ABSTRACT

Title of Dissertation: THE ROLE OF FUNCTIONAL TRAITS IN DRIVING SPECIES RELATIVE ABUNDANCE IN PLANT COMMUNITIES

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Tropical forests harbor remarkable levels of biodiversity characterized by an exceptional number of rare species and few common species. Human and natural disturbances are increasingly threatening the condition of these forests, especially the persistence of species with low population sizes. Thus, disentangling the drivers of species relative abundance represents a central goal in ecology and critical step in order to maintain and predict future changes in biodiversity. One potential explanation for the variation in abundance relays on the idea that species exhibit differential abilities to exploit resources that are heterogeneously distributed in space. This ability is expected to be associated with different organisms' attributes (functional traits) that affect the individual performance and ultimately their distribution and abundance. The trait-base approach serves as a general framework for this dissertation that examines the role of species' traits in influencing the observed variation in species relative abundance across plant communities. In the first chapter, I examine changes in functional composition of tropical tree communities during a key life-history transition, the seed-to-seedling transition, in order to determine the main ecological forces driving the high mortality occurring during these early stages. In the second chapter, I evaluate the importance of intra-specific trait variation as related with the species abundance. I show that abundant species have lower magnitude of intraspecific trait variation than rare species. In the third study, I compile a set of functional traits across several plant communities including tropics and temperate forest to quantify the contribution of rare species to the functional diversity of the communities. In the fourth chapter, I assemble individual-level trait information together with performance to predict seedling growth rates as related with trait dissimilarity. Together, these findings expand our knowledge on the ecological forces underlying patterns of species relative abundance and will help to foster decisions devoted to preventing biodiversity loss in tropical forests.

THE ROLE OF FUNCTIONAL TRAITS IN DRIVING SPECIES RELATIVE ABUNDANCE IN PLANT COMMUNITIES

by

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Chapter 1: Introduction

A widely sustained generality about natural communities, is that they contain few common species and many rare species (Fisher 1943; Preston 1948; Lawton 1999). Regardless of the type of organisms studied, ecologists and naturalists have repeatedly documented this ubiquitous pattern since the 1800's (Darwin 1859, Wallace 1878) and today it is considered as one of the few general laws in ecology (Lawton 1999). For tropical communities, the number of rare species becomes even larger and many of the rare species exhibit extremely low abundance, in many cases, represented by single individuals across communities of more than 20,000 individuals (Hubbell and Foster 1986*a,b*; Hubbell 2001). Despite its generality, the main drivers of the pattern that describes the species abundance distribution remain largely unsolved (McGill 2006; McGill et al. 2007). Thus, disentangling the causes of species relative abundances constitutes a major goal in ecology and conservation of biodiversity.

The observed variation in species relative abundance is the result of differences in survival rates and establishment. Species that are able to attain higher survival would be able to attain higher population size, while species with lower survival chances would likely attain lower population sizes. This variation in demography has been often explained as result of differences in the use of resources that are heterogeneously distributed in space and time (Motomura 1932; MacArthur 1957, 1960; Whittaker 1965). However, the variation in resources is not always strongly linked to the distribution and abundance of all the different species in communities (Hanski 1982; Harms et al. 2001). One factor that could provide further insights into the current limited understanding of the variation in species abundance is the role of phenotypic differences across species. Species traits provide a useful way to determine the species strategies that allow individuals to establish and be successful within communities (McGill et al. 2006).

Species exhibit a broad arrangement of different traits that allow the interactions with their surrounding environment (through biotic interactions and exploiting different resources) (McGill et al. 2006; Violle et al. 2007). For example, seed mass represents a tradeoff between species that produce numerous and low quality seeds that are often not stress tolerant but able to disperse widely, and species that produce few but high quality seeds able to tolerate stressful environments (Muller-Landau 2010). Species with different traits will exhibit variation in their demographic performance given that some strategies will be favored over others which eventually will result in the observed variation of species abundance (Arnold 1983; Violle et al. 2007). Thus, integrating trait-based approached into the questions on the relative abundance of the species will shed light on the ecological forces underlying the pattern.

This dissertation concerns the species relative abundance distribution and how this pattern is linked with the variation in traits. I present three studies in which I test different hypotheses on how species-level, and individual-level traits should be related to the variation in species abundance. Then, in a fourth study I evaluate how individual performance (relative growth rates) responds to variation in several traits measured at the individual level and linked to resource acquisition strategies. Combined, these four projects represent an assemblage of evidence on the role of traits as related to the patterns of abundance. The conclusions presented here provide a deeper understanding on how tree species are differentially related with their environment and how the species-environment relationships are influencing species population sizes.

In *chapter 2*, I evaluate the ecological forces driving community structure and functional composition across one of the most important life-history transitions for plant communities, the seed to seedling transition. This ontogenetic transition is considered a key step for understanding patterns of species abundance, given that a high percentage of the individuals die, affecting species population sizes. The results from this study suggest that there are at least two contrasting forces shaping the species composition and functional structure of seedlings communities. One force is restricting the total range of functions from seed to seedling stage, while the other is promoting species diversity through conspecific negative density processes.

In *chapter 3*, I examine the role of intraspecific trait variation in relation to patterns of species relative abundance for seedlings in two tropical rain forests. The main goal of this project is to evaluate whether the magnitude of intraspecific trait variation is variable across species and related with the relative abundance of the species. The results show that common species tend to be less variable in performance and several traits associated with resource acquisition strategies than rare species, and tend to occupy central positions within the functional space of the community. On the other hand, rare species tend to occupy peripheral positions within the total volume of functional space. Together these findings suggest that common and rare species exhibit differences in ecological requirements and temporal dynamics.

In *chapter 4*, I investigate the contribution of rare species to the functional diversity of the community and their patterns of local spatial distribution across plant communities from temperate and tropical regions. The results show that rare species tend to occupy peripheral positions in the functional space suggesting that they are key contributors of the functional diversity in tree communities. Further, rare species tend to be more clustered than common species. This evidence shows that locally rare tree species disproportionally contribute to community functional diversity highlighting the importance of considering rare species in future strategies aimed at conserving both tree species and functional diversity.

In *chapter 5* I explore the effect of trait dissimilarity in a neighborhood scale together with the role of traits itself and density of neighboring individuals on patterns of relative growth rates of tropical seedling communities. The result show that functional dissimilarity in traits related to resource acquisition strategies are not strongly linked to growth rates of seedlings, however seedling performance is enhanced for seedlings that invest in leaf biomass and that are surrounded by few conspecifics.

The results presented in this dissertation show that the generality of the pattern of species relative abundance underlies a variety of ecological processes that shape the functional structure of plant communities at individual and species level. Specifically I show that: (i) beyond the species differences in phenotypes, considering individual-level differences in traits is a necessary step to understand the linkage that translates individual interactions into a population and community levels which ultimately results in the variation of species relative abundance; (ii) given that the species abundance distribution is an emergent outcome of the variations in demography among individuals, assembling information on performance together with functional traits is a key step to foster understanding into the forces leading variations in species abundance.

Chapter 2: Inter-specific functional convergence and divergence and intra-specific negative density dependence underlie the seed-to-seedling transition in tropical trees.

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Abstract

The seed-to-seedling transition constitutes a critical bottleneck in the life history of plants and represents a major determinant of species composition and abundance. However, we have surprisingly little knowledge regarding the forces driving this ontogenetic transition. Here we utilize information regarding organismal function to investigate the strength of intra- and inter-specific negative density dependence during the seed-to-seedling transition in Puerto Rican tree species. Our analyses were implemented at individual sites and across an entire 16-ha forest plot, spanning six years. The functional richness of seedling assemblages was significantly lower than expected given the seed assemblages, but the functional evenness was significantly higher than expected indicating the simultaneous importance of constraints on the overall phenotypic space and trait differences for successful transitions from seed to seedling. The results were consistent across years. Within species, we also found evidence for strong intra-specific negative density dependence where the probability of transition was proportionally lower when in a site with high conspecific density. These results suggest that filtering of similar phenotypes across species and strong negative density dependence within and among species are simultaneously driving the structure and dynamics of tropical tree assemblages during this critical life-history transition.

Introduction

Identifying the mechanistic drivers of the assembly and structure of diverse plant communities remains a key challenge in empirical and theoretical ecology (Wright 2002; Kraft et al. 2008; Swenson 2013). Diverse tropical tree assemblages have been particularly challenging to untangle given the lifespan, abundance, and diversity of the species involved. Despite these challenges, ecologists have made progress through analyzing long-term forest dynamics datasets (e.g., Condit et al. 2006; Wills et al. 2006; Swenson et al. 2012b; Muscarella et al. 2013). Recent studies have shown that non-random mortality is particularly high in the smallest size classes in tropical tree communities and this leaves a disproportionally large imprint on patterns of co-existence through to adulthood (Metz et al. 2010; Paine et al. 2012; Bagchi et al. 2010, 2014; Green et al. 2014). Uncovering the ecological mechanisms that determine the seed-to-seedling transition and their effects on tropical tree co-existence and community dynamics (Levine & Murell 2003) is an essential goal.

The number of individuals in the seed community is usually much larger that that in the established seedling community at any particular location, with more than 75% of the seeds that land in a site being unable to successfully establish and grow (Howe et al. 1985; Schupp 1988). Seedling and sapling studies have argued for the importance of negative density dependence (Harms et al. 2000; Metz et al. 2010), abiotic filtering (Uriarte et al. 2010) or stochastic survivorship (Paine & Harms 2009). However, it is more likely that all of these factors act at the same time (e.g., Swenson & Enquist 2009), making it important to disentangle their importance in structuring tropical tree communities through space and time.

There have been many temporally static investigations of seedling assemblages (Augspurger 1984*a*; Nicotra 1999; Norden et al. 2007; Paine et al. 2012) and some dynamic investigations of the seedling-to-sapling transition (Norden et al. 2012, Green et al. 2014), but there are few detailed forest-wide investigations of perhaps the biggest demographic bottleneck of all: the seed-to-seedling transition (Harms et al. 2000; Paine & Harms 2009; Norden et al. 2009; Muscarella et al. 2013). One of the best-known of these investigations comes from Harms et al. (2000) who found that the seed-to-seedling transition in a Panamanian tropical forest assemblage was strongly influenced by negative density dependence. Intra-specific negative density dependence is expected to have a higher per capita mortality rate at higher population densities than at lower population densities. Thus, it is expected that proportionally fewer individuals will successfully transition from seed-to-seedling when there is a higher local conspecific density. Using a log-log regression of the number of seedlings against the number of seeds at a site, Harms et al. (2000)

proposed that a linear regression slope less than one would be indicative of intra-specific negative density dependence (Figure 2.1).

Although the Harms et al. (2000) approach can provide insights into intra-specific negative density dependence, it does not integrate information pertaining to plant function in the form of trait data. Adding such information is important because the successful transition from seed to seedling is influenced by traits that affect the individuals' establishment, growth and survival, and ultimately fitness (Arnold 1983; Reich 2003; McGill et al. 2006). Individuals with trait values that are favored in a given abiotic and biotic context will have increased probabilities of growth and survival, thereby enabling the plant to advance to the next ontogenetic stages. From a study of seed and seedling densities alone we cannot understand the functional mechanisms underlying the observed patterns of density change. Integrating traits into analyses of the seed-to-seedling transition in tropical tree communities is critical because of the potentially large number of functionally similar species (Hubbell and Foster 1986). For example, although negative density dependence has been demonstrated within species of tropical trees (Harms et al. 2000; Bagchi et al. 2014), one might also expect stronger negative density dependence between species with similar traits, due to negative interactions such as inter-specific competition for similar resources. As a result, we would expect negative density dependence to maximize the local species and functional richness and mean nearest neighbor distance of the community (i.e. the total trait range and the mean trait distance between the nearest neighbors) (Villeger et al. 2008). Under this *negative density dependence hypothesis*, the proportion of seeds that become established as seedlings will be reduced if there are more conspecifics or functionally similar heterospecifics in the neighborhood. The pattern resulting from such a mechanism is that the functional richness of seedlings will be similar to the functional richness of seeds, which arrived at that site.

An alternative to the *negative density dependence hypothesis* described above would emphasize functional similarity among species. Under *the functional convergence hypothesis*, species have an increased probability of transitioning from seed to seedling due to one of two main processes: abiotic filtering or hierarchical competition for resources. An abiotic filtering process dictates that species with similar functions are the only ones capable of successfully colonizing a given habitat (Keddy 1992; Weiher & Keddy 1995). The hierarchical competition process states that functionally similar species co-exist by being superior competitors (Mayfield & Levine 2010) such that the competitive superiority of a species is related to its relative position in trait space and not trait dissimilarity *per se* (Kunstler et al. 2012). In both cases, the resulting pattern would be a seedling assemblage with a functional richness that is significantly lower than that expected given the functional richness of species represented in the seed assemblage.

A final *hybrid hypothesis* must be considered where multiple mechanisms are operating at the same time to influence the seed-to-seedling transition. Specifically, negative density dependence may be a dominant force not only within species but also among species when they are functionally very similar; thus, the overall range of functions would be governed by abiotic filtering or hierarchical competition, which would eliminate extreme phenotypes. The pattern resulting from this *hybrid* *hypothesis*, would be a seedling assemblage that has smaller functional range or volume than the potential range given the arriving seeds, combined with evidence that the proportion of seeds successfully transitioning to established seedlings within species critically relies on the number of conspecific seeds and the high functional similarity among species. Both the *functional convergence* and the *hybrid hypotheses* outlined above, which invoke the importance of abiotic filtering, could not be uncovered without information on functional traits.

In the present work, we aim to investigate the critically important seed-to-seedling transition in tropical trees. First, we perform a series of null model analyses where we simply quantify whether the trait range or multivariate trait volume for seedlings at each individual site in the forest is higher or lower than expected given the trait range and volumes for the species arriving at that same site. These analyses were performed in order to test the three hypotheses presented - *the negative density dependence, abiotic filtering and hybrid hypotheses*. The expectation is that if the *negative density dependence hypothesis* is supported, trait ranges or volumes in seedlings will be similar in size to that found for the species of seeds. In addition we also expect that species will be more evenly spaced in trait space. Conversely, if the *functional convergence hypothesis* is supported, we predict a smaller than expected range and spacing of trait values for seedlings given the trait values of the seed assemblage. It is possible that both abiotic filtering and negative density dependence are operating simultaneously. Under this *hybrid hypothesis*, we expect seedling assemblages to have a smaller range or volume of trait values, but species within this range or volume will be evenly spaced. A second goal of the present study was to quantify whether there was evidence for intra-specific negative density dependence forest-wide. To address this we utilize the framework developed by Harms et al. (2000) designed to detect within species negative density dependence by comparing the number of established seedlings to the number of seeds of a species (Figure 2.1).

The four specific questions, related to our three main hypotheses that we address in this research are: Is inter-specific negative density dependence an important force promoting the observed changes in functional diversity across the seed-to-seedling transition?; Is there a detectable influence of both intra- and inter-specific negative density dependence during the seed-to-seedling transition?; Are the answers to the first two questions consistent across different axes of plant function, which are related to different limiting resource axes?; and how does the strength of these processes influencing the seed-to-seedling transition change across time?

Methods

Study area

The study used data on 62 species found as seeds in seed traps or as seedlings in seedling plots from 120 stations distributed across the 16-ha Luquillo Forest Dynamics Plot (LFDP), part of a National Science Foundation Long Term Ecological Research (LTER) site in eastern Puerto Rico. The LFDP is classified as subtropical wet forest according to the Holdridge life zone system (Ewel & Whitmore 1973) with elevation ranging from 333 to 428 m a.s.l. and a mean annual rainfall of 3500 mm (Thompson et al. 2002).

Seed traps and seedling plots

Each station (120 in total) consisted of one 0.5 m^2 trap and three 1 m^2 seedling plots placed in a random direction and 2 m from three of the edges of the trap. Each trap was built with a PVC frame that held a 1mm wire-mesh bag suspended approximately 1 m above the ground. Fruits and seeds were collected every 2 weeks from each trap and all seedlings were counted, tagged, and identified from each seedling plot once per year from 2007 to 2012. Data are available at Luquillo LTER: http://luq.lternet.edu/data/luqmetadata175 (Zimmerman 2014).

Trait data

We compiled trait data for all tree species present in the LFDP (data available in the Dryad digital repository http://dx.doi.org/10.5061/dryad.j2r53, Swenson and Umaña 2015). We used eight functional traits that represent the major ecological strategies of trees using standard protocols (Swenson & Enquist 2008; Swenson et al. 2012a, b). All traits used in the analysis reported here come from adult individuals except seed mass (data collected by J.F-M and LTER staff). Leaf traits for seedlings have been measured for some of our study species in this forest by N.G.S., R.M. and M.N.U. We performed exploratory analyses to determine whether using seedling traits altered our findings. We found that the qualitative results and inferences were not different from those we display and that the rank correlation between seedling and adult traits was strong (Figure A1.5). We therefore used only the adult traits so that the traits from the leaves and wood came from individuals of the same ontogenetic stage and not different stages (i.e. we avoided mixing wood trait data from adults and leaf trait data from seedlings).

Leaf area was measured to reflect the area deployed for light capture. Leaf %C, %N, %P and specific leaf area (SLA) are a part of the leaf economics spectrum (LES), which indicates where a leaf occurs along a continuum of resource capture rates and leaf lifespans. Maximum height was measured to represent the adult light niche of species. It was included in this study on seedlings as it is linked to growth rates across life stages (Iida et al. 2014; Lasky et al. in press). Seed mass was measured as it represents where a species is located on an axis between producing few well provisioned offspring versus producing many poorly provisioned offspring where provisioning is expected to be strongly related to success along resource availability gradients. Lastly, wood density was measured to represent the wood economics spectrum (Chave et al. 2009), where species fall along a continuum of fast volumetric growth and high mortality rates versus slow volumetric growth and low mortality rates.

Sampling and data analysis

The analyses required that the seed and seedling data were directly and logically comparable. To this end, we performed the following steps. First, all seeds falling into a single seed trap for an entire year were tallied into one assemblage for that year. Thus, we had one single seed assemblage for each station by year (2007-2012) that could be compared to the seedling census from the same year. Second, the seedling assemblage for each year was the combined assemblage of the three small seedling inventory plots surrounding a single seed trap. Some of the seedling plots recruited species that were not recorded in the seed traps, indicating that the seed traps did not capture 100% of the species dispersing to the site. This could have unintentionally inflated our analyses of the importance of negative density dependence. To avoid this problem we combined the seed and seedling data for each station and year into a single matrix and used this as the original species pool data. In other words, we defined the pool of species that arrived at each site as the combination of species found in the seed trap and seedling plots at a single location.

In order to compare the functional composition of the seed and seedling assemblages, we calculated the functional richness, functional evenness, and mean nearest neighbor distance of the assemblage (Villéger et al. 2008; Laliberte & Legendre 2010). The functional richness metric calculates the multi-dimensional volume occupied by the community in trait space. This metric is an approximation of the range of traits in the sample that is not weighted by species abundance. The functional evenness metric measures the regularity of the spacing of species and their abundances in trait space using a minimum-spanning tree (Villéger et al. 2008; Laliberté & Legendre 2010). If limiting similarity was important, we would expect a higher functional evenness value than expected if the probability of an individual transitioning from seed to seedling transition was random with respect to its function. If hierarchical competition and/or abiotic filtering were important, we would expect dominant species to be on one end of the trait range and consequently a lower mean nearest neighbor distance value than expected if the probability of an individual transitioning from seed to seedling transition was random with respect to its function, but not necessarily a lower functional evenness value. This is because functional evenness calculates the evenness given the observed trait range, whereas mean nearest neighbor distance calculates the shortest trait distance between neighboring species given the total trait range of the system. Thus, it is expected that functional evenness and mean nearest neighbor distances have similar trends, but mean nearest neighbor distance may be more informative regarding hierarchical competition. Trait data were centered, scaled and subjected to a principal component analysis (PCA) in order to diminish redundancy. We used the positions of species along the first two PCA axes, which together explained 51% of the total variation for the multivariate analyses. Previous research on static adult tropical tree assemblage datasets has shown that the degree of local trait diversity varies by trait reflecting divergence and convergence operating simultaneously on the functional similarity (e.g. Swenson & Enquist 2009). Thus we performed the uni-variate and multivariate analyses described below. All analyses were replicated across years to quantify temporal variability of the results.

Null model analyses

We conducted the null model analyses on two levels: the inter- and intra-specific level. For the inter-specific analyses we studied individual sites in the forest by comparing the functional richness, functional evenness and mean nearest neighbor distance values in seedling assemblages at a site to that of the seed + seedling assemblages at the same site. In the null models for the site level, the species pool could only contain those species found in the individual site being considered. We are aware that this species pool is missing some species that either were not able to germinate or when germination did not last long enough to be counted in the seedling census. These unseen species would increase the size of the pool, which would mean that our analyses are probably underestimating the functional diversity of the species in the pool, and underestimating the narrowing of functional diversity during the seed-to-seedling transition. Our null models were performed by randomizing the names of species on the seed + seedling species list, comparing the random functional richness, functional evenness and mean nearest neighbor distance values to the observed values and calculating a SES value for each site (Swenson 2014). All randomizations maintained the observed species richness. Negative values indicated lower than expected values for a given metric (i.e., functional richness, functional evenness or mean nearest neighbor distance) given the observed species richness in the seed + seedling assemblage. Conversely, positive values indicated higher than expected values for a metric (i.e., functional richness, functional evenness or mean nearest neighbor distance) given the observed species richness. A forest-wide analysis was also conducted and the methods are discussed in Appendix 1.

Our intra-specific analyses aimed to evaluate the strength of negative density dependence within species by comparing the abundances of seeds and seedlings at individual sites across the forest. Our method follows the approach developed by Harms et al. (2000) who examined the logarithmic relationship ($R=aS^b$) between the density of recruits (R) and the density of seeds (S). To avoid spurious results from the regression analyses, we conducted the same tests that Harms et al. (2000) performed. As a result some of the species were excluded and we only implemented the analyses with a subset of species (10 species for 2007, 11 for 2008, 9 for 2009, 2010, 2011 and 2012). For this analysis the seed density was obtained by counting the total number of seeds of each species collected in a seed trap over a year and dividing by 0.5 m^2 (area of the seed trap). The seedling recruit density was obtained from the total number of individuals of each species in the 3 1 m^2 seedling-plots for each site divided by three and calculated for each census. These values are then log-transformed and the density of seedlings was regressed against the density of seeds. Slope values lower than one indicate that the density of seedlings was lower than would be expected under intra-specific negative density dependence (Figure 2.1).

Results

Overall, our results provide support for the *hybrid hypothesis*, where the seed-to-seedling transition is the outcome of multiple mechanisms acting simultaneously. In the following we present the detailed results for inter-specific and intra-specific analyses.

At the site level for the multivariate analyses (Figure 2.2), the seedling functional richness values were lower than expected given the observed functional richness in all years. When the analyses were performed at the individual trait level, we found that seed size and leaf traits associated with the leaf economic spectrum (LES) showed the same trend as the multivariate results (Figure A1.6). However, the functional richness SES values for trait maximum tree height of adults and wood density showed no positive or negative trend (Figure A1.6). Only leaf area (Figure A1.6) exhibited functional richness SES values higher than expected by chance. In general, these results provide support for abiotic filtering or hierarchical competition as expected under the *functional convergence hypothesis*. When functional evenness and mean nearest neighbor distance were considered, most of the observed values were higher than expected given the observed species richness (Figure 2.3 and A1.7). In other words, the spacing of seedling abundances in trait space was larger than expected given the seed assemblage, indicating an important role of negative density dependence processes occurring between functionally similar species. The functional evenness and mean nearest neighbor distance analyses performed on individual traits were generally consistent with the overall functional evenness and mean nearest neighbor distance results with the exception that leaf nutrients, SLA and seed mass were less evenly dispersed than expected (Figure A1.8 and A1.9). The results from site level were consistent with analyses conducted on the forest-wide scale (Appendix 1).

When all of the results were considered across the six years we found that functional patterns for the multivariate and uni-variate analyses were generally consistent (Figures 2.2, 2.3, A1.7). The results for forest-wide analyses, showed generally similar trends to the site level analyses, however for wood density and the leaf economic spectrum traits, we found a decreasing pattern in functional richness across time (Figure A1.2).

We also analyzed the direction of the filtering by comparing the mean trait values in the pool and at seedling stage *ad hoc*. The mean seed mass, wood density and leaf area values were generally higher for the seedling assemblages than for the seed + seedling assemblages whereas the mean LES and maximum height values were more likely to be smaller than the total seed + seedling assemblages (Figure A1.10).

Lastly, we conducted an analysis to quantify whether there was evidence for intra-specific negative density dependence. The results of our intra-specific analyses generally found a log-log slope less than 1 between the seed and the seedling density indicating a decrease in the per capita transition rate as conspecific density increased (i.e. negative density dependence). The only exception was *Guarea guidonia* (Meliaceae) in 2010 which had a slope higher than 1 (Figure 2.4).

Discussion

The transition from seed to seedling represents one of the great population bottlenecks for tree communities. This bottleneck leaves a lasting imprint on the structure of adult tree assemblages. Thus, uncovering the mechanisms underlying this transition is essential for our understanding of the structure and dynamics of tree communities (Green et al. 2014). Here we have tested three hypotheses regarding the seed to seedling transition in tree communities that make clear predictions regarding the role of functional similarity among species during this critical transition. Specifically, we tested: (*i*) a *negative density dependence hypothesis* that predicts functionally dissimilar are more likely to transition from seed to seedling; (*ii*) *a functional convergence hypothesis* where functional similar species are more likely to transition from seed to seedling due to abiotic filtering or hierarchical competition; and (*iii*) *a hybrid hypothesis* that predicts that there is functional convergence during the seed to seedling transition, but also negative density dependent processes that evenly space species within a constrained trait space.

The first main finding from our study is that consistent with the *functional convergence hypothesis,* functionally similar species are more likely to transition from seed to seedling (Figures 2.2 and A1.2). This could be the result of one of two processes: an abiotic constraint on the phenotypes that can successfully establish at a site (Keddy 1992) or hierarchical competition (Mayfield & Levine 2010; Kunstler et al. 2012). Further analyses that considered the evenness of species abundance in trait space (i.e. analyses of mean nearest neighbor distances and functional evenness) found that seedling assemblages are more evenly spaced in trait space than expected given the seed assemblages (Figures 2.3, A1.3, A1.4 and A1.7). Consistent with the *negative density dependence hypothesis* this result indicates a thinning of individuals with similar functions during the seed-to-seedling transition and is generally consistent with trait-based negative density dependence. A final analysis of intra-specific negative density dependence based on the Harms et al. (2000) method (see Figure 2.1) uncovered consistently strong negative density dependence (Figure 2.4). Considering the results together, we find support for the *hybrid hypothesis* where inter-specific and intra-specific negative dependence and abiotic constraints both influence the seed to seedling transition. In the following sections we discuss these results and inferences in detail.

Changes in the Assemblage of Functional Diversity During the Seed-to-Seedling Transition

To determine the changes in functional diversity of the total species dispersed to a site and the seedling population that established, we compared the functional richness, functional evenness and mean nearest neighbor distance of the species in our seedling plots to the species that could have recruited to the plots using a null modeling approach (Figures 2.2, 2.3, A1.2, A.13, A1.4 and A1.7). Specifically, we asked whether the observed functional richness, functional evenness and mean nearest neighbor distance values were higher, lower or no different from that expected if seeds had a random chance of transitioning to seedlings.

The majority of the sites showed negative standardized effect size (SES) values of functional richness indicating a smaller than expected functional richness in the seedling communities given the seeds that are present in the same location (Figure 2.2). This result was consistent across years. When considering individual traits we found that leaf area had higher than expected functional richness, but the remaining traits: wood density, leaf economics spectrum (LES) traits (i.e. SLA, leaf N and P), and seed mass had less functional richness than expected given the seedling assemblages (Figure A1.2, A1.6). Our finding that most functional traits (all except leaf area) were lower in the seedling than seed communities demonstrates that the species able to successfully establish as seedlings represent a significantly smaller range of trait values compared to that found in the seed species assemblages. This indicates that the traits measured related to resource capture and interactions with the abiotic environment, strongly limit seedling establishment. For example, during the seedling stage, light availability has been shown to be one of the most important requirements for successful seedling establishment as very small seeded species have limited resources for initial seedling growth and survival and therefore require more light at an earlier stage than large seeded species, with greater stored resources (Denslow 1987; Chazdon et al. 1996; Nicotra et al.1999; Montgomery & Chazdon 2001; Dalling et al. 2004; Muller-Landau 2010). The seed mass results indicate a constraint that is most likely associated with the fecundity-stress trade-off (Muller-Landau 2010). Indeed, mean seed mass values of the species that established as seedlings tended to be high compared with the mean values for the pool (seed + seedlings) (Figure A1.10). Previous work from this forest (Francis & Rodriguez 1993, Muscarella et al. 2013) has also demonstrated that large seeds have a germination advantage suggesting that only a small subset of seed sizes might be expected to establish in a habitat that is relatively temporally stable. In forests with a well-developed canopy, low light in the understory and few canopy gaps, it is likely that there will be few opportunities for small seeded light demanding species to be able to successfully establish (Comita et al. 2009). Lastly, our wood density results are likely linked to the importance of water availability for establishment where a dense wood conservative strategy has a higher probability of survival in resource limited conditions (Chave et al. 2009). Indeed seedling assemblages tended to have higher wood density values than the seed + seedling assemblages. Thus, we infer that abiotic filtering (e.g. Keddy 1992) and/or competitive hierarchies where functionally similar species with superior performance in a given abiotic context competitively exclude functionally dissimilar species (e.g. Mayfield & Levine 2010) are affecting the seed-to-seedling transition.

While our functional richness results are informative, quantifying how species are arrayed in trait space is essential for disentangling the influence of hierarchical competition and abiotic filtering and for determining whether inter-specific negative density dependence is also important as predicted by the *hybrid hypothesis*. We therefore compared the observed functional evenness and mean nearest neighbor distance of the seedling assemblages to that expected given the seed assemblages. We found that seedling assembles have higher than expected functional evenness and mean nearest neighbor distance (Figure 2.3 and A1.7). This result indicates the abundance in the seedling assemblages is evenly spread over multivariate trait space, which is consistent with trait-based inter-specific negative density dependence and not hierarchical competition. Taken together, our results demonstrate that a constrained range of phenotypes transition from seeds to seedlings, but within that constrained space a thinning of individuals from similar species also occurs. This is consistent with our *hybrid hypothesis* where an abiotic constraint and functionally driven inter-specific negative density dependence operating simultaneously.

When we considered the functional evenness and mean nearest neighbor distance of individual traits, we found that not all traits are behaving similarly as has been noted in previous tropical tree research comparing multivariate and individual trait dispersion patterns (e.g. Kraft et al. 2008; Swenson and Enquist 2009). Specifically, wood density and leaf area showed higher functional evenness and mean nearest neighbor distance than expected, indicating a thinning of individuals with similar wood density and leaf area values. Interestingly, the distribution of these traits is highly variable at different sites within the forest indicating that the forest is highly heterogeneous (Figure A1.9). We believe this pattern reflects the effect of disturbance from past land use history that was more intense in the northern part of the LFDP and hurricane disturbance (Zimmerman 1994; Thompson et al. 2002; Comita et al. 2010*b*). For the other traits, the functional evenness was usually lower than expected indicating that traits associated with photosynthetic capacity (i.e. SLA, leaf nutrients) and stress tolerance (i.e. seed mass). A higher rate of establishment success is expected for species sharing similar conservative leaf and seed economies in dark tropical forest understories (Poorter 2007). Thus, it is possible that competitive hierarchies on these individual trait axes are also important, but when considering the overall phenotype, assemblages become more evenly spaced during the seed-to-seedling transition as expected by limiting similarity theory.

When evaluating the functional evenness and mean nearest neighbor distance results for all traits combined across the six years, we found no major changes through time. The functional evenness as well as the mean nearest neighbor distance in seedling assemblages was consistently higher than expected from 2007 to 2012, indicating that the strength of inter-specific negative density dependence remains the same across time. Different results were obtained for the functional richness analyses where we found that a decrease in functional richness across years during the transition was present. In particular, traits such as those associated with the leaf economics spectrum and wood density had a relatively consistent decrease in functional richness during the seed-to-seedling transition across years. A potential reason for this trait convergence over time may be a delayed turnover in species composition caused by hurricane disturbance (Hurricane Hugo in 1989, Hurricane

Georges in 1998), where species adapted to non-disturbed conditions and low understory light levels may take long time to arrive and dominate in the seedling population. In previous work, Swenson et al. (2012a) found that the functional turnover in the adult tree assemblage in this forest increased as light demanding trees established in canopy gaps after Hurricane Georges in 1998, but converged by 2005.

Intra-Specific Negative Density Dependence During the Seed-to-Seedling Transition

In addition to the dynamics occurring on the inter-specific level, that are mainly determined by functional differences among species, we also wanted to evaluate the importance of intra-specific negative density dependence. We estimated the strength of intra-specific negative density dependence for all the species using the methodology developed by Harms et al. (2000) (Figure 2.1). We found strong intra-specific negative density dependence across the seed-to-seedling transition for nearly all species included in the analysis (Figure 2.4). The only exception was *Guarea guidonia* (Meliaceae), a common seedling in the LFDP forest, with generally high recruitment. Our results are also consistent with investigations of tropical tree communities that have inferred the importance of intra-specific negative density dependence (e.g. Harms et al 2000). Thus, deterministic negative interactions between conspecifics, such as shared enemies and competition, appear to play a consistently important role in defining seedling and adult tree community structure.

Caveats and Suggestions

Most traits in our study do show a decrease in range during the seed-to-seedling transition, but some do not and, of course, there are many other traits that could potentially be considered (Swenson 2012, 2013). For example, traits related to interactions with pests and pathogens would be very informative particularly with respect to intra-specific negative density dependence. We therefore wish to highlight that our inferences are based on a limited number of axes of plant function and those axes that we did consider are primarily related to resource acquisition and rather than direct biotic interactions.

A second important consideration is that most functional trait based studies of tree communities utilize species mean trait values and ignore intra-specific variation making it impossible to quantify whether there is functional displacement between co-occurring conspecifics (see Paine et al. 2011). More research is clearly needed particularly to increase our understanding of seedling community dynamics where the performance of individual phenotypes, and their interactions with other individuals and their phenotypes can be quantified.

Conclusions

During their lifetime, trees are subjected to several transitions across different life history stages, in order to disperse, establish, grow, survive and reproduce, which represents significant challenges. At all life stages trees must deal with environmental stresses and biotic interactions that will have a range of impacts depending upon the life stage, but that will determine survival and a successful transition to future stages. We have developed new techniques for quantifying the changes in the community composition of functional traits during the seed-to-seedling transition utilizing functional trait information. We found that along with strong intra-specific negative density dependence, there is evidence that seedling assemblages represent only a small proportion of the total functional volume found in seed assemblages and within these constrained volumes seedlings are more evenly spaced than expected. Together, these results argue for a greater appreciation of the simultaneous contribution of multiple deterministic processes that drive community structure and population dynamics and the way that these processes vary in their importance within and among species.

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Figures

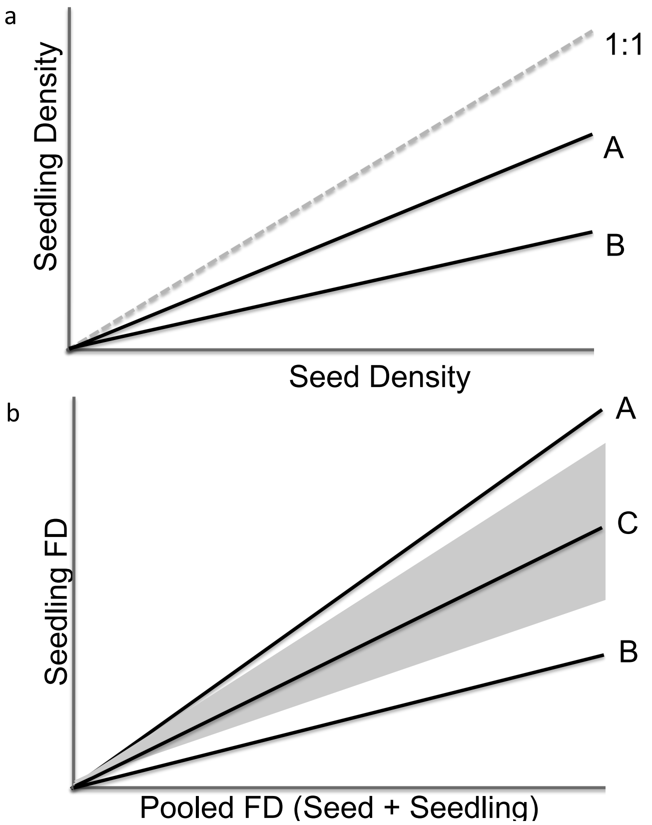

Figure 2. 1. A schematic figure comparing the Harms et al. (2000). The slope lines correspond to the regression line for one species where species B is experiencing stronger negative density dependence than species A.

