

Large- and small-seeded species have contrasting functional neighborhoods in a subtropical forest

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Abstract. Forest community composition is the outcome of multiple forces, including those that increase taxonomic and functional divergence and those that promote convergence in traits. The mechanisms underlying these forces may not operate homogeneously within communities; individuals of different species are never perfectly mixed, and thus, species tend to be surrounded and interact with different subsets of species. In fact, taxonomic and functional composition of neighborhoods of different focal species can be highly variable. Here, we examine whether mechanisms driving species-level neighborhoods relate to intrinsic characteristics of focal species such as differences in life-history and resource-uptake strategies and in turn relate to species survival. We focus on two key characteristics: (1) seed mass, which defines a dominant axis of life-history strategies related to stress tolerance, and (2) understory light preferences that sort species from light-demanding pioneers to shade-tolerant. We monitored seedling communities over 10 yr in Puerto Rico and calculated neighborhood trait dispersion in species-level neighborhoods using seven functional traits. We examined whether species-level characteristics, seed mass and preferred light conditions, influence patterns of functional dispersion in seedling neighborhoods using linear models. Then, we examined how species-level functional neighborhoods impact seedling survival. We found that small- and large-seeded species diverge in the type of functional neighborhoods they associate with. Large-seeded species associate with neighbors that are more similar than expected in leaf economic traits, but more different than expected in seed mass and leaf area traits, while the opposite was found for small-seeded species. This variation in species functional neighborhood was important in determining seedling survival. In sum, our results suggest that divergent and convergent forces do not operate homogeneously over entire communities. Their relative role changes in space, and on a species-by-species basis, probably with a deterministic foundation linked to traits such as seed mass.

Key words: canopy openness; Luquillo Forest Dynamics Plot; neighborhood trait dispersion; Puerto Rico; seed mass; seedlings; survival.

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INTRODUCTION

Understanding the underlying mechanisms driving diversity and structure in tropical forests has proved an enduring challenge in ecology. In the past, several studies have focused on examining the amount of trait dispersion within communities as an approach to infer ecological forces driving community structure (Weiher and Keddy 1995, Kraft et al. 2008, Swenson and Enquist 2009, Paine et al. 2011, Baraloto et al. 2012). These forces, in general, can vary from those that increase taxonomic and functional divergence to those that promote convergence in traits, for a given number of species. Trait over-dispersion is typically interpreted as a predominance of divergent processes (i.e., competitive interactions that promote niche differentiation), while trait under-dispersion is interpreted as a prevalence of convergent forces (i.e., if many combinations of trait values are incompatible with survival or reproduction, co-occurring species will tend to be relatively similar to each other at that scale; MacArthur and Levins 1967, Agren and Fagerström 1984). However, examining patterns of trait dispersion based on average community-level values might offer inaccurate information about the diversity of ecological processes occurring at neighborhood scales. This is particularly true in species-rich ecosystems where local composition at the scale of few meters includes a relatively smaller subset of the local assemblage, forcing local interactions to vary importantly in space and time (Hubbell and Foster 1986). If species show variation in the biotic and abiotic interactions at the neighborhood scale, this could result in differences in patterns of trait dispersion within their neighborhoods. Here, instead of looking at the forest as a single and unique assemblage, we focus on multiple species-level neighborhoods to assess to what extent divergent/convergent forces can vary in tropical forests at the neighborhood scale. These species-level neighborhoods can be thought of as the preferred sub-assemblage with which each species tends to associate locally.

Some species might associate with sub-assemblages more controlled by convergent forces than others. We can expect this variation to relate with the physiological or life strategies of the species. If that is the case, variations in the type of sub-

assemblage with which the different species associate (i.e., convergent vs. divergent assemblages) would be the result of deterministic processes, and not just the result of chance. In particular, we can expect stress-tolerant species to be specialized in specific harsh habitats from which stress-intolerant species are absent, and thus be surrounded by similar neighbors (Goldberg and Landa 1991, Kunstler et al. 2012). In contrast, stress-intolerant or more opportunistic species might be influenced by divergent processes if they, for example, avoid direct competition by occupying peripheral niches in the places where they appear (Umaña et al. 2015, 2017). Thus, species differences in the tolerance of stressful conditions could reveal differences in the role of convergent and divergent processes structuring neighborhood communities.

In the present study, we use seed mass as a proxy for tolerance of stressful conditions (Westoby 1998, Westoby et al. 2002, Moles 2018). Seed mass relates to the amount of resources that embryos use to grow in early life stages (Turnbull et al. 1999, Leishman et al. 2000, Moles et al. 2004, Moles 2018). Greater reserves of large-seeded species allow plants to survive better and thrive in sites where resources are scarce while reserves of small-seeded species are more limited, making their individuals less tolerant of stress and weaker in general (Henery and Westoby 2001, Coomes and Grubb 2003, Moles et al. 2004, Muller-Landau et al. 2008, Muller-Landau 2010, Larson and Funk 2016). In addition, seed mass is important in determining the ability to tolerate effects of conspecific negative density-dependent processes that severely impair seedling performance in tropical forests (Lebrija-Trejos et al. 2016). In particular, large-seeded species are less affected by conspecific negative density dependence than small-seeded species and can survive in neighborhoods with a higher density of conspecifics than small-seeded species (Lebrija-Trejos et al. 2016).

