finding that has been documented in the literature (Katabuchi et al. 2012). Second, our analyses provide insights into which traits are most consistent with habitat filtering, and third, they indicate which soil gradients filter traits the most. Since fine scale soil gradients are insufficiently studied, our results regarding the role they play in community assembly are particularly important (McGill et al. 2006). Finally, by studying canopy and understory species separately we were able to explore the relationship between shade tolerance and intolerance and plant functional traits. We found striking differences in CWM-trait correlations when analyzing all species together, canopy species, and understory species. These differences indicate that plant functional traits have meaningfully different effects on community assembly. Therefore, it is important to study these functional groups separately.

One of our main goals was to determine which traits are most influenced by habitat filtering. We found that across all soil gradients, CWMs from only understory species showed maximum DBH as the trait that is most influenced by habitat filtering. Studying CWMs from only canopy species shows leaf size as the trait most influenced by habitat filtering. When habitat filtering occurs, we would expect low variance in a trait versus soil gradient graph because specific localities should have similar trait values (e.g. Fig. 3a and Fig. 3c). This means that across soil gradients, maximum DBH values in understory species are relatively similar at any given point on the soil gradient; however, maximum DBH values do not show this pattern in canopy species. On the other hand, canopy species have similar leaf size values at any given

point on a soil gradient, across the soil gradients, while understory species do not. These results indicate that the functional groups may be filtered by different traits, implying that processes of community assembly operate differently depending on the functional group.

Another main objective was to determine which soil gradients play a strong role in community assembly. We found that the strength of correlations between plant functional traits and soil gradients is more consistent when looking at a trait across all soil gradients. Looking at a given soil gradient across all of the traits shows more variability in the strength of correlations (Table 6, Table 7 and Table 8). For instance, if we look at maximum DBH (based on CWMs from all species), across all soil gradients the smallest r-value (using absolute value) is 0.49 and the largest is 0.76 (range = 0.27; the highest range in soil gradient values for a given trait). On the other hand, if we look at pH across all traits, the smallest r-value is 0.23, and the largest is 0.76 (range = 0.53; the highest range in trait values for a given soil gradient). This finding – that strength of correlations is more consistent for a trait, across soil gradients – remained the same when we studied CWMs from only canopy species and only understory species (Tables 7 and 8). Even so, it is still worthwhile to acknowledge which gradients, regardless of traits, have stronger influences on community assembly.

We found that canopy and understory species show striking similarities in the role soil gradients play in community assembly. None of the soil gradients show results that are strongly consistent with habitat filtering, but pH is somewhat consistent with this process for CWMs from all species, only canopy, and only understory species (Tables 6, 7 and 8). Thus, pH is the soil gradient that best filters traits. In all species combined, nitrogen is the least consistent with habitat filtering. However, in only canopy species and in only understory species, phosphorus is the least consistent. Therefore, it is important to recognize that functional groups are less

consequential when examining the importance of soil gradients on community assembly than when examining the extent to which traits are filtered.

We found weak relationships and the least significant correlations for wood density across the soil gradients when using CWMs from all species. However, when we studied canopy and understory species separately we found remarkably strong and significant relationships. Given that wood density is a critical predictor of growth and survival rates (Swenson 2012), we anticipated important findings regarding wood density. Other studies have found that analyses of wood density do not generate results consistent with habitat filtering (Kraft et al. 2008), so we did not necessarily expect findings consistent with habitat filtering. Regardless, after separating CWMs for canopy and understory species, we saw drastic increases in the strength of relationship between wood density and the soil gradients. Our results therefore indicate that within each functional group, habitat filtering is an important process for community assembly. In fact, within each functional group wood density was the second most consistent trait with habitat filtering.

Looking specifically at the relationship between wood density and pH, we saw remarkable differences when studying CWM-soil gradient correlations using CWMs from all species, only canopy, and only understory species (Fig. 4). Using CWMs from only canopy species and from only understory species, the strength of the correlation between wood density and pH is higher than when using CWMs from all species. Furthermore, in canopy species, wood density and pH are negatively correlated while in understory species they are positively correlated. These findings imply that this trait assembles differently among canopy species and understory species. Canopy species succeed in higher light environments while understory species persist in lower light environments. These differences imply that species in one

functional group should have different biological life strategies than those in the other group, a hypothesis consistent with our findings. The exact implications for community assembly remain unclear but it is undeniable that future studies using CWMs for plant functional traits, particularly in temperate forests, should study the CWMs separately for canopy and understory species. This should reduce confounding and contradictory effects that the functional groups might have on each other.