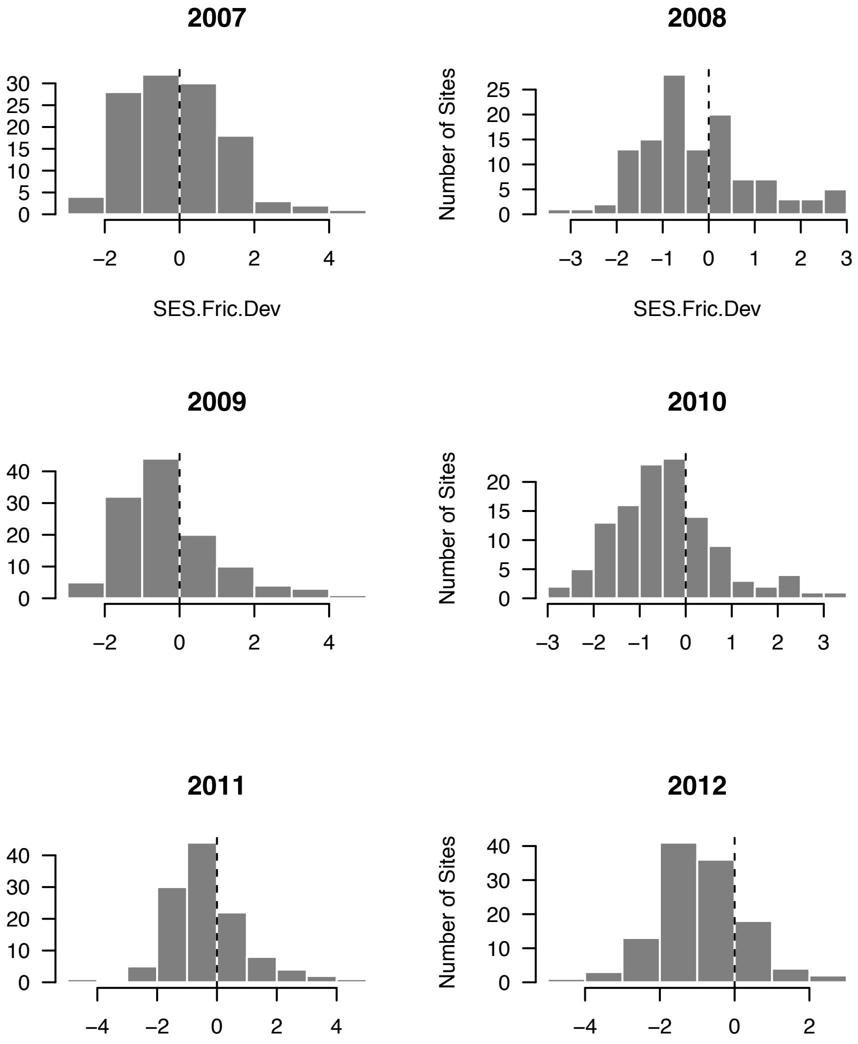

Figure 2. 2. Site-level results for the standardized effect size (SES) of functional richness across 6 years. Negative SES of functional richness values indicate lower functional richness in the seedling assemblage than expected. Positive SES of functional richness values indicate higher functional richness in the seedling assemblage than expected. LES refers to traits that represent the leaf economic spectrum; FRic refers to functional richness.

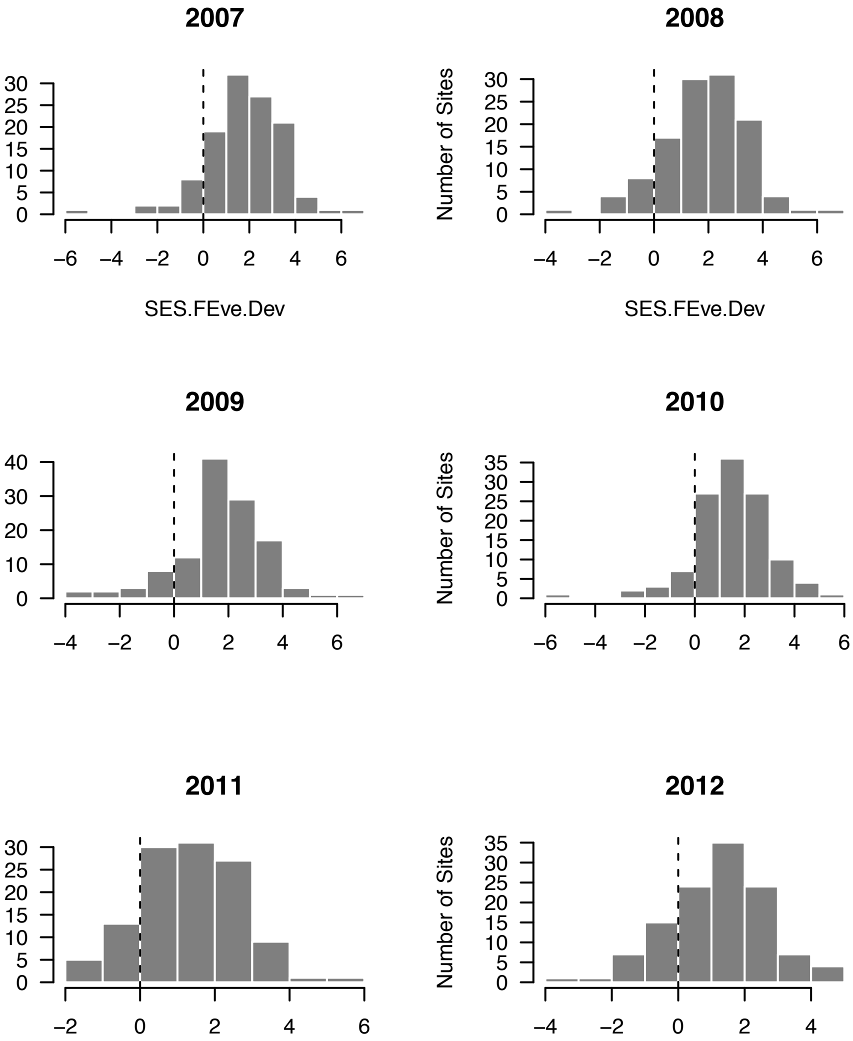

Figure 2. 3. Site-level results for the standardized effect size (SES) of functional evenness across 6 years. Negative SES of functional evenness values indicate lower functional evenness in the seedling assemblage than expected. Positive SES of functional evenness values indicate higher functional evenness in seedling assemblages than expected. LES refers to traits that represent the leaf economic spectrum; FEve refers to functional evenness.

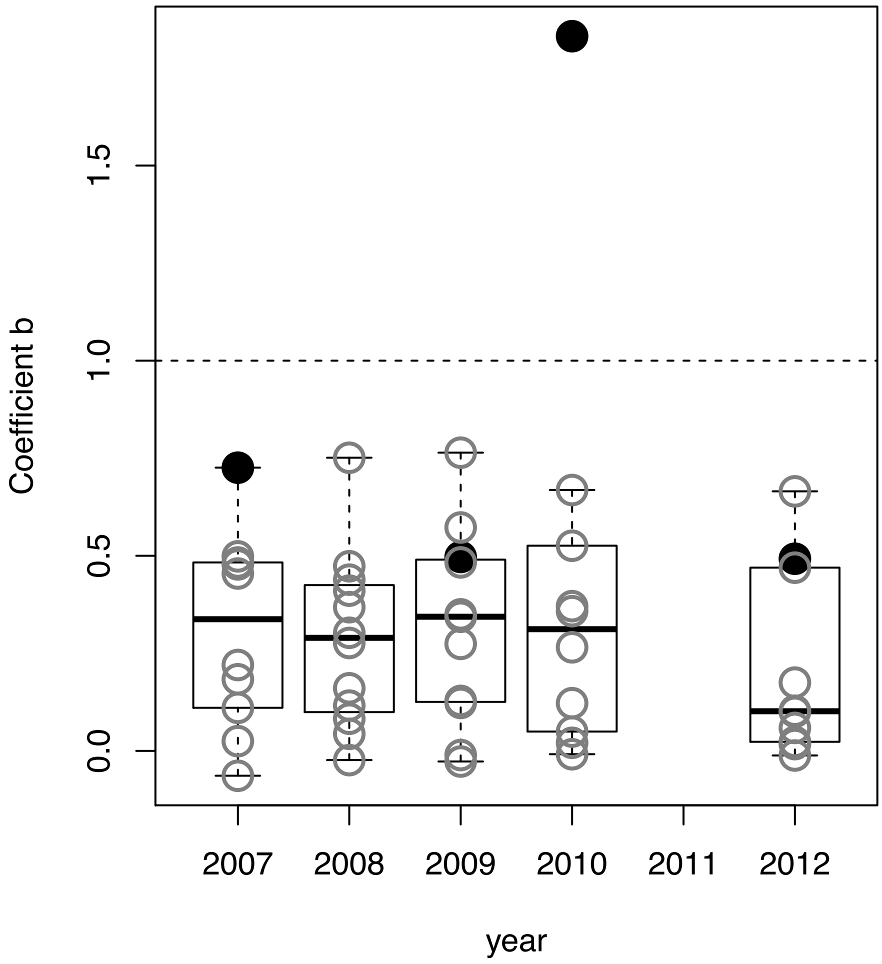

Figure 2. 4. Boxplot representing the regression slope values between seed and seedling densities. The black point represents the slope values for *Guarea guidonea* (Meliaceae). Smaller slope values are indicative of stronger intra-specific negative density dependence whereas slope values of one indicate no intra-specific density dependence (Harms et al. 2000).

Chapter 3: Commonness, rarity, and intra-specific variation in traits and performance in tropical tree seedlings

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Abstract

One of the few rules in ecology is that communities are composed of many rare and few common species. Trait-based investigations of abundance distributions have generally focused on species-mean trait values with mixed success. Here, using large tropical tree seedling datasets in China and Puerto Rico, we take an alternative approach that considers the magnitude of intra-specific variation in traits and growth as it relates to species abundance. We find that common species are less variable in their traits and growth. Common species also occupy core positions within community trait space indicating they are finely tuned for the available conditions. Rare species are functionally peripheral and are likely transients struggling for success in the given environment. The work highlights the importance of considering intra-specific variation in trait-based ecology and demonstrates asymmetry in the magnitude of intra-specific

variation among species is critical for understanding of how traits are related to abundance.

Introduction

Ecology is a discipline with few universal laws or consistent emergent patterns (Lawton 1999). Among these is the presence of few common and many rare species in communities (e.g. Preston 1948; MacArthur 1957). The relative consistency in this pattern across systems suggests shared foundational principles that determine community structure and dynamics (McGill et al. 2007; Morlon et al. 2009). Uncovering the mechanisms underlying patterns of species abundance distributions (SADs) therefore represents one of the grand challenges motivating a great deal of research in ecology (Brown 1995; Hubbell 2001).

An outstanding challenge for those studying SADs is that most hypotheses predict a "hollow curve" shape, where most species are rare and few are dominant (McGill et al. 2007). Recent work has approached this problem by employing Maximum Entropy (MaxEnt) principles where multiple emergent ecological patterns (e.g. SADs, species area curves) can simultaneously be predicted using only a few constraints (e.g. Harte et al. 2008). For example, the shape of the SAD can be predicted with a high degree of accuracy (>70% variation explained) by knowing the total number of individuals and species (White et al. 2012; Locey & White 2013). While this work impressively predicts the shape of the SAD, it is still unknown what factors control the commonness and rarity of individual species within the SAD. In other words, ecologists are still challenged by the question of: what causes a particular to be species common or rare?

The consideration of organismal function is likely key for understanding why some species are common while others are rare (McGill et al. 2006). Indeed, classic models of the SAD consider not just its shape, but also how it should be related to niche or resource axes (e.g. MacArthur 1957; Sugihara 1980). Given that functional traits are expected to be linked to resource use strategies and performance (e.g. Westoby et al. 2002), traits should be related to abundance (McGill et al. 2006). However, recent meta-analyses have shown that species traits are typically not correlated with relative abundances in communities indicating that linking traits and abundance is not a simple task (Murray et al. 2002). Additional investigations that rely on MaxEnt type approaches that include trait information (e.g. Shipley et al. 2006; Laughlin et al. 2012) have been used to predict the relative abundances. Though, some of this work has been criticized (Shipley et al. 2006) when the number of constraints imposed is high relative to the number of predicted values (Haegeman & Loreau 2008). In sum, community ecologists and macroecologists are still struggling to clearly link functional traits with abundance and ultimately performance.

A major outstanding question in trait-based community ecology is the relative importance of intra-specific variation and how incorporating such information may help us understand community structure and dynamics (e.g. Bolnick et al. 2011). For example, recent work has taken up this challenge by quantifying whether our perception of trait dispersion changes if we consider individual-level trait values

(Paine et al. 2011) or by testing whether models that consider intra-specific trait distributions provide stronger predictions of relative abundance compared to MaxEnt models utilizing species level mean trait values (Laughlin et al. 2012). However, we have very few studies in the rapidly growing functional trait literature that examine how intra-specific variation itself is related to the abundance of a species. This is, perhaps, surprising given that trait variation among individuals within a population can alter interactions with other species and should therefore be key for understanding community dynamics (Van Valen 1965; Roughgarden 1972; Bolnick et al. 2003; Bolnick et al. 2011).

There are two main predictions for how trait variation within a species could be related to its abundance. First, in a highly heterogeneous environment, common species may be expected to be generalists with broad tolerances. Such species should be more variable or flexible in their traits allowing them to perform well under a variety of abiotic and biotic conditions, whereas rare species may be more phenotypically constrained or specialized on a spatially or temporally rare resource thereby limiting their ability colonize and perform well (Gaston et al. 1997). Conversely, in a less heterogeneous environment, we would expect common species to have a superior phenotype across sites that should therefore be under stabilizing selection, whereas rare species may have phenotypes ill-suited to most of the available habitats and may be more variable in their struggle to adjust to the available sites (Brown 1984). In both of the above cases, we may expect common species to have lower variation in their performance (e.g. growth) compared to rare species that may fail or succeed depending upon their ability to adjust to local conditions or disperse to a favorable site.

Importantly, the above two predictions can be unified into a general framework relating intra-specific trait variation and abundance across scales. We expect the link between intra-specific variation and abundance to critically rely upon the environmental heterogeneity of the system and therefore spatial scale. Specifically, on local scales where environmental heterogeneity is reduced, common species will be those with phenotypes that best fit the environment and individuals within those species with large deviations from the optimal phenotype will disadvantaged thereby reducing phenotypic variation in common species. However, on larger spatial scales where there is more environmental heterogeneity, common species in the system will most likely be those species that can colonize and increase their population sizes in a variety of different environments where the optimum phenotype will differ thereby increasing phenotypic variation in common species. Thus, we expect the link between intra-specific variation and abundance to be intimately tied to the degree of environmental heterogeneity and therefore changing from negative relationship locally to a positive relationship regionally, but these predictions remain largely untested on any spatial scale in the functional trait literature.

Perhaps nowhere are patterns of relative abundance more striking and fascinating than in diverse communities (Dobzhansky 1950; Lynch & Neufeld 2015). For example, upwards of 50% of the species in tropical tree communities may be considered 'rare' (e.g. Hubbell & Foster 1986). Locally rare tropical tree species may simply be explained by ecological equivalence and probabilistic birth-death given the relative abundance distribution in a meta-community (Hubbell 2001). However, rare species may be functionally divergent and simply ill-suited to most of the available habitats and/or more susceptible to pests and pathogens or specialized on rare habitats. Ill-suited rare species may be expected to be more variable in their phenotypes, whereas specialized rare species may be less variable. Despite the large interest in the relative abundances of tropical trees we have no clear tests of these fundamental predictions.

In diverse tropical tree communities, the seedling stage is critical for determining the relative abundance and species composition of the entire forest. Specifically, the transition from seedling to sapling represents a major demographic bottleneck that severely reduces population sizes differentially across species thereby greatly influencing the structure of tree communities in later ontogenetic stages (Green et al. 2014). This demographic bottleneck makes the study of seedling dynamics essential for our understanding of the processes that determine the relative abundance distributions and species composition of diverse tropical tree assemblages.

Here we tested the above predictions by quantifying the relationship between species relative abundance and the variance in growth rates and traits, by using data from 1974 seedling individuals of 142 species in a tropical rain forest in China and 1771 seedling individuals of 53 species in a tropical rain forest in Puerto Rico. These seedlings were monitored during one year for growth in 218 and 200 plots, respectively, and then harvested for trait measurements. Using this data we specifically asked: (1) What is the relationship between intra-specific trait variation and relative abundance?; (2) What is the relationship between intra-specific growth rate variation and relative abundance?; (3) Do common species have higher growth rates compared to rare species?; and (4) Are rare species occupying extreme positions of the community trait distribution, while dominant species occupy a core position?

Methods

Study Sites

This study was conducted in two tropical rain forests. The first study site was located in Xishuangbanna, Yunnan, China (101º 34′ E, 21º 36′N). This region is characterized by monsoon climate with a strongly seasonal variation between dry (November - April) and wet season (May- October). The annual mean temperature is 21.8ºC and mean annual rainfall is 1493 mm (Cao et al. 2008). The second study site is located in the El Yunque National Forest, in Puerto Rico (65°47′ W, 18°19′ N). El Yunque also has a seasonal climate with heaviest rains falling during the Atlantic Ocean hurricane season (June - December) with a mean annual rainfall of 3548 mm and an average temperature of 23 ºC.

Seedling Plots

In Xishuangbanna, we established 218 1x1m seedling plots arrayed in a regular grid to monitor seedling dynamics during 12 months (2013-2014). The sampling grid was located in an area forest that is relatively homogeneous with respect to elevation and light levels as compared to the heterogeneity found in the entire forest. All free-standing seedlings smaller than 50 cm in height were tagged, identified and measured.

Not all species could be identified to the species level, 5% were determined to the genus level and were ultimately recorded as clearly distinguishable morphospecies. The seedlings were monitored every two months to assess growth and survival. New recruits were also tagged, measured, identified and incorporated into the census. Relative growth rates were calculated for each seedling using basal diameter and height measurements.

In El Yunque, Puerto Rico, we established 200 1x1m plots that were also arrayed in a regular grid and seedling dynamics were monitored for the same year as in China. The seedling measurements followed the same procedure as the one described for China and 3% of the species were determined to the morphospecies level. Because part of this study sought to investigate intra-specific variation in traits and growth, we only used those individuals that were present from the first to the last census.

Trait Measurement and Abundance

Recent work has highlighted the importance of trait variation across ontogenetic stages and its influence on inferences regarding community assembly (e.g. Spasojevic et al. 2014). In this study all trait data were measured from the individuals in our seedling plots and all of the abundance values in our analyses represent the seedling abundance of the species in our seedling plots. Thus, trait and abundance data from other ontogenetic stages or outside of our seedling plots was not used in this study.

After one year of monitoring, all surviving individual seedlings were extracted from the soil and collected permitting the quantification of leaf functional traits as well as plant allocation traits for each individual. For each individual we measured the fresh leaf area (LA in cm^2) of 1 to 3 fully expanded leaves. These leaves were then weighed and leaf thickness was measured using the middle section of leaf lamina avoiding primary and secondary veins. Roots were cleaned and separated from the main stem and the length of the main stem was measured (cm). All the leaves and leaflets, stems and roots were then dried in an oven for 72 hours at 70ºC and measured for dry mass (g). Specific leaf area (SLA) was calculated as: SLA = LA/dry mass. Leaf mass fraction (LMF) was calculated as: LMF = leaf dry mass/total plant dry mass. Stem mass fraction (SMF) as: SMF = stem dry mass/total plant dry mass. Root mass fraction (RMF) as: root dry mass/total plant dry mass. Leaf area ratio (LAR) was calculated as: LAR = leaf area/total plant dry mass. Stem specific length (SSL) was calculated as: SSL = stem length/stem dry mass (Poorter et al. 2012). LMF, SMF, RMF, SSL and LAR are traits that provide information about the allocation strategies of plants, while SLA, leaf thickness and LA are considered non-integrative traits specific to resource acquisition by leaves.

Growth Rate

The relative growth rate (RGR) of seedlings was calculated as the change in log-transformed basal diameter and total height from the first to last census. All seedlings were marked on their stem at the initial point of measurement and subsequent measurements were made at the same location. The total height of each seedling was measured from the mark to the most distant part of the main stem. The RGR was estimated in cm/year and all negative values were discarded.

Data Analyses

Because of the substantial variation in sample size (i.e. abundance) between species in our study, we utilized rarefaction to generate comparable estimates of variation in traits and RGR across species. Specifically, for those species with 4 or more individuals, we randomly sampled without replacement 4 individuals and calculated the variation in the trait and RGR values for those individuals. This procedure was repeated 999 times to generate 95% confidence intervals and a mean variance value. All trait data were transformed for normality and scaled prior to analyses. For the trait variation analyses we considered all traits individually, but because many of our traits may co-vary we also performed a principal components analysis (PCA) to mitigate trait redundancy using all individuals across species at a single site (i.e. China or Puerto Rico). A PCA was used over other ordination techniques as we utilize continuous trait data and we were interested in the Euclidean distance separating individuals in multivariate space. The first three resulting PC axes explained 70.7% and 72.9% of the total trait variation in China and Puerto Rico, respectively (Table S1). The position of individuals along these three axes was also used in the rarefaction analyses. For each species, the estimated mean variance for each trait, each PC axis and both RGR, was then correlated with the log-transformed total abundances of the species in the study site using a Pearson's correlation coefficient.

Next, we were asked whether mean RGR using the height and basal diameter data was significantly related to abundance. This calculation included all species in the study even if they had fewer than 4 individuals. A Pearson's correlation coefficient was then calculated to relate the mean RGR values to the log-transformed total abundances of the species in the study site.

In order to evaluate the relative position of species along the total breadth of functional trait space, we performed analyses with the individual trait data positions of individuals on the PC axes. Specifically, we wanted to address whether rare species occupy peripheral positions along single trait axis while common species occupy core positions. To do this, we subtracted the mean trait value for the entire community from the median trait value computed for each species. Thus, the displacement of a species from the overall community trait distribution was calculated. We also quantified the deviation of the median trait value of species from the median community trait value and found similar results and therefore only provide the deviation of the median trait value for a species from the mean of the community distribution. Smaller deviation values indicate that a species is close to the mean trait value of the community, whereas a large value indicates a species occupies an extreme position in the community-wide trait distribution. To evaluate if there was a significant correlation between the relative position of a species in functional trait space and its abundance, we calculated Pearson's correlation coefficients between the absolute values of the deviations against the log-transformed abundance. Negative coefficient correlation values indicated that abundant species had mean trait values closer to the median of the community, while rare species tended to have mean trait values more distant from the median of the community.

Results

In total 1974 seedling individuals from 142 species were harvested and measured for traits in China and a total of 1771 from 53 species in Puerto Rico. For the aspect of the study focusing on intra-specific variation, we used only species with 4 or more individuals. Thus, for the intra-specific variation results described below, we analyzed 1614 individuals from 62 species in China and 617 seedlings from 28 species in Puerto Rico.

This study quantified intra-specific variation in traits and relative growth rates (RGR) for seedling communities and related this variation to relative abundance. The results from China and Puerto Rico were generally consistent. Specifically, we found a negative correlation between intra-specific variation in traits and relative abundance, indicating that common species tend to exhibit lower variance in traits when compared to relatively rare species (Table 3.1, Figure A2.1, Figure A2.2). However, intra-specific variation in some individual traits was not related to abundance. For example, in China we found that leaf thickness, root mass fraction (RMF) and specific stem length (SSL) were not significantly correlated with species abundance and in Puerto Rico leaf area (LA) and leaf thickness were not significantly related to abundance and SLA, while LAR had marginal p-values (Table 3.1, Figure A2.3, Figure A2.4). The correlation between species relative abundance and intra-specific variation in RGR was only significant for growth based on height measurements in the seedlings from China and growth based in basal diameter for seedlings from Puerto Rico (Table 3.2, Figure A2.5, Figure A2.6, in Appendix 2).

Thus, the results provide mixed support for common species having lower variation in RGR.

Mean RGR was variable among species and not consistently related to relative abundance, where some common species had higher mean RGR while other exhibited lower RGR than expected by chance. Similar patterns were found irrespective of whether we measured RGR using basal diameter or total height data for China and Puerto Rico (Table 3.3, Figure A2.7, Figure A2.8, in Appendix 2).

Next, we quantified the relative position of rare and common species within the entire range of trait values for the entire community. For seedlings in China, we found that for LAR, SSL, LMF, SMF and RMF, common species tended to occupy core positions within the functional trait space for the total community (Figure 3.1, Figures A2.9-A2.12), while rare species tended to occupy extreme positions. In other words, for most traits, rare species occupied the periphery of community trait space. For LA, SLA and leaf thickness, the results did not show a consistent pattern since dominant species were found across the total trait range, as were rare species (Figure A2.13-A2.15). In Puerto Rico, we found that LAR was the only trait that showed common species occupying central position within the community (Figure 3.2, Figures A2.16-A2.22).

Discussion

A major goal in ecology is to uncover the main forces that generate emergent patterns across ecosystems. The hollow curve of species abundance distributions (SADs) in communities, where most species are rare and relatively few are dominant, is one such emergent pattern. Despite the progress made in predicting this pattern based on a few parameters (Hubbell 2001; Harte et al. 2008), determining the mechanisms that cause particular species to be common or rare in a given SAD is a major open avenue of research. Our results advance research on SADs by moving beyond determining the shape of the curve and providing a framework for understanding what species make up the rare and common species within any given curve by including information regarding intra-specific variation in organismal traits and performance. Here we have provided the results from tropical tree seedlings demonstrating that variance in traits and relative growth rates are often negatively related to species abundance. Additional analyses indicate that common species are not necessarily faster growing and in many cases, particularly in one study site, rare species tend to occupy the periphery of trait space. In the following we discuss these results in greater detail.

Abundance and Intra-Specific Variation

The low intra-specific trait variation found for common species (Table 3.1), indicates a convergent strategy that emphasizes a core physiological association with the habitat allowing high efficiency in exploiting available resources (Grime et al. 2006) We posit that common species have traits optimized for resource use in the given environment and deviations from these optimal values have negative consequences thereby reducing intra-specific variation. Trait convergence has been discussed in previous trait-based community ecology studies, but generally on the inter-specific scale (Weiher et al. 1998; Swenson & Enquist 2009). Here we show that trait convergence is also evident at intra-specific level for common species. Contrary to the pattern found for common species, rare species tended to exhibit higher trait variation (Table 3.1).

When these results are considered in their ecological context, where both sites are located in tropical forests with little topographic complexity, we infer that common species, that have low variation around optimal trait values, are able to easily dominate; whereas, high intra-specific trait variation for rare species may be indicative of their struggle to adjust to the given environment. However, on larger spatial scales with larger environmental heterogeneity or in other local scale sites exhibiting more environmental heterogeneity we might expect the opposite result. For example, high intra-specific trait variation is expected to facilitate the colonization of new or sub-optimal habitats across a region (Gonzáles-Suárez et al. 2015). Indeed, some studies have reported that invasive species vary greatly in shoot-root ratios in order to maximize water uptake under variable levels of drought (Brock & Galen 2005). Thus, future research investigating whether regionally common species have higher intra-specific trait variation to ensure success across multiple habitats and whether species have similar levels of intra-specific variation across their range are needed. Furthermore, our predicted relationships between intra-specific variation and abundance across scales should not only apply to tropical tree assemblages, but to other ecosystems and taxa. Therefore future work is also needed to test whether our predictions are supported more generally.

When considering individual traits, we found that most traits followed the same pattern observed with the multivariate trait analyses. However, intra-specific variation in leaf thickness from seedlings in Puerto Rico and China was not related to abundance. This result is not totally surprising given that previous studies have shown that leaf thickness is highly variable across all species (Onoda et al. 2011). In addition to leaf thickness, stem specific length (SSL) and root mass fraction (RMF) did not show the expected pattern for seedlings in China nor did leaf area (LA) for seedlings in Puerto Rico. These results may arise from the fact that species may not be able to be equally variable across all trait axes and that variation, particularly as it relates to relative allocation to leaves, is likely more important.

Although variation may be beneficial, it is not necessarily linked to increased growth, establishment success or persistence (Robinson et al. 2013). Our results show that rare species tend to have higher intra-specific variation in RGR compared to common species (Table 3.2). In sum, common species are less variable in traits and RGR when compared to rare species. The observed differences in the magnitude of intra-specific variation in traits and RGR between common and rare species suggests not only differences in their ecological requirements, but also likely their permanence of these species in the community (Hanski 1982; Magurran & Henderson 2003). Species that are better adjusted to the present conditions are expected to have superior permanence. Species that are more variable in their traits and performance could arrive occasionally to the community, disappear, and re-colonize later thereby being effectively transient species with sink populations ill-suited to the presently available habitats. Although our results do not demonstrate the transient nature of rare species due to a lack of multi-year census data, it emerges as one potential explanation of the high variability in traits (Magurran & Henderson 2003). Common species, on the other hand, would represent core components of the community strongly associated with environmental conditions that will allow them persist for long periods and attain large population sizes.

Abundance and Relative Growth Rates

The RGR of species may be positively related to abundance given that faster growing species may achieve maturity more rapidly. However, we found no support for this expectation (Table 3.3). These results are not necessarily surprising given that fast growing species also have higher mortality rates (e.g. Wright et al. 2010) thereby regulating the number of individuals that achieve reproductive maturity. For example, species from the genera *Cecropia* (Urticaceae) and *Macaranga* (Euphorbiaceae) are broadly known as pioneer fast growing species in the Neo- and Paleo-tropics, respectively; however they exhibit high mortality rates as well (e.g. Condit et al. 2006; Wright et al. 2010) and are not dominant species in relatively undisturbed forests. Further, a recent study that measured the correlation between abundance and growth rates in eastern North American trees found that where trees are most abundant they are rarely growing well (McGill 2012).

Do Rare Species Occupy the Periphery of Trait Space?

The final goal of the present work was to quantify whether rare species tended to occupy the periphery of community trait space. Our individual trait-based analyses results show that, for most traits (i.e., LAR, SSL, LMF, SSL, SMF and RMF) for seedlings growing in China, abundant species tend to exhibit median trait values closer to the mean trait values for the entire community. This indicates that common species tended occupy core positions within the entire community trait distribution, while less abundant species tended to occupy marginal positions in the community trait distribution. Similar results have been reported in a previous study arguing that rare species disproportionately contribute to ecosystem function (Mouillot et al. 2013). Our findings, however, highlight that while rare species do often occupy the periphery of community trait distributions, they are also highly variable in their trait values.

Although, in general, trait values from abundant species in China were close to the median values for the entire community, leaf thickness, leaf area (LA) and specific leaf area (SLA) were exceptions. One explanation for these results may be allocation traits such as LMF or SMF are more likely to be adjusted in order to fit the environment while organ level traits like leaf thickness, LA and SLA are less well understood without contextual information regarding whole plant allocation (Marks 2007). In particular, traits linked to light availability appear to be important for the ontogenetic stage analyzed in this study. For example, LAR reflects how much leaf area is present for unit of plant mass; LMF corresponds to the fraction that the plant allocated to leaves relative to roots and stem, these traits are all related to photosynthetic and respiration rates and therefore are expected to be related to growth (Poorter et al. 2012). Therefore, these results suggest that gas exchange rates are likely of key importance during the early ontogenetic stages studied as seedlings are actively adjusting their allocational strategies to exploit available light resources.

Our results from Puerto Rico were not totally consistent with our findings from China. Specifically, rare species were only peripheral with respect to leaf area ratios (LAR). Although these results contrast somewhat with our China results, we argue that the Puerto Rico findings are manly the result of past disturbance in the forest. Puerto Rico has been severely affected by two hurricanes (Thompson et al. 2002) and has long history of human disturbance that altered the species and functional composition of the plant community such that species that are typically rare in older growth forests are now more common due to a still recovering canopy.

Caveats

Although our results are generally consistent for both of the sites evaluated, it remains to be seen if they are totally applicable to other sites. We expect that additional local scale studies in similarly homogeneous environments will find that common species exhibit less intra-specific trait variation. However, we expect that future studies conducted on larger spatial scales or on local scales with more environmental heterogeneity should generally find the opposite result where common species must be variable enough to persist in a large variety of habitats and rare species will be specialized on a spatially or temporally rare habitat. In sum, the future development of a framework relating traits to abundance will require information regarding individual-level trait measurements and measures of environmental heterogeneity across scales.

A second caveat to our study is that the traits considered do not represent the entire spectrum of strategies for tree seedlings (Swenson 2013). Traits related to defense likely also have an important role in structuring seedling communities. Thus, we recognize that although the traits considered in this study represent the main axis for resource acquisition, there are additional traits that might reflect other important axes of plant function.

Conclusion

Given the generality of species abundance distributions (SADs), ecologists have frequently focus their research on the shape of SADs and where species fall in the SAD. In this regard, trait-based analyses of abundance distributions have had mixed success. Such work typically focuses on correlating species mean trait values with abundance. Here we have taken an alternative approach that considers how intra-specific variation in traits and growth rates are linked to abundance in order to provide novel insights into the mechanisms underlying patterns of commonness and rarity in tropical tree communities. We show that the degree of intra-specific variation in traits and growth is itself variable across species and negatively related to abundance. Common species tend to occupy core positions within the total range of traits relevant for acquiring limiting resources and the variance in these traits is usually less than that found in rarer species. Given these results we propose that common species are well-suited for the available environmental conditions where deviations from their optimal trait values are detrimental whereas rare species are likely to be transient species ill-suited to available conditions and exhibiting high phenotypic variation in their struggle for success. Despite these insights, future studies will be needed to determine whether rare species are actually transient and inherently more phenotypically plastic or have greater genetic diversity, whether common species are phenotypically divergent on very local scales as may be an expected result from competition and whether low trait and growth variation in locally common species is potentially linked to the hyperdominance of a few species in a large and relatively homogeneous environments in regions like the Amazon Basin (ter Steege et al. 2013; Fauset et al. 2015).

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Tables

Table 3. 1. Pearson's correlations between species relative abundance and variance in traits and PC axes.

Variable	**site**	**r**	**P-value**	**df**	**t**
PCA1	XTBG, China	-0.25	0.04 *	60	-1.9
PCA2	XTBG, China	-0.32	0.008**	60	-2.66
PCA3	XTBG, China	-0.29	0.02*	60	-2.34
Leaf Area	XTBG, China	-0.31	0.01**	60	-2.57
Specific Leaf Area	XTBG, China	-0.28	0.03*	60	-2.19
Leaf Area Ratio	XTBG, China	-0.25	0.04*	60	-2.01
Leaf Mass Fraction	XTBG, China	-0.31	0.01**	60	-2.54
Stem Mass Fraction	XTBG, China	-0.29	0.02*	60	-2.41
Root Mass Fraction	XTBG, China	-0.18	0.15	60	-1.42
Leaf thickness	XTBG, China	-0.14	0.25	60	-1.15
Specific Stem Length	XTBG, China	-0.19	0.13	60	-1.51
PCA1	El Yunque, Puerto Rico	-0.43	0.02*	26	-1.85
PCA2	El Yunque, Puerto Rico	-0.41	0.04*	26	-2.15
PCA3	El Yunque, Puerto Rico	-0.46	0.01**	26	-2.55
Leaf Area	El Yunque, Puerto Rico	-0.33	0.1	26	-1.7
Specific Leaf Area	El Yunque, Puerto Rico	-0.36	0.05	26	-1.86
Leaf Area Ratio	El Yunque, Puerto Rico	-0.37	0.05	26	-1.95
Leaf Mass Fraction	El Yunque, Puerto Rico	-0.46	0.01**	26	-2.54
Stem Mass Fraction	El Yunque, Puerto Rico	-0.53	0.006**	26	-2.99
Root Mass Fraction	El Yunque, Puerto Rico	-0.45	0.02*	26	-2.45
Leaf thickness	El Yunque, Puerto Rico	-0.31	0.11	26	1.318
Specific Stem Length	El Yunque, Puerto Rico	-0.44	0.02*	26	-2.35

Asterisks represent the level of significance: **, $P \leq 0.01$; *, $P < 0.05$.

Table 3. 2. Pearson's correlations between species relative abundance and variance in relative growth rate (RGR). RGR was based on measurements of basal diameter (-b) and height (-h). Asterisk represent the level of significance: *, $P < 0.05$.

Variables	**Site**	**r**	**P-value**	**df**	**t**
Variance RGR-b	XTBG, China	-0.16	0.24	60	-1.13
Variance RGR-h	XTBG, China	-0.27	0.02*	60	-2.26
Variance RGR-b	El Yunque, Puerto Rico	-0.41	0.04*	26	-2.16
Variance RGR-h	El Yunque, Puerto Rico	-0.042	0.83	26	-0.2

Table 3. 3. Pearson's correlations between species relative abundance and mean RGR. RGR was based on measurements of basal diameter (-b) and height (-h).

Variable	**Site**	**r**	**P-value**	**df**	**t**
Mean RGR-b	XTBG, China	0.18	0.16	60	1.42
Mean RGR-h	XTBG, China	-0.11	0.39	60	-0.85
Mean RGR-b	El Yunque, Puerto Rico	0.14	0.47	26	0.72
Mean RGR-h	El Yunque, Puerto Rico	-0.38	0.06	26	-2

Figures

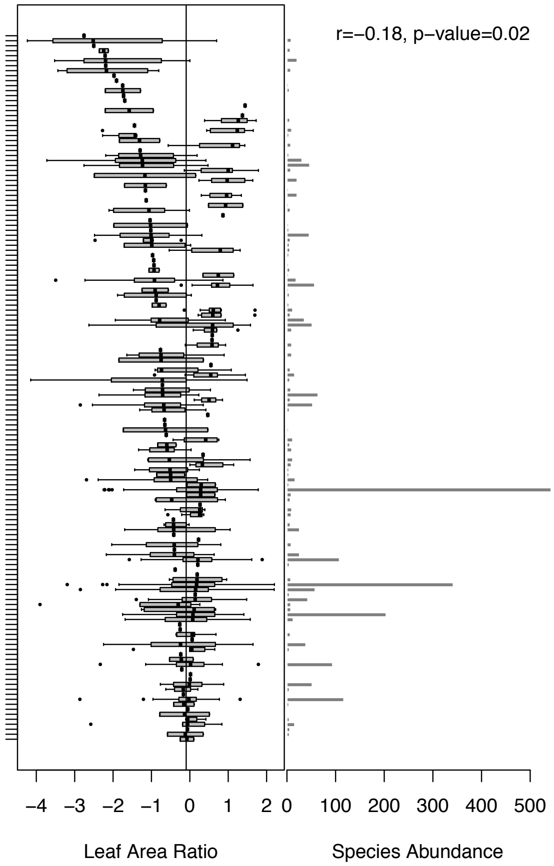

Figure 3. 1. The relative position of species in the leaf area ratio (LAR) distribution in Xishuangbanna, China. Left Panel: the x-axis represent the difference between median LAR species trait and mean LAR for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of LAR by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and mean of the community against the log-transformed abundance of the species.

