

Interspecific Functional Convergence and Divergence and Intraspecific 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 interspecific 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 6 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 intraspecific 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.

Keywords: community assembly, functional ecology, functional richness, seed-to-seedling transition, tropical tree ecology.

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 life span, abundance, and diversity of the species involved. Despite these challenges, ecologists have made progress through analyzing long-term forest dynamics data sets (e.g., Condit et al. 2006; Wills et al. 2006; Swenson et al. 2012b; Muscarella et al. 2013). Recent studies have shown that nonrandom mortality is particularly high in the smallest size classes in tropical tree communities, and this leaves a disproportionately large imprint on patterns of coexistence through to adulthood (Bagchi et al. 2010, 2014; Metz et al. 2010; Paine et al. 2012; Green et al. 2014). Uncovering the ecological mechanisms that determine the seed-to-seedling transition and their effects on tropical tree coexistence and community dynamics (Levine and Murell 2003) is an essential goal.

The number of individuals in the seed community is usually much larger than that in the established seedling community at any particular location, with more than 75% of the seeds that land in a site 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 and Harms 2009). However, it is more likely that all of these factors act at the same time (e.g., Swenson and 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; Nicotra 1999; Norden et al. 2007; Paine et al. 2012) and some dynamic investiga-

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tions 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 largest demographic bottleneck of all: the seed-to-seedling transition (Harms et al. 2000; Norden et al. 2009; Paine and Harms 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. Intraspecific 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 1 would be indicative of intraspecific negative density dependence (fig. 1).

Although the Harms et al. (2000) approach can provide insights into intraspecific 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, 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

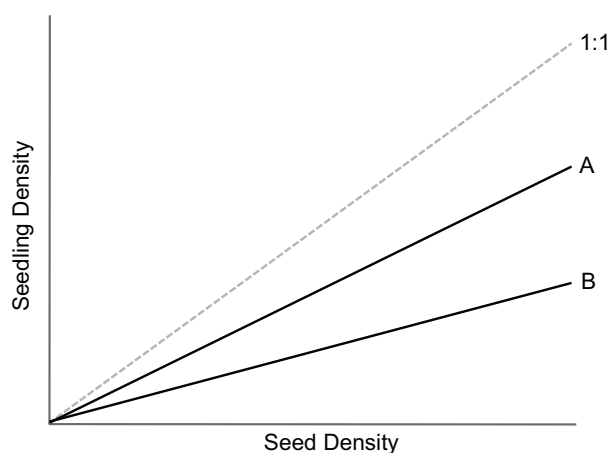


Figure 1: Schematic figure comparing the Harms et al. (2000) approach. The slope lines correspond to the regression line for one species where species B is experiencing stronger negative density dependence than species A.

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 interspecific competition for similar resources. As a result, we would expect negative density dependence to maximize the local species and functional richness and the mean nearest neighbor distance of the community (i.e., the total trait range and the mean trait distance between the nearest neighbors; Vileger 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 that 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 and Keddy 1995). The hierarchical competition process states that functionally similar species coexist by being superior competitors (Mayfield and 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 a 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 this 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 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 our study was to quantify whether there was evidence for intraspecific 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 (fig. 1).

There are four specific questions related to our three main hypotheses that we address in this research: (1) Is interspecific negative density dependence an important force promoting the observed changes in functional diversity across the seed-to-seedling transition? (2) Is there a detectable influence of both intra- and interspecific negative density dependence during the seed-to-seedling transition? (3) Are the answers to the first two questions consistent across different axes of plant function, which are related to different limiting resource axes? (4) How does the strength of these processes influencing the seed-to-seedling transition change across time?

Methods

Study Area

Our 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 a subtropical wet forest according to

the Holdridge life zone system (Ewel and Whitmore 1973), with elevation ranging from 333 to 428 m asl and a mean annual rainfall of 3,500 mm (Thompson et al. 2002).

Seed Traps and Seedling Plots

Each station (120 in total) consisted of one 0.5-m² trap and three 1-m² seedling plots placed in a random direction 2 m from three of the edges of the trap. Each trap was built with a PVC frame that held a 1-mm 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 via 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 analyzed eight functional traits that represent the major ecological strategies of trees using standard protocols (Swenson and Enquist 2008; Swenson et al. 2012a, 2012b). All traits used in the analysis reported here come from adult individuals, except seed mass (data collected by J. Forero-Montaña and LTER staff). Leaf traits for seedlings have been measured for some of our study species in this forest by N. G. Swenson, R. Muscarella, and M. N. Umaña. 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 (fig. S1; figs. S1–S6, A1–A4 are available online). 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, and %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 life spans. Maximum height was measured to represent the adult light niche of species. It was included in this study of seedlings, as it is linked to growth rates across life stages (Iida et al. 2014; Lasky et al. 2015). Seed mass was measured, as it represents where a species is located on an axis between producing few well-provisioned offspring and producing many poorly provisioned offspring, where provisioning is expected to be strongly related to success along resource availability gradients. Last, 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.