Our study indicates that certain traits are consistent with a known ecological process of assembly. However, our analyses do not provide sufficient evidence that this process is necessarily the primary driver in the assembly of the corresponding traits. Other processes, such as limiting similarity, can lead to dissimilar trait values, and could have potentially been at play in this ecosystem. Further and more rigorous analysis of these processes (such as a null model approach, as in Kraft et al. 2008 and Katabuchi et al. 2012) is necessary to provide the evidence needed to draw these conclusions. What we have found are indications that this process may be important. We also found that there are drastic differences in results when using CWMs from all species, and from canopy and understory species separately. These findings are important for determining directions of future research. It is important now, more than ever, that we work to unravel the various mechanisms governing community assembly. Plant functional traits can provide important insight into how species will respond to environmental changes, and may therefore reveal how communities will assemble in light of those changes. With global warming threatening society, we can anticipate shifts in the natural world, and a better understanding of community assembly and biodiversity may help us understand the changes we will all likely face.

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References

- Chase J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B*.
- 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* 12:351-366.
- Condit, R. 1998. *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer-Verlag Berlin Heidelberg and R.G. Landes Company Georgetown, Texas, USA.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steeg, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A Handbook of Protocols for Standardised and Easy Measurement of Plant Functional Traits Worldwide. *Australian Journal of Botany* 51:335-380.
- Cornwell W. K., D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*. 79:109-126.
- Davies, S. J., S. Tan, J.V. LaFrankie, and M.D. Potts. 2005. Soil-Related Floristic Variation in a Hyperdiverse Dipterocarp Forest. Pages 22-34 *in* D. W. Roubik, S. Sakai, and A. A. H. Karim, editors. *Pollination Ecology and the Rain Forest*. Springer Science+Business Media, Inc., New York, New York, USA.
- Grossman, G. D. 1982. Dynamics and Organization of a Rocky Intertidal Fish Assemblage: The Persistence and Resilience of Taxocene Structure. *The American Naturalist* 119:611-631.
- Hampe, C. L. 1984. A Description of Species Composition, Population Structures, and Spatial Patterns in a Missouri Oak-Hickory Forest. MS Thesis.

- 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.
- John, R., J. W. Dalling, K. E. Harms, J. B. Yavitt, R. F. Stallard, M. Mirabello, S. P. Hubbell, R. Valencia, H. Navarrete, M. Vallejo and R. B. Foster. 2007. Soil Nutrients Influence Spatial Distributions of Tropical Tree Species. *PNAS* 104: 864-869.
- Katabuchi, M., H. Kurokawa, S. J. Davies, S. Tan, and T. Nakashizuka. 2012. Soil Resource Availability Shapes Community Trait Structure in a Species-rich Dipterocarp Forest. *Journal of Ecology* 100:643–651.
- Kitajima, K, J. A. Myers. 2008. Seedling ecophysiology: strategies toward achievement of positive net carbon balance. Pages 172-188 *in* M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *Seedling Ecology and Evolution*. Cambridge University Press, New York, USA.
- Kraft, N. J. B., R. Valencia, and D. D. Ackerly. 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. *Science* 322:580–582.
- Laliberté, E., and P. Legendre (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305.
- Laliberté, E. and B. Shipley. (2011). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11.
- Lavergne, S., N. Moquet, W. Thuiller, and O. Ronce. 2010. Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities. *Annual Review of Ecology, Evolution, and Systematics* 41:321-350.

- Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrough, S. Berman, F. Quétier, A. Thébault, and A. Bonis. 2008. Assessing Functional Diversity in the Field – Methodology Matters! *Functional Ecology* 22:134-147.
- MacArthur, R., and R. Levins. 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist* 101:377-385.
- Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13:1085-1093.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding Community Ecology from Functional Traits. *Trends in Ecology and Evolution* 21:178–185.
- Moles, A. T., and M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 91:371-383.
- Osazuwa-Peters O., and A. E. Zanne. 2011. Wood density protocol. Prometheus Wiki. <<http://prometheuswiki.publish.csiro.au/tiki-index.php?page=Wood+density+protocol>>
- Paine, C. E. T., C. Baraloto, J. Chave, and B. Hérault. 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* 120:720–727.
- Paine, C. E. T., N. Norden, J. Chave, P. M. Forget, C. Fortunel, K. G. Dexter, and C. Baraloto. 2012. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters* 15:34–41.
- R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

- Reich, P. B., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Science* 164:S143-S164.
- Russo, S. E., S. J. Davies, D. A. King, and S. Tan. 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Ecology* 93:879-889.
- Russo, S. E., P. Brown, S. Tan, and S. J. Davies. 2008. Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of Ecology* 96:192-203.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9:671-675.
- Seed Information Database. Kew Royal Botanic Gardens.
<<http://data.kew.org/sid/sidsearch.html>>
- Shipley, B., C. E. T. Paine, and C. Baraloto. 2012. Quantifying the importance of local niche-based and stochastic processes to tropical tree community assembly. *Ecology* 93:760-769.
- Swenson, N. G. 2011. The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. *American Journal of Botany* 98:472-480.
- Swenson, N. G. 2012. The Functional Ecology and Diversity of Tropical Tree Assemblages Through Space and Time: From Local to Regional and from Traits to Transcriptomes. *ISRN Forestry* 2012:1-16.
- Valladares, F., and U. Niinemets. 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annual Review of Ecology, Evolution, and Systematics*. 39:237-257.

- Weihner E., P. A. Keddy. 1995. Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns. *Oikos* 74:159-164.
- 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* 428:821-827.
- Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, S. Diaz, B. M. J. Engelbrecht, K. E. Harms, S. P. Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, and A. E. Zanne. 2010. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* 91:3664–3674.
- Zimmerman, J. K., E. M. Everham III, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology* 82:911-922.