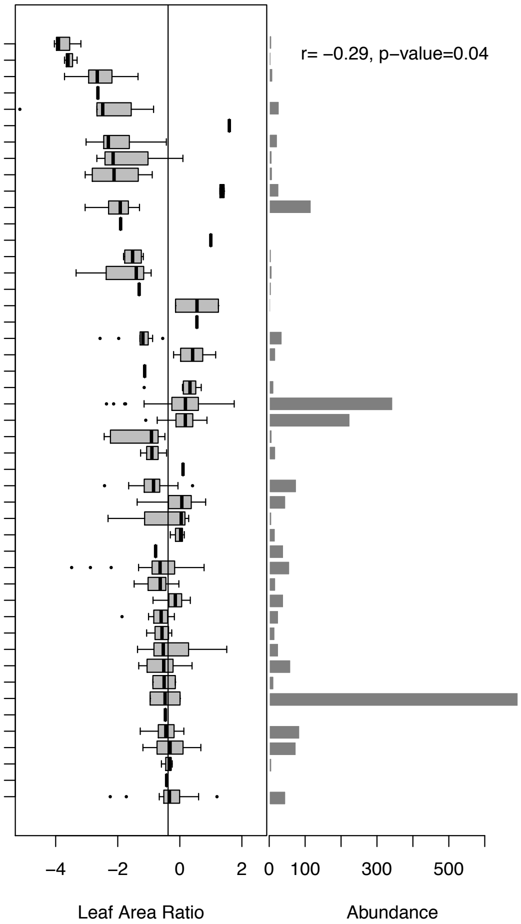

Figure 3. 2. The relative position in the leaf area ratio (LAR) distribution in El Yunque, Puerto Rico. Left Panel: the x-axis represent the difference between median LAR species trait and mean LAR for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of LAR by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and mean of the community against the log-transformed abundance of the species.

Chapter 4: The role of functional uniqueness and spatial aggregation in explaining rarity in trees

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Abstract

Aim: Determining the drivers of species rarity is fundamental for our understanding and conservation of biodiversity. The rarity of a given species within its community may arise due to exclusion by other ecologically similar species. Conversely, rare species may occupy habitats that are rare on the landscape or they may be ill-suited to all available habitats. The first mechanism would lead to common and rare species occupying similar ecological space defined by functional traits. The second mechanism would result in common and rare species occupying dissimilar ecological space and spatial aggregation of rare species either because they are specialist in rare habitats, or because of rare species tend to be dispersal limited. Here, we quantified the contribution of locally rare species to community functional richness, and the spatial aggregation of species across tree communities worldwide to address these hypotheses.

Location: Asia and the Americas.

Methods: We compiled a dataset of functional traits from all the species present in 8 tree plots around the world to evaluate the contribution of locally rare species to tree community functional diversity using multi- and uni-variate approaches. We also quantified the spatial aggregation of individuals within species at several spatial scales as it relates to abundance.

Results: Locally rare tree species in temperate and tropical forests tended to be functionally unique and are consistently spatially clustered. Furthermore, there is no evidence that this pattern is driven by pioneer species being locally rare.

Main conclusions: This evidence shows that locally rare tree species disproportionally contribute to community functional diversity and we therefore can reject the hypothesis that locally rare species are suppressed by ecologically similar, but numerically dominant, species. Rather, locally rare species are likely specialists on spatially rare habitats or they may be ill-suited to the locally available environments.

Introduction

Virtually every natural community is comprised of a few common species and many rare species (Wallace 1878; Preston 1948; Hubbell & Foster 1986; Brown 1995;

Lawton & Lawton 1999). The large number of rare species in ecological communities becomes even more pronounced in tropical regions where community ecology effectively becomes a study of rare species (Hubbell & Foster 1986; Pitman et al. 1999; Ricklefs 2000). Thus, our understanding of how ecological communities are themselves structured depends on our ability to uncover the processes driving rarity. Further, identifying the drivers of rarity is of fundamental importance for society's efforts to conserve biodiversity through space and time.

In tree communities, the rarity of species can be explained by a few, potentially overlapping, processes. First, a species may be locally rare because its niche is being occupied by ecologically similar species that are more numerically dominant in the community. For example, priority effects could promote the rarity of late arriving species even though these late arrivals are ecologically similar to the early arriving individuals (Chase 2007). Second, a species may be a habitat specialist and the habitat it specializes on is itself rare in the landscape (MacArthur 1957; Macarthur & Macarthur 1961; Sugihara 1980; Kunin & Gaston 1997). A prediction arising from the first possibility is that rare species should be functionally similar to common species. The second hypothesis, however, predicts that rare species should be functionally dissimilar to common species because they specialize on different and rarer habitats than common species. Further, rare species may be spatially clustered on a preferred habitat that is itself aggregated (Kunin & Gaston 1997). Given that in undisturbed forests pioneer species, specializing on light gap environments, may be rare in the community (Hubbell & Foster 1986; Denslow 1987), a possibility that emerges is that rare species will be functionally dissimilar from common species. For example, pioneer species are characterized by having low wood density, high specific leaf area, high leaf nutrients (Bazzaz 1980) and are often clumped distributed in gaps (Seidler & Plotkin 2006).

Despite the great interest in rarity in ecology (Rabinowitz 1981; Rabinowitz et al. 1986; Gaston 1994; McGill 2006), quantitative tests of the hypotheses described above are lacking. Specifically, comparative quantitative tests of the contribution of rare versus common species to community functional diversity and whether rare species tend to be spatially aggregated on spatially rare habitats are needed.

In this study, we analyzed long-term forest plot data from the temperate zone to the tropics. Four of the plots are located in Asia and four are located in the Americas. In each forest plot, we quantified several plant functional traits that are associated with species performance, functional trade-offs and ecological strategies. Our approach is a trait-based extension of a method recently proposed by Mi et al. (2012) that integrates relative abundance distributions with phylogenetic diversity measures (Figure 4.1). The specific questions we addressed in this study are: (*1*) do locally rare tree species contribute more than expected to community functional diversity by virtue of their being on the periphery of community trait space?; (*2*) do species with pioneer traits consistently occupy peripheral positions within the trait space of tree communities?; (*3*) are locally rare tree species more spatially clustered than common species?; The answers to these key questions are largely consistent across forest plots from the temperate zone to the tropics on two continents. Specifically, rare species tend to contribute more than expected to community functional diversity, species with pioneer traits are not consistently occupying the peripheral positions, and rare species tend to be more spatially aggregated than common species.

Methods

Data collection

This study analyzed eight forest dynamics plots from Asia and the Americas. For each forest plot, all individuals with a diameter at breast height greater than or equal to one centimeter were identified, measured and spatially mapped. The Guanacaste forest plot in Costa Rica, was the only exception, where only individuals greater than or equal to three centimeters were recorded. The plots have experienced relatively little disturbance recently aside from the Luquillo forest plot in Puerto Rico which has experienced severe hurricane damage from Hurricane Hugo in 1989 and Hurricane Georges in 1998 (Zimmerman et al. 1994; Comita et al. 2009) and the Wabikon Lake, Wisconsin forest plot has experienced selective logging in the past (early 1900's). The forest plots are located in temperate, subtropical and tropical regions and the plot species richness ranges from 34 with 27,861 individuals in Indiana, USA to 469 with 95,609 individuals in Xishuangbanna, China (Table 4.1).

At each forest plot, we compiled trait data for each of the species and calculated a species-level mean value for six functional traits: leaf area (LA), maximum height, specific leaf area (SLA), leaf nitrogen content (%N), leaf phosphorus content (%P) and wood specific gravity. The trait database for the Xishuangbanna forest plot did not contain %N, %P or wood specific gravity values. Rather, these axes of function were represented by leaf chlorophyll content and wood specific resistance (measured with a resistograph; Rennitech Co., Germany). Leaf chlorophyll content and wood resistance values have been shown to be highly correlated with %N, and %P and wood density, respectively (Vos & Bom 1993; Loh et al. 2002; Isik & Li 2003; Netto et al. 2005; Yang et al. 2014). Thus the leaf and wood axes of plant function were measured in each of the forest plots. Trait data were collected from the plots or in some instances from the area immediately next to them and followed standardized methodology (Cornelissen et al. 2003). For further details on trait data collection please see Appendix 3.

The traits quantified approximate the position of species along a continuum of ecological strategies on several axes (Díaz et al. 2015). The SLA, %N, %P and chlorophyll content of a species are components of the 'leaf economics spectrum' (Wright et al. 2004). Leaves with low structural and high nutrient investment tend to have higher photosynthetic rates and shorter leaf lifespans. The wood specific gravity and its correlate, wood specific resistance, represent the 'wood economics spectrum' (Chave et al. 2009). Species with low wood specific gravity or resistances tend to exhibit rapid volumetric growth rates and higher mortality rates compared to those species with higher wood specific gravities and resistances. The maximum height of species relates to the adult light niche of species and light gradient partitioning. Finally, the LA reflects the leaf area deployed for resource (i.e. light) capture and is known to vary along forest scale abiotic gradients as well as along local light gradients (Dolph & Dilcher, 1980; Cornelissen et al. 2003).

Measuring functional diversity

This work integrates functional diversity with the species rank abundance distribution in forest plots. It is important to note that this means that our approach and inferences are limited to the topic of local rarity and not the regional scale rarity of species. Our approach provides information about the relative contribution of each of the species to the community functional diversity (Gaston 2012; Mi et al. 2012). We quantified functional diversity using the functional richness (FRic) metric from Laliberté & Legendre (2010). The FRic is the volume of a convex hull encompassing the multivariate trait space of the species in a sample and therefore approximates the multivariate range of traits in the samples. The FRic metric is a good indicator of environmental filtering acting on the edges of trait space and it conceptually aligns with the goals of the present work, which asks whether increasingly rare species tend to occupy the periphery of multivariate trait space (Cornwell et al. 2006). Furthermore, it does not include abundance information, which is critical for our study that required a measure of functional diversity that is independent of the abundance distribution. We utilized the function *dbFD* in R package 'FD' (Laliberté and Legendre 2010) to calculate FRic. Trait values were log-transformed, if necessary, to approximate normality prior to the *dbFD* analyses. The *dbFD* function scales all trait data and performs a principal coordinate analysis (PCoA) to provide orthogonal axes prior to calculating FRic. The number of PCo axes selected to calculate FRic followed Laliberté & Legendre (2010) where the number of PCo axes retained is equal to the number of the species in the community minus 1.

Integrating abundance distributions and functional richness

To quantify the contribution of locally rare species to community functional richness for each assemblage, we integrated the standardized effect size (SES) for FRic with species rank abundance. In the following, we will describe the method to obtain the SES FRic values and how we compared it with the species abundance rank values. Our method follows that developed by Mi et al. (2012) who related phylogenetic diversity to rank abundance distributions. The first step was to calculate the observed FRic values. This method first computes the functional richness for the first and second most abundant species in the forest. Next, the third most abundant species is added to the sample and the functional richness metric is again computed and recorded. This is repeated adding increasingly rare species to the sample until the second most rare species is added (Figure 4.1).

The FRic metric is correlated with species richness (Laliberté and Legendre 2010). Thus, it is not possible to compare the FRic value across samples including increasingly rare species that differ in their number of species. A null model is, therefore, necessary to produce the expected distribution of FRic values given the observed species richness of a sample. Thus, for the second step in our analyses we generated a null distribution of values to estimate standardized FRic values. The null model was accomplished by randomizing the names of species 999 times on the trait data matrix in a plot. Thus, the species pool for the randomizations consisted of only the species within each plot. The FRic values for samples with increasingly rare species were computed as before, but this time with randomized trait data. At the end we had a distribution of 999 random FRic-abundance relationships that could be compared to our observed relationship. For each species along the species abundance rank distribution we calculated a SES FRic by subtracting the mean of the null distribution of FRic values for that species from the observed FRic and divided by the standard deviation of the null distribution. Therefore, positive SES FRic values indicated a higher than expected observed FRic value and negative SES FRic values indicated a lower than expected observed FRic value. Since a FRic of only one species cannot be computed the most abundant species is never analyzed by itself and the rarest species is never analyzed because the standardized effect size must be zero when all species are sampled (i.e. there is no variance in the null distribution). At the end we obtained a set of SES FRic values equal to the length of the total number of species minus two for each plot.

The last step was to compare the SES FRic values along the species rank abundance axis. On the left-hand side of the x-axis is the sample containing only the two most abundant species and increasingly rare species are added as one moves along the x-axis. A change in the y-axis value, the SES FRic, is expected if the added species to the sample (i.e. the next rarest species) increases or decreases the functional diversity more than expected based on a randomly added species. If there is a decreasing trend in SESs along the x-axis this indicates that as one adds less and less abundant species to the sample, less than expected functional diversity accumulates. In other words, the less abundant species are generally functionally similar to the more abundant species already in the sample. Conversely, if there is an increasing trend in the SESs along the x-axis, less abundant species are more functionally diverse than expected and functionally divergent from the more abundant species already in the sample.

Quantifying trends in functional diversity along the abundance distribution

Trends in the SES FRic values along the rank abundance distribution are used to indicate the relative contribution of increasingly rare species to community FRic. Thus, a critical step for interpreting FRic-rank abundance relationships is to determine: first, whether there are breaking points along the curve that indicate a change in the trend of the curve; and second, whether the trends in the curve are significantly increasing or decreasing, which would be indicative of rarer species adding more than expected or less than expected functional diversity to the community. Thus, we first used piece-wise regression to identify subseries (i.e. significant breakpoints) in each of the analyses and significance was assessed with a structural change test using the Chow's F- statistic method as described in Mi et al. (2012). We used Akaike information criteria (AIC) to compare a simple linear model with the piecewise linear model. For all the plots piece-wise linear models were consistently better than simple linear model (lower AIC values for piece-wise linear models than for simple linear models, Appendix 4 Table A4.1). Second, we used a Mann-Kendall test to quantify whether each sub-series exhibited a non-randomly increasing or decreasing trend in the standardized effect size values. Since the Mann-Kendall test may be sensitive to autocorrelation in the data a permutation approach using block bootstrapping is recommended (Wilks 1997). We utilized block bootstrapping to quantify whether trends were significant given the observed autocorrelation where block size was set at the maximum size at which continuous lag correlations were significant. Thus, blocks were randomly sampled with replacement to construct null sub-series of standardized effect sizes. A Mann-Kendall was then calculated for the null sub-series and this was repeated 999 times to generate a null distribution to which the observed Mann-Kendall for that sub-series could be compared and a p-value could be estimated. We utilized the function *MannKendal* in R package 'Kendall' and function *tsboots* in R package 'boot' to perform these analyses.

Evaluating individual trait ranges

In order to determine: (a) whether rare species increase FRic because they are potentially pioneer species with low wood density, high leaf nutrient content (i.e. %P and %N) or high specific leaf area (Bazzaz 1980) and (b) whether increases in FRic with rarity across all forests are generally associated with the increase in the range for a particular trait across all forests, we plotted the range of individual trait values as increasingly rare species are added. This allowed us to visualize how the range of an individual trait changes as increasingly rare species are added and it is the uni-variate analog to our multivariate FRic analyses. As in our multivariate analyses, our uni-variate analyses also estimated breakpoints and performed the structural test using the Chow's F- statistic method to evaluate whether the increases in the ranges of leaf traits and decreases in wood specific gravity were consistently associated with rare species. We used piece-wise regression to identify subseries in relationships between maximum trait range and rank abundance as well as minimum trait range and rank abundance.

Quantifying spatial aggregation of individuals within species

We quantified the spatial aggregation of individuals within species at several scales by computing the omega (Ω) metric developed by Condit et al. (2000). Omega evaluates the population density of each focal tree of each species within concentric circles with radii of 5, 10, 20, 30, 40 and 50 m. Thus, for a given species, Ω indicates the density of conspecifics in the neighborhood. This value is divided by the total population density of a particular species for the entire plot. Omega values equal to one indicate a perfectly random distribution. At short distances, Ω values higher than one indicates aggregation and Ω values lower than one indicates more even spacing. To ensure that our aggregation analyses were not inherently biased by differences in species abundance, we used a complete spatial randomness simulation to test whether species had Ω values that were significantly higher or lower than expected from a randomly dispersed species. In particular, we calculated 999 random Ω values by shuffling species names across the XY locations of all individuals in the forest plot each time calculating an Ω value for each species. This randomization considers the simplest null scenario assuming complete spatial randomness and independence. The mean of the null distribution of Ω values was subtracted from the observed Ω values and divided by the standard deviation of the null omega values to result in a standardized effect size (SES) of Ω. A SES of Ω higher than zero indicates a species is more spatially aggregated than expected whereas a SES Ω value less than zero indicates a species is more evenly dispersed in space than expected. In order to examine whether rare species tended to be more spatially clustered than common species, we performed Spearman correlations between SES Ω values and log-transformed species abundance. If rare species are more spatially clustered than common species, then a negative Spearman correlation is expected.

Results

The results from six of the eight forest plots (Indiana, Changbaishan, Fushan, Guanacaste, Gutianshan and Xishuangbanna) were consistent with downward trends on the left side and upward trends on the right side of the SES FRic curves (Figure 4.2, Appendix 4 Table A4.1, Table A4.2). The breakpoints for these six plots were located in the right hand of the curve (rare species) indicating that there are significant changes of these downward trends to upward trends (Figure 4.2, Appendix 4 Table A4.1). In other words, the rarest species in these forest plots were adding more to the overall community FRic than expected.

We further considered the results using an ad-hoc criterion for describing rare species (<1 individuals for a species per hectare) (Hubbell & Foster 1986) to evaluate if the breakpoints were associated with what may commonly be considered "rare" species. The results show that, in general, the breakpoints were very close to values that match the criteria for "rare" species used by Hubbell and Foster (1986) (Figure 4.2). Combined, the results for the trends and the breakpoints, indicate that the progressively rare species add more than expected to the functional diversity of the tree community (Figure 4.2, Appendix 4 Table A4.1, Table A4.2). For the other two plots (Wabikon Lake and Luquillo), the trends were more complex and rare species did not consistently contribute more than expected to the functional diversity of the community (Figure 4.2, Table A4.1, Table A4.2). For these two plots, the breakpoints were located on both the left and the right hand of the curve (Table A4.1), and the trends were downwards (Figure 4.2, Table A4.2).

When the ranges of individual traits were evaluated, we found no consistent trends across the different plots indicating that traits related with pioneer species (i.e. low wood density, high leaf nutrient content, high specific leaf area) are not consistently associated with the rarest species (Appendix 4 Table A4.3 Figures A4.1-A4.8). Specifically, for Indiana, Changbaishan, Fushan, Guanacaste, Gutianshan and Xishuangbanna plots, the breakpoints on the right hand of the curve (rare species) were not consistently found for leaf trait maximum values and wood density minimum values (Table A4.3, Figures A4.1-A4.8). The results for the plots with historical disturbance, Wabikon Lake and Luquillo showed significant changes in the trends in the left-hand of the curves (common species), but again the traits were not always consistent with the expectation for pioneer species (Table A4.3). Overall, we found no consistent support for our results being due to pioneer species being rare. We further tested for evidence regarding whether rare species are spatially aggregated. This was done by evaluating the correlation between species abundance and SES Ω values. The results show strong evidence that rare species tend to be more spatially aggregated than common species in all forests and spatial scales (Figure 4.3, Appendix 4 Table A4.4). Common species tended to have negative SES Ω values while rare species tended to have positive SES Ω values. Some rare species were highly clustered distributed at the smallest annulus size (5m) (Figure 4.3) as shown in the Wisconsin, Luquillo, Guanacaste and Gutianshan plots (Figure 4.3b, e, f, g).

Discussion

A central goal of this study was to quantify whether rare species are functionally distinct from more common species, thereby adding more than expected functional diversity to tree communities worldwide (Lawton 1999; Gaston 2012). Our results show that in six of the eight plots, rare species tend to be functionally unique indicating rare species are not rare because functionally similar species have pre-empted or excluded them. These results suggest that species abundance distribution is not only the result of historically contingent factors where the sequence and timing of functionally similar species arriving is the main determinant of their abundance (Chase 2003, 2007; Fukami 2015). Instead the combination of traits that characterize rare species may allow them to exploit different resources and therefore play an alternative role within the community as suggested by similar results for other taxa (Mouillot et al. 2011, 2013; Leitaõ et al. 2016). However, in two of our study plots, the Wabikon Lake, Wisconsin and Luquillo, Puerto Rico, the results showed different trends and the breakpoints were associated to common species. These two forests have both experienced past human disturbance via selective logging. The Luquillo plot has experienced two major hurricanes in the past 30 years (Thompson et al. 2002) and the dynamics at Luquillo plot have shown a higher functional turnover during the last 10 years compared with a non-disturbed tropical forest in Panama (Swenson et al. 2012). It is possible that this disturbance has affected the dynamics of these forests having an important effect on the functional composition of the plant communities. As forested ecosystems become increasingly disturbed in the future, it may well be that functional diversity will be reduced through the loss of rare functionally divergent species, and functional homogenization through space and along the abundance distribution may become more common.

Rarity and specialization

A potential explanation for unifying the results for the eight plots is that weedy pioneer tree species with unique peripheral trait values (Bazzaz 1980) are driving all of the observed results across forests. Specifically, in the six undisturbed forests, pioneer species, usually described as rare members of pristine communities and specialized on rare gap environments, might be the species responsible of the observed pattern of functionally distinct rare species (Hubbell & Foster 1986). Under this scenario, rarity would primarily be driven by the availability of habitats and functional specialization. However, upon examination of increases in individual trait ranges as progressively rare species are added in each forest plot, we find no clear and consistent evidence that pioneer species with unique trait values are the determinant of our results. For example, some leaf traits showed increases associated with rare species, as it is the case for *Trevesia palmata* (Araliaceae)*,* a tree characterized by big leaves and no side branches, which is a very rare species in the Xishuangbanna tree community. However, the increases in leaf traits for other non-disturbed forest plots were not always evident or were also associated with significant decreases in leaf trait values. For example, *Lonicera monantha* (Caprifoliaceae) is one of the rarest species in the Changbaishan plot, but it is not a pioneer species, instead is an understory tree and shade tolerant. Therefore, these results provide little support for the pioneer habitat specialization hypothesis linked to rarity.

Rare species might not be necessarily pioneers, but they may be specialized in other ways. We attempted to explore this possibility by analyzing the strength of the association between rare species and elevationally rare habitats compared to common species, suggesting potential specialization to particular elevations (Appendix 5). Elevation, typically linked to other topographical variables, has been found to play an important role in determining species distribution in tropical forest and potentially a key factor determining habitat associations (Harms et al. 2001; Baldeck et al. 2013). We evaluated the preferred elevation of species, ordered from most rare to most common, against the relative abundance of the elevation bins ordered from most rare to most common. We failed to find evidence supporting the habitat specialization for rare species aside from a very weak positive correlation in a few plots and this was consistent across bin sizes (Appendix 5). However, we caution that the analytical approach used had several flaws that hinder our ability to completely reject the rare species-specialists relationship. Specifically, other habitat variables that were not measured that are not or loosely correlated with elevation in the plots may be axes upon which rare species specialize. Furthermore, it is also important to recall that our analyses concern local rarity both in species and elevation and we cannot speak to whether the rare species-specialists relationship is supported at larger spatial scales.

Rarity and spatial aggregation

We further tested whether locally rare species are spatially aggregated. Our results show that locally rare species are more spatially aggregated than common species in all forests and spatial scales suggesting that populations of locally rare species are small because: (1) they are specialized on rare habitats; (2) locally rare species are sink populations and their spatial dispersion is limited due to rare dispersal events and a lack of reproduction and population spread, which combined drive the clustered individual spatial patterns. Although previous studies have found similar patterns, where locally rare species tend to be more clumped than common species (Hubbell 1979; Condit 2000; Li et al. 2009), one additional hypothesis that would help to clarify the role of rare species should be to evaluate their performance. In this respect, Hubbell (1979), showed that for a tropical forest analyzed in this study (Guanacaste, Costa Rica), rare species tend to exhibit poor reproductive performance compared with common species, suggesting that specialization might not be the main factor driving rarity. Supporting these results, recent work by Mangan et al. (2010) experimentally demonstrated that rare species are more susceptible to pathogens. However, previous work by Wills et al. (2006) that included two of our study forests showed that rare species have preferential recruitment, but quantifying demographic rates for rare species can be challenging (Condit et al. 2006). Wills et al. (2006) argued that their results were evidence of frequency-dependent selection favoring rare species thereby maintaining tree diversity. Thus, more studies are needed in order to fully support or reject it the specialization hypothesis.

In some ways, it may be useful to consider our results in the context of the core-satellite hypothesis (Hanski 1982). Hanski (1982) presented a classification of species according to their abundance and spatial distribution (regionally). In this context, locally small populations in a region may be considered satellite and perhaps sink populations, whereas locally large populations in a region may be considered core and perhaps source populations. One prediction arising from this would be that the locally rare populations like those we presently analyze are satellite and perhaps sink populations ill-suited to the local environment. Due to data limitations we were unable to strongly address whether locally rare species were ill-suited to local conditions and we have in many cases little information regarding whether the species in our forest plots are locally and regionally rare. Thus, at present we cannot fully address the predictions arising from the core-satellite literature. It is interesting to note, however, that recent work by Ricklefs & Renner (2012) has indicated that there is phylogenetic signal in local abundance in forest plots worldwide. This may indicate that there is inherent rarity in lineages that is evident locally and regionally, but it is still unclear from this evidence whether this rarity is due to specialization on rare habitats or some other process.

Together, our results fail to support the notion that rarity is driven by the ecological similarity between rare species and competitively superior or earlier arriving common species. Also, we present tentative evidence that did not support the link between specialization and rarity based upon our analyses of elevational data and shade tolerance strategies. We do note, however, that soil nutrient and light data would be preferred for such an analysis and future work on this topic is merited. Our results have additional implications beyond those for community structure and assembly. First, because locally rare species disproportionally contribute to community functional diversity, it is expected that they may also disproportionally contribute to ecosystem function (Tilman et al. 1997; Mouillot et al. 2011). Recent work has indicated this may be the case in several tropical systems (Mouillot et al. 2013). The present work show that rare species tend to be functionally unique, but they may not be disproportionally influencing present day functioning. However, functionally unique rare species are still likely to be critical for the stability of ecosystems undergoing change. Thus, the loss of rare species in ecosystems not only reduces the species and functional dimensions of biological diversity (Hector & Bagchi 2007), but it also likely has the potential to negatively impact the ability of ecosystems to respond to change or forcing. Second, a great deal of emphasis is now being placed on building large plant trait and spatial datasets for the purpose of mapping the distribution and diversity of plant function worldwide to facilitate vegetation modeling and biodiversity science (Kattge et al. 2011; Lamanna et al. 2014; van Bodegom et al. 2014). Such databases will inevitably be biased towards the inclusion of locally common species and the exclusion of locally rare species. This problem will be exacerbated in tropical systems where it is likely that such efforts will be prone to under-estimate of tropical functional diversity compared to temperate functional diversity. Thus, future analyses should attempt to avoid such biases and, just as importantly, a great deal more information regarding the functional diversity of entire tropical assemblages will be needed.

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Tables

Table 4. 1. Location and description of the forest dynamic plots.

Forest Plot	**Latitude**	**Forest Type**	**Plot Size (ha)**	**Census Year**	**Species Richness**
Lilly Dickey Woods, Indiana, U.S.A.	39.2361	Temperate forest	25	2012	34
Wabikon Lake, Wisconsin, U.S.A	45.5508	Temperate forest	25.6	2008	38
Changbaishan, China	42.3833	Korean pine mixed forest	25	2004	51
Fushan, Taiwan	24.7614	Subtropical evergreen forest	25	2002	110
Luquillo, Puerto Rico	18.3262	Lowland moist forest	16	2012	125
Guanacaste, Costa Rica	10.8833	Tropical dry forest	14.44	2006	136
Gutianshan, China	29.2500	Subtropical evergreen forest	24	2012	159
Xishuangbanna, China	21.6117	Tropical forest	20	2007	469

Figures

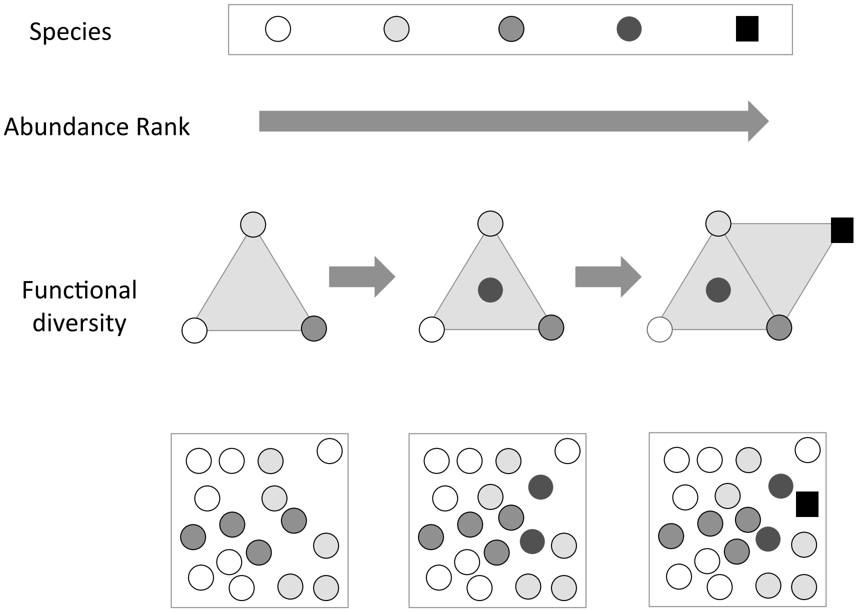


Figure 4. 1. A conceptual figure depicting how the species rank abundance was integrated with functional diversity. In this highly simplified example there are five individual species represented by different colors and shapes, sorted from most to least abundant based on the number of individuals in the forest plot. Notice that in this example the rarest species in the community is functionally unique and that is why its shape is different from the other species. The multivariate trait volume (in this simplified example, represented by the gray area) for the first three most abundant species is computed to represent the functional diversity. This measure is also referred to as functional richness. The volume is measured again including the fourth most abundant species. Here, the fourth species does not expand the volume. This process is repeated until we add the rarest species, which in this case adds substantially to the functional richness.

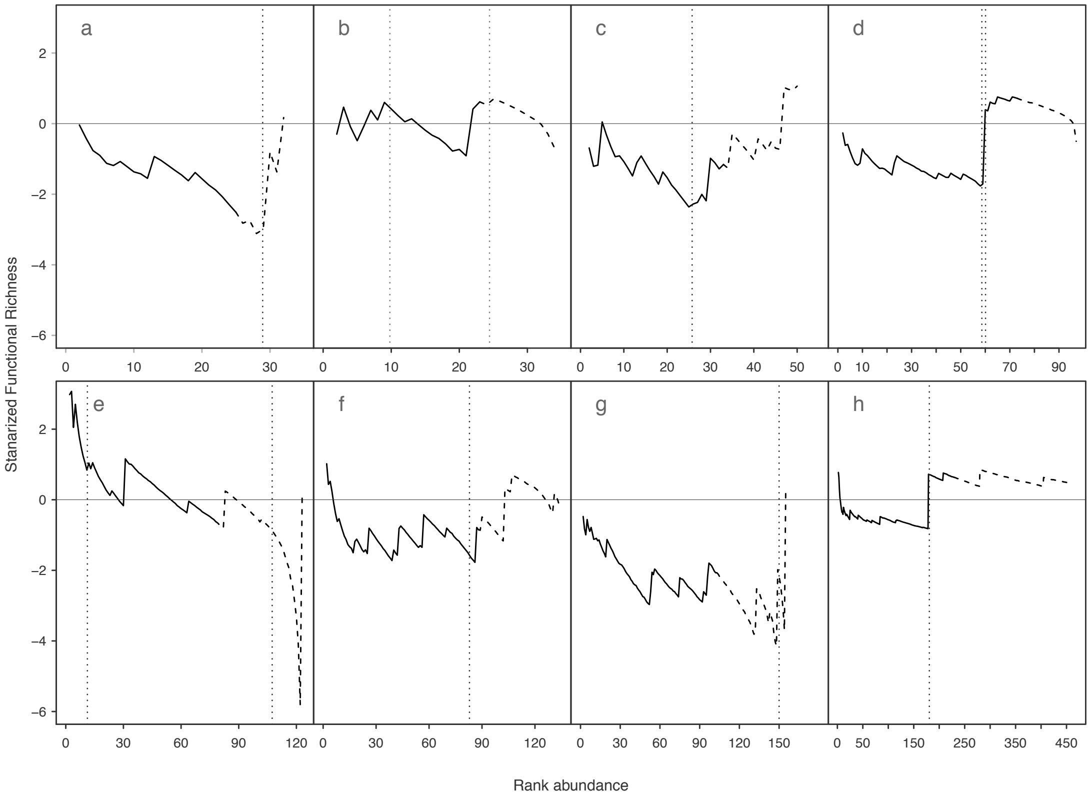


Figure 4. 2. The standardized effect sizes of functional richness. a) Indiana, USA, b) Wisconsin, USA, c) Changbaishan, China, d) Fushan, Taiwan, e) Luquillo, Puerto Rico, f) Guanacaste, Costa Rica, g) Gutianshan, China, h) Xishuangbanna, China. Positive values on the y-axis indicate that the species included in that calculation contribute more than expected to the functional diversity and negative values indicate that they contribute less than expected to the functional diversity. Positive trends indicate that increasingly rare species are disproportionally increasing the functional diversity of the system. Vertical doted grey lines in the panels indicate significant breakpoints in the piecewise regression (Appendix 4 Table A4.1). Dashed portions of the trend lines indicate species that have less than one individual per hectare, which is a commonly used categorization for 'rarity' in tree communities.

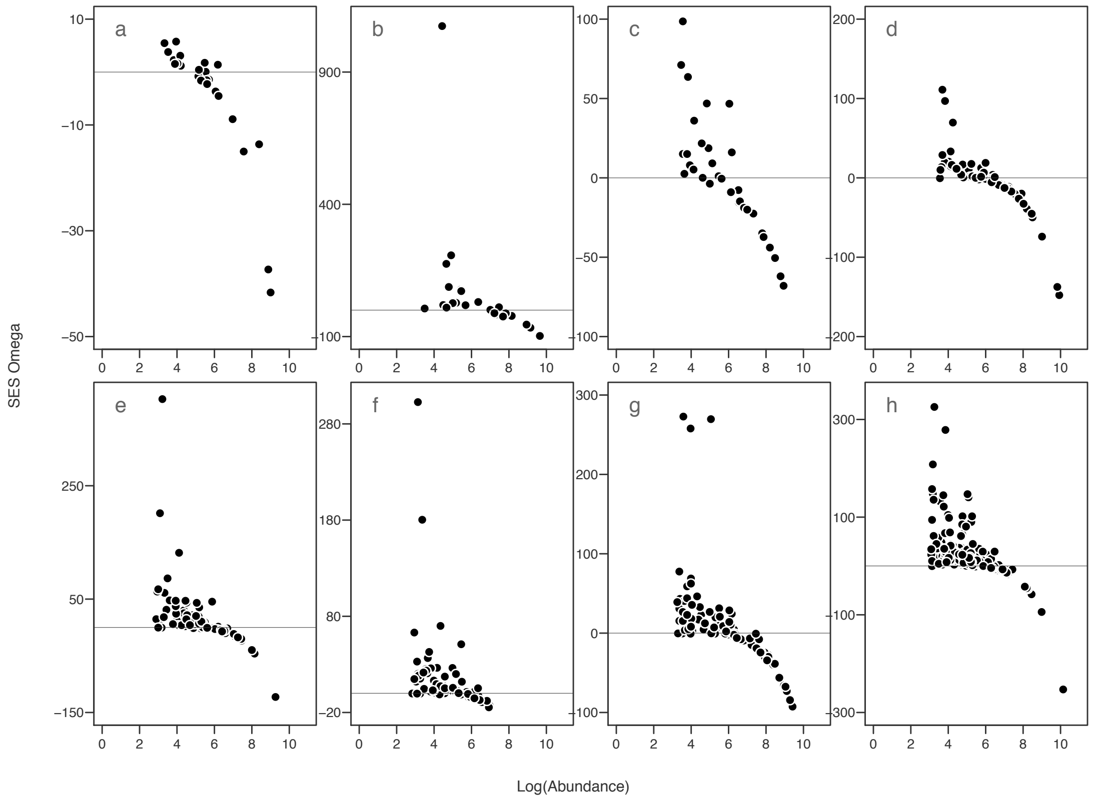


Figure 4. 3. The degree of spatial aggregation of individuals within a species. SES Ω values were plotted against their forest-wide abundance. a) Indiana, USA, b) Wisconsin, USA, c) Changbaishan, China, d) Fushan, Taiwan, e) Luquillo, Puerto Rico, f) Guanacaste, Costa Rica, g) Gutianshan, China, h) Xishuangbanna, China. The radius circle (Ω) surrounding each individual used for this figure was 5m. Positive SES Ω values indicate a higher degree of spatial aggregation. All correlations were statistically significant ($P < 0.01$). Species with no conspecific individuals within the 5m radius were omitted from these analyses but the correlations were still significant. Overall the trends show that rare species tend to be more clustered than common species.

Chapter 5: Intraspecific trait variation and negative density dependence drive growth rates in tropical tree seedlings

Abstract

Individual-level interactions with neighbors and the surrounding environment are key factors influencing performance that ultimately structure and maintain the diversity of tropical plant communities. However, discerning the main drivers of individual performance and how they are linked to individual phenotypic variation within communities remains unknown. We address these outstanding challenges by utilizing an unprecedented dataset containing individual-level demographic and functional trait data for tropical tree seedlings to quantify the influence of trait dissimilarity among neighbors and individual trait variation on survival and growth. The results show traits associated with resource acquisition do not explain observed negative density dependence occurring in seedling communities. However, irrespective of the trait dissimilarity among neighbors, individuals with relatively larger investments in leaf allocation are able to attain higher growth rates. Combined, these results indicate that focal individual trait values govern seedling growth, but the functional traits of neighbors related to resource acquisition do not influence focal individual growth rates or observed negative density dependence thereby also suggesting a strong role for shared host-specific pests in tropical tree communities.