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; Laliberté and 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 and 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 were 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; consequently, we would expect a lower mean nearest neighbor distance value than expected if the probability of an individual transitioning from seed to seedling were 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 dis-

tances 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) 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 data sets 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 and Enquist 2009). Thus, we performed the univariate 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: inter- and intraspecific. For the interspecific 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 contain only 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 had germination 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 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 standardized effect size (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 the appendix, available online.

Our intraspecific 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 implemented only the analyses with a subset of species (10 species for 2007, 11 for 2008, and 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 1 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 three 1-m^2 seedling plots for each site divided by three and calculated for each census. These values were then log transformed, and the density of seedlings was regressed against the density of seeds. Slope values lower than 1 indicate that the density of seedlings was lower than would be expected under intraspecific negative density dependence (fig. 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 interspecific and intraspecific analyses.

At the site level for the multivariate analyses (fig. 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 LES showed the same trend as the multivariate results (fig. S2). However, the functional richness SES values for trait maximum tree height of adults and wood density showed no positive or negative trend (fig. S2). Only leaf area (fig. S2) exhibited functional richness SES values higher than those 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 (figs. 3, S3). 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 (figs. S4, S5). The results from site level were consistent with analyses conducted on the forest-wide scale (appendix).

When all of the results were considered across the 6 years, we found that functional patterns for the multivariate and univariate analyses were generally consistent (figs. 2, 3, S3). The results for forest-wide analyses showed trends that were generally similar to the site-level analyses; however, for wood density and the leaf economics spectrum traits, we found a decreasing pattern in functional richness across time (fig. A2).

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 (fig. S6).

Last, we conducted an analysis to quantify whether there was evidence for intraspecific negative density dependence. The results of our intraspecific 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 (fig. 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 that functionally dissimilar species are more likely to transition from seed to seedling, (ii) a functional convergence hypothesis where functionally 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 (figs. 2, A2). 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 and Levine 2010; Kunstler et al. 2012). Further analyses that considered the evenness of species abundance