Figures and Tables

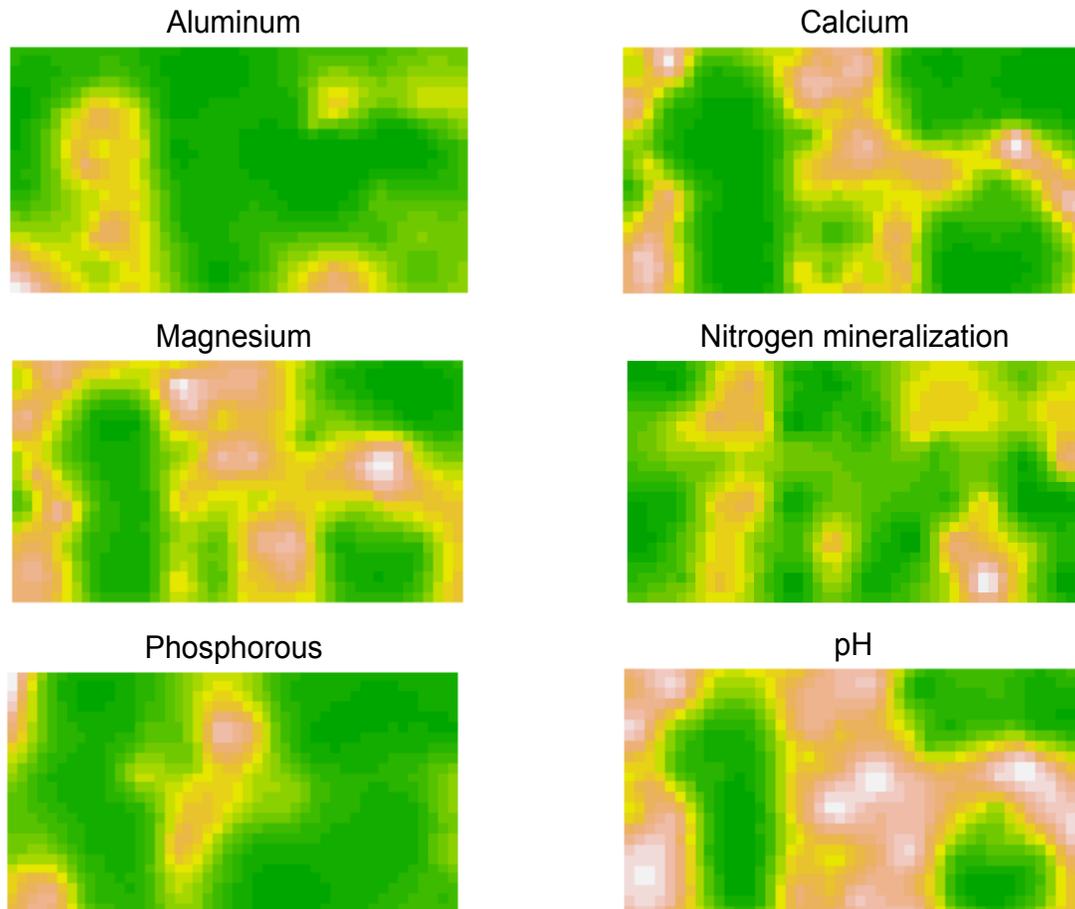


FIG. 1. Maps of several soil gradients that were measured across the Tyson FDP. Calcium and magnesium, included in this figure, were not included in our analysis because they were highly correlated with other soil gradients. In this paper we refer to “nitrogen mineralization” as simply “nitrogen.” Potassium is the only soil gradient we used that is not included in this figure.