Introduction

Explaining the remarkable levels of diversity in tropical forests has been one of the main challenges for ecologists during the last 50 years (Hubbell 2001; Wright 2002). Community structure and composition ultimately result from a combination of ecological forces that simultaneously influence individual performance. Negative density dependence, where individual performance and population growth diminishes as the density of conspecific individuals increases, is believed to play a central role in maintaining species diversity in natural communities by providing an advantage to rare species and preventing monodominance (Janzen 1970; Webb and Peart 1999; Harms et al. 2000; Wright 2002). Ecological theory highlights the role of conspecific competition and host-specific pests as main factors governing negative density dependence (Janzen 1970). Together with negative density dependence, individual variation in resource acquisition strategies should simultaneously create variation in individual performance. Beyond biotic interactions among co-occurring conspecifics, the local abiotic resource environment and how well individuals fit that environment should also impact demographic rates. Therefore, disentangling the role of these different mechanisms in driving the observed patterns of individual performance is critical for understanding the underlying causes of community assembly.

Species' phenotypes are powerful means to investigate the role that abiotic environments and biotic interactions play in structuring natural communities. Individual-level phenotypic information, in particular, is critical for investigating the drivers of community structure since individual-level interactions scale up to produce emergent community-level patterns (Clark 2010; Bolnick et al. 2011). Despite growing interest in understanding individual-level dynamics, large challenges remain. First, conspecific tropical tree seedlings vary considerably in their phenotypes and the degree of intra-specific variation is related to species abundance (Umaña et al. 2015). Trait-based analyses predicting performance have typically ignored this variation and have applied a species mean trait value to all individuals within a species. This, coupled with the fact that analyses of plant neighborhoods generally find that the number of neighboring conspecifics has a far greater impact on focal tree demography than the trait values of neighboring hetero-specific species (Kunstler et al. 2015), suggests that incorporating individual-level trait variation is an essential next step for understanding how biotic neighborhoods influence demographic patterns. Second, neighborhoods are highly dynamic and the number of neighbors may increase if new seedlings are recruited, or may decrease if some seedlings die during the observation period. This generates biotic uncertainty within the neighborhood of focal trees that might alter the perceived influence of local interactions. Considering the effect of this change in neighborhood composition would aid in understanding the role of biotic interactions on performance.

We utilized an unprecedented dataset containing individual-level growth and trait data for tree seedlings in a Chinese tropical rainforest to address the key challenges outlined above. We hypothesized that if negative density dependence mainly results from strong intra-specific competition for limited resources, then high conspecific densities and similarity or dissimilarity in resource acquisition traits would reduce individual growth performance. While high trait similarity can reflect strong competitive interactions (Macarthur and Levins 1967), other studies have suggested that larger differences in traits may lead to strong competitive interactions due to asymmetrical interactions (Weiner et al. 2001). The present study considered both hypotheses. Additionally, decreasing the number of conspecifics is expected to alleviate the negative effects of other conspecific neighbors and reduce the risk of disease transmission by species-specific pests. Thus, we expect that seedling performance will be enhanced via a reduction in conspecific density. An alternative hypothesis is that intra-specific competition at the seedling stage is not strong (Paine et al. 2008) and species-specific pathogens and herbivores drive a decrease in the demographic performance of individuals when in the presence of many conspecifics. In this case, we expect to find negative density dependent effects manifested only through changes in density, but not related to the similarity of resource acquisition traits in neighboring individuals since these traits are not involved in plant defense. Furthermore, we would expect that if local abiotic conditions also do influence seedling growth irrespective of neighborhood composition, variation in focal individual traits should determine growth.

To test our predictions, we collected trait and demographic data for all individual seedlings found in 218 1x1m plots from a hyper-diverse tropical rain forest in Xishuangbanna, China. The main goal of this study was to quantify negative density dependent effects and the role of individual-level phenotypic variation on seedling growth using information regarding the identity and traits of all individuals in the neighborhood (1x1m plot) of focal individuals. To accomplish this, we built a hierarchical model to evaluate the role of initial neighborhood density, change in the number of neighbors during the observation period, variation in individual-level traits and neighborhood trait dissimilarity in predicting relative growth rate (RGR) of seedlings.

Materials and Methods

Study site and data collection

This study evaluated seedling communities across 218 1x1m plots established next to a 20-ha forest dynamics plot in a tropical seasonal rainforest in Xishuangbanna, Yunnan, China (101º 34′ E, 21º 36′N). The Xishuangbanna region has a typical monsoon climate with a dry season between November and April and a rain season from May to October (Cao et al. 2008). In each seedling plot, we tagged, identified and measured all freestanding individuals smaller than 50 cm in height. Only 5% could not be identified and were thus recorded as clearly distinguishable morpho-species. We calculated species abundance as the total abundance of all observed individuals for each species across all the seedling plots during the first census.

We collected all seedlings for trait measurements after one year of monitoring changes in maximum height of each individual in the field. We measured eight traits related to leaf morphology and biomass allocation: leaf thickness, leaf area (LA), specific leaf area (SLA), leaf mass fraction (LMF), stem mass fraction (SMF), root mass fraction (RMF), leaf area ratio (LAR) and specific stem length (SSL) (Westoby 1998; Wright et al. 2004; Poorter et al. 2012). For leaf traits we used 1-3 fully expanded and undamaged leaves that were scanned and posteriorly dried in an oven for 72 h at 70°C. For biomass allocation traits, all leaves, stem and roots were manually separated and dried for 72h at 70°C to measure dry mass.

Growth rates

We monitored all individuals for one year for survival and changes in total height and basal diameter. The relative growth rate (RGR) was computed as $\log(M_{t+\Delta t} - M_t) / \Delta t$, were M indicates height and basal diameter at successive time steps *t* (Hoffmann and Poorter 2002). RGR was estimated in cm/y and all negative values were discarded (~7%).

Trait dissimilarity

Since the eight traits used in this study (SLA, LA, leaf thickness, LMF, SMF, RMF, LAR and SSL) may co-vary, we diminished trait redundancy by applying a principal component analysis (PCA) (Table A6.1 Appendix 6). We selected the three first PC axes (that explained 70% of the variation) and these orthogonal axes were used in further analyses (Table A6.2, Appendix 6). We calculated the trait dissimilarity (Td) as the mean Euclidean pairwise distance in traits (or PC axes) between each focal seedling individual and its seedlings neighbors within each plot. For ease of interpretation, this variable was centered at their community average and divided by its standard deviation.

Model implementation

We evaluated the effect of neighborhood seedling density, change in the number of neighbors and trait dissimilarity on individuals' relative growth rates (RGR). We only used individuals that had at least one conspecific in the plot at the time of sampling: in total we used 1009 seedlings, from 60 species distributed in 171 plots. The base-level of the model describes the relative growth rate of seedling *i,* of a species *j*, as a function of trait dissimilarity (Td) among conspecifics and hetero-specifics, density of conspecifics and hetero-specifics, change in the number of conspecifics neighbors and hetero-specific neighbors, three PC- trait axes, initial seedling size, and a plot-level random effect (denoted τ_k for plot *k*). Mean and range values for all predictor variables is in Table A6.3, Appendix 6.The variation in relative growth rates at given trait dissimilarity and plot effect is modeled using a normal distribution:

$$G_{ijk} \sim \mathrm{N}(\lambda_{jik}, \sigma_{\lambda}) \quad (1)$$

$$\lambda_{jik} = \alpha0_j + \alpha1_j \times \mathrm{Td.Co.sp}_{ijk} + \alpha2_j \times \mathrm{Td.Het.sp}_{jik} + \alpha3 \times \mathrm{Ch.Co.sp}_i + \alpha4 \times \mathrm{Ch.Het.sp} + \alpha5 \times \mathrm{Dens.Co.sp} + \alpha6 \times \mathrm{Dens.Het.sp} + \alpha7 \times \mathrm{Init.Size}_{ijk} + \alpha8 \times PC1_i + \alpha9 \times PC2_i + \alpha10 \times PC3_i + \tau_k \quad (2)$$

where λ represents the relative growth rate for each seedling *i* from species *j* and plot *k*, Td.Co.sp represents the trait dissimilarity among conspecifics, Td.Het.sp represents the trait dissimilarity among hetero-specifics, Ch.Co.sp represents the change in the number of conspecific neighbors for the time period evaluated in this study, Ch.Het.sp represents the change in the number of conspecific neighbors for the time period evaluated in this study, Init.Size presents the initial size of the seedlings when the first census started, PC1, PC2 and PC3 represent the 3 PC axes for the principal component analysis using all traits (Table A6.2) . The intercept $\alpha 0_j$ was modeled assuming that each species *j* was a random effect, drawn from a normal distribution with mean $\mu_{\alpha 0}$ and standard deviation $\sigma_{\alpha 0}$. Plot variation was modeled as a random effect:

$$\tau_k \sim \mathrm{N}\left(0, \sigma_{plot}\right)(3)$$

were τ_k represents the variation in seedling growth among plots. In addition to the expected influence of trait dissimilarity (Td) on seedling survival, we also hypothesized an indirect effect of species relative abundance on growth (Comita et al. 2010*a*). To evaluate this effect we added an additional component to our model to estimate the slope of trait dissimilarity effect on growth ($\alpha 1$ and $\alpha 2$)for each species *j*. The values for each $\alpha 1_j$ and $\alpha 2_j$ were modeled as a function of species abundance (*abundance*):

$$\alpha 1_j \sim \mathrm{N}(\mu_{\alpha 1}, \sigma) \ (4)$$

$$\mu_{\alpha 1, j} = \beta_0 + \beta_1 \times \log(Abundance_j) \ \ (5)$$

In addition to the model presented above, we also fit an additional model that not included seedling initial size, since this predictor variable was correlated with PC1 (r= -0.5, *P*<0.01). We compared both models using the deviance information criteria (DIC) (Gelman et al. 1995; Gelman and Hill 2007) and kept this model for the further results.

The models were fitted using Markov Chain Monte Carlo (MCMC) sampling techniques in *JAGS 3.4.0* interfaced using the *r2jags* package (Su and Yajima 2015). We set un-informative prior distributions for all parameters (Appendix 6). We ran three parallel chains with random initial values. We examined convergence visually with a threshold of 1.1for the Gelman and Rubin convergence diagnostic for all parameters (Gelman et al. 1995). For the growth models, we used 70,000 iterations, a burn-in period of 10,000 iterations and thinned by 10. We computed the mean and the 95% credible intervals of all model parameters (Figure A6.1, and Table A6.1).

Results

Firstly, our model evaluated the role of negative density dependence forces by testing the effect of initial density of conspecifics and the change in the density of conspecifics on seedlings growth rates. We found evidence for negative density dependent growth (Figure 5.1). A higher density of conspecifics decreased seedling relative growth rates across all 60 species. In addition, the change in the number of conspecific neighbours was negatively, but weakly, related to seedling growth (Figure 5.1).

Our model also evaluated the effects of density and change in the number of heterospecifics on seedling growth rates. We found that heterospecific coefficients were not significant (Table A6.1). However, initial density of heterospecifics had a weak positive effect on seedling growth (Table A6.1), indicating that seedlings tend to increase growth at higher densities of heterospecifics.

Next, in the same model, we evaluated the role of trait dissimilarity among conspecifics and heterospecifics on seedling growth rates. Seedling growth was not related to the trait dissimilarity of conspecifics or hetero-specifics in the neighbourhood and species relative abundance was not related to the strength of negative density dependence (Figure 5.2). The widespread negative density dependent effect was, therefore, not related to resource acquisition traits in the neighbourhood even when measured on the individual level.

Finally, we evaluated the role of PC traits measured for each individual seedling on seedling growth rates. We found that the resource acquisition trait values of the focal individual were, a strong predictor of seedling growth rates (Figure 5.3), suggesting that the local abiotic context exerts an important influence on individual performance. These results indicate that, although trait dissimilarity was not strongly linked to seedling performance, focal traits have an important role in determining growth rates in plants at early ontogenetic stages.

Discussion

Our results show that individual-level demographic performance in tropical tree seedlings is related to individual-level variation in traits linked to resource acquisition measured on the focal individual. Specifically, seedlings that invest more in leaf tissue, exhibiting leaves with high specific leaf area (PC2) and high biomass allocation in roots and stems (PC3) exhibit enhanced growth rates. However, the trait values of neighboring individuals had no impact on focal individual demographic performance. Rather, the observed negative impact of neighboring conspecifics on focal individual performance was not linked to resource acquisition traits indicating traits related to natural enemies are likely the drivers of negative density dependence in these communities. This supports recent arguments that analyses of tropical forests focusing on resource acquisition related functional traits and not traits related to defense may fail to infer key demographic processes such as negative density dependence driven by natural enemies (Coley and Kursar 2014). Overall, we infer from our results that there is generally weak intra- and inter-specific competition for resources among seedlings, but an important role for the fit of an individual's phenotype to the local environmental context. Thus, although tropical seedlings are strongly limited by light (Augspurger 1984*b*; Chazdon and Fetcher 1984), they are not necessarily intensely competing for this resource in a pair-wise manner. In tropical tree seedling communities where overlapping canopies or root systems are not common, the growth of one individual has little direct impact on the ability of neighboring seedlings to acquire resources. Rather, seedlings are mainly tolerating low level of resources, which makes competition more diffuse among neighbors. Thus, we suggest that resource levels *per se* and not competition for resources, governs seedling growth. Combined, our results reflect the slow growth of individuals responding to a resource-limited environment that survive due to a low density of neighboring conspecific individuals.

One additional factor that was evaluated in our approach was the effect of a changing neighborhood composition through time. Immediate neighbors are not static, and this variability may affect local interactions. Negative density dependent effects on growth rates might be hidden by the fact that the observed density of conspecifics at one particular moment can change rapidly, especially at early ontogenetic stages (Wright et al. 2005; Hubbell 2006). Given this, one may not be able to capture negative density dependent dynamics if changes in local conspecific density are not considered. We found a negative, although weak, effect on seedling growth related to a change in the number of conspecifics through time (Figure 5.1), but this effect was not observed when hetero-specifics were considered (Table A6.1). The negative effect of an increasing number of conspecifics and the null effect of the change in hetero-specific density highlights once again the important role of conspecific effects on focal seedling performance and the diffuse effects from other species. Further, the effect of variable numbers of neighbors also highlights the fact that biotic interactions are highly unpredictable across time and space such that the predicted differences among species as result of character displacement by direct inter-specific competition might be diluted. In particular, for species-rich systems the unpredictability in the identity of neighboring species is higher than in other less diverse forest and this uncertainty occurs on short temporal scales typically not considered in studies of negative density dependence (Hubbell 1980; Hubbell and Foster 1986). Our results suggest that pairwise interactions among species are likely diluted due to the high turnover of individuals occurring at the early ontogenetic stages. Thus, the implications of the effect of species turnover at neighborhood scale on species coexistence should be explored in future studies.

Based upon the evidence, we argue that a combination of different ecological forces drive the demographic patterns of tropical communities in its early life stages. On the one hand, negative density dependence is key for regulating populations through differential survival, promoting species co-existence and maintaining local levels of species diversity (Janzen 1970; Harms et al. 2000). We have shown that this key process is manifested in tropical tree seedlings by a decrease in growth rates at higher conspecific local densities. Additionally, the functional traits of neighboring conspecific and hetero-specific seedlings had no impact on focal seedling survival or growth. From this we infer a lesser role for direct resource competition and a greater role for interactions with shared natural enemies. Lastly, we have shown that individual trait values are significant predictors of individual demographic rates irrespective of neighborhood composition indicating that the phenotypic fit of an individual to a resource limited environment where increased investment in traits related to photosynthesis rather than over root drive demographic success. Together, these findings indicate that tropical seedling communities are structured by both abiotic and biotic interactions. Biotic interactions drive negative density dependence that regulates local population sizes and these forces are not linked to commonly measured functional traits related to resource acquisition indicating diffuse or non-existent competition for resources among seedlings. Abiotic interactions are realized via differential growth rates resulting from among individual variation in resource acquisition traits as they relate to local resource environments.

Acknowledgments

We acknowledge many field assistants who conducted the seedling censuses and helped with the trait measurements. We also like to thank to two anonymous reviewers that provide insightful comments and suggestions on an earlier version of the manuscript. Financial support was provided by National Science Foundation (DEB-1046113, DEB-1241136), by the National Key Basic Research Program of China (2014CB954104), the National Natural Science Foundation of China (31370445, 31570430), the Southeast Asia Biodiversity Research Institute of Chinese Academy of Sciences (2015CASEABRI004) and the Science and Technology Service Network Initiative of Chinese Academy of Sciences (KFJ-EW-STS-126).

Figures

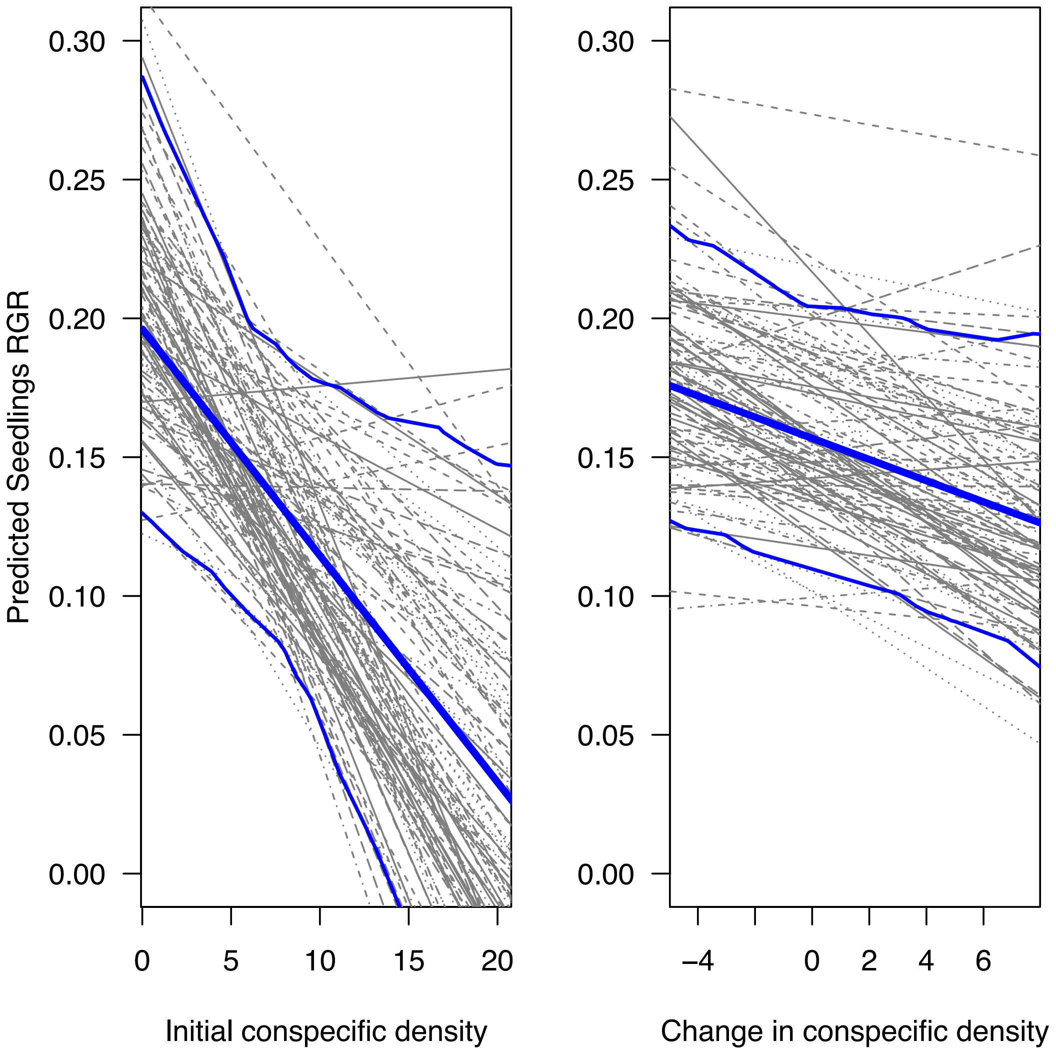


Figure 5. 1. Predicted relationship between relative growth rate and conspecific density. Left, considering the initial density of seedlings. Right, considering the change in the total number of conspecific neighbors between the two censuses. Thick blue line represents the mean and the 2 thin lines represent the 95% confidence intervals.

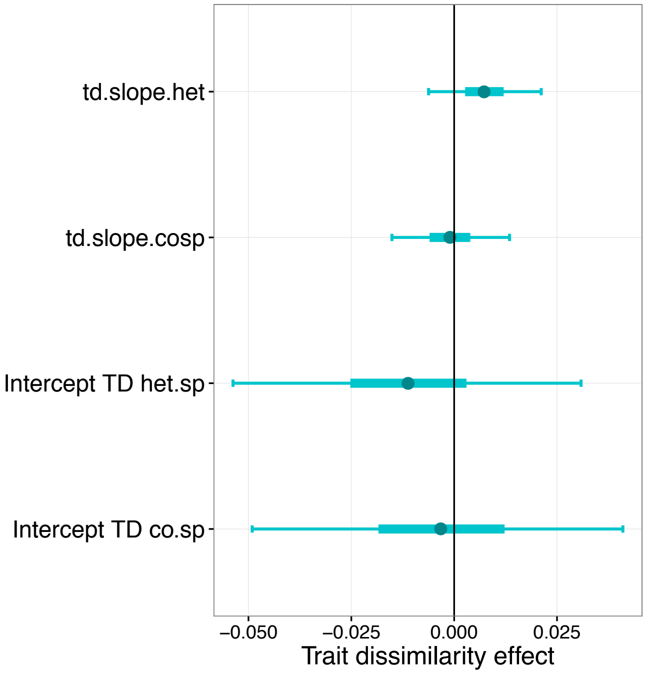


Figure 5. 2. Conspecific and hetero-specific coefficient effects from hierarchical Bayesian model of seedling growth. Blue dots represent the mean value and the segments represent the 50% (thick) and 95% (thin) credible intervals for each species.

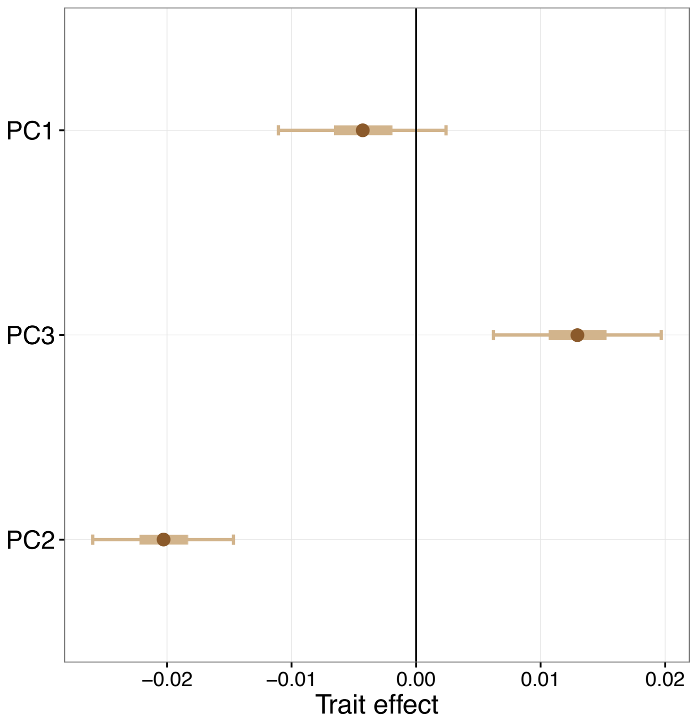


Figure 5. 3. Trait PC axes coefficient effects on seedling relative growth rate. Brown dots represent the mean value and the segments represent the 50% (thick) and 95% (thin) credible intervals for each species. The three PC axes explain 76% of the total variation of traits.

Appendices

Appendix 1. Functional diversity at forest-wide level

Text: Quantifying inter-specific functional negative density dependence during the seed-to-seedling transition at forest-wide level.

We aimed to quantify whether the relationship between trait similarity and the seed-to-seedling transition across the entire forest. To address this we built off of the framework developed by Harms et al. (2000) designed to detect within species negative density dependence by comparing the number of established seedlings to the number of seeds of a species (Figure A1.1). We extended this approach to quantify the degree of inter-specific functional negative density dependence during the seed-to-seedling transition (Figure A1.1). Specifically, we used a linear regression constrained to pass through the origin to evaluate the relationship between the functional richness, functional evenness, or mean nearest neighbor distance of the total pool of species (i.e., the species found in the seed traps and seedling plots) and the functional richness, functional evenness, or mean nearest neighbor distance of seedling plots. These slopes were then compared to a null distribution of slopes where null slopes were calculated using the null communities assembled for our site level analyses. Standardized effect sizes (SES) were calculated where negative SES values indicated a slope that is shallower than expected and positive SES values indicated a steeper than expected slope. It is important to note that a steeper than expected slope does not indicate that the seedling assemblage has a higher functional diversity than the seed assemblage. Rather, it is lower in absolute terms, but simply higher than expected. Negative SES results for this analysis indicate less functional richness, functional diversity, or mean nearest neighbor distance than expected in the seedling assemblages in sites forest-wide given the functional richness, functional evenness, or mean nearest neighbor distance in the species that have dispersed to those sites. This result would reflect the pattern predicted if abiotic filtering or hierarchical competition reduced the range of phenotypes able to establish in a site. Conversely, positive SES values indicated a slope that is steeper than expected demonstrating that seedling functional richness, functional evenness or mean nearest neighbor distance in sites forest-wide is higher than that expected given the species that have dispersed to the sites. This result would reflect the pattern predicted under an inter-specific functional negative density dependence mechanism such as limiting similarity.

We found that the multivariate functional richness of the seedlings was lower than expected given the functional richness of the total seed + seedling assemblages that were dispersed across all sites in each of the six years 2007 to 2012 (Figure A1.2). When individual traits were analyzed, we found that wood density, seed size and leaf traits associated with the leaf economic spectrum (LES) showed the same trend as the multivariate results (Figure A1.2). However, the functional richness SES values for maximum tree height (Figure A1.2) showed no consistent pattern being positive in two years and negative in four years. Leaf area (Figure A1.2) exhibited slopes higher than expected by chance. The functional evenness and mean nearest neighbor distance values for the seedlings assemblages exhibited higher observed values than expected in each of the six years (Figure A1.3 and A1.4). When individual traits were examined, the wood density and leaf area functional evenness and mean nearest neighbor distance values for the seedling assemblages were higher than expected given the functional evenness and mean nearest neighbor distance values for seeds (Figure A1.3 and A1.4). Leaf economics spectrum traits and seed mass for seedlings had lower than expected functional evenness and mean nearest neighbor distance values. The seedling functional evenness and mean nearest neighbor distance results for maximum height were inconsistent across years (Figure A1.3 and A1.4).

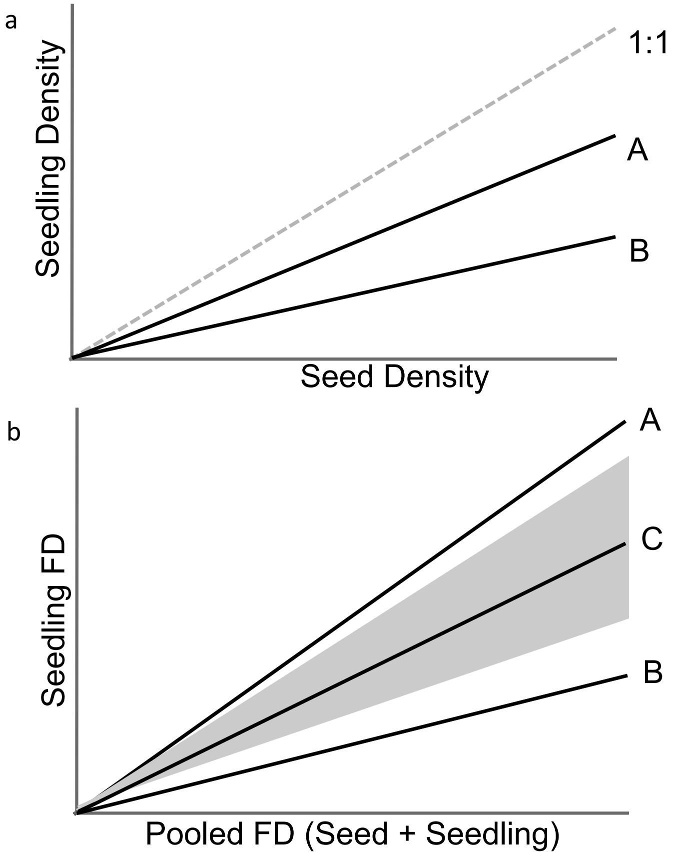


Figure A1.1. A schematic figure comparing the Harms et al. (2000) approach (top panel) with our trait-based approach (bottom panel). In the top panel, the slope lines correspond to the regression line for one species where species B is experiencing stronger negative density dependence than species A. In the bottom panel, the shaded area corresponds to the null distribution, slope lines correspond to regressions for sites forest-wide where the seedling assemblages, for example A, have higher than expected functional richness given the functional richness in the seed + seedling assemblage, assemblages in example B have lower than expected functional richness given the functional richness in the seed + seedling assemblage, and assemblages in example C have functional richness values no different from that expected given the functional richness in the seed + seedling assemblage.

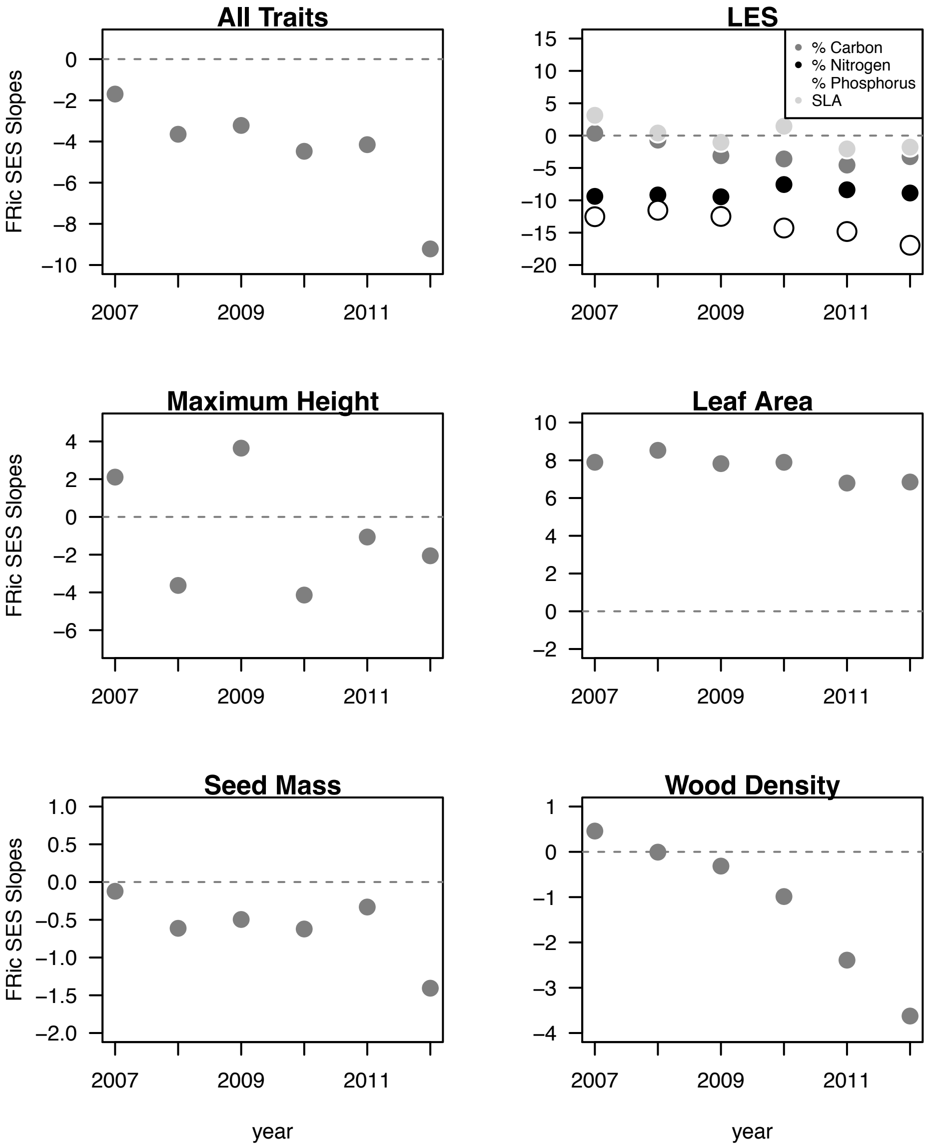


Figure A1.2. Forest-wide results for the standardized effect size (SES) of functional richness across 6 years. Negative SES of functional richness values indicate the observed slope is shallower than expected. Positive SES values indicate the observed slope is steeper than expected. LES refers to traits that represent the leaf economic spectrum; FRic refers to functional richness.

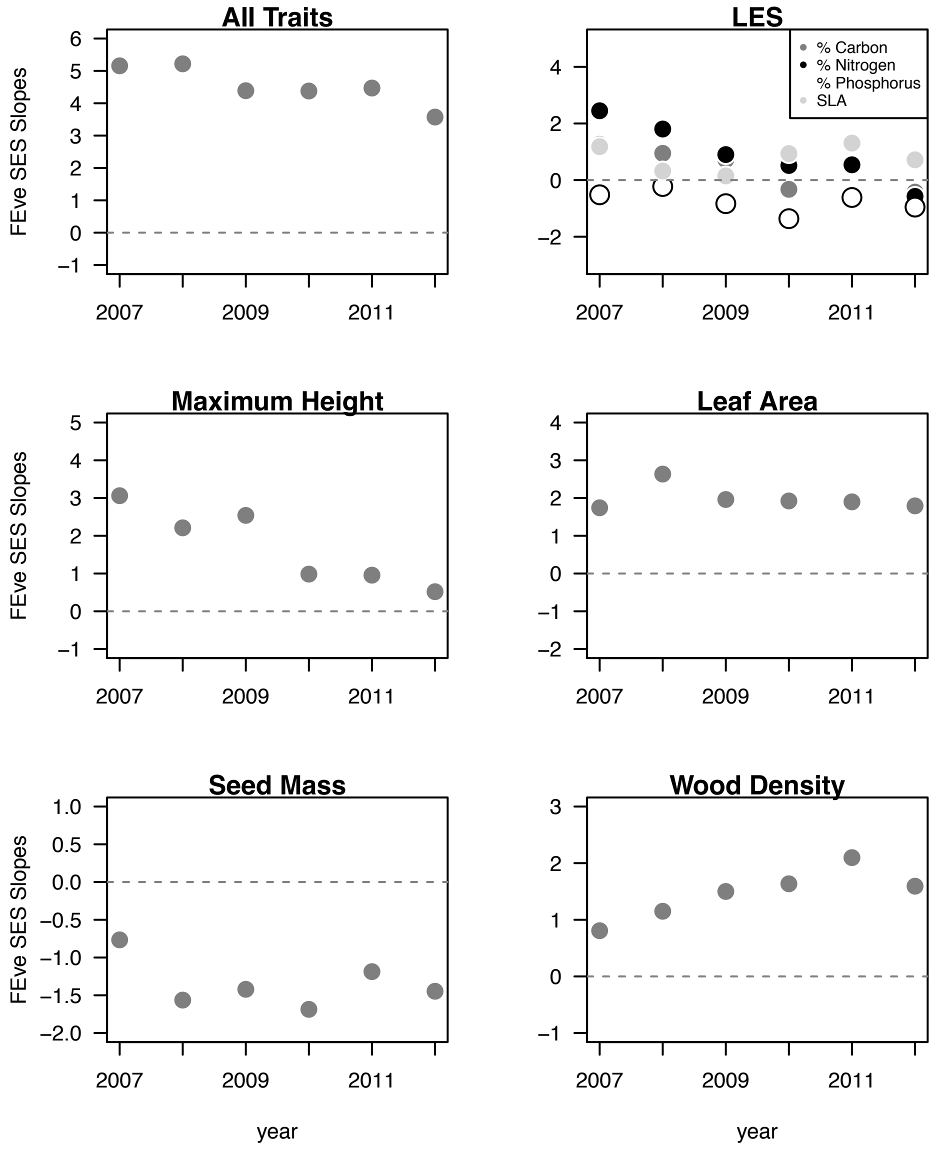


Figure A1.3. Forest-wide results for the standardized effect size (SES) of functional evenness across 6 years. Negative SES of functional evenness values indicate the observed slope is shallower than expected. Positive SES values indicate the observed slope is steeper than expected. LES refers to traits that represent the leaf economic spectrum; FEve refers to functional evenness.