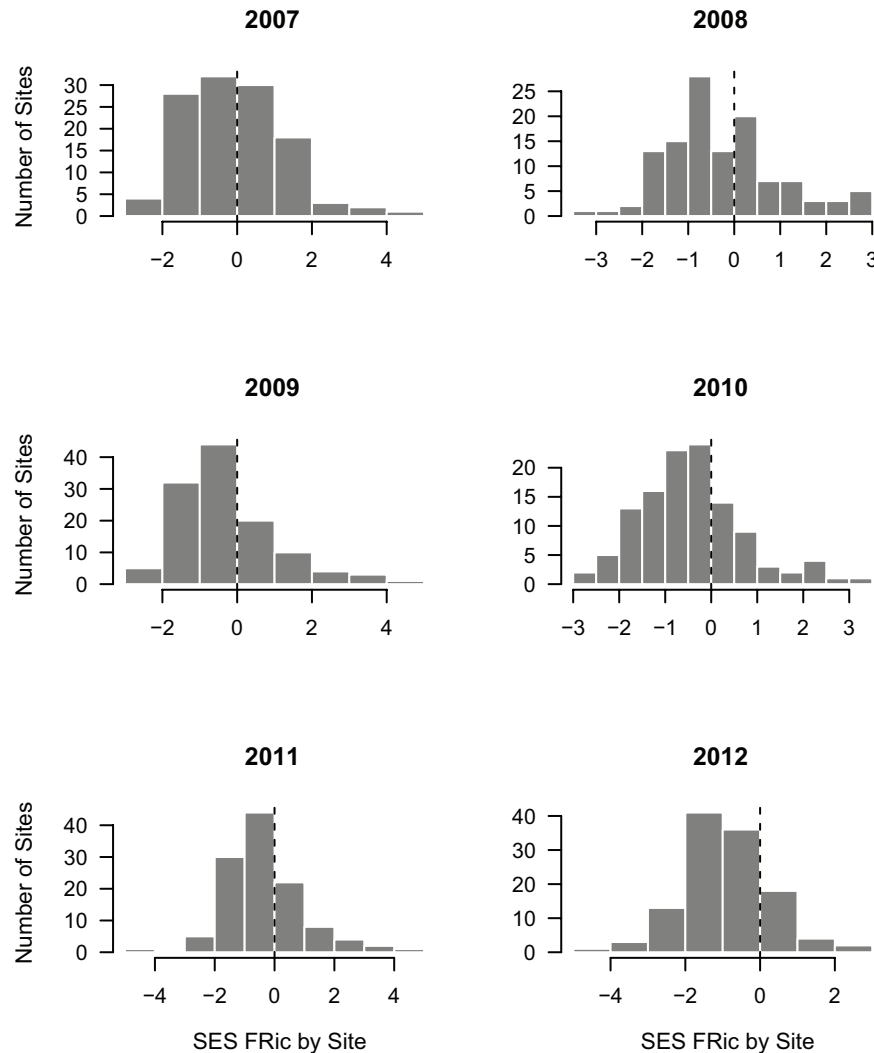


Figure 2: Site-level results for the standardized effect size (SES) of functional richness across 6 years. Negative functional richness SES values indicate lower functional richness in the seedling assemblage than expected. Positive functional richness SES values indicate higher functional richness in the seedling assemblage than expected. FRic = functional richness.

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 (figs. 3, S3, A3, A4). 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 intraspecific negative density dependence based on the Harms et al. (2000) method (see fig. 1) uncovered consistently strong negative density dependence (fig. 4). Considering the results together, we find support for the hybrid hypothesis, where interspecific and intraspecific negative dependence and abiotic constraints both influence the seed-to-seedling tran-

sition. 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 (figs. 2, 3, S3, A2–A4). Specifically, we asked whether the observed functional richness, functional evenness, and mean nearest

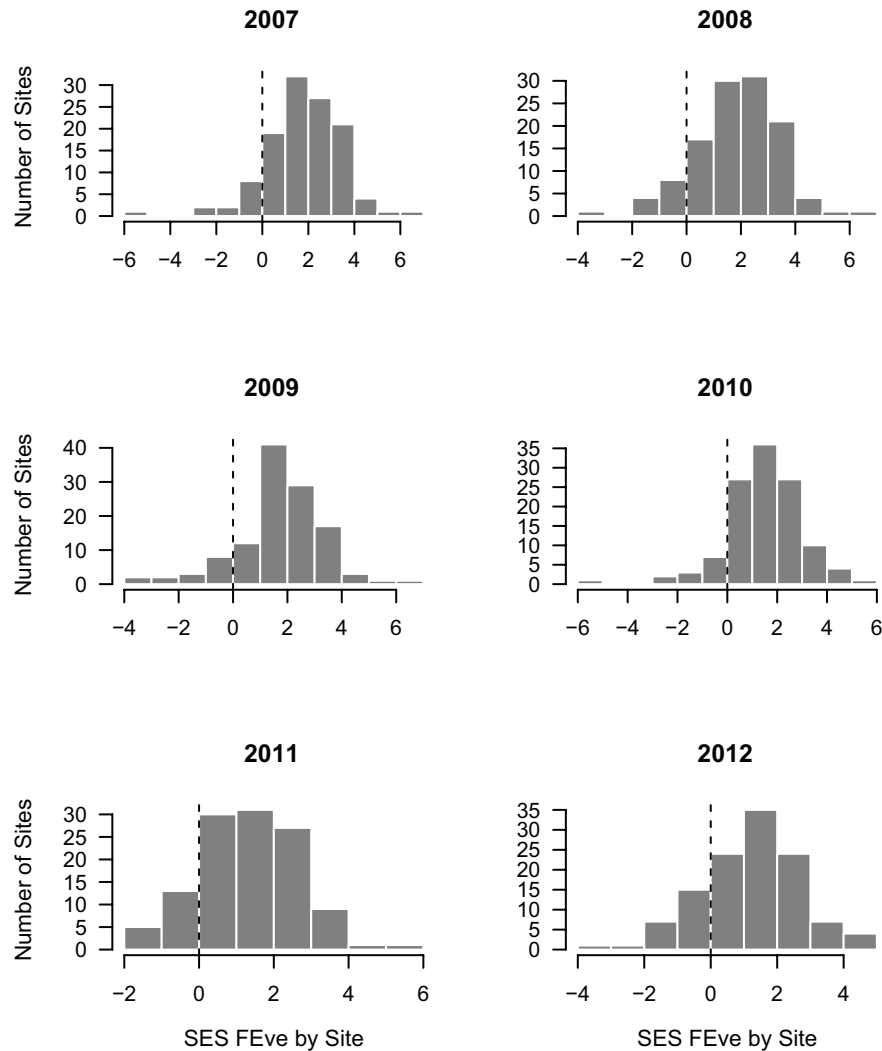


Figure 3: Site-level results for the standardized effect size (SES) of functional evenness across 6 years. Negative functional evenness SES values indicate lower functional evenness in the seedling assemblage than expected. Positive functional evenness SES values indicate higher functional evenness in seedling assemblages than expected. FEve refers to functional evenness.