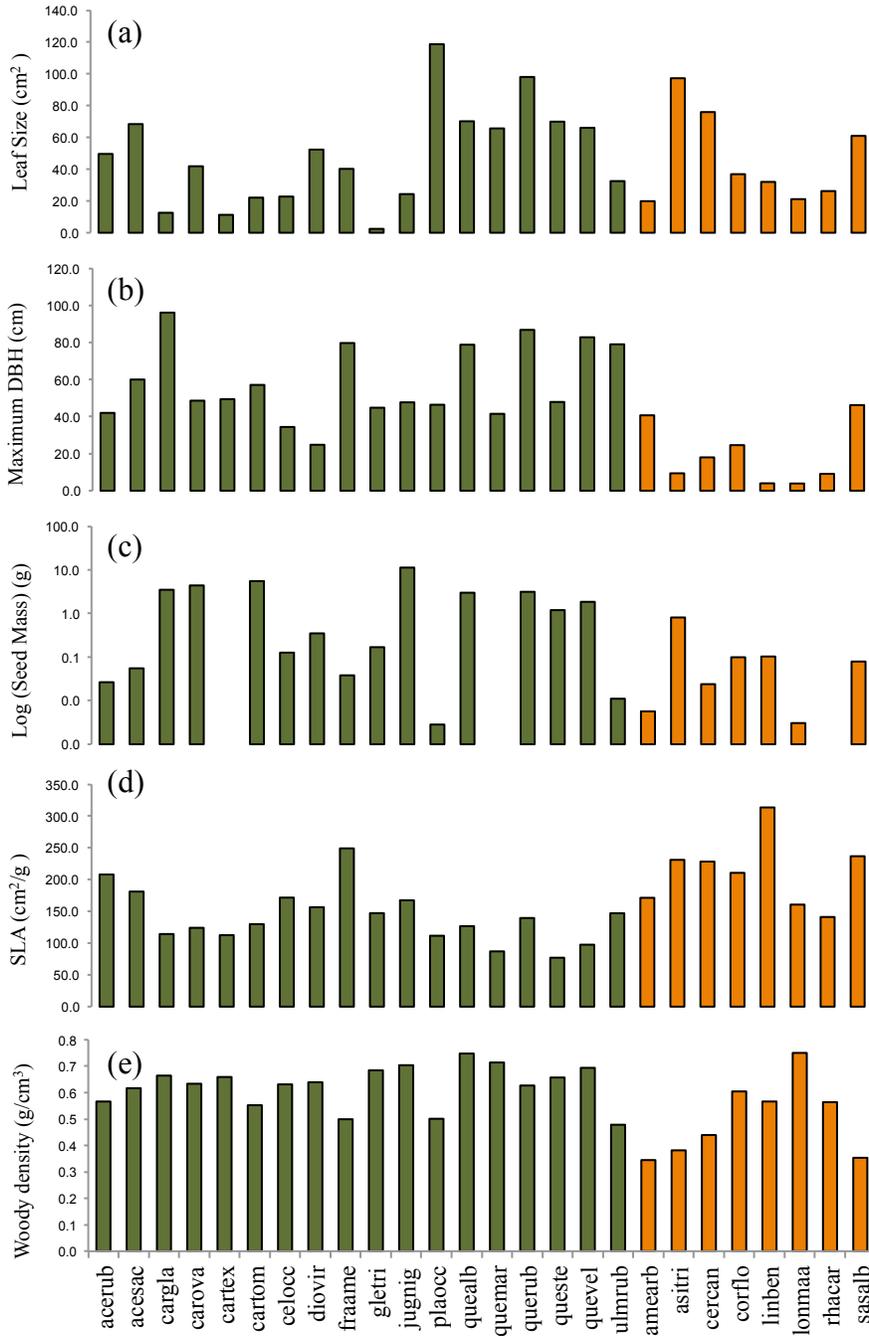


FIG. 2. Bar graphs show the average value of a given trait for each species. Green bars correspond to canopy species, and orange bars correspond to understory species. The y-axis shows plant functional traits values, and the x-axis shows species; species codes are used, consisting of the first three letters of the genus, and the first three letters of the species (see species names, Table 2). Graph (c) is on a logarithmic scale due large variations in highest and lowest values. Graph (c) is also missing data for three species (cartex, quemar and rhacar).