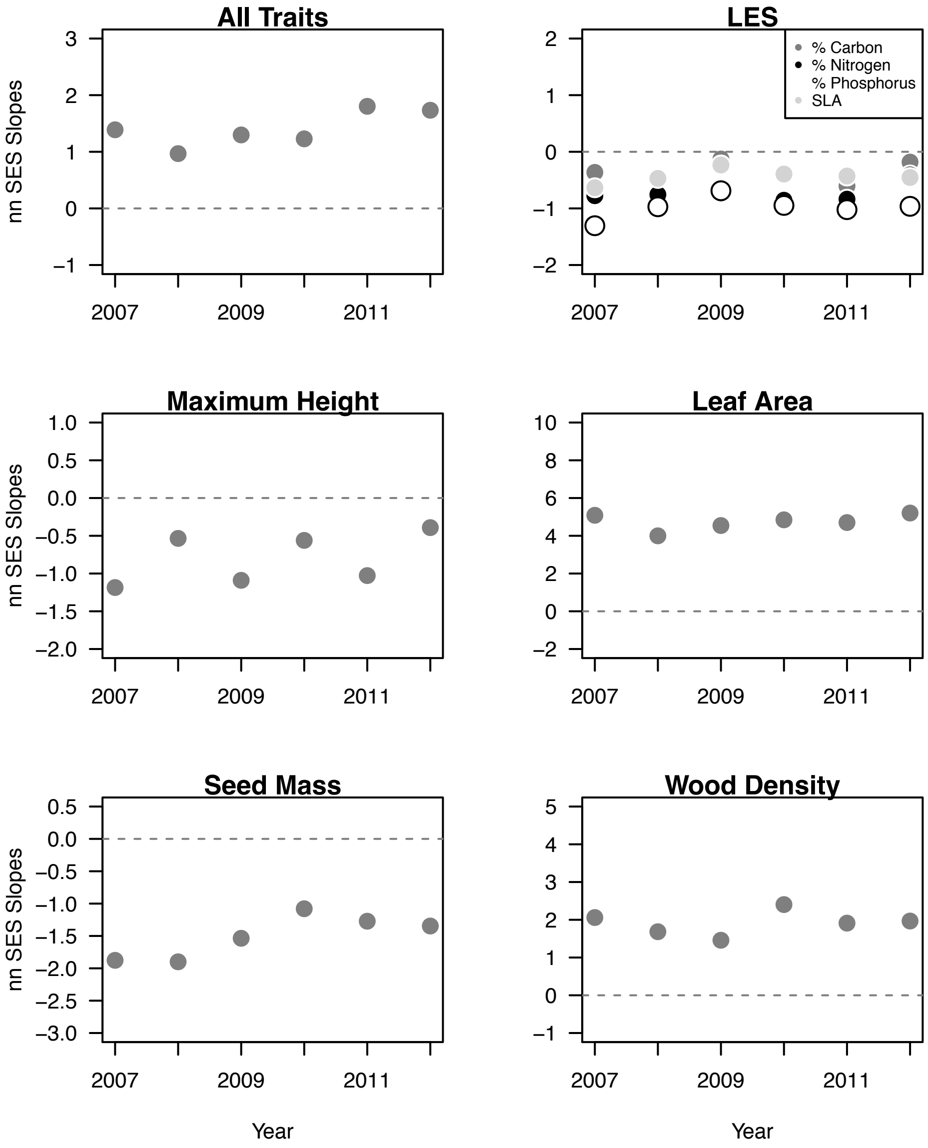


Figure A1.4. Distribution of SES of mean nearest neighbor distance slope values across 6 years. Negative SES mean nearest neighbor distance values indicate the observed slope is shallower than expected. Positive SES values indicate the observed slope is steeper than expected. LES refers to traits that represent the leaf economic spectrum; nn refers to mean nearest neighbor distance.

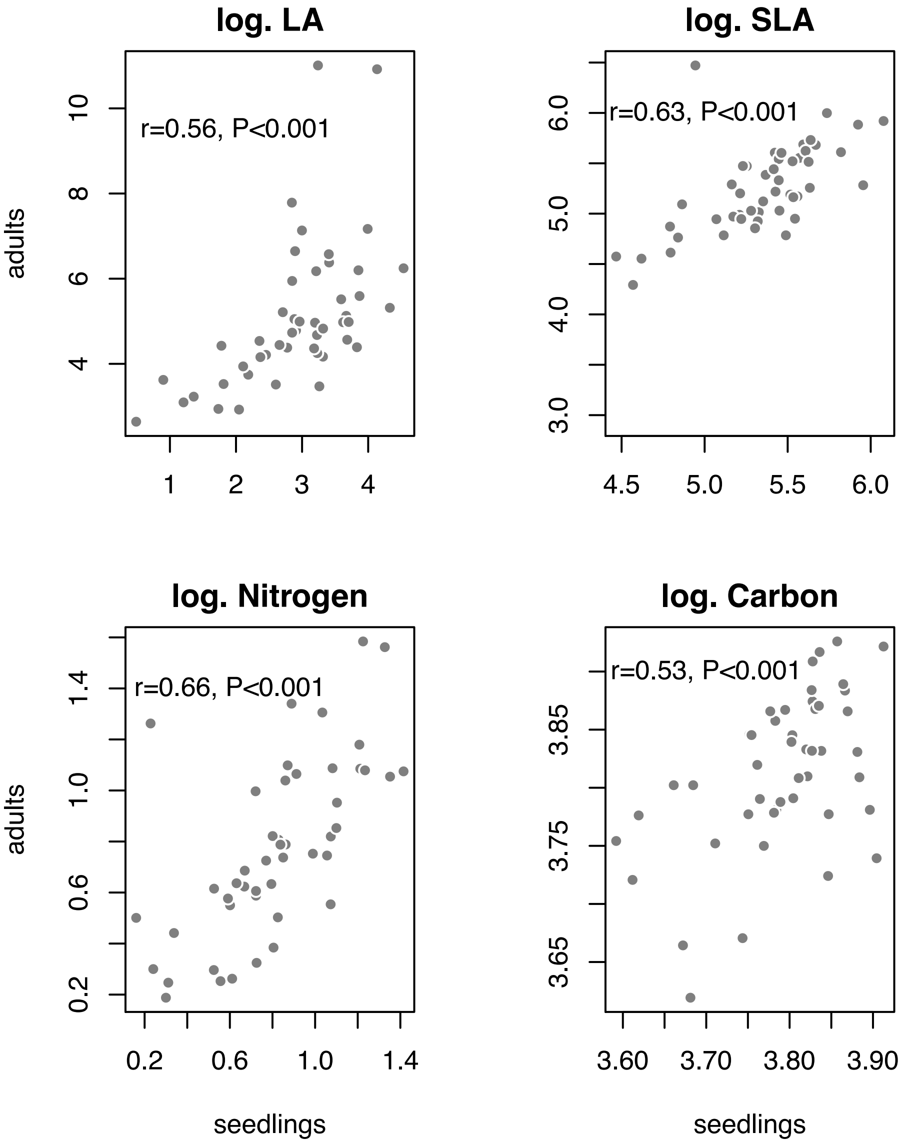


Figure A1.5. Correlation figures between individual traits at seedling and adult stage. The general pattern shows a high correlation in trait values in the two ontogenetic stages.

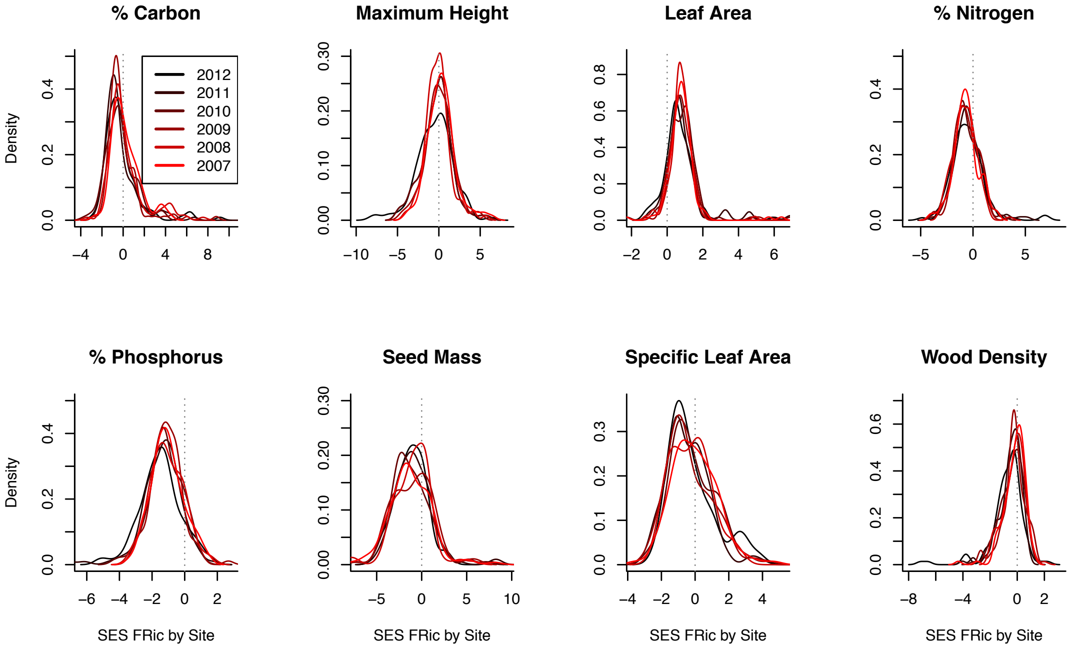


Figure A1.6. Site-level results for functional richness for individual traits. Density plots of SES of functional distance by site. Each line represents one year from 2007 to 2011. FRic refers to functional richness.

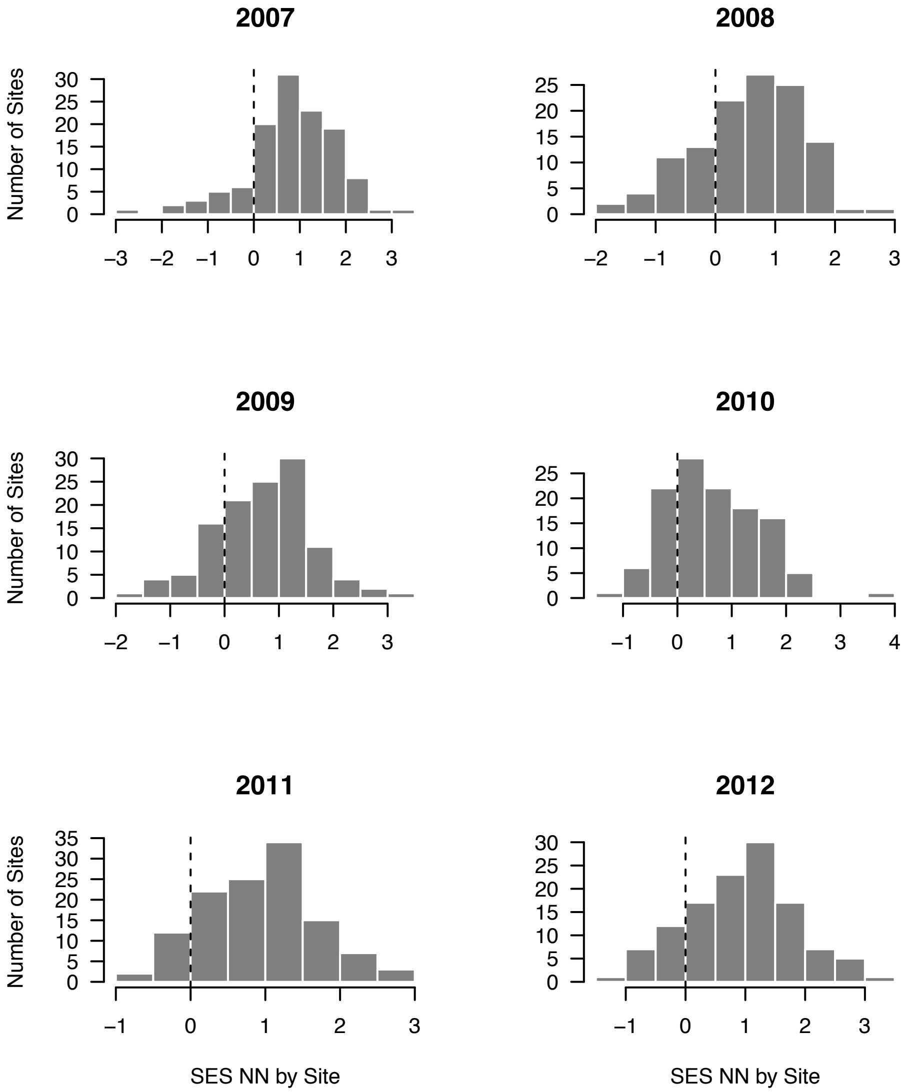


Figure A1.7. Site-level results for mean nearest neighbor distance. Frequency distribution of SES of mean nearest neighbor distance values combining all traits across different years. Negative SES mean nearest neighbor distance values indicate lower functional richness in seedling assemblages than expected. Positive values indicate the mean nearest neighbor distance values in the seedling assemblage was higher than expected. NN refers to mean nearest neighbor distance.

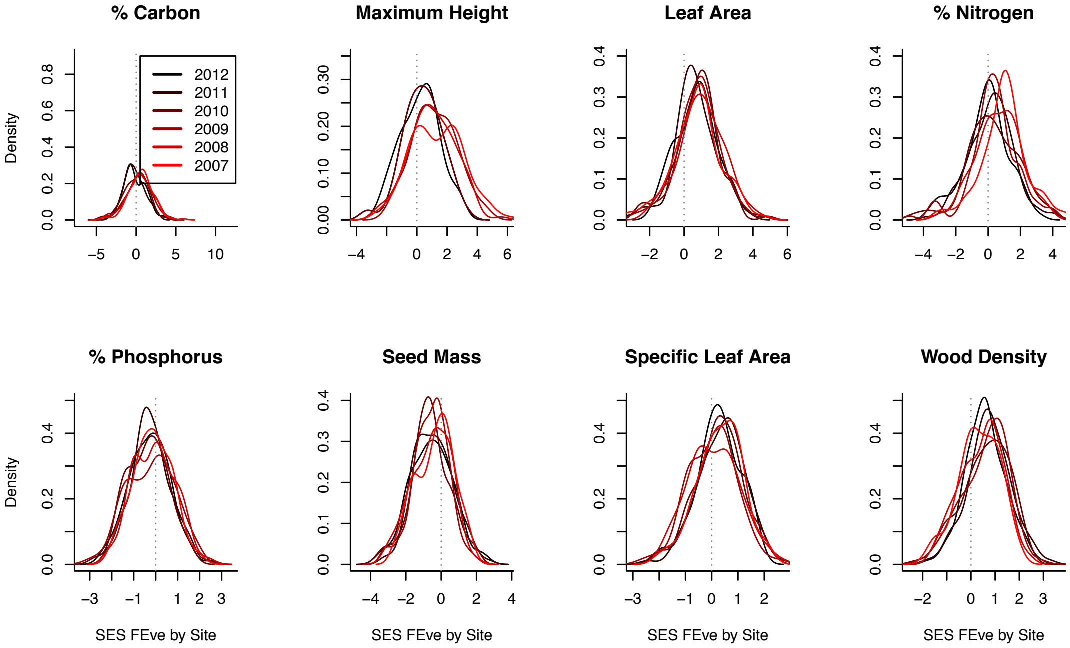


Figure A1.8. Site-level results for functional evenness for individual traits. Density plots of SES of Functional evenness values by site. Each line represents one year from 2007 to 2012. FEve refers to functional evenness.

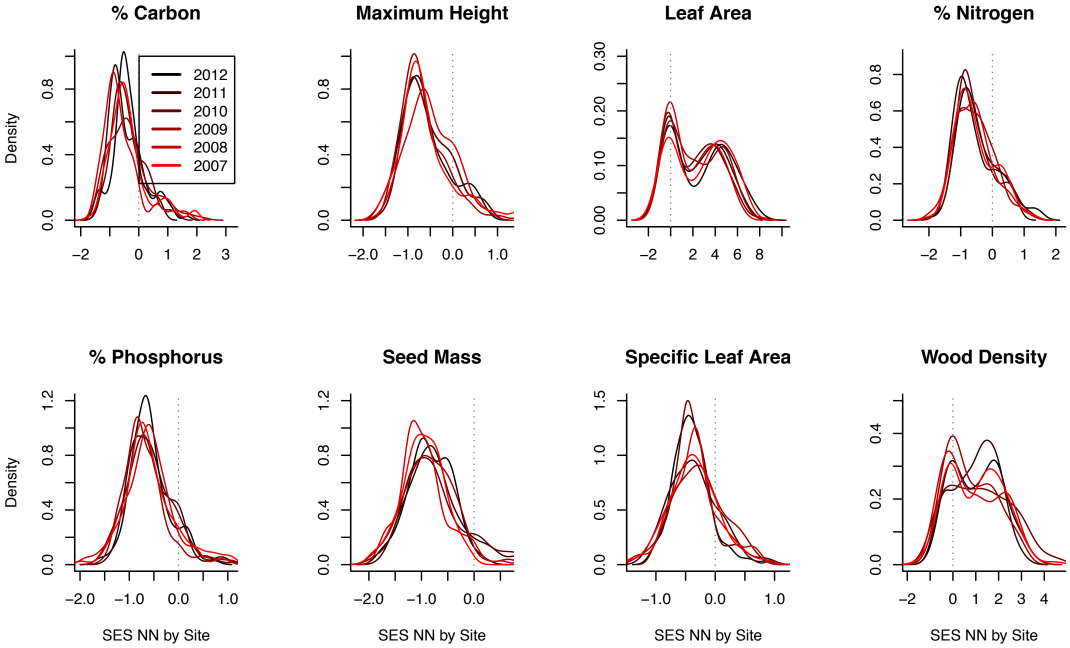
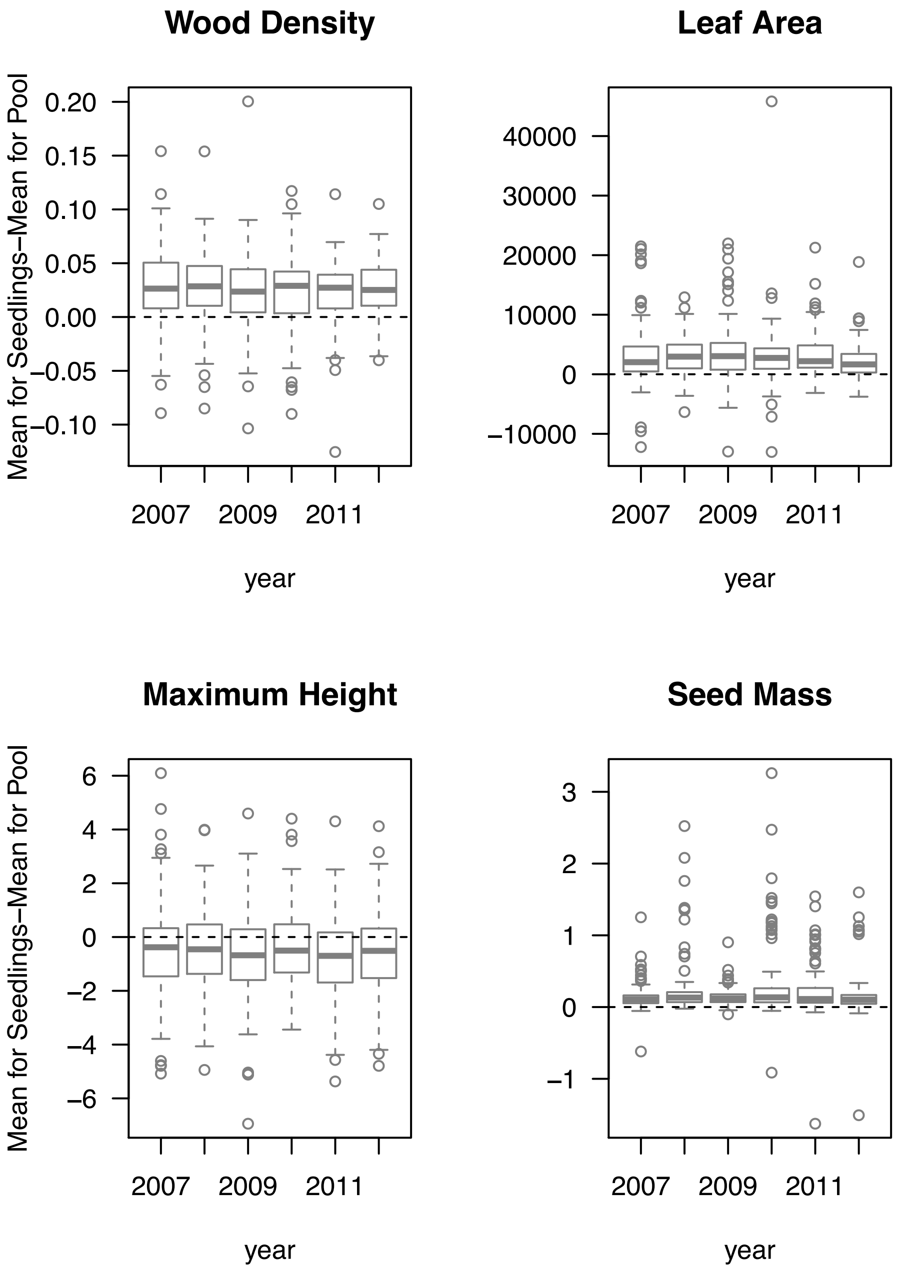


Figure A1.9. Site-level results for mean nearest neighbor distance for individual traits. Density plots of SES of mean nearest neighbor distance values by site. Each line represents one year from 2007 to 2012. NN refers to mean nearest neighbor distance.


Wood Density
Leaf Area
Maximum Height
Seed Mass
Mean for Seedlings−Mean for Pool
Mean for Seedlings−Mean for Pool
0.20
0.15
0.10
0.05
0.00
−0.05
−0.10
40000
30000
20000
10000
0
−10000
6
4
2
0
−2
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−6
3
2
1
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−1
2007
2009
2011
year
year
year
year

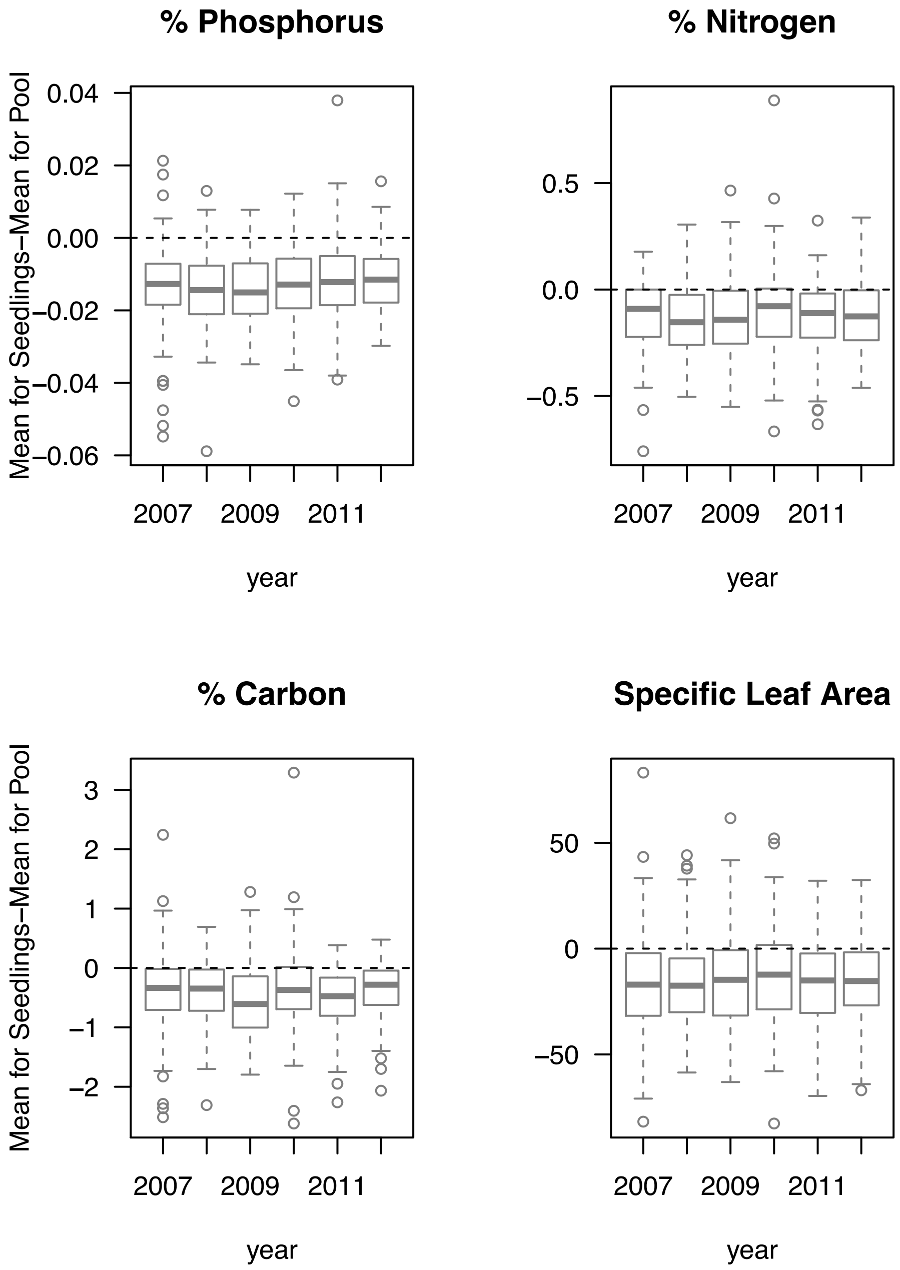

Figure A1.10. Boxplot showing the difference in mean traits values between the seedlings assemblages and the seed + seedling assemblages for every trait in each year. Positive values indicate mean trait values at seedling stage are higher than the trait values for the seeds + seedling assemblage and negative values indicate mean trait values at seedling stage are smaller than the trait values for the seed + seedling assemblages.

Appendix 2. Additional results for China and Puerto Rico

Table A2. 1. PCA loadings for 8 functional traits and cumulative proportion explained by each orthogonal axis for China and Puerto Rico seedlings data set.

	China			**Puerto Rico**		
Trait	**Comp. 1**	**Comp. 2**	**Comp. 3**	**Comp. 1**	**Comp. 2**	**Comp. 3**
Leaf Area	0.452	-0.204		0.54		0.285
Specific leaf area	-0.413	0.288	-0.126	-0.505	-0.197	0.115
Leaf thickness	0.28		0.302	0.27	0.233	-0.421
Specific stem length	-0.55		0.233	-0.474	-0.365	-0.237
Leaf area ratio	-0.445	-0.207			-0.538	
Leaf mass fraction		-0.703		0.279	-0.521	-0.183
Stem mass fraction	-0.121	0.138	-0.715	-0.212	0.438	-0.353
Root mass fraction	0.161	0.564	0.439	-0.164	0.112	0.713
Cumulative proportion	0.34	0.55	0.71	0.29	0.56	0.73

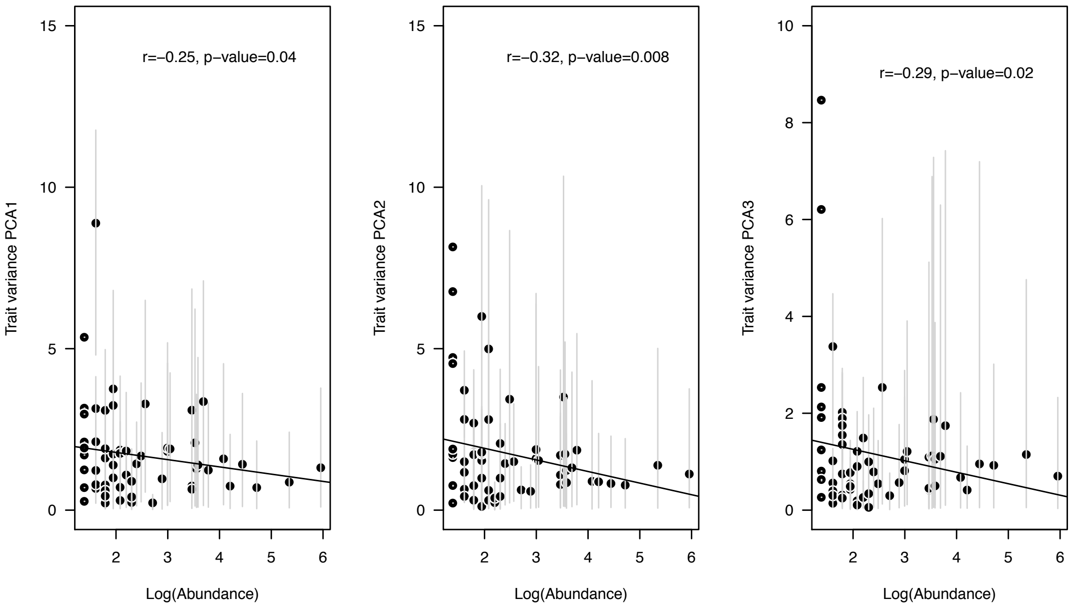

Figure A2.1. Correlation plots between species relative abundance and PCA axes, China.

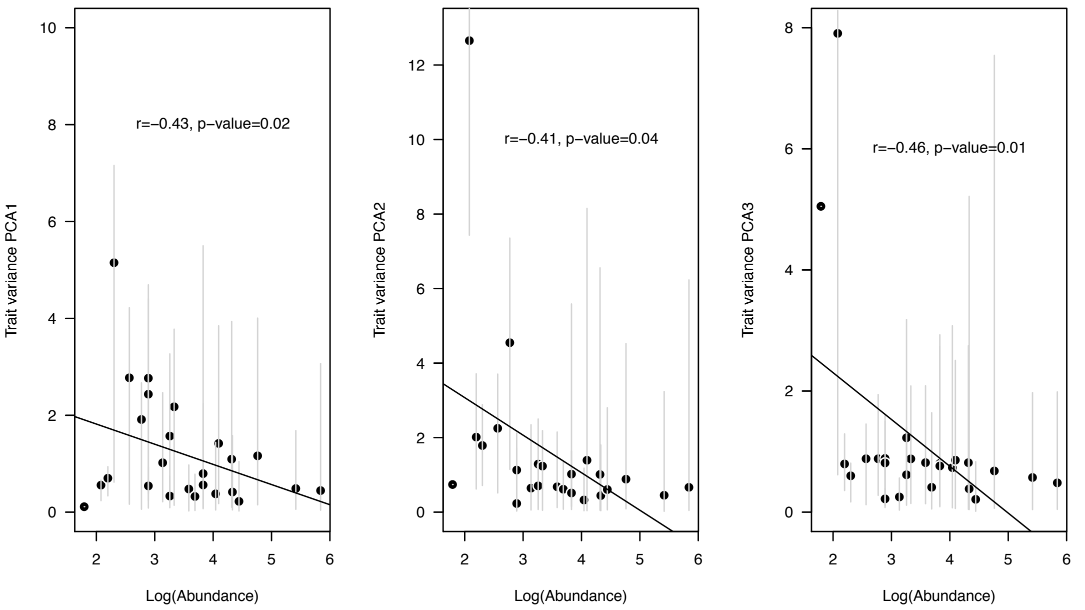

Figure A2.2. Correlation plots between species relative abundance and PCA axes, Puerto Rico.

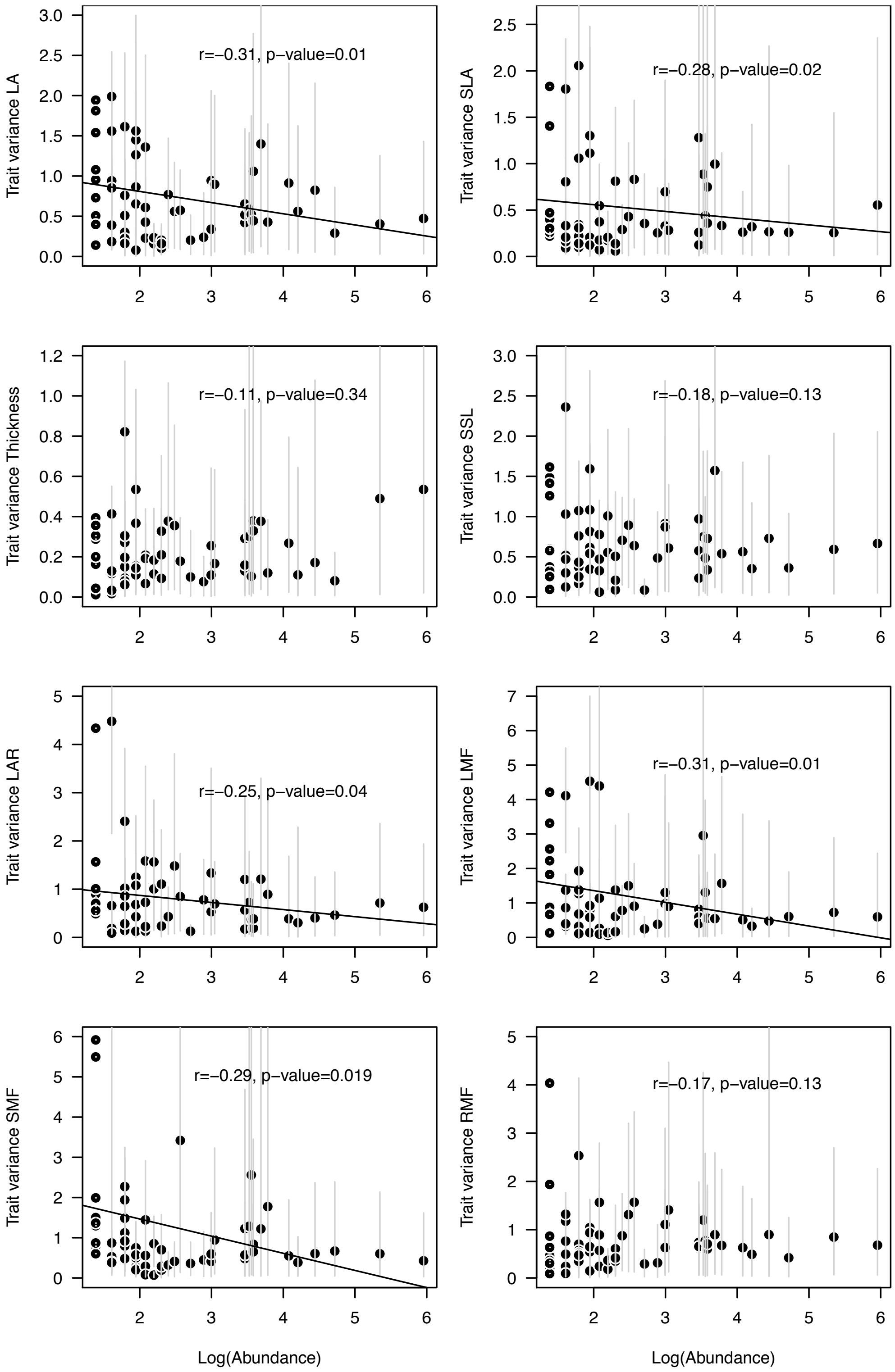

Figure A2.3. Correlation plots between species relative abundance and individual traits, China.

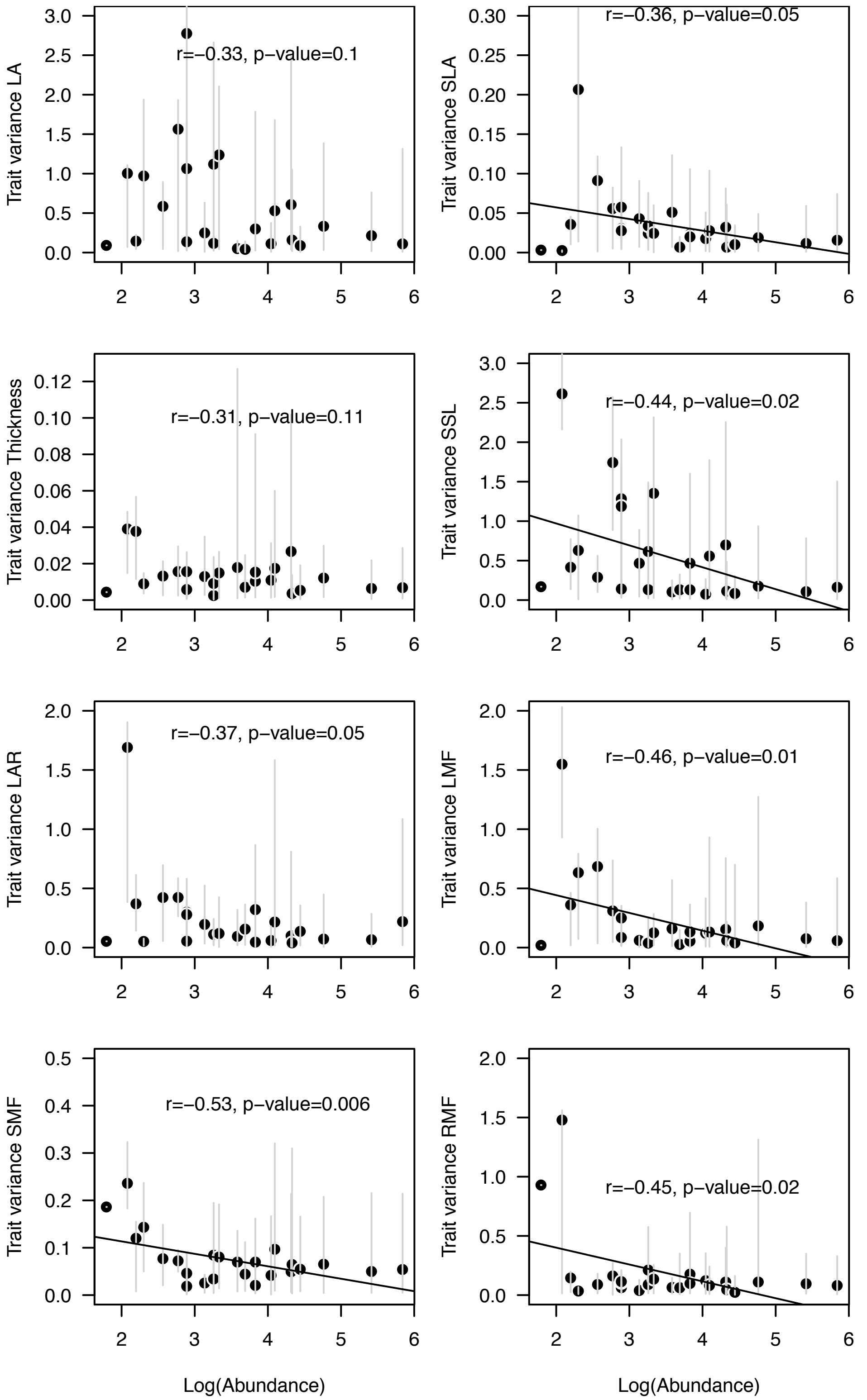

Figure A2.4. Correlation plots between species relative abundance and individual traits, Puerto Rico

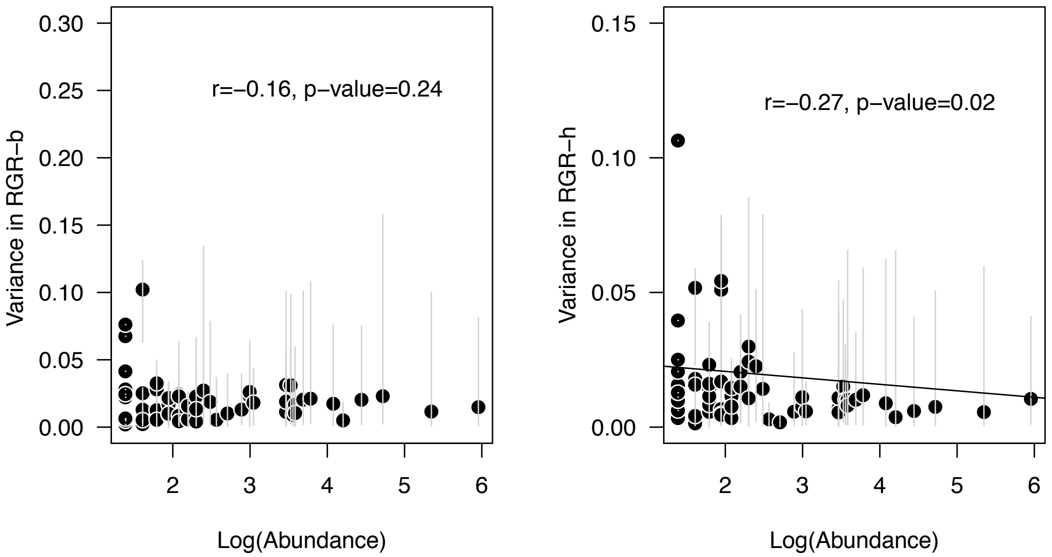

Figure A2.5. Correlation plots between species relative abundance and variance in relative growth rates (RGR), China. RGR was based on measurements of basal diameter (-b) and height (-h).