The type of neighborhoods species are associated with is not only affected by stress tolerance. The variation in functional neighborhoods can also be associated with preferences for certain abiotic conditions. Here, we focus on light availability, a major limiting resource in tropical understories (Denslow 1980, 1987, Condit et al. 1992). In particular, in the Luquillo Forest

Dynamics Plot (LFDP) in Puerto Rico, human and natural disturbances have resulted into a highly heterogeneous understory with great influence in species distributions (Zimmerman et al. 1994, Thompson et al. 2002, Foster et al. 2003, Lugo and Helmer 2004). Given the wide spatial heterogeneity in understory light conditions in this forest, one could expect that species-level neighborhoods vary according to species preferences for particular understory light conditions. For example, species that prefer gaps are usually pioneer species that tend to require good light conditions (Denslow 1980, 1987) and would associate with neighborhoods that display similar functions, while shaded sites tend to have plants with a wider range of ecological strategies, given that the vast majority of species in tropical forests are shade-tolerant (Hubbell 2005). Whether these differences in response to light conditions are relevant for determining functional neighborhoods of species remains largely unknown.

Ultimately, variation in functional neighborhoods across species should impact plant performance of focal individuals (i.e., survival; Uriarte et al. 2010). Specifically, if performance is enhanced through mechanisms of niche complementarity where individual success within the neighborhood is determined by the use of different resources (MacArthur and Levins 1967), then species associated with functionally dissimilar neighborhoods will attain higher survival than species associated with functionally similar neighborhoods. On the other hand, if individual performance is enhanced through mechanisms that promote functional convergence such as environmental filtering or hierarchical competition (Keddy and Shipley 1989, Kunstler et al. 2012), then individual survival may correlate with the similarity of neighborhoods.

In this study, we investigated whether species-level characteristics (seed mass and response to understory light conditions) influence patterns of trait dispersion in species-level neighborhoods for seedling communities. We focus on seedlings given that at this stage the high mortality rates have a strong long-lasting impact on community composition of later life stages (Harper 1977). The results from this study clarify whether the relative role of ecological forces driving neighborhood structure in plant communities is

variable within communities and related to ecological characteristics of the focal taxa. These results could apply to other systems and communities where species exhibit variation in seed mass. If true, community-level analyses could lead to inaccurate generalizations about drivers of community structure and composition. To address this, we used ten years of annual censuses on seedling communities from a subtropical wet forest in Puerto Rico combined with data on seven functional traits that describe a broad range of resource-uptake strategies for plants. We asked:

1. How does neighborhood functional composition change across species with different seed mass? We predict that neighbors of large-seeded species will have greater trait similarity between them than neighbors of small-seeded species. This will happen if large-seeded species are concentrated in low-resource and highly stressful environments where only a limited range of traits can persist (Kunstler et al. 2012), and/or if negative density-dependent effects are less severe for these species allowing higher densities of conspecifics (i.e., highly similar neighbors) at local scales (Lebrija-Trejos et al. 2016). Small-seeded species, in contrast, are severely impacted by negative density dependence and, more generally, competitive exclusion by similar species (Rees 1995, Turnbull et al. 1999, Lebrija-Trejos et al. 2016). Consequently, they could succeed in sites where neighbors use different resources. Therefore, we expected functional neighborhoods of small-seeded species will be more dissimilar than for large-seeded species.
2. How does neighborhood functional composition change across species that vary in their preference regarding understory light conditions? We predict that functional neighborhoods of species that are mainly distributed in high light conditions will be more trait-similar than neighborhoods of species that are distributed in shaded understories.
3. What is the relationship between species-level functional neighborhood and seedling survival? If niche partitioning determines

seedling survival, then we expect that functional over-dispersion in the neighborhood would lead to higher survival. In contrast, if abiotic filtering or hierarchical competition determines seedling survival, then we expect higher survival in functionally under-dispersed neighborhoods.