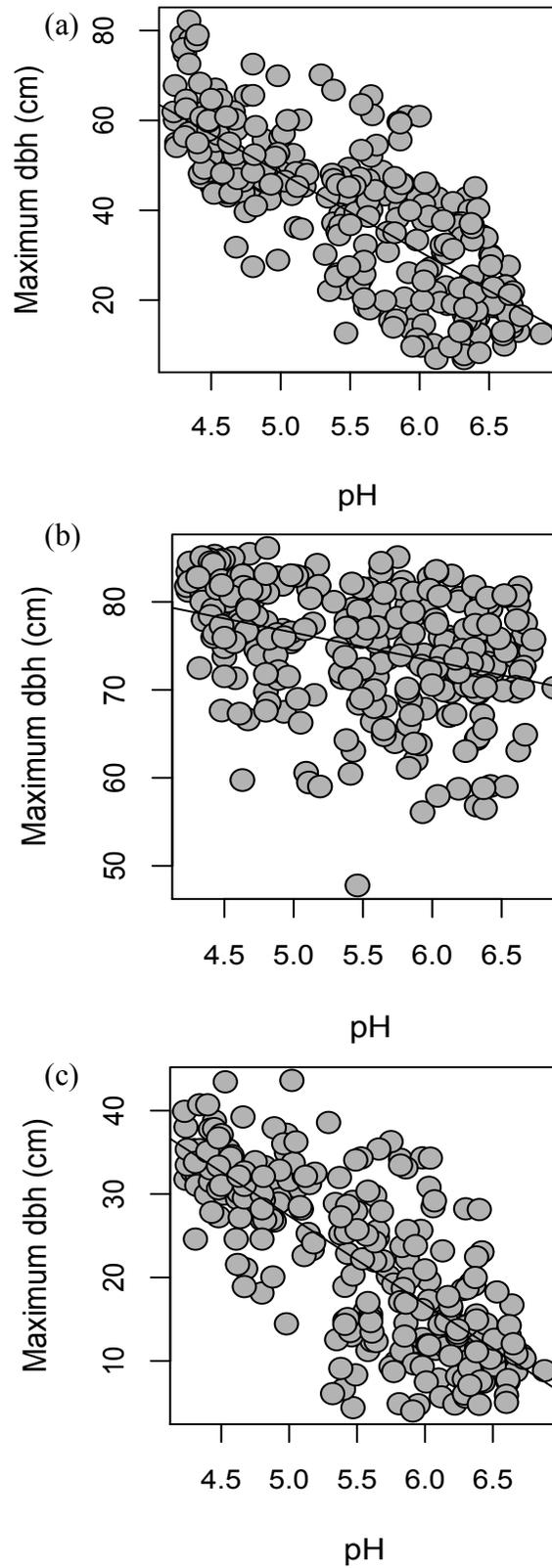


FIG. 3. Regressions for maximum DBH versus pH. Graph (a) is using CWMs from all species combined, graph (b) is using CWMs from canopy species only and graph (c) is using CWMs from understory species only. See Table 6, 7, and 8 for relevant r-values.

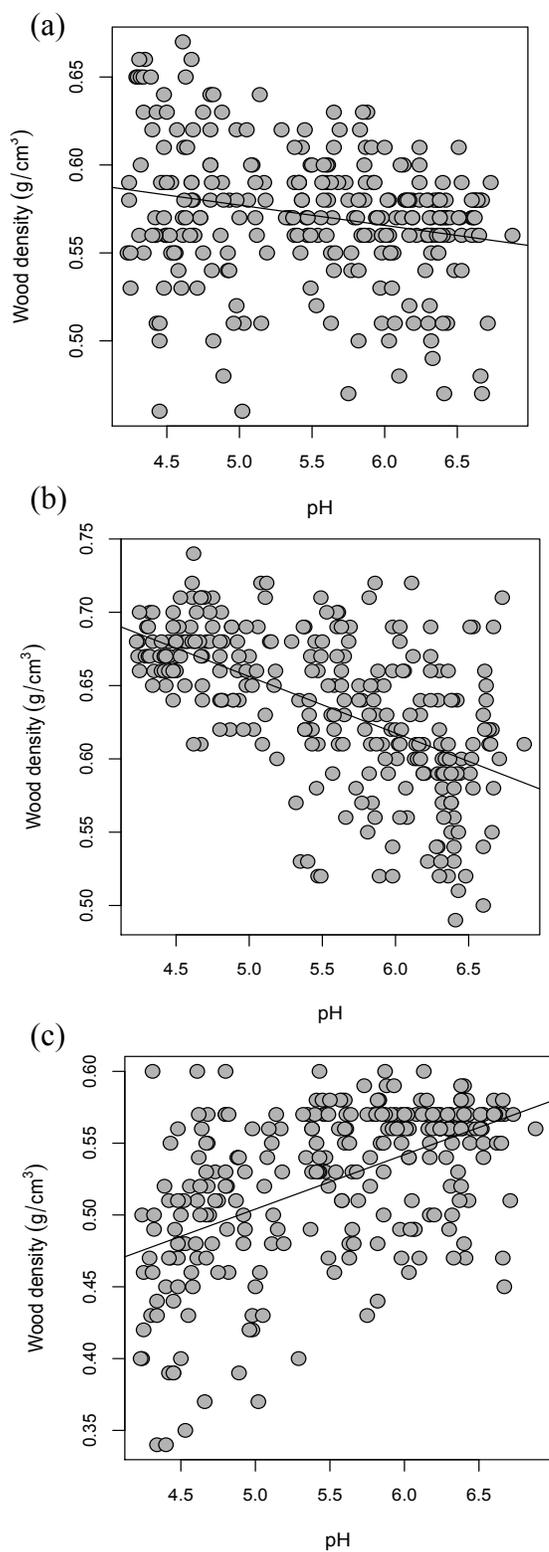


FIG. 4. Regressions for wood density versus pH. Graph (a) is using CWMs from all species combined, graph (b) is using CWMs from canopy species only and graph (c) is using CWMs from understory species only. See Table 6, 7, and 8 for relevant r-values.

TABLE 1. Plant functional traits measured and used in this study, including units, equation used to measure trait, functional value of studying the trait and reference source.