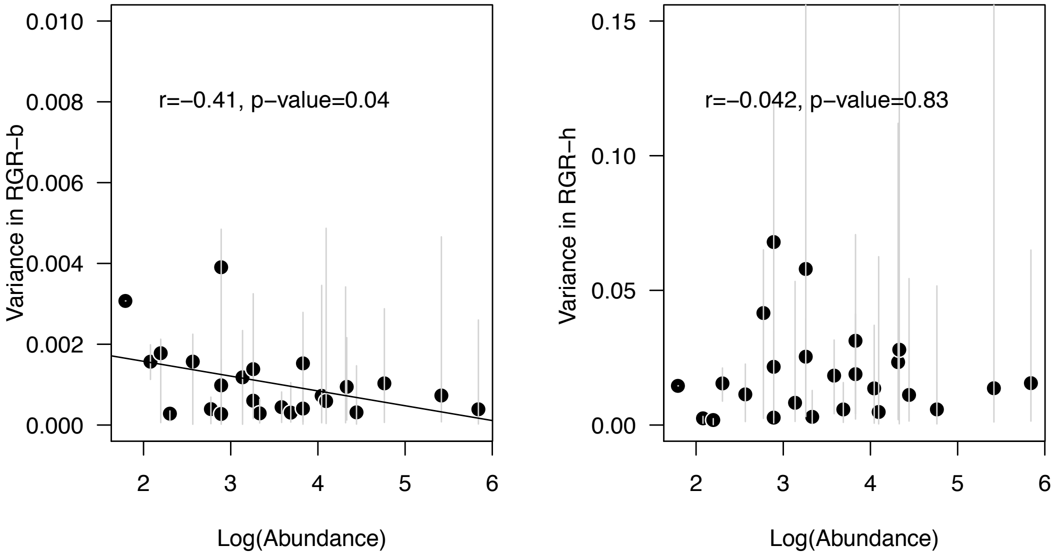

Figure A2.6. Correlation plots between species relative abundance and variance in relative growth rates (RGR), Puerto Rico. RGR was based on measurements of basal diameter (-b) and height (-h).

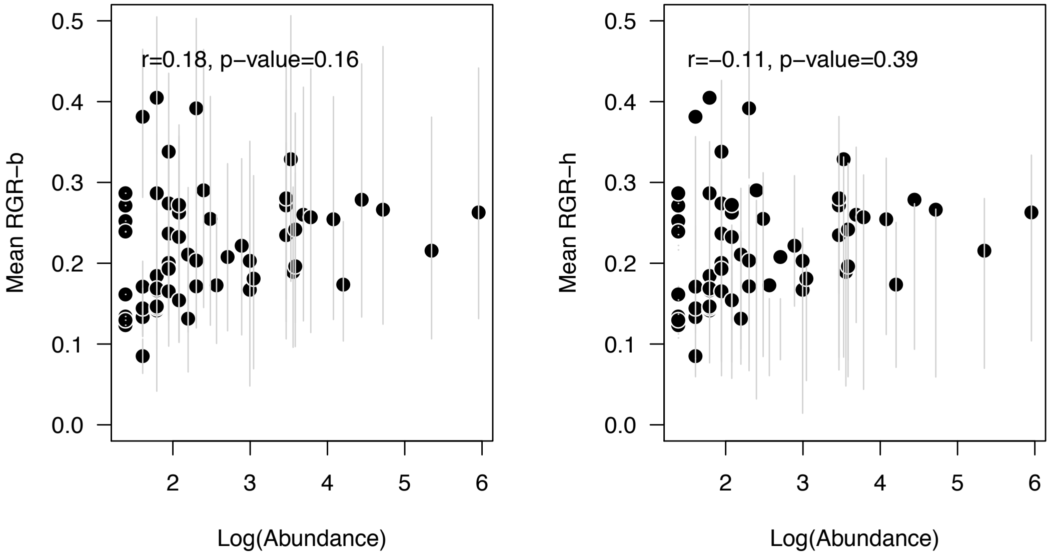

Figure A2.7. Correlation plots between species relative abundance and mean relative growth rates (RGR), China. RGR was based on measurements of basal diameter (-b) and height (-h).

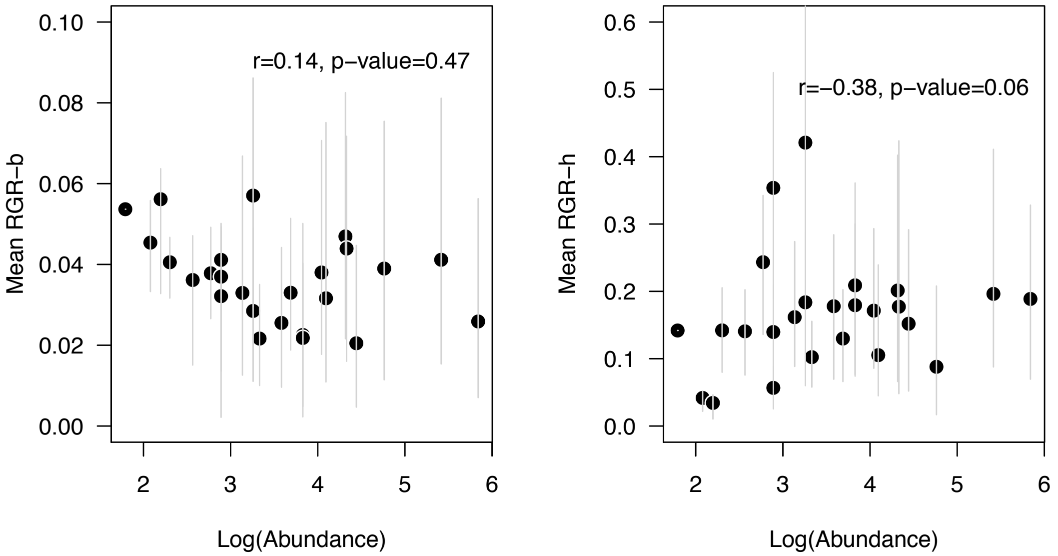

Figure A2.8. Correlation plots between species relative abundance and mean relative growth rates (RGR), Puerto Rico. RGR was based on measurements of basal diameter (-b) and height (-h).

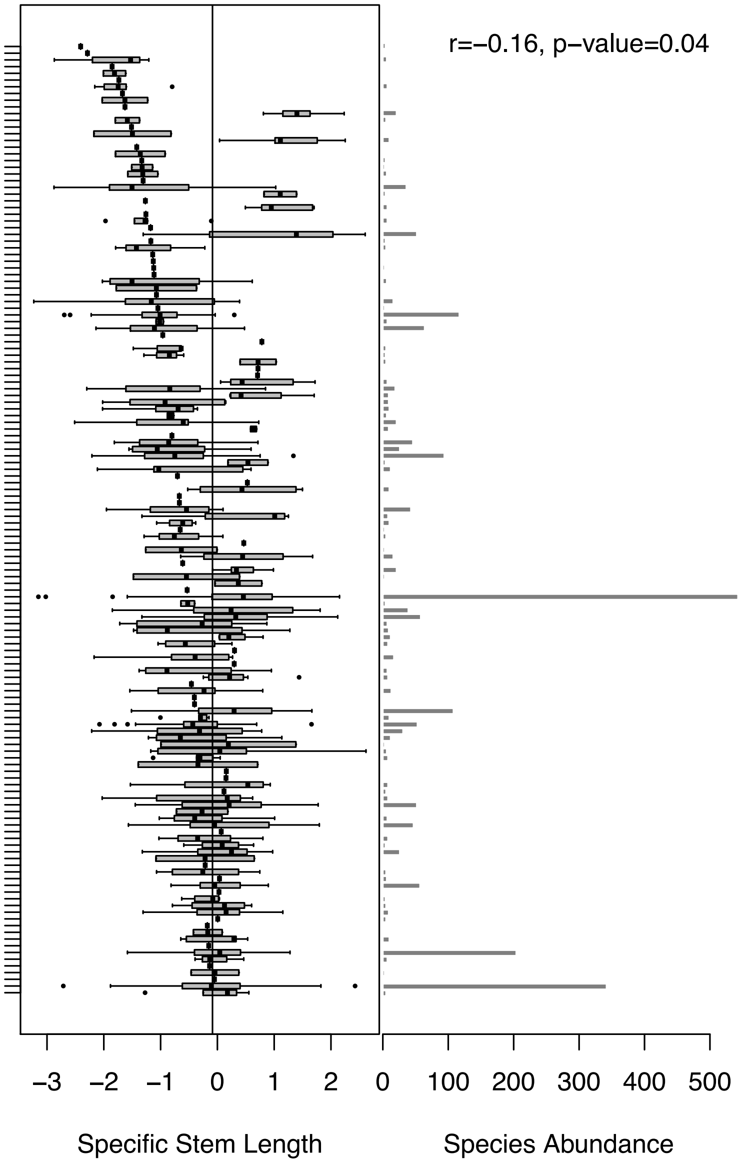

Figure A2.9. The relative position of species in the stem specific length (SSL) distribution in Xishuangbanna, China. Left Panel: the x-axis represent the difference between median SSL species trait and mean SSL for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of SSL by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

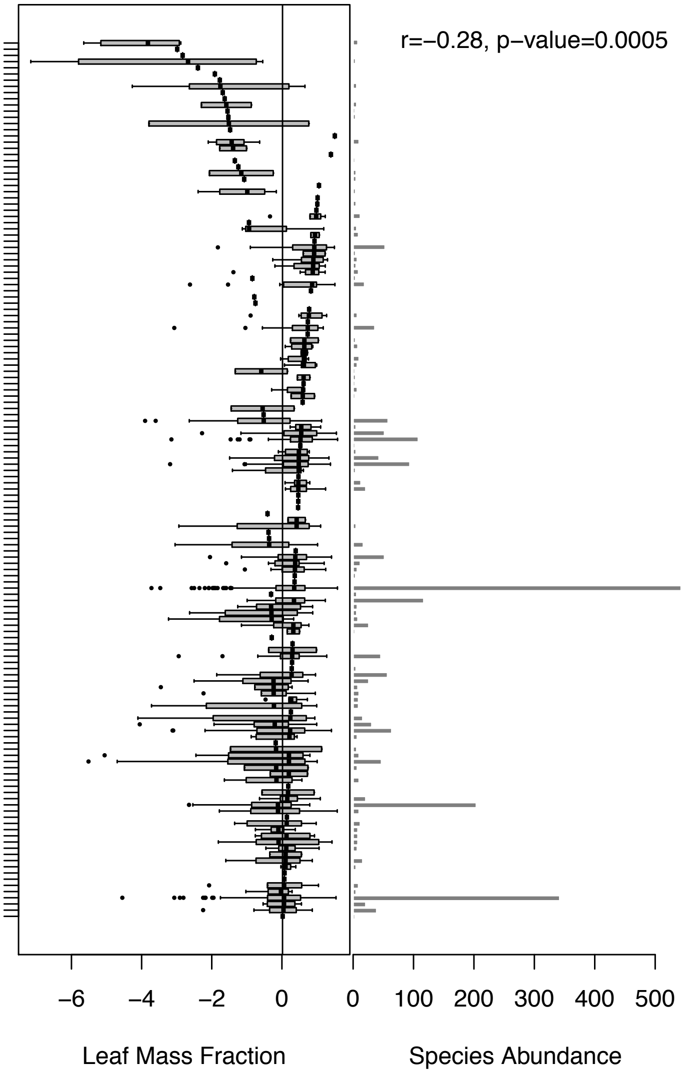

Figure A2.10. The relative position of species in the leaf mass fraction (LMF) distribution in Xishuangbanna, China. Left Panel: the x-axis represent the difference between median LMF species trait and mean LMF for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of LMF by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

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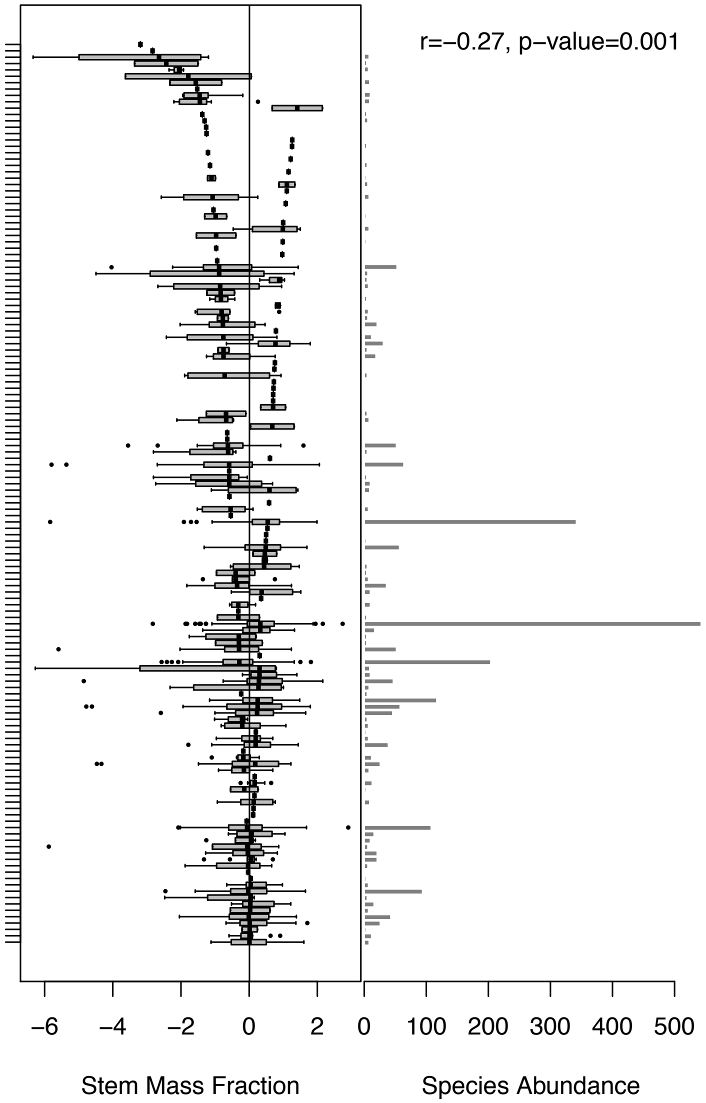

Figure A2.11. The relative position of species in the stem mass fraction (SMF) distribution in Xishuangbanna, China. Left Panel: the x-axis represent the difference between median SMF species trait and mean SMF for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of SMF by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species

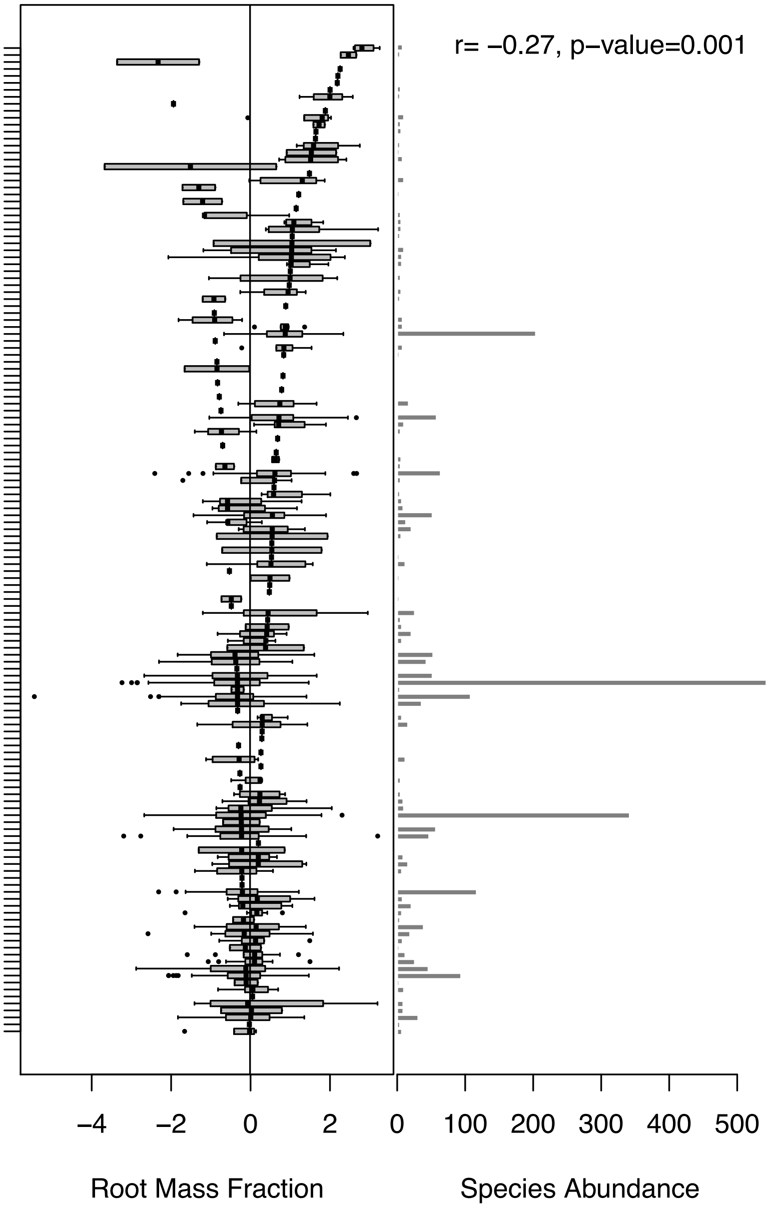

Figure A2.12. The relative position of species in the root mass fraction (RMF) distribution in Xishuangbanna, China. Left Panel: the x-axis represent the difference between median RMF species trait and mean RMF for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of RMF by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

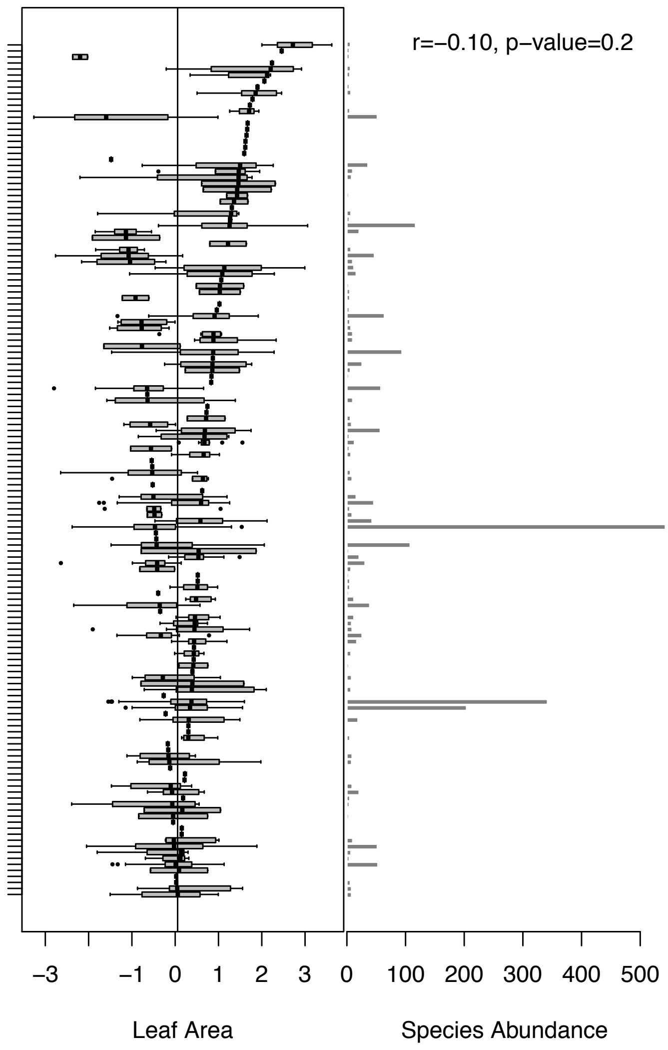

Figure A2.13. The relative position of species in the leaf area (LA) distribution in Xishuangbanna, China. Left Panel: the x-axis represent the difference between median LA species trait and mean LA for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of LA by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

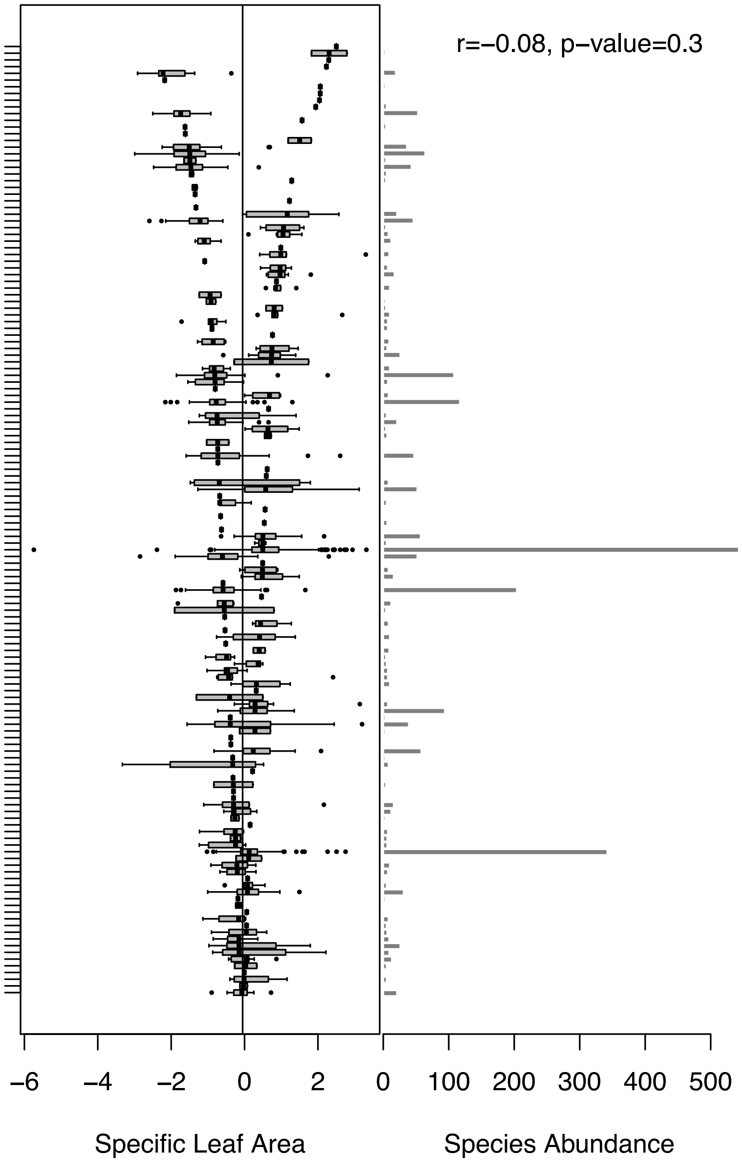

Figure A2.14. The relative position of species in the specific leaf area (SLA) distribution in Xishuangbanna, China. Left Panel: the x-axis represent the difference between median SLA species trait and mean SLA for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of SLA by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

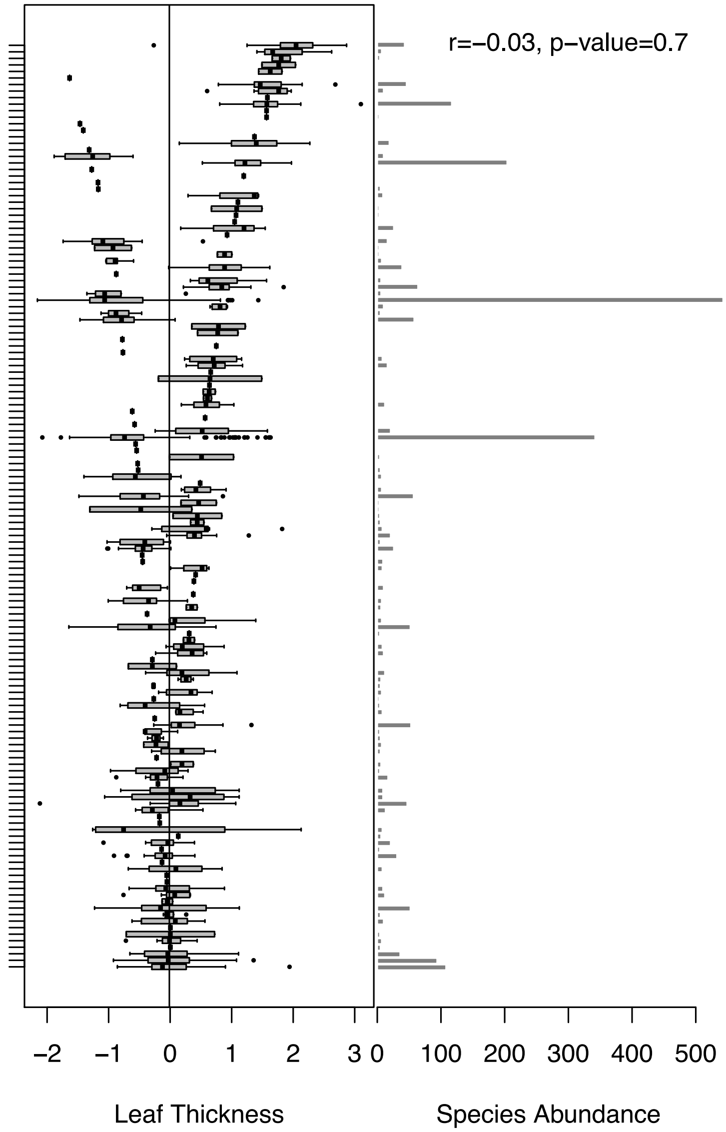

Figure A2.15. The relative position of species in the leaf thickness distribution in Xishuangbanna, China. Left Panel: the x-axis represent the difference between median thickness species trait and mean thickness for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of thickness by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

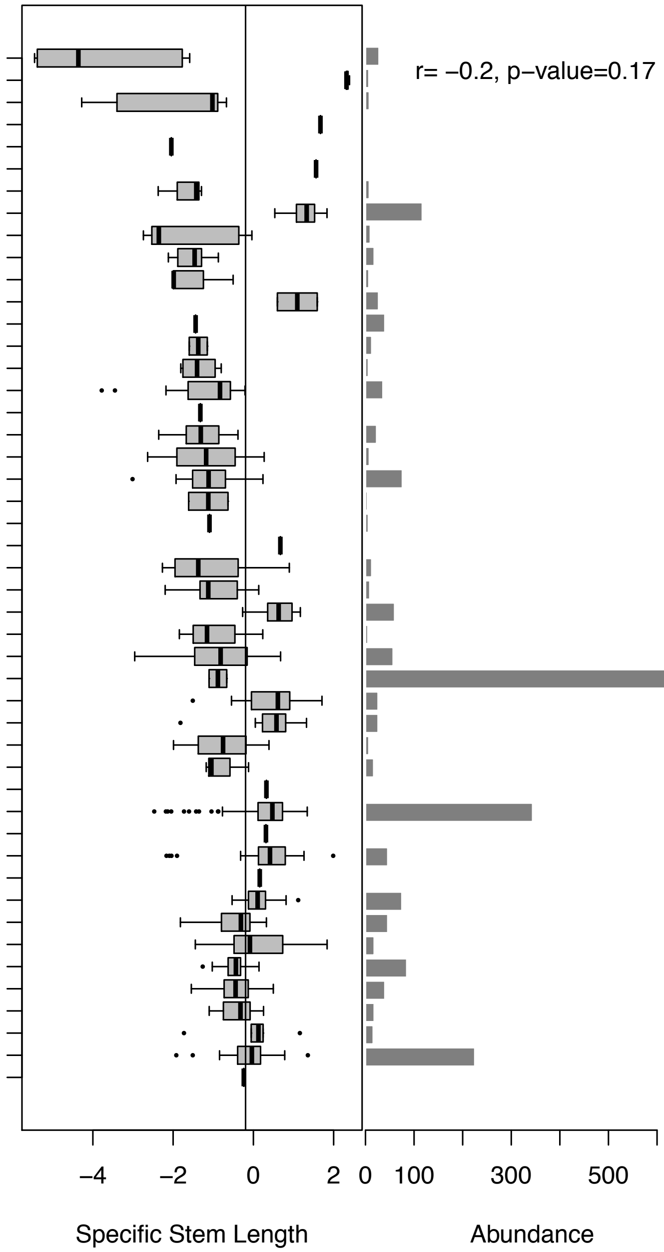

Figure A2.16. The relative position of species in the stem specific length (SSL) distribution in El Yunque, Puerto Rico. Left Panel: the x-axis represent the difference between median SSL species trait and mean SSL for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of SSL by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

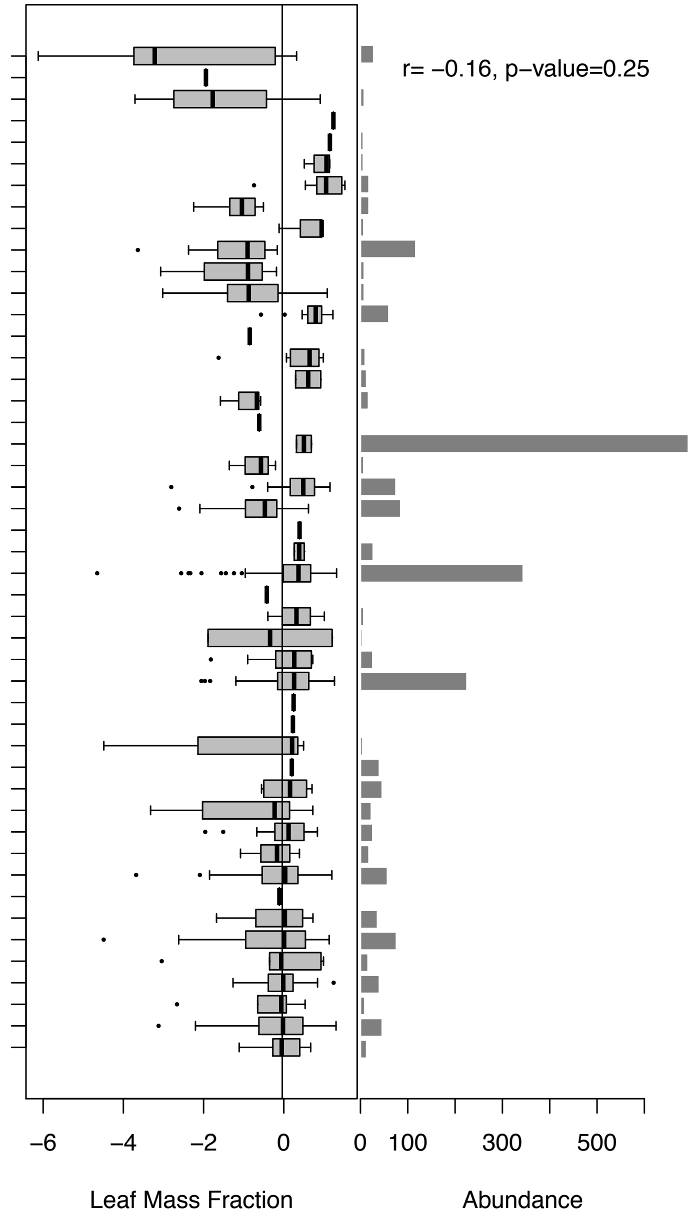

Figure A2.17. The relative position of species in the leaf mass fraction (LMF) distribution in El Yunque, Puerto Rico. Left Panel: the x-axis represent the difference between median LMF species trait and mean LMF for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of LMF by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

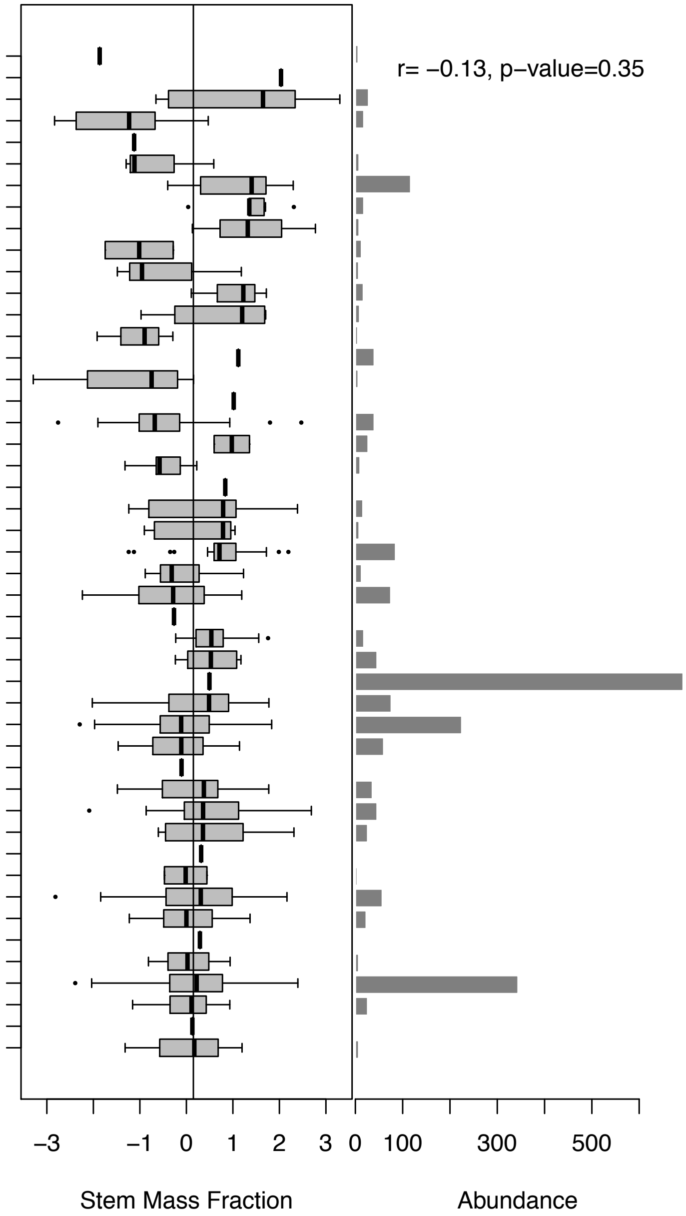

Figure A2.18. The relative position of species in the stem mass fraction (SMF) distribution in El Yunque, Puerto Rico. Left Panel: the x-axis represent the difference between median SMF species trait and mean SMF for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of SMF by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

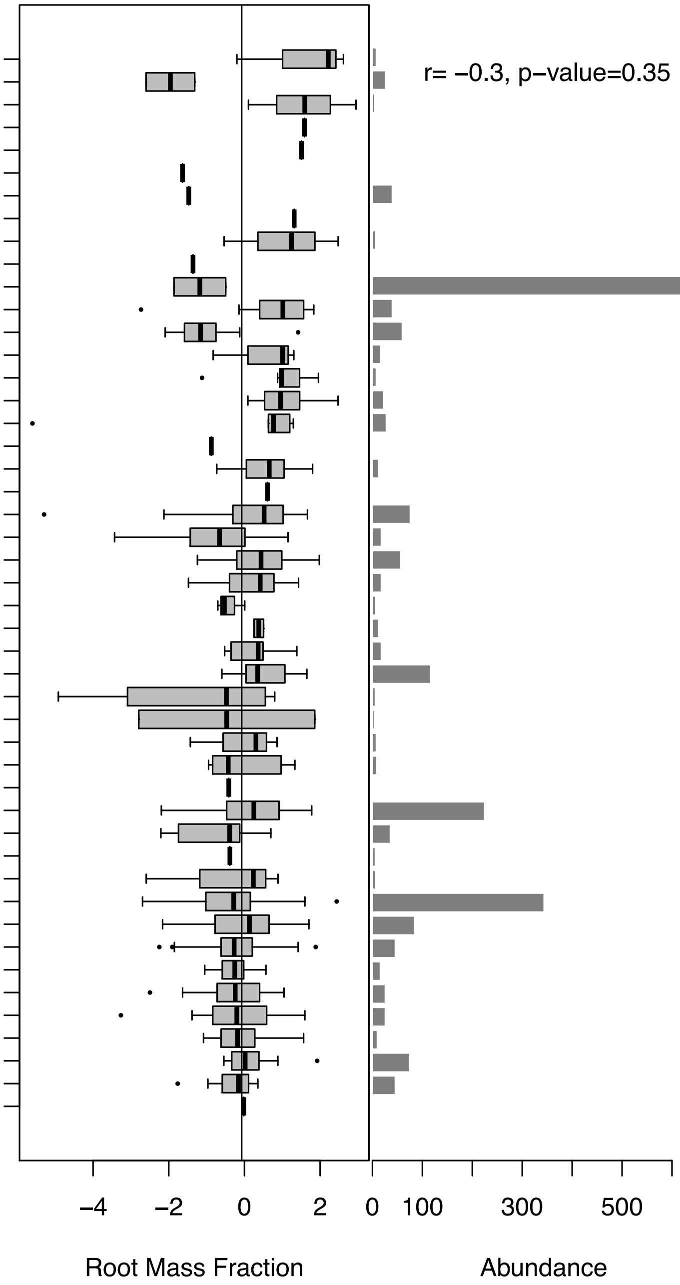

Figure A2.19. The relative position of species in the root mass fraction (RMF) distribution in El Yunque, Puerto Rico. Left Panel: the x-axis represent the difference between median RMF species trait and mean RMF for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of RMF by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