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 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 (fig. 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, LES traits (i.e., SLA and leaf N and P), and seed mass—had less functional richness than expected given the seedling assemblages (figs. S2, A2). Our finding that most functional traits (all except leaf area) were lower in the seedling than seed communities demonstrates that the species able to success-

fully 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, which have greater stored resources (Denslow 1987; Chazdon et al. 1996; Nicotra et al. 1999; Montgomery and 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-

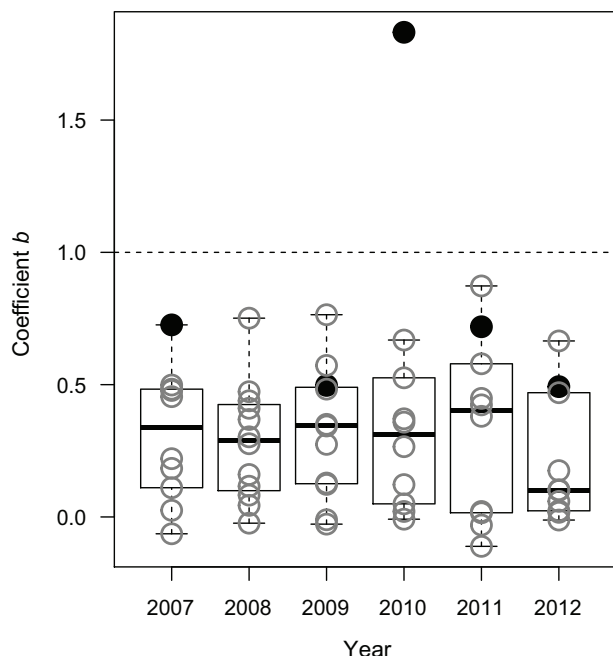


Figure 4: Boxplot representing the regression slope values between seed and seedling densities by species by year. Black circles represent the slope values for *Guarea guidonea* (Meliaceae). Smaller slope values are indicative of stronger intraspecific negative density dependence, whereas slope values of 1 indicate no intraspecific density dependence (Harms et al. 2000).

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; fig. S6). Previous work from this forest (Francis and 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). Last, 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 and 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 interspecific 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 assemblages have higher than expected functional evenness and mean nearest neighbor distance (figs. 3, S3). This result indicates that the abundance in the seedling assemblages is evenly spread over multivariate trait space, which is consistent with trait-based interspecific 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 interspecific negative density dependence are 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 (fig. S5). We believe that 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). For the other traits, the functional evenness was usually lower than expected, indicating that traits associated with photosynthetic capacity (i.e., SLA and leaf nutrients) and stress tolerance (i.e., seed mass) are more successful in making the ontogenetic transition (Poorter 2007). 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 6 years, we found no major changes through time. The functional evenness as well as the mean nearest neighbor dis-

tance in seedling assemblages were consistently higher than expected from 2007 to 2012, indicating that the strength of interspecific 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 LES 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 and Hurricane Georges in 1998), where species adapted to nondisturbed conditions and low understory light levels may take a 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.

Intraspecific Negative Density Dependence during the Seed-to-Seedling Transition

In addition to the dynamics occurring on the interspecific level that are mainly determined by functional differences among species, we also wanted to evaluate the importance of intraspecific negative density dependence. We estimated the strength of intraspecific negative density dependence for all the species using the methodology developed by Harms et al. (2000; fig. 1). We found strong intraspecific negative density dependence across the seed-to-seedling transition for nearly all species included in the analysis (fig. 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 intraspecific 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 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 intraspecific negative density dependence. We therefore wish to highlight that our inferences are based on a limited number of axes of plant func-

tion, and those axes that we did consider are primarily related to resource acquisition 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 intraspecific 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 represent significant challenges. At all life stages, trees must deal with environmental stresses and biotic interactions that will have a range of impacts depending on 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 intraspecific negative density dependence, there is evidence that seedling assemblages represent only a small proportion of the total functional volume found in seed assemblages and that 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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