METHODS

Study site

The LFDP is a 16-ha permanent plot located at El Verde field station in northeastern Puerto Rico (18°20' N, 65°49' W). The forest of this research area is classified as subtropical wet according to Holdridge life zones (Ewel and Whitmore 1973) with a mean annual rainfall of 3500 mm and an elevation range that varies from 330 to 428 m (Thompson et al. 2002). The vegetation is dominated by *Dacryodes excelsa* (Burseraceae), and *Prestoea acuminata* (a palm). In the past, the forest experienced human and natural disturbances that altered the composition and dynamics of plant communities (Guzman-Grajales and Walker 1991, Thompson et al. 2002, Uriarte et al. 2005). Before 1934, the northern two-thirds of the LFDP was used for agriculture, while the southern third was used for selective logging and remained relatively unaltered (Zimmerman et al. 1994, Foster et al. 1999, Thompson et al. 2002). This past land use left a signature in the plot, with greater prevalence of pioneer species and more dynamic gap formation in the areas that were cleared for agricultural uses, and a darker and more homogeneous light environment in the understory in those areas that were only selectively logged (Thompson et al. 2002). Besides past land use, hurricanes are a major driver of the dynamics at the site. In 1989 and 1998, Hurricanes Hugo (category 4) and Georges (category 3) impacted the island. Although the LFDP was heavily impacted by category 5 Hurricane Maria in 2017, the data used in this paper were collected prior to this event.

Field surveys

This study used information on 120 seedling stations that were established in 2007 throughout the LFDP. Each seedling station consisted of three 1 × 1 m seedling plots located ~2 m away

from each other and distributed along a trail that crosses the 16-ha plot from south to north. Every year from 2007 to 2016, seedling censuses were carried out during January–May. Each census included recruits and survival observations for all freestanding woody stems that do not reach 1 cm of diameter at breast height (1.30 m). This definition of seedling follows standard census methods for large forest dynamic plots (Anderson-Teixeira et al. 2015). We excluded a few stems broken below 1.30 m that were obviously not seedlings. Woody ferns were not included in the census. During each survey, all new recruits were tagged and identified. We analyzed data on 48,660 seedling observations, including at least one observation on 26,289 individual seedlings representing to 66 species. The mean number of individuals per seedling plot was 14, ranging between 1 and 597 (standard deviation = 22).

Trait data

We collected seven functional traits from adult trees present in the LFDP following standardized methods (Cornelissen et al. 2003). The traits collected represent major resource acquisition ecological strategies (Westoby et al. 2002, Díaz et al. 2015) and included specific leaf area (leaf area per unit of dry mass, SLA), leaf phosphorus content (LPC), leaf nitrogen content (LNC), leaf carbon content (LCC), leaf area, seed mass, wood specific gravity, and maximum height. Specific leaf area, LPC, and LNC summarize the leaf economic spectrum (Wright et al. 2004). Leaf carbon content reflects investment in structural support (Niinemets 2007). Leaf area represents the area displayed for light capture and has been shown largely uncorrelated with leaf economic traits (Poorter and Rozendaal 2008). Wood specific gravity reflects the three-fold trade-off between (1) transport safety, (2) transport efficiency, and (3) mechanical support (Chave et al. 2009). Seed mass reflects the amount of resources that an embryo is provided with and relates to stress tolerance (Chapin 1991).

Liana species are very common at the seedling stage in this forest (Umaña et al. 2019), but our trait collection was based on tree species. Our trait dataset contained 70% of the woody species and 46% of the woody individuals found in the seedling plots. The other 30% of the woody species and 54% of the woody individuals were

lianas and very rare tree species that were not collected for trait measurements in the site (Uriarte et al. 2010). The interpretation of the results will consider this limitation of the data. Mean trait values per species were calculated from a total of 25 samples (10 for wood specific gravity) per species. Although traits were collected from adult individuals, significant correlations between seedling and adult traits have been reported for this forest (Umaña et al. 2016). We used adult traits instead of seedling traits because for seedlings we did not have LPC, LCC, LPC, and wood density traits. All traits (except wood specific gravity) were log-transformed to reduce skewness and fulfill the requirements of the linear models employed. Additionally, we summarized the trait variation with the first three axes from a principal component analysis (PCA; see Appendix S1: Table S1 for correlations between traits); these three axes captured 67% of the trait variation (Fig. 1; Appendix S1: Table S2). PC1 was negatively correlated with the leaf economic traits (LNC, LPC, and SLA; leaf economic axis). PC2 was strongly and negatively correlated with leaf area and seed mass (leaf area–seed axis). PC3 was strongly and negatively correlated with LCC.

Species-level canopy openness

To evaluate the effect of light conditions in the understory, we used hemispherical photographs that were taken with a camera and a fisheye lens (Nikkor; Nikon, Tokyo, Japan). The camera was positioned at 1 m height in the center of each seedling plot under uniform light conditions (either at dawn or during uniformly cloudy days). The photographs were taken during January and May every year between 2008 and 2015. Each photograph was analyzed following the iterative selection thresholding algorithm (Ridler and Calvard 1978) to calculate a gap light index as a measure of canopy openness (Canham 1988). Then, we calculated median canopy openness conditions for each species as an overall estimate of gap vs. shade preference and relative specialization to light environments.

Quantification of species-level neighborhood functional similarity

To quantify trait