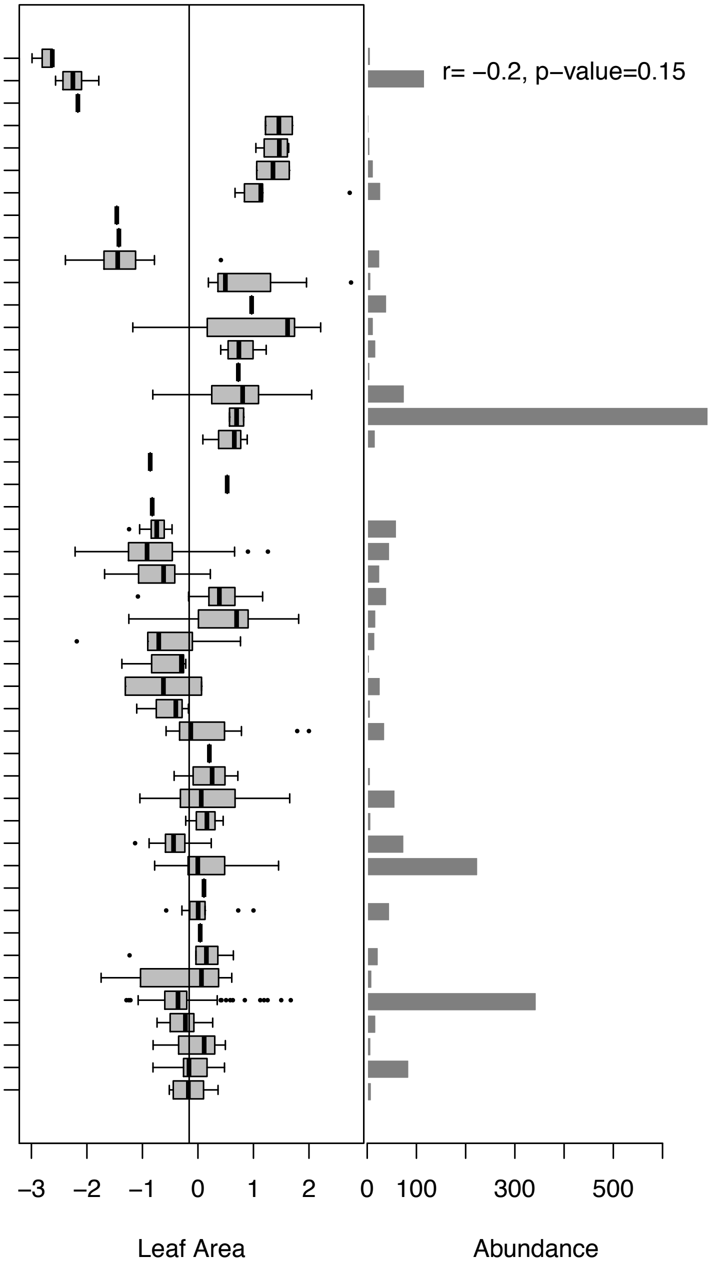

Figure A2.20. The relative position of species in the leaf area (LA) distribution in El Yunque, Puerto Rico. Left Panel: the x-axis represent the difference between median LA species trait and mean LA for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of LA by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

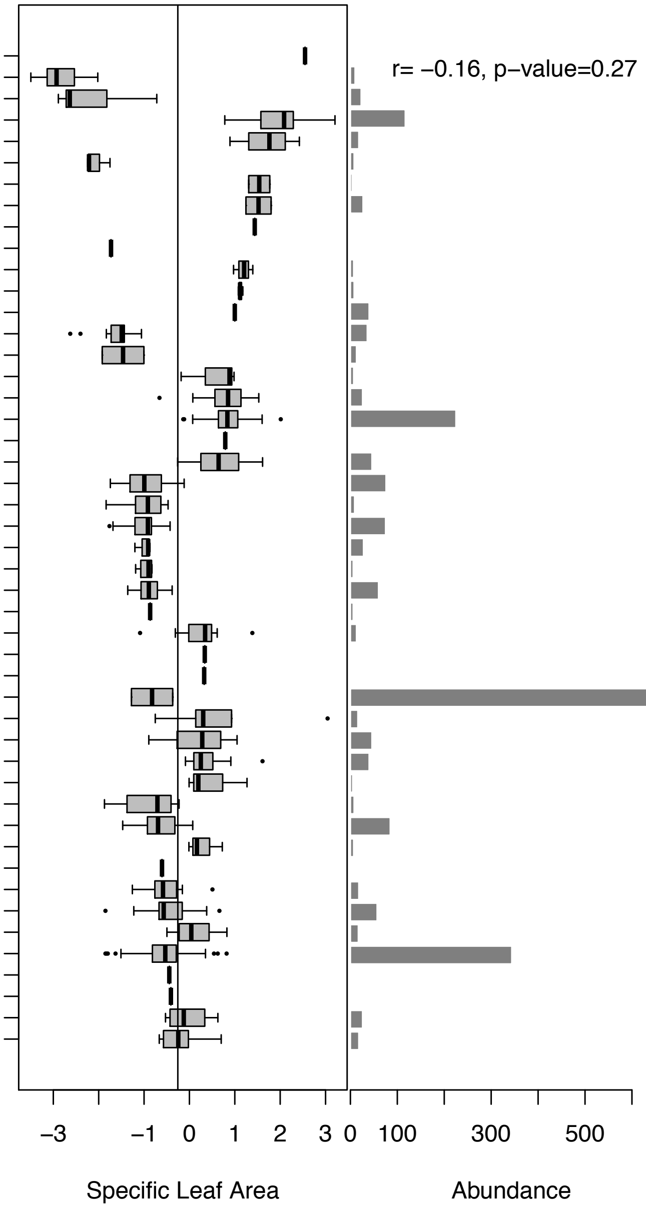

Figure A2.21. The relative position of species in the specific leaf area (SLA) distribution in El Yunque, Puerto Rico. Left Panel: the x-axis represent the difference between median SLA species trait and mean SLA for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of SLA by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

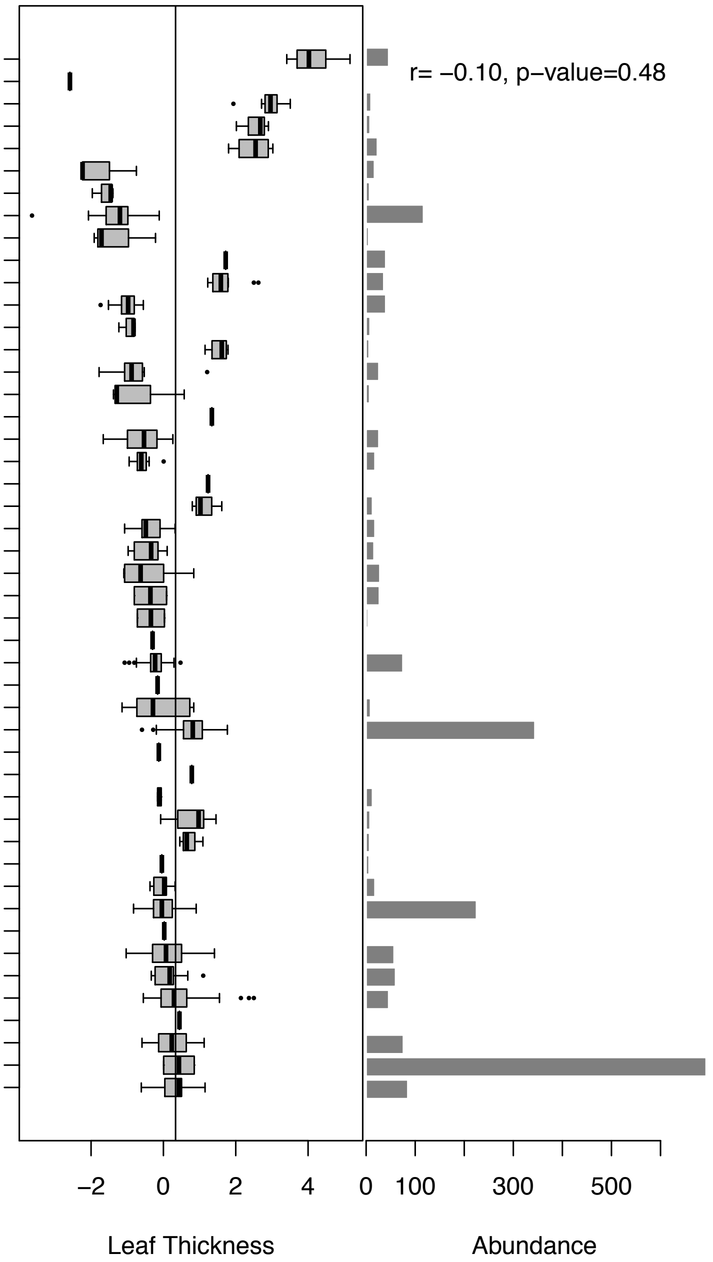

Figure A2.22. The relative position of species in the leaf thickness distribution in El Yunque, Puerto Rico. Left Panel: the x-axis represent the difference between median thickness species trait and mean thickness for the entire community. The y-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of thickness by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and median of the community against the log-transformed abundance of the species.

Appendix 3. Supplementary methods on trait data collection for 8 permanent plots.

Text: Supplementary methods on trait data collection.

Traits were collected from 5-10 individuals per species from the area within and around the forest dynamics plots when possible or all available individuals when not possible. In some instances, the trait data were not collected in, or in the area immediately around, the forest plot. Specifically, maximum height was compiled from literature. For the species in Lilly Dickey Woods, Indiana, traits were collected during 2010 from forests in Michigan and Wisconsin. Trait data for Wabikon Lake, Wisconsin were collected in 2010 in the plot; trait data for Changbaishan, China were collected in 2011 in the plot; trait data for Fushan, Tawian were collected in 2011 in the plot; trait data for Luquillo, Puerto Rico were collected between 2007 and 2008 in the plot; trait data for Guanacaste, Costa Rica, were collected between 2006 and 2007 in the plot; trait data for Gutianshan, China were collected between 2009 and 2010 in the plot; and trait data for Xishuangbanna, China species were collected between 2010 and 2011 in the plot. Table A3.1 shows all the ranges fro the different traits across all the plots.

Table A3.1. Trait ranges for all the plots.

Plot	Maximum Height	WSG/ WSR	%P /Chlorophyll content	%N	SLA	LA
Indiana, USA	3	0.3	0.1	1.3	30.0	0.5
	60	0.8	0.9	3.9	585.2	405.5
Wisconsin, USA	8	0.3	0.1	1.0	77.6	1.1
	150	0.7	0.4	2.9	585.2	530.3
Changbaishan, China	1.5	0.3	1.2	1.3	57.1	6.0
	32	0.7	2.9	3.6	585.0	796.1
Fushan, Taiwan	2.3	0.2	0.0	0.9	86.8	4.4
	28.6	0.8	0.3	4.1	400.2	1658.8
Luquillo, Puerto Rico	1.524	0.3	0.0	1.0	18.8	10.0
	30.48	1.0	0.3	5.1	1304.2	60383.3
Guanacaste, Costa Rica	3	0.2	0.0	1.3	33.5	1.4
	45	1.0	0.2	5.8	406.0	212.4
Gutianshan, China	0.8	0.3	0.0	0.9	59.6	0.5
	45	0.8	0.2	3.7	460.9	229.5
Xishuangbanna, China	2	11.22	24.98	NA	14.48	1.86
	60	1109.39	67.12	NA	394.34	2395.26

Note: The plot in Xishuangbanna, China did not contain wood specific gravity, %N and %P values, instead these axes of function were represented by leaf chlorophyll content and wood specific resistance (WSR). WSG represents wood specific gravity, SLA represents specific leaf area, LA represents leaf Area.

Appendix 4: Supplementary results on breaking points and spatial aggregation patterns

Table A4.1. Breakpoints and significance values associated to the structural change test for relationships between SES FRic values and rank species abundance.

Plot	Estimated breakpoint	F	P-value (<)	AIC(seg)	AIC(lm)
Indiana, USA	28.92	61.91	8.21E-11	31.34695	68.24729
Wisconsin, USA	9.809	3.74	0.03598	50.64894	47.86799
Wisconsin, USA	24.44	3.38	3.38E-06		
Changbaishan, China	25.76	60.29	1.86E-13	58.69107	116.7757
Fushan, Taiwan	58.96	900.01	2.20E-16	66.14535	200.8568
Fushan, Taiwan	60.1	162.14	2.20E-16		
Luquillo, Puerto Rico	11.25	13.04	7.68E-06	195.2497	269.1527
Luquillo, Puerto Rico	107.4	69.61	2.20E-16		
Guanacaste, Costa Rica	82.43	33.66	1.72E-12	198.3929	247.3509
Gutianshan, China	154.1	255.00	2.20E-16	211.5991	284.6906
Xishuangnanna, China	180.6	996.32	2.20E-16	326.2578	453.2756

Table A4.2. Mann-Kendall trend test for each plot and block bootstrap results.

Plot	Kendall's tau statistic (τ)	Probability	Abundance rank range
Indiana, USA	-0.846	<0.001	(2-28)
	0.733	0.975	(26-32)
Wisconsin, USA	-0.415	0.061	(2-10)
	0.667	0.912	(11-24)
	-0.867	0.009	(24-34)
Changbaishan, China	-0.732	<0.001	(2-26)
	0.620	0.999	(27-52)
Fushan, Taiwan	-0.599	<0.001	(2-59)
	0.145	0.858	(60-110)
Luquillo, Puerto Rico	-0.867	0.028	(2-11)
	-0.653	<0.001	(12-107)
	-1.000	<0.001	(108-125)
Guanacaste, Costa Rica	-0.927	0.015	(2-82)
	0.227	0.934	(83-136)
Gutianshan, China	-0.892	<0.001	(2-154)
	0.333	0.494	(155-159)
Xishuangbanna, China	-0.602	<0.001	(2-180)
	0.156	0.995	(180-469)

Note: Positive Mann-Kendal's statistic value indicates that the data tend to increase along the species abundance rank; a negative trend indicates the opposite. The probability column represents the probability that an observed *tau* value is greater that in null *tau* values. The rank abundance range column represents the species rank range that was used.

Table A4.3. Breakpoints and significance values associated to the structural change test for correlations between maximum trait values or minimum trait values and rank abundance.

Plot	Trait	Maximum Range				Lower range			
		Breakpoint	Sp. Ab	F	P-value	Breakpoint	Sp. Ab	F	P-value
Indiana, USA	LA	18.90	73	2.22	2E-04	28.99	5	1.79	7E-03
	SLA	5.31	1158	1.96	2E-03	28.31	5	1.55	3E-02
	N	**28.41**	**5**	**1.63**	**2E-02**	4.76	1974	2.13	5E-04
	P	**28.78**	**5**	**1.60**	**2E-02**	22.54	45	2.24	2E-04
	WD	25.03	28	1.63	2E-02	2.97	7912	1.14	3E-01
Wisconsin, USA	LA	4.25	3457	1.27	2E-01	4.66	3457	2.33	8E-05
	SLA	15.95	176	2.17	3E-04	4.95	3457	2.21	2E-04
	N	8.00	1751	2.25	2E-04	4.70	3457	2.07	8E-04
	P	6.01	2172	2.29	1E-04	4.69	3457	1.63	2E-02
	WD	23.99	32	1.88	3E-03	5.13	2517	2.24	2E-04
Changbaishan, China	LA	12.75	681	2.58	7E-06	7.33	1598	2.25	2E-04
	SLA	**46.06**	**2**	**1.94**	**2E-03**	7.62	1598	2.71	2E-06
	N	13.30	515	2.33	8E-05	7.72	1598	2.79	7E-07
	P	17.00	251	2.55	9E-06	6.41	2468	2.79	7E-07
	WD	41.23	17	1.55	3E-02	38.32	18	1.49	5E-02
Fushan, Taiwan	LA	12.98	2343	2.36	6E-05	39.34	355	3.40	4E-10
	SLA	38.56	371	3.33	1E-09	9.57	2984	3.43	3E-10
	N	63.67	64	2.73	1E-06	60.00	86	3.17	7E-09
	P	33.20	489	3.36	6E-10	77.02	17	2.24	2E-04
	WD	14.19	2256	3.73	3E-12	**79.93**	**13**	**2.22**	**2E-04**
Luquillo, Puerto Rico	**LA**	**96.50**	**6**	**2.75**	**1E-06**	2.03	3972	3.99	6E-14
	SLA	**104.74**	**4**	**2.01**	**1E-03**	88.11	9	3.04	4E-08
	N	39.69	164	3.91	2E-13	59.09	69	3.44	2E-10
	P	7.96	1802	2.83	5E-07	38.42	185	3.98	7E-14
	WD	3.86	3292	2.15	4E-04	8.00	1517	4.37	1E-15
Guanacaste, Costa Rica	LA	72.83	30	4.13	6E-15	25.41	232	4.10	9E-15
	SLA	5.00	624	4.63	4E-16	21.97	311	3.20	5E-09
	N	23.48	243	4.30	4E-16	35.37	148	3.46	2E-10
	P	46.57	79	2.89	2E-07	30.81	191	2.67	3E-06
	WD	39.49	101	4.10	1E-14	3.64	921	2.71	2E-06
Gutianshan, China	LA	67.01	140	4.28	4E-16	28.49	1334	4.65	3E-07
	SLA	**146.00**	**2**	**2.66**	**3E-06**	98.39	28	3.29	2E-09
	N	71.91	93	3.97	8E-14	38.32	567	4.61	5E-07
	P	111.00	**16**	3.89	3E-13	118.32	13	2.73	1E-06
	WD	11.18	3508	4.06	2E-14	123.18	**9**	2.62	5E-06
Xishuangb	**LA**	**260.12**	**14**	**7.89**	**2E-16**	264.34	13	6.45	4E-16

anna, China	**SLA**	**235.36**	**20**	**8.10**	**3E-16**	295.02	8	7.39	2E-14
	Chlorophyll	123.32	104	7.73	2E-16	383.60	2	4.78	2E-16
	WSG	380.89	2	6.25	1E-15	**378.39**	**2**	**4.92**	**2E-16**

Note: The breakpoint column indicates the abundance rank value where the trait value changed in its trend (maximum or minimum). The Sp.Ab represents the abundance of the species at the breaking point. Bold values show the candidate pioneer traits.

* For Luquillo, Puerto Rico and Wisconsin, USA, we checked for pioneer traits associated to common species instead of rare species, according to our original hypothesis.

Table A4.4. The degree of spatial aggregation of species in all forest dynamic plot communities.

Plot	Omega	rho	statistic S	P-value
Indiana, USA	5	-0.90	4376	<0.001
	10	-0.99	4580	<0.001
	20	-0.99	4586	<0.001
	30	-0.99	4574	<0.001
	40	-1.00	4590	<0.001
	50	-0.99	4584	<0.001
Wisconsin, USA	5	-0.78	3606	<0.001
	10	-0.75	3550	<0.001
	20	-0.84	3728	<0.001
	30	-0.87	3786	<0.001
	40	-0.89	3826	<0.001
	50	-0.91	3862	<0.001
Changbaishan, China	5	-0.86	10139	<0.001
	10	-0.90	10349	<0.001
	20	-0.96	10709	<0.001
	30	-0.98	10794	<0.001
	40	-0.99	10864	<0.001
	50	-1.00	10899	<0.001
Fushan, Taiwan	5	-0.92	140575	<0.001
	10	-0.96	143041	<0.001
	20	-0.97	143957	<0.001
	30	-0.99	145340	<0.001
	40	-0.99	145818	<0.001
	50	-0.99	145911	<0.001
Luquillo, Puerto Rico	5	-0.80	131458	<0.001
	10	-0.79	131252	<0.001
	20	-0.90	139019	<0.001
	30	-0.97	143898	<0.001
	40	-0.99	145542	<0.001
	50	-0.99	145599	<0.001
Guanacaste, Costa Rica	5	-0.64	192632	<0.001
	10	-0.82	213463	<0.001
	20	-0.84	216340	<0.001
	30	-0.92	225283	<0.001
	40	-0.95	229140	<0.001
	50	-0.96	230807	<0.001
Gutianshan, China	5	-0.87	311219	<0.001
	10	-0.91	318239	<0.001
	20	-0.94	323775	<0.001

	30	-0.96	326615	<0.001
	40	-0.98	329504	<0.001
	50	-0.98	329980	<0.001
Xishuangbanna, China	5	-0.67	4086361	<0.001
	10	-0.72	4205348	<0.001
	20	-0.86	4562793	<0.001
	30	-0.91	4688648	<0.001
	40	-0.95	4773076	<0.001
	50	-0.97	4826073	<0.001

Note: The results correspond to Spearman correlations between SES Ω and their forest-wide abundance. All species with abundances lower than one individual by hectare were removed from the analysis.

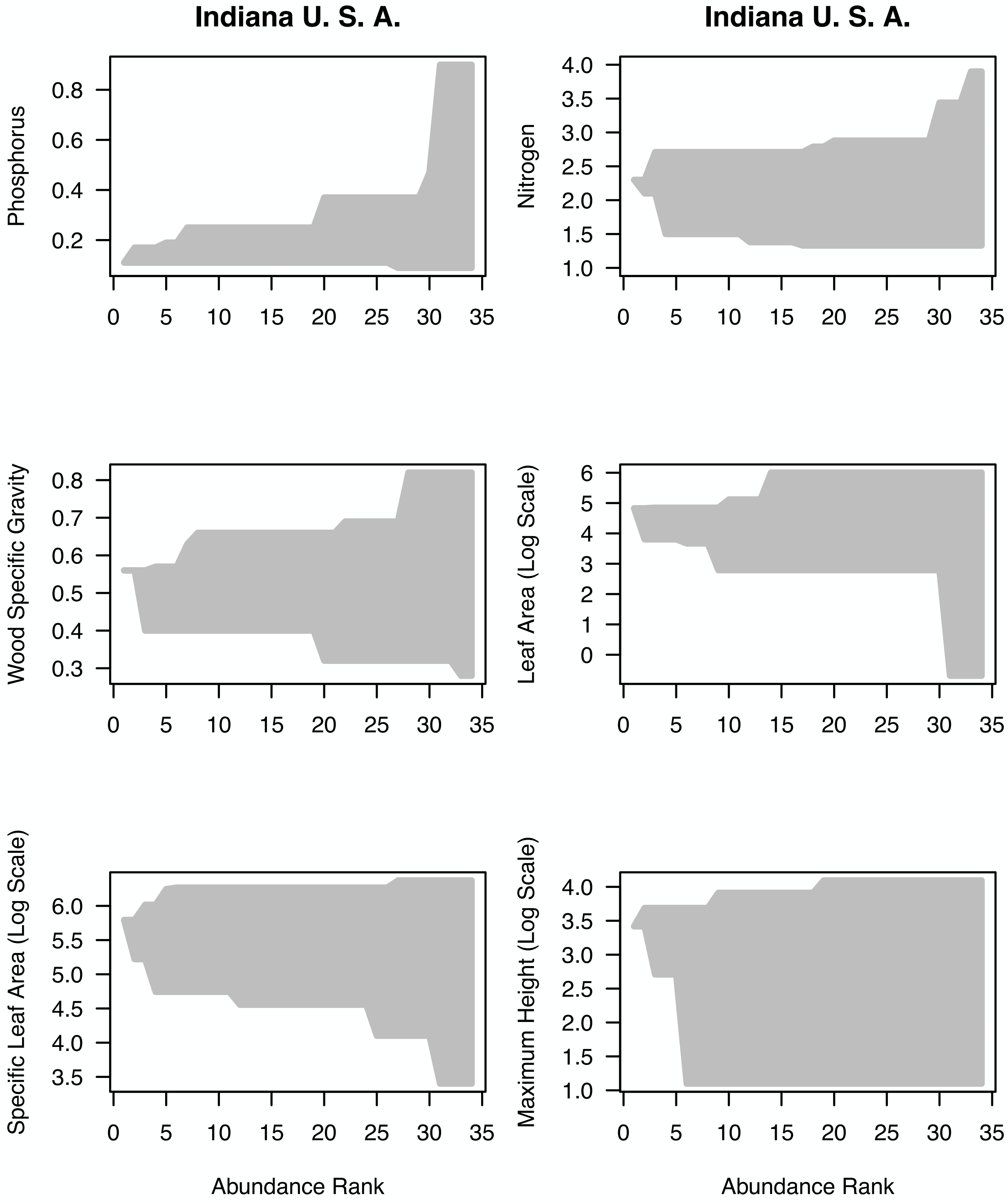

Figure A4.1. Change in trait ranges for the Indiana, U. S. A. forest plot as a function of rank abundance where increasingly rare species are added from left to right.

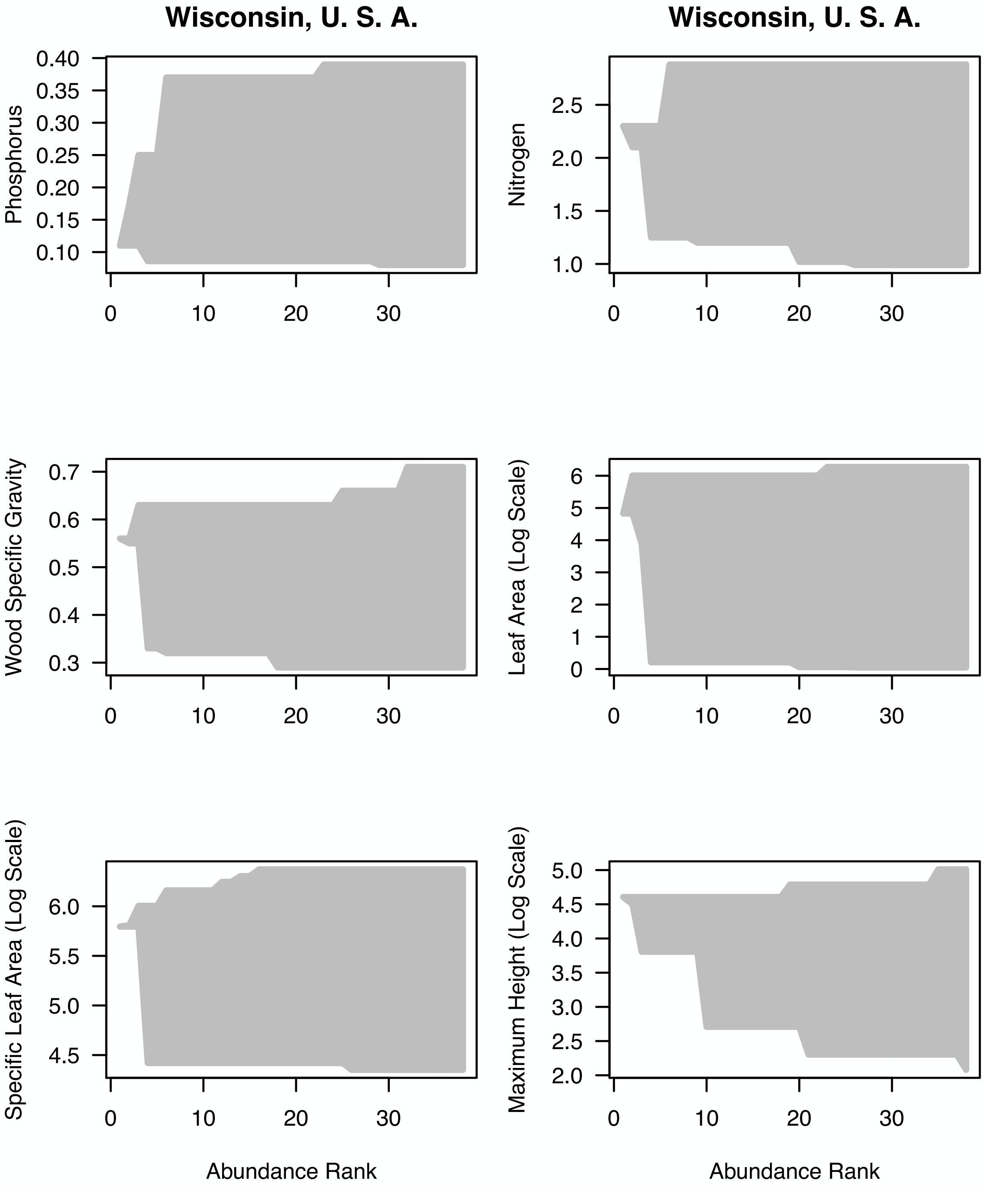

Figure A4.2. Change in trait ranges for the Wisconsin, U. S. A. forest plot as a function of rank abundance where increasingly rare species are added from left to right.

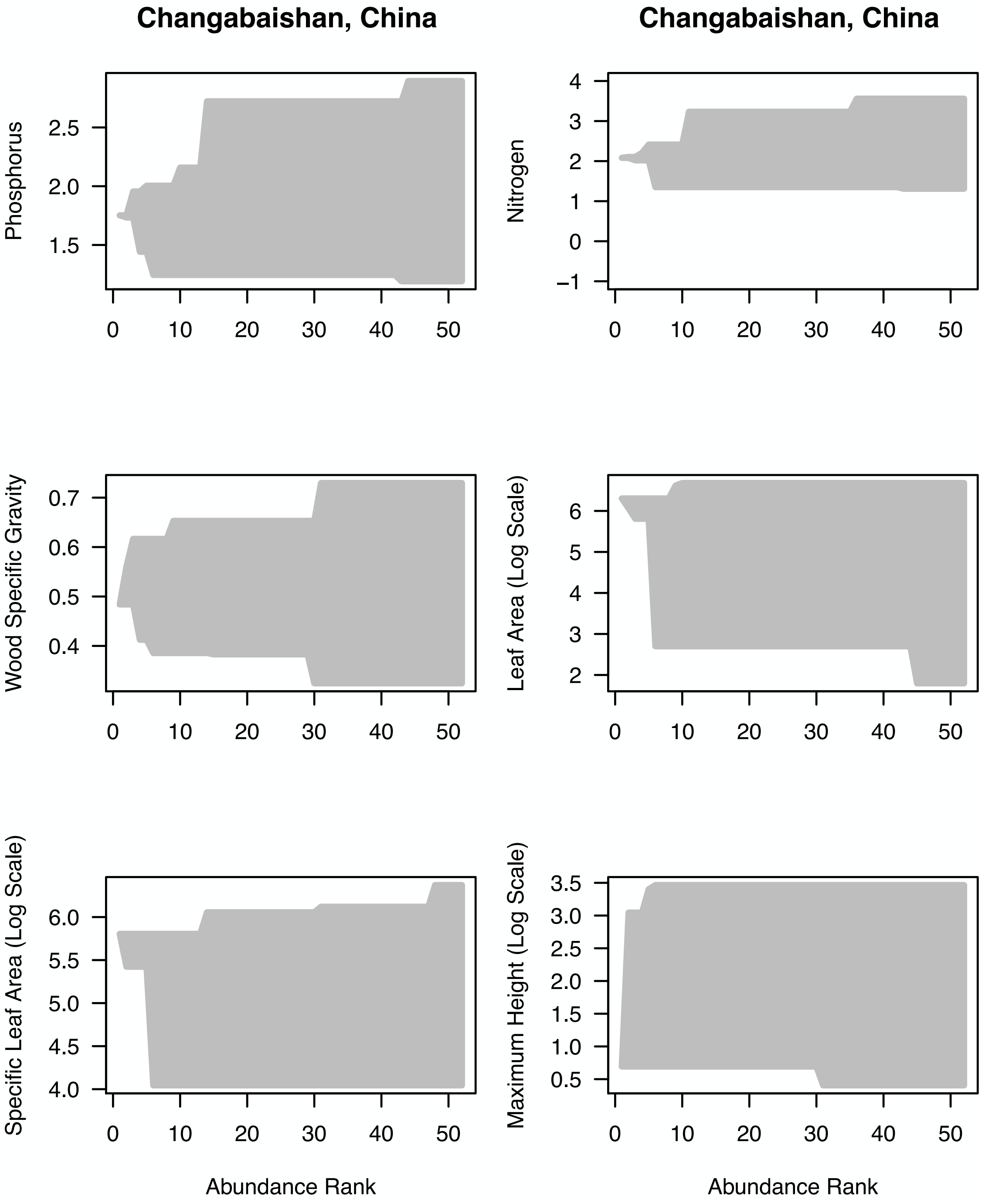

Figure A4.3. Change in trait ranges for the Changbaishan, China forest plot as a function of rank abundance where increasingly rare species are added from left to right.

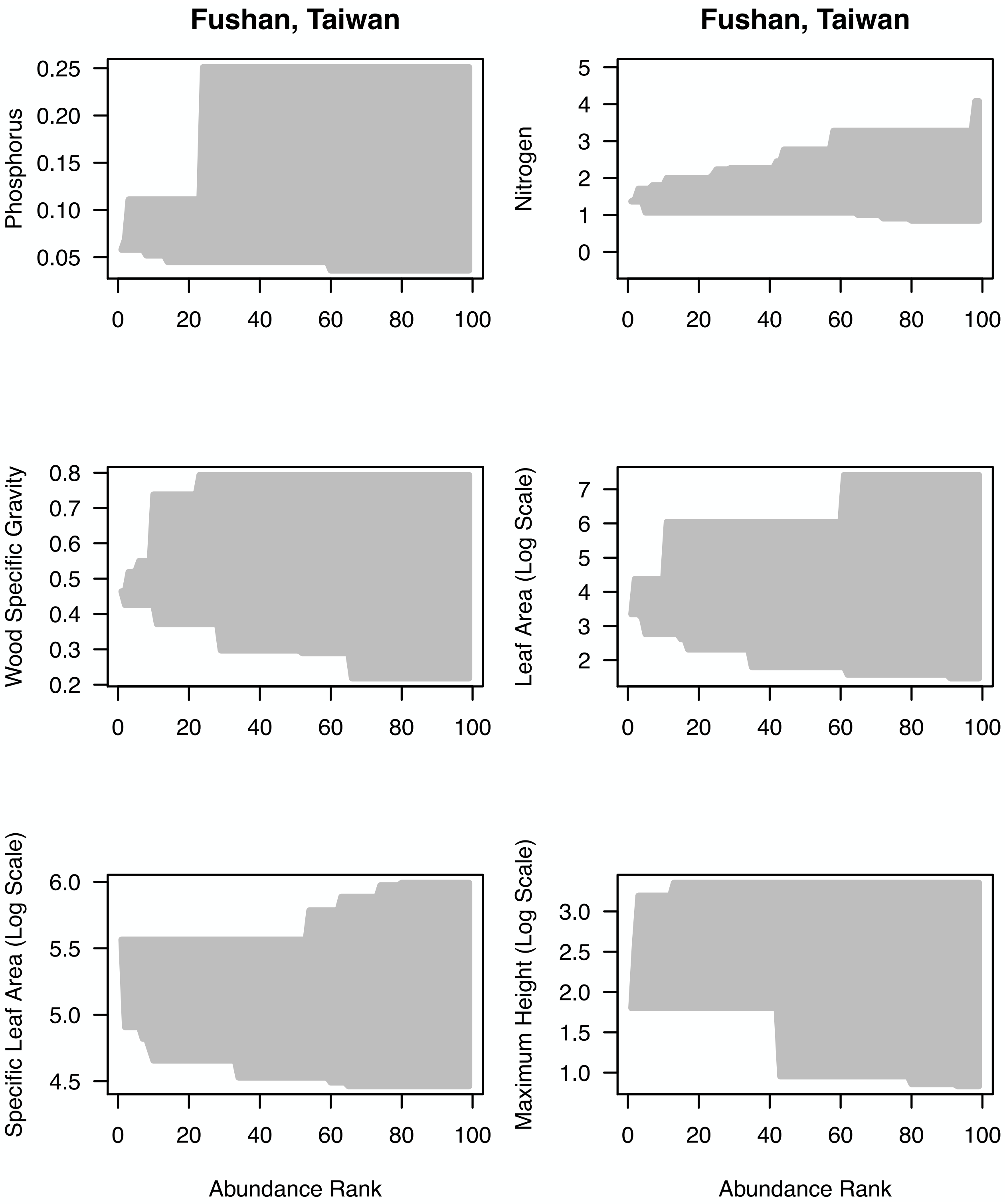

Figure A4.4. Change in trait ranges for the Fushan, Taiwan forest plot as a function of rank abundance where increasingly rare species are added from left to right.