Trait	Unit	Equation	Function	Reference
Leaf Size	cm ²	Main leaf area	Energy and water uptake	Cornelissen et al. 2003
Maximum DBH	cm	-	Related to maximum size/height, an indicator of competition for light	-
Seed Mass	g	-	Dispersal and provisioning of offspring	Cornelissen et al. 2003
SLA	cm ² /g	Leaf area / Oven dry mass	Photosynthetic rates and longevity of leaves	Cornelissen et al. 2003
Wood Density	g/cm ³	Dry Wood Mass / Fresh Wood Volume	Mechanical strength	Wright et al. 2010

TABLE 2. Species most commonly found in the 12-ha Forest Dynamics Plot, Tyson Research Center, Missouri. Includes species name, common name, family, canopy vs. understory species, and mode of dispersal.

Species Name	Common Name	Family	Habitat	Dispersal
<i>Acer rubrum</i>	Red maple	Aceraceae	Canopy	Wind
<i>Acer saccharum</i>	Sugar maple	Aceraceae	Canopy	Wind
<i>Amelanchier arborea</i>	Serviceberry	Rosaceae	Understory	Bird, Mammal
<i>Asimina triloba</i>	Pawpaw	Annonaceae	Understory	Mammal
<i>Carya glabra</i>	Pignut hickory	Juglandaceae	Canopy	Mammal
<i>Carya ovata</i>	Shagbark hickory	Juglandaceae	Canopy	Mammal
<i>Carya texana</i>	Black hickory	Juglandaceae	Canopy	Mammal
<i>Carya tomentosa</i>	Mockernut hickory	Juglandaceae	Canopy	Mammal
<i>Celtis occidentalis</i>	Common hackberry	Ulmaceae	Canopy	Bird, mammal
<i>Cercis canadensis</i>	Eastern redbud	Fabaceae	Understory	Mammal, Wind
<i>Cornus florida</i>	Flowering dogwood	Cornaceae	Understory	Bird, Mammal
<i>Diospyros virginiana</i>	Common persimmon	Ebenaceae	Canopy	Bird, Mammal
<i>Fraxinus americana</i>	White ash	Oceaceae	Canopy	Wind
<i>Gleditsia triacanthos</i>	Honeylocust	Fabaceae	Canopy	Bird, Mammal
<i>Juglans nigra</i>	Black walnut	Juglandaceae	Canopy	Mammal
<i>Lindera benzoin</i>	Northern spicebush	Lauraceae	Understory	Bird, Mammal
<i>Lonicera maackii</i>	Amur honeysuckle	Caprifoliaceae	Understory	Bird, Mammal
<i>Platanus occidentalis</i>	American sycamore	Platanaceae	Canopy	Wind
<i>Quercus alba</i>	White oak	Fagaceae	Canopy	Mammal
<i>Quercus marilandica</i>	Blackjack oak	Fagaceae	Canopy	Mammal
<i>Quercus rubra</i>	Northern red oak	Fagaceae	Canopy	Mammal
<i>Quercus stellata</i>	Post oak	Fagaceae	Canopy	Mammal
<i>Quercus velutina</i>	Black oak	Fagaceae	Canopy	Mammal
<i>Rhamnus caroliniana</i>	Carolina buckthorn	Rhamnaceae	Understory	Mammal
<i>Sassafras albidum</i>	Sassafras	Lauraceae	Understory	Bird, Mammal
<i>Ulmus rubra</i>	Slippery elm	Ulmaceae	Canopy	Wind

TABLE 3. Summary of r-values for an ANOVA using community weighted mean trait values, and comparing each plant functional trait with every other trait. All species were included in this analysis.

Trait	Leaf Size	Max DBH	Seed Mass	SLA	Wood Density
Leaf Size		0.80***	0.53***	-0.35***	0.23***
Max DBH	0.80***		0.62***	-0.58***	0.36***
Seed Mass	0.53***	0.62***		-0.69***	0.52***
SLA	-0.35***	-0.58***	-0.69***		-0.40***
Wood Density	0.23***	0.36***	0.52***	-0.40***	

Note: p-values were determined, with ranges designated by the following number of stars:
 *** $p \leq 0.001$ ** $0.001 < p \leq 0.01$ * $0.01 < p \leq 0.05$ $p > 0.05$

TABLE 4. Summary of r-values for an ANOVA using community weighted mean trait values, and comparing each plant functional trait with every other trait. Only canopy species were included in this analysis.

Trait	Leaf Size	Max DBH	Seed Mass	SLA	Wood Density
Leaf Size		0.42***	0.37***	-0.44***	0.72***
Max DBH	0.42***		0.39***	-0.51***	0.37***
Seed Mass	0.37***	0.39***		-0.59***	0.59***
SLA	-0.44***	-0.51***	-0.59***		-0.70***
Wood Density	0.72***	0.37***	0.59***	-0.70***	

Note: p-values were determined, with ranges designated by the following number of stars:
 *** $p \leq 0.001$ ** $0.001 < p \leq 0.01$ * $0.01 < p \leq 0.05$ $p > 0.05$

TABLE 5. Summary of r-values for an ANOVA using community weighted mean trait values, and comparing each plant functional trait with every other trait. Only understory species were included in this analysis.

Trait	Leaf Size	Max DBH	Seed Mass	SLA	Wood Density
Leaf Size		-0.02	0.69***	0.31***	-0.15*
Max DBH	-0.02		-0.41***	-0.19**	-0.74***
Seed Mass	0.69***	-0.41***		0.09	0.06
SLA	0.31***	-0.19**	0.09		0.05
Wood Density	-0.15*	-0.74***	0.06	0.05	

Note: p-values were determined, with ranges designated by the following number of stars:
 *** $p \leq 0.001$ ** $0.001 < p \leq 0.01$ * $0.01 < p \leq 0.05$ $p > 0.05$

TABLE 6. Summary of r-values for an ANOVA using community weighted mean trait values, and comparing each plant functional trait with all soil variable gradients of study. All species were included in this analysis.

Soil Variable	Plant Functional Traits				
	Leaf Size	Max DBH	Seed Mass	SLA	Wood Density
Aluminum	0.39***	0.49***	0.38***	-0.42***	0.18**
Nitrogen	0.35***	0.52***	0.18**	-0.25***	0.08
Phosphorus	-0.35***	-0.55***	-0.17**	0.29***	-0.19**
pH	-0.59***	-0.76***	-0.39***	0.41***	-0.23***
Potassium	-0.48***	-0.63***	-0.25***	0.32***	-0.23***

Note: p-values were determined, with ranges designated by the following number of stars:
 *** $p \leq 0.001$ ** $0.001 < p \leq 0.01$ * $0.01 < p \leq 0.05$ $p > 0.05$

TABLE 7. Summary of r-values for an ANOVA using community weighted mean trait values, and comparing each plant functional trait with all soil variable gradients of study. Only canopy species were included in this analysis.

Soil Variable	Plant Functional Traits				
	Leaf Size	Max DBH	Seed Mass	SLA	Wood Density
Aluminum	0.52***	0.37***	0.26***	-0.26***	0.30***
Nitrogen	0.62***	0.25***	0.21***	-0.33***	0.49***
Phosphorus	-0.37***	0.05	0.10	0.12*	-0.25***
pH	-0.73***	-0.35***	-0.26***	0.46***	-0.57***
Potassium	-0.52***	-0.16**	-0.07	0.34***	-0.44***

Note: p-values were determined, with ranges designated by the following number of stars:
 *** $p \leq 0.001$ ** $0.001 < p \leq 0.01$ * $0.01 < p \leq 0.05$ $p > 0.05$

TABLE 8. Summary of r-values for an ANOVA using community weighted mean trait values, and comparing each plant functional trait with all soil variable gradients of study. Only understory species were included in this analysis.

Soil Variable	Plant Functional Traits				
	Leaf Size	Max DBH	Seed Mass	SLA	Wood Density
Aluminum	-0.19**	0.49***	-0.21***	-0.26***	-0.30***
Nitrogen	-0.24***	0.61***	-0.33***	-0.05	-0.41***
Phosphorus	0.13*	-0.49***	0.25***	0.08	0.20**
pH	0.21***	-0.77***	0.38***	0.11	0.52***
Potassium	0.09	-0.61***	0.26***	0.03	0.32***

Note: p-values were determined, with ranges designated by the following number of stars:
 *** $p \leq 0.001$ ** $0.001 < p \leq 0.01$ * $0.01 < p \leq 0.05$ $p > 0.05$