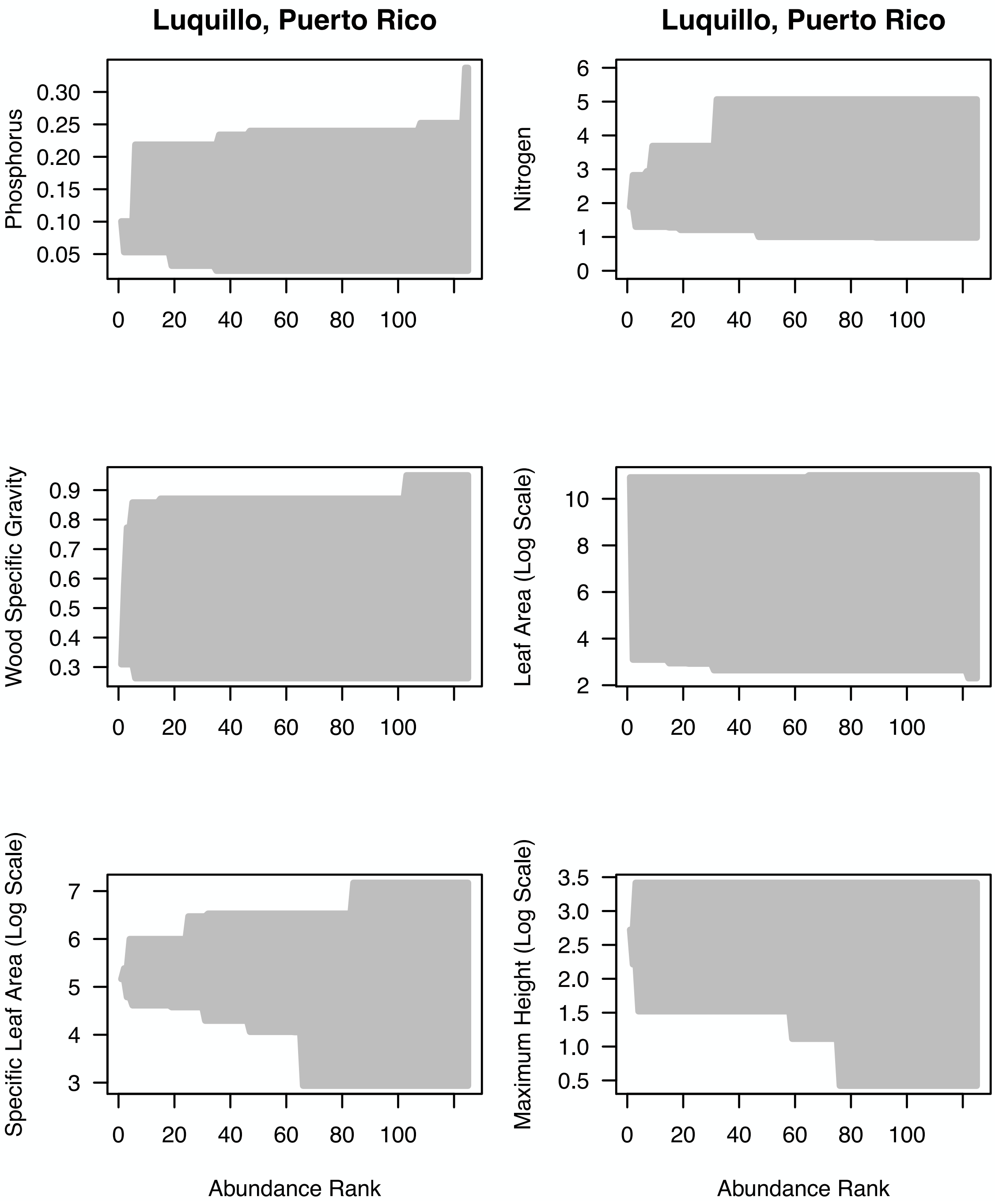

Figure A4.5. Change in trait ranges for the Luquillo, Puerto Rico forest plot as a function of rank abundance where increasingly rare species are added from left to right.

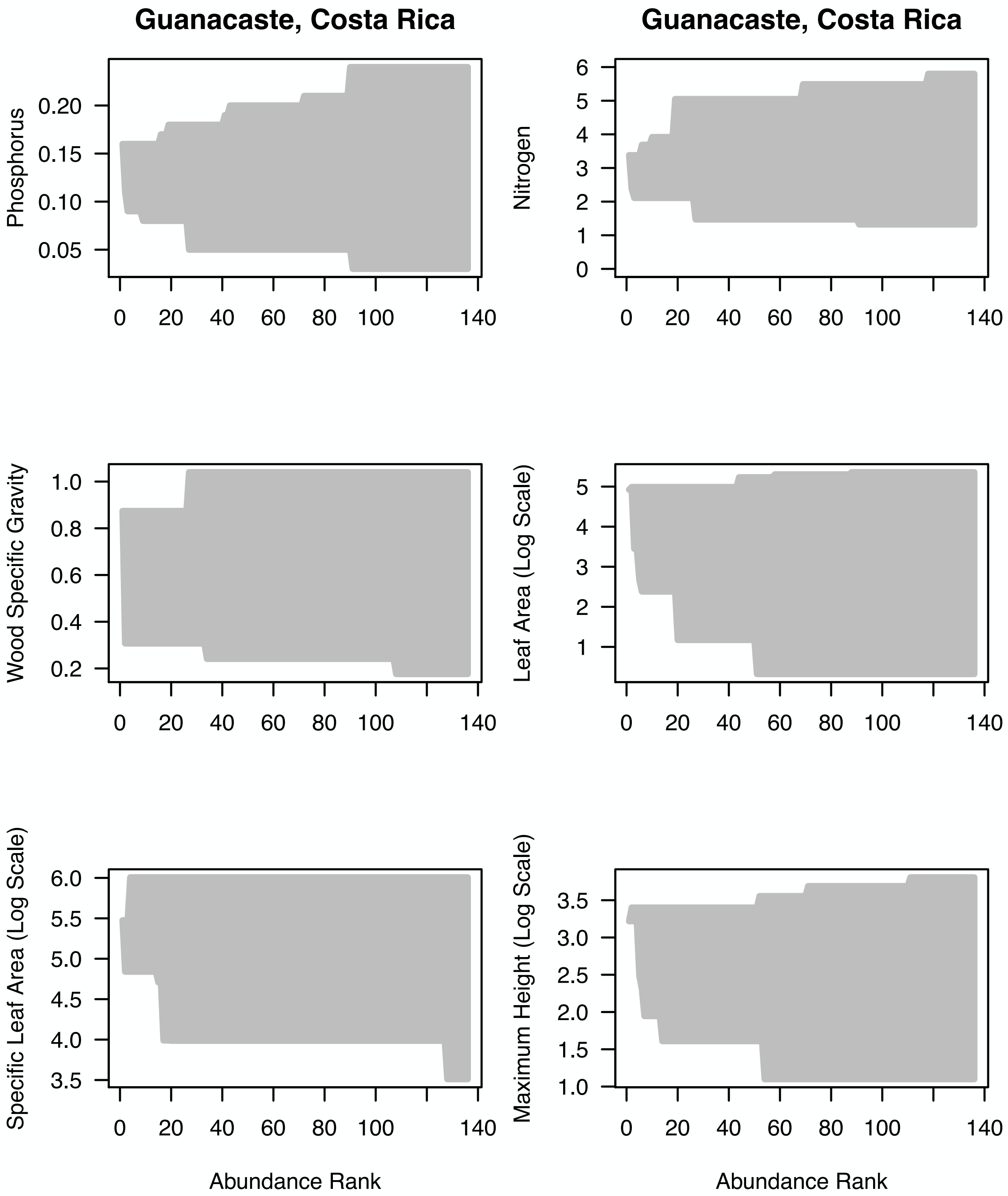

Figure A4.6. Change in trait ranges for the Guanacaste, Costa Rica forest plot as a function of rank abundance where increasingly rare species are added from left to right.

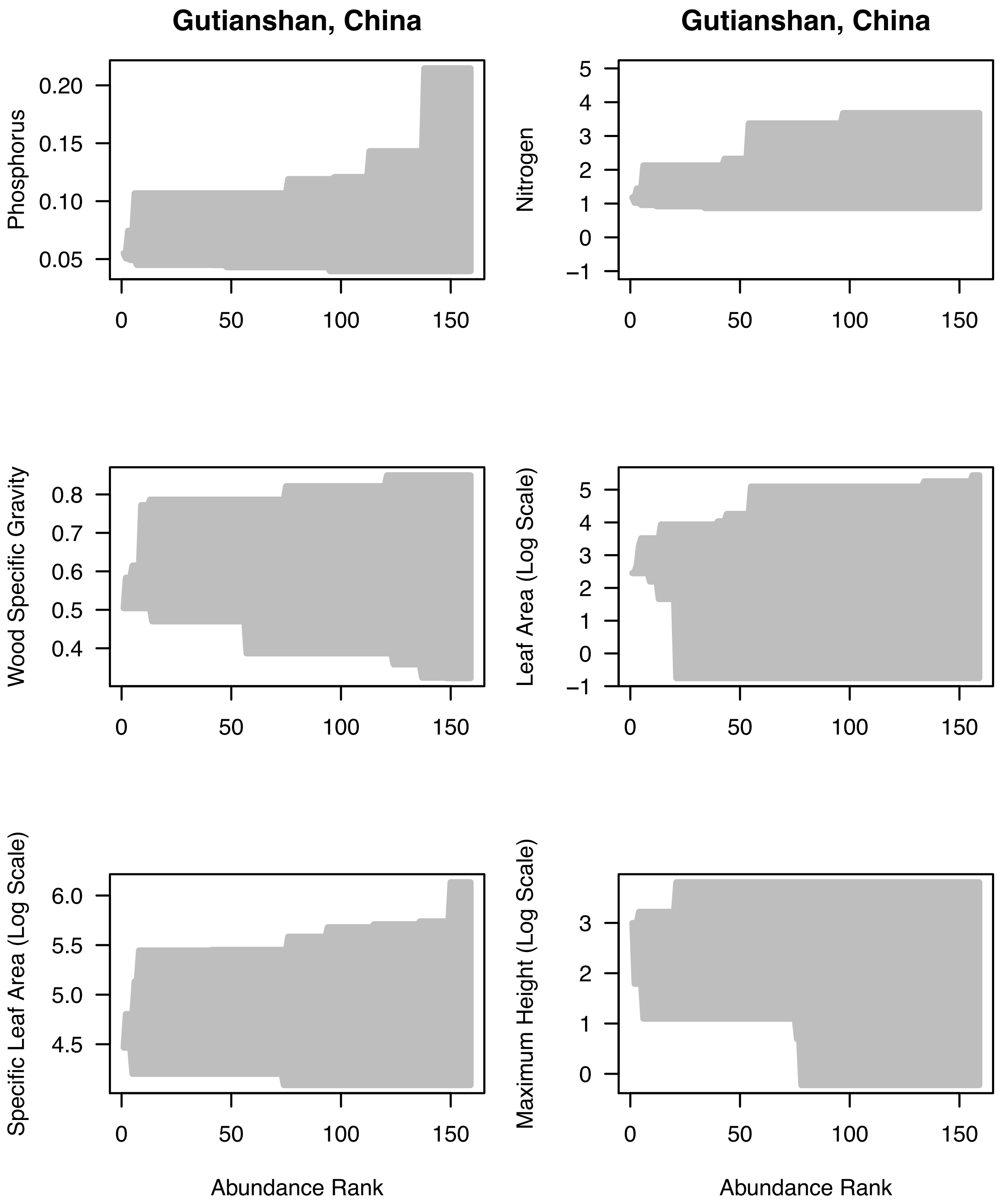

Figure A4.7. Change in trait ranges for the Gutianshan, China forest plot as a function of rank abundance where increasingly rare species are added from left to right.

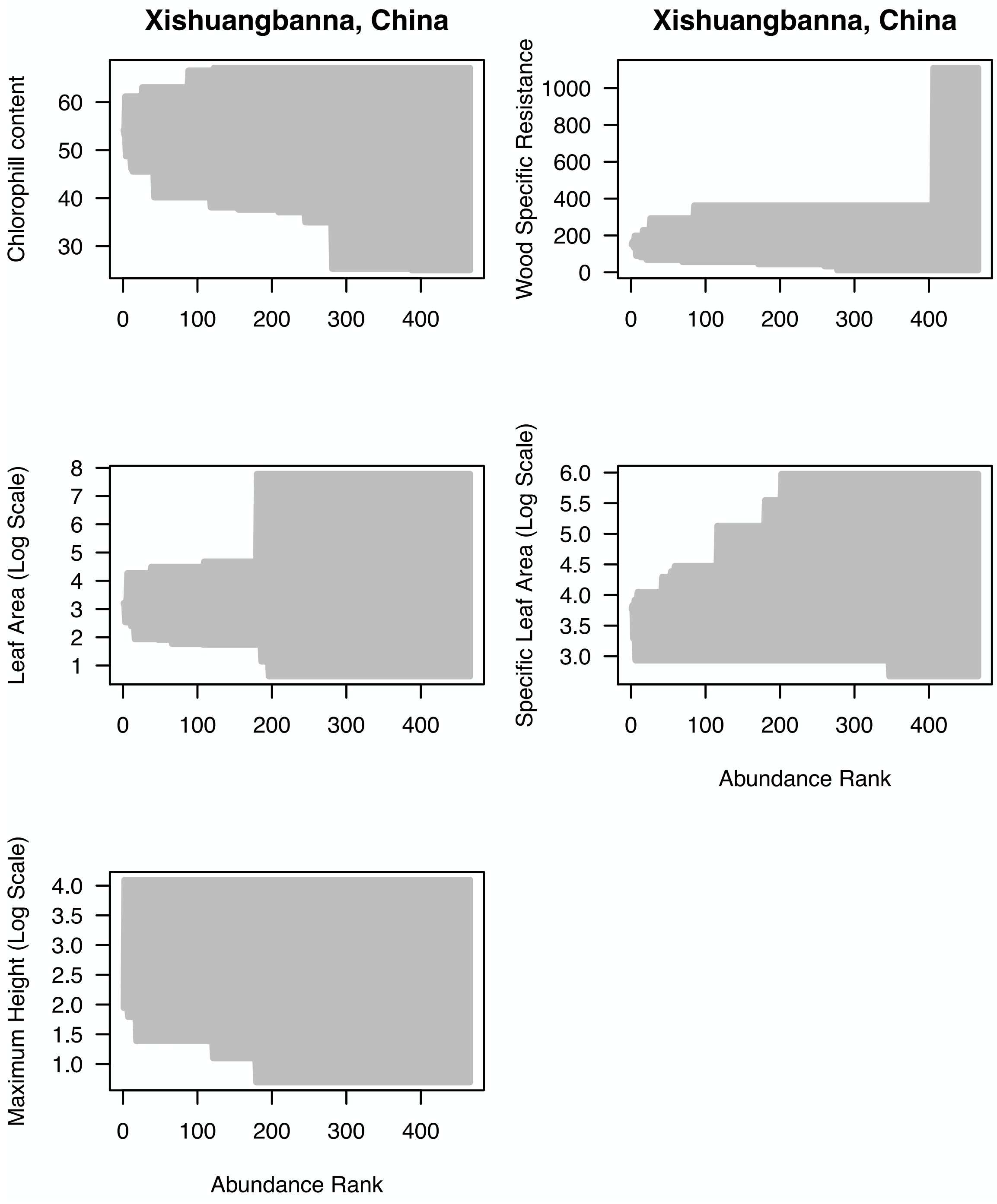

Figure A4.8. Change in trait ranges for the Xishuangbanna, China forest plot as a function of rank abundance where increasingly rare species are added from left to right.

Appendix 5: Supplementary methods on quantifying whether rare species prefer elevationally rare habitats.

Text: methods

We used fine-scale elevation data in order to evaluate whether the relative abundances of species in a plot were related to the relative abundances of different elevations within each plot. Ideally, additional information regarding light habitats and soil nutrients would be incorporated into our analyses, but at present this information is not available. Further, elevation tends to be a correlate of soil nutrients and water gradients in forest dynamics plots suggesting that it is a reasonable proxy of soil habitats (John et al. 2007).

To accomplish our analyses we utilized the known elevation of each 20 x 20 m subplot in each forest plot. Thus, we obtained a distribution of elevations for each plot. This distribution was then binned every 1, 5 and 10 m. The number of 20 x 20 m subplots per bin represented the relative abundance of the bin. Because bin size decisions may influence the results we utilized three size intervals to quantify sensitivity to our binning decisions. Next, we calculated the elevation of each individual of each species in a plot and estimated the median value. This median value was used to estimate the preferred elevation for the species. The median values were translated into elevation bin numbers. Species and elevation bins were then sorted by their respective relative abundances and plotted against each other with the rarest species and bin nearest the origin of the *xy*-plot. A spearman correlation was calculated with the expectation that if rare species are rare because they specialize on rare habitats, then there should be a positive rank correlation.

Text: Results

The results showed in general no significant correlation between the abundance and the elevation and only in few cases very weak positive correlation and this was consistent across bin sizes (Table A5.1, Table A5.2, Figures A5.1-A5.4). Thus, rare species generally do not appear to be associated with rare topographic habitats in the forests we investigated.

Table A5.1. Ranges of elevation (in meters) for each plot.

Plot	**Min elevation (m)**	**Max elevation (m)**	**Difference**
Lilly Dickey Woods, Indiana, U.S.A.	230.03	302.8	72.77
Wabikon Lake, Wisconsin, U.S.A	488	514	26
Changbaishan, China	791.8	809.5	17.7
Fushan, Taiwan	400	1400	1000
Luquillo, Puerto Rico	335	371	36
Guanacaste, Costa Rica	140	779.9	639.9
Gutianshan, China	42.72	57.12	14.4
Xishuangbanna, China	724.4	842.4	118

Table A5.2. Correlation between species rank abundance and its preferred elevation.

	bin=1		**bin=5**		**bin=10**	
Plot	**Rho**	**P-value**	**Rho**	**P-value**	**Rho**	**P-value**
Indiana, USA	0.43	0.01	0.57	<0.001	0.55	<0.001
Wisconsin, USA	0.29	0.07	0.26	0.10	NA	NA
Changbaishan, China	0.28	0.06	0.28	0.05	NA	NA
Fushan, Taiwan	0.15	0.80	-0.1	0.28	-0.05	0.60
Luquillo, Puerto Rico	0.02	0.80	0.24	<0.001	0.28	<0.001
Guanacaste, Costa Rica	0.11	0.15	0.13	0.11	0.39	<0.001
Gutiashan, China	0.16	0.07	0.12	0.12	0.19	<0.001
Xishungbanna, China	0.1	0.02	0.08	0.06	0.1	0.03

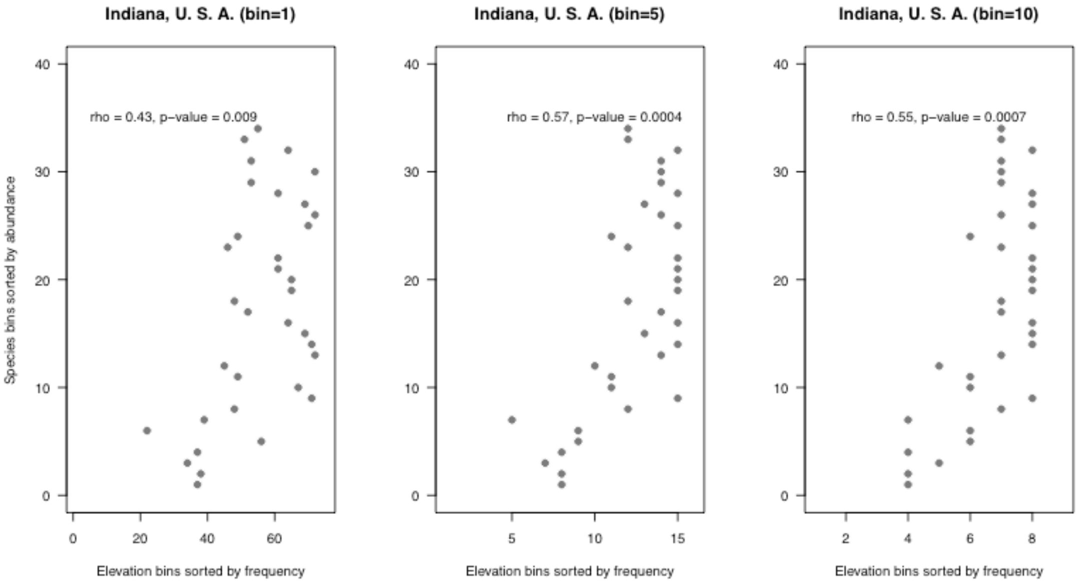

Figure A5.1. The relationship between species rank abundance (y-axis) ordered from rarest to most common and its preferred elevation ranked from the most rare elevation bin to the most common for species in the Indiana, U.S.A. forest plot. The panels represent the three elevation bin sizes used (1m, 5m, and 10m). Spearman rho correlations are provided.

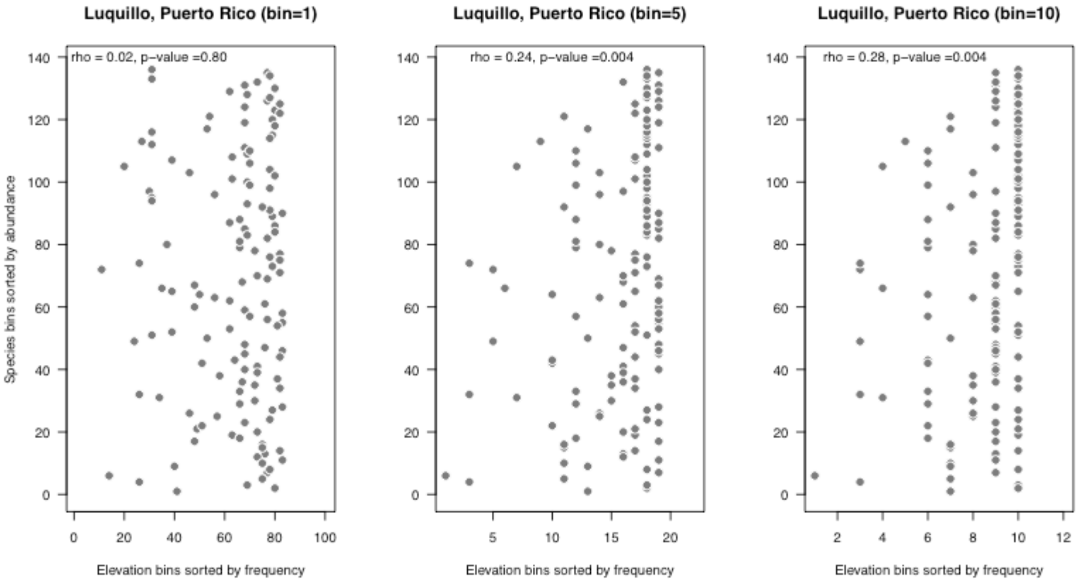

Figure A5.2. The relationship between species rank abundance (y-axis) ordered from rarest to most common and its preferred elevation ranked from the most rare elevation bin to the most common for species in the Luquillo, Puerto Rico forest plot. The panels represent the three elevation bin sizes used (1m, 5m, and 10m). Spearman rho correlations are provided.

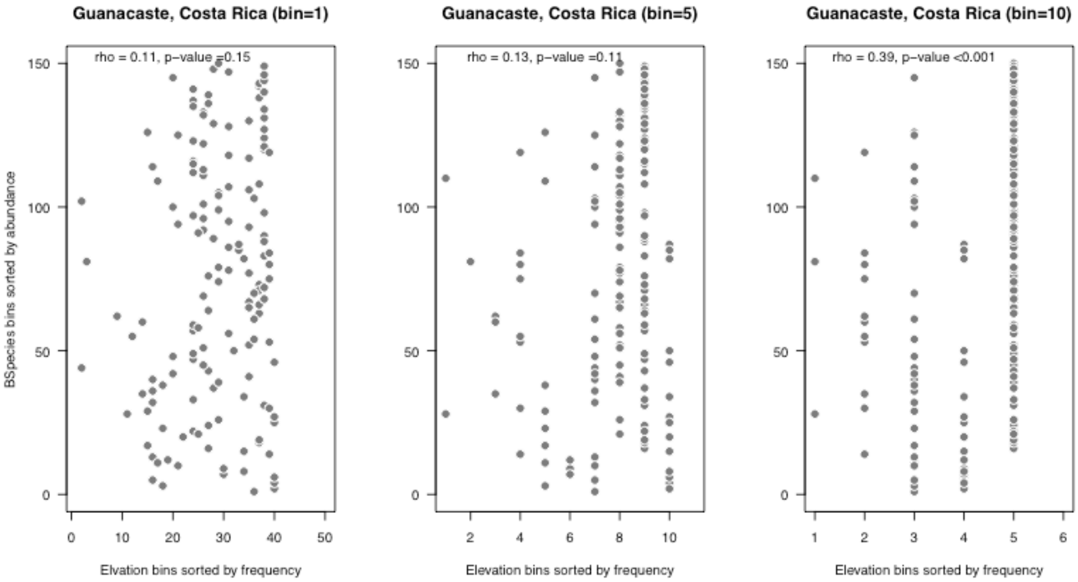

Figure A5.3. The relationship between species rank abundance (y-axis) ordered from rarest to most common and its preferred elevation ranked from the most rare elevation bin to the most common for species in the Guanacaste, Costa Rica forest plot. The panels represent the three elevation bin sizes used (1m, 5m, and 10m). Spearman rho correlations are provided.

Appendix 6: Supplementary results on seedling growth model

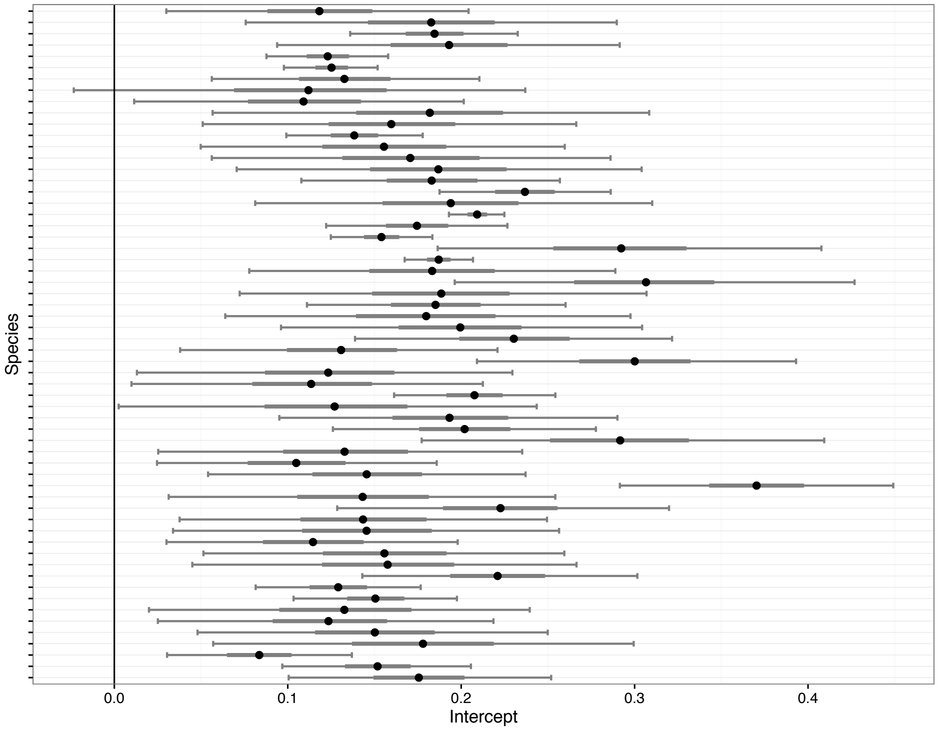

Figure A6.1. Intercept coefficients. Black dots represent the mean value and the segments represent the 50% (thick) and 95% (thin) credible intervals for each species.

Table A6.1. PCA loadings for 8 functional traits and cumulative proportion explained by each orthogonal axis for China.

Trait	PC1	PC2	PC3
Leaf area	-0.30	-0.45	0.15
Specific leaf area	0.32	0.40	0.04
Leaf thickness	-0.32	-0.16	-0.21
Specific stem length	0.42	0.31	-0.34
Leaf area ratio	0.52	-0.29	-0.09
Leaf mass fraction	0.36	-0.54	-0.12
Stem mass fraction	0.04	0.22	0.77
Root mass fraction	-0.36	0.31	-0.44
Cumulative proportion	0.33	0.6	0.76

Table A6.2. Range and mean value for all the predictor variables.

Variable	Minimum	Maximum	Mean
Initial density of conspecifics	0.0	21.0	4.9
Initial density of hetero-specifics	3.0	32.0	11.2
Change in conspecific neighbors	-5.0	8.0	-0.1
Change in hetero-specific neighbors	-6.0	9.0	-0.2
Traits dissimilarity among conspecifics	0.1	6.6	2.0
Traits dissimilarity among hetero-specifics	0.9	6.2	2.5
Initial height (cm)	6	50	22.88

Table A6.3. Coefficients for initial size effect and plot-level parameters.

Parameter	Mean	CI 2.5	CI 97.5
Change het.sp	-0.002	-0.006	0.003
Dens-0 het.sp	0.005	-0.004	0.01
Initial size	-0.05	-0.06	-0.05
Plot1	0.001	-0.064	0.068
Plot2	-0.039	-0.095	0.015
Plot3	-0.045	-0.090	-0.002
Plot4	0.019	-0.036	0.073
Plot5	-0.005	-0.063	0.053
Plot6	-0.028	-0.079	0.021
Plot7	-0.022	-0.077	0.032
Plot8	0.000	-0.065	0.064
Plot9	-0.002	-0.058	0.053
Plot10	-0.014	-0.080	0.051
Plot11	-0.010	-0.070	0.051
Plot12	-0.028	-0.085	0.027

Plot13	0.016	-0.032	0.064
Plot14	-0.025	-0.071	0.022
Plot15	0.013	-0.044	0.071
Plot16	-0.004	-0.070	0.062
Plot17	-0.016	-0.078	0.045
Plot18	-0.019	-0.066	0.026
Plot19	0.009	-0.045	0.065
Plot20	0.003	-0.055	0.061
Plot21	-0.007	-0.067	0.053
Plot22	-0.003	-0.055	0.047
Plot23	0.005	-0.061	0.071
Plot24	-0.012	-0.070	0.046
Plot25	-0.009	-0.067	0.048
Plot26	-0.001	-0.062	0.059
Plot27	0.012	-0.048	0.072
Plot28	-0.041	-0.097	0.015
Plot29	-0.024	-0.062	0.014
Plot30	-0.003	-0.057	0.051
Plot31	-0.005	-0.048	0.039
Plot32	0.007	-0.049	0.064
Plot33	-0.006	-0.056	0.043
Plot34	-0.011	-0.063	0.040
Plot35	-0.024	-0.071	0.020
Plot36	-0.019	-0.060	0.022
Plot37	0.005	-0.058	0.070
Plot38	-0.019	-0.068	0.029
Plot39	0.044	-0.018	0.108
Plot40	0.011	-0.028	0.052
Plot41	-0.008	-0.059	0.043
Plot42	-0.001	-0.051	0.049
Plot43	-0.027	-0.075	0.022
Plot44	-0.027	-0.077	0.021
Plot45	0.010	-0.034	0.053
Plot46	0.003	-0.047	0.055
Plot47	0.009	-0.036	0.054
Plot48	0.000	-0.055	0.055
Plot49	-0.025	-0.076	0.026
Plot50	0.015	-0.023	0.054
Plot51	0.010	-0.040	0.060
Plot52	-0.013	-0.072	0.045
Plot53	-0.046	-0.104	0.009
Plot54	-0.032	-0.087	0.022
Plot55	-0.008	-0.051	0.035

Plot56	0.010	-0.039	0.059
Plot57	0.017	-0.039	0.073
Plot58	0.018	-0.034	0.071
Plot59	0.004	-0.050	0.056
Plot60	0.019	-0.028	0.065
Plot61	0.038	-0.014	0.089
Plot62	-0.043	-0.091	0.006
Plot63	-0.008	-0.067	0.049
Plot64	-0.026	-0.073	0.021
Plot65	-0.004	-0.056	0.048
Plot66	-0.003	-0.051	0.044
Plot67	-0.021	-0.062	0.019
Plot68	-0.012	-0.067	0.043
Plot69	0.050	0.014	0.087
Plot70	-0.006	-0.068	0.055
Plot71	0.052	0.011	0.093
Plot72	0.003	-0.041	0.047
Plot73	0.000	-0.046	0.047
Plot74	0.065	0.023	0.107
Plot75	-0.015	-0.059	0.029
Plot76	0.038	-0.007	0.083
Plot77	0.007	-0.055	0.069
Plot78	0.025	-0.036	0.086
Plot79	-0.005	-0.047	0.037
Plot80	-0.054	-0.095	-0.012
Plot81	-0.008	-0.043	0.027
Plot82	0.002	-0.040	0.044
Plot83	0.031	-0.013	0.076
Plot84	0.018	-0.035	0.071
Plot85	0.036	-0.002	0.073
Plot86	-0.022	-0.087	0.042
Plot87	-0.016	-0.069	0.037
Plot88	-0.002	-0.049	0.045
Plot89	-0.008	-0.055	0.038
Plot90	0.000	-0.045	0.044
Plot91	-0.038	-0.080	0.002
Plot92	0.001	-0.053	0.054
Plot93	-0.010	-0.055	0.034
Plot94	0.000	-0.059	0.058
Plot95	-0.010	-0.062	0.042
Plot96	0.019	-0.016	0.055
Plot97	0.023	-0.031	0.080
Plot98	-0.014	-0.073	0.046

Plot99	-0.007	-0.053	0.039
Plot100	0.010	-0.045	0.064
Plot101	0.013	-0.040	0.067
Plot102	0.027	-0.017	0.070
Plot103	-0.014	-0.060	0.034
Plot104	0.000	-0.049	0.047
Plot105	-0.002	-0.057	0.051
Plot106	0.019	-0.040	0.079
Plot107	0.043	0.005	0.080
Plot108	0.034	-0.015	0.084
Plot109	-0.026	-0.086	0.031
Plot110	0.005	-0.047	0.058
Plot111	-0.020	-0.066	0.027
Plot112	0.033	-0.019	0.086
Plot113	0.026	-0.025	0.079
Plot114	-0.006	-0.059	0.045
Plot115	0.002	-0.059	0.064
Plot116	-0.006	-0.062	0.050
Plot117	-0.009	-0.061	0.042
Plot118	-0.011	-0.062	0.039
Plot119	0.009	-0.039	0.059
Plot120	-0.012	-0.065	0.041
Plot121	-0.010	-0.075	0.054
Plot122	0.008	-0.042	0.060
Plot123	-0.005	-0.073	0.063
Plot124	0.004	-0.059	0.068
Plot125	0.046	-0.006	0.099
Plot126	0.036	-0.010	0.083
Plot127	0.011	-0.030	0.054
Plot128	-0.003	-0.062	0.055
Plot129	0.003	-0.049	0.056
Plot130	0.017	-0.027	0.061
Plot131	0.007	-0.051	0.066
Plot132	0.006	-0.062	0.073
Plot133	-0.006	-0.074	0.059
Plot134	0.060	0.010	0.110
Plot135	-0.020	-0.074	0.033
Plot136	0.014	-0.049	0.079
Plot137	-0.020	-0.072	0.031
Plot138	-0.002	-0.071	0.066
Plot139	-0.002	-0.057	0.053
Plot140	-0.003	-0.069	0.065
Plot141	-0.009	-0.060	0.043

Plot142	-0.010	-0.052	0.030
Plot143	0.001	-0.050	0.051
Plot144	0.025	-0.023	0.072
Plot145	0.072	0.022	0.124
Plot146	0.020	-0.035	0.076
Plot147	-0.012	-0.057	0.032
Plot148	-0.007	-0.067	0.054
Plot149	0.000	-0.050	0.052
Plot150	-0.005	-0.065	0.055
Plot151	-0.003	-0.060	0.055
Plot152	0.046	-0.013	0.108
Plot153	-0.006	-0.043	0.032
Plot154	0.010	-0.035	0.055
Plot155	-0.010	-0.055	0.035
Plot156	0.001	-0.040	0.042
Plot157	-0.010	-0.070	0.049
Plot158	0.015	-0.032	0.061
Plot159	0.004	-0.052	0.059
Plot160	-0.004	-0.063	0.055
Plot161	-0.007	-0.066	0.050
Plot162	-0.044	-0.105	0.015
Plot163	-0.026	-0.086	0.033
Plot164	0.051	-0.008	0.114
Plot165	-0.033	-0.084	0.017
Plot166	0.040	-0.010	0.090
Plot167	-0.011	-0.064	0.041
Plot168	-0.008	-0.044	0.027
Plot169	-0.004	-0.072	0.061
Plot170	-0.023	-0.078	0.031
Plot171	-0.012	-0.059	0.034

Model: RGR and neighborhood trait dissimilarity

Variables:

G: log(RGR+1)

co.ini: number of conspecifics in 1 m^2. ($co.ini_{obs}$-mean.co.ini)/SD.co.ini.

het.ini: number of hetero-specifics in 1 m^2. ($het.ini_{obs}$-mean.het.ini) /SD.het.ini.

cosp: change in the number of alive conspecifics across the period studied

hetsp: change in the number of alive hetero-specifics across the period studied.

td.cons: Trait dissimilarity among conspecifics. (TD_{obs}-meanTD)/SD TD.

td.het: Trait dissimilarity among hetero-specifics. (TD_{obs}-meanTD) /SD TD.

PC1: trait PC axis 1

PC2: trait PC axis 2

PC3: trait PC axis 3

ini.size: seedling height at first census. ($ini.size_{obs}$-mean.ini.zise)/SD.ini.size.

log.abun: log-transformed species relative abundance

J: total number of species

K: total number of plots

```
model{

   #### PRIORS
   tau.G <- 1/(sigma.G * sigma.G)
   sigma.G ~ dunif(0,100)
   a3 ~  dnorm(0,0.01)
   a4 ~  dnorm(0,0.01)
   a5 ~  dnorm(0,0.01)
   a6 ~  dnorm(0,0.01)
   a7 ~  dnorm(0,0.01)
   a8 ~  dnorm(0,0.01)
   a9 ~  dnorm(0,0.01)
   a10 ~  dnorm(0,0.01)

   ### species loop
   tau.a0 ~ dgamma(0.001,0.001)
   mu.a0 ~ dnorm(0,0.01)
   tau.a1 ~ dgamma(0.001,0.001)
   inter.a1 ~ dnorm(0,0.01)
   slope.a1 ~ dnorm(0,0.01)
   tau.a2 ~ dgamma(0.001,0.001)
   inter.a2 ~ dnorm(0,0.01)
   slope.a2 ~ dnorm(0,0.01)

   ### plot loop slope hyperpriors
   tau.plot ~ dgamma(0.001,0.001)

   ###LIKELIHOOD
   for (i in 1:nInd){
```

```
   G[i]~ dnorm(G.hat[i], tau.G)
   G.hat[i] <- a0[species[i]]+a1[species[i]]*td.cons[i]+a2[species[i]]*td.het[i]+
a3*co.sp[i]+ a4*het.sp[i]+a5*co.ini[i]+a6*het.ini[i]+a7*ini.size[i]
+a8*pc1[i]+a9*pc2[i]+a10*pc3[i] +a11[plot[i]]
   }

   for (j in 1:J){
   a0[j] ~ dnorm(mu.a0, tau.a0)

   a1[j] ~ dnorm(mu.a1[j], tau.a1)
   mu.a1[j] <- inter.a1 + slope.a1*log.abun[j]

   a2[j] ~ dnorm(mu.a2[j], tau.a2)
   mu.a2[j] <- inter.a2 + slope.a2*log.abun[j]
   }

   for (k in 1:K){
   a11[k]~ dnorm (0, tau.plot)
   }

   }
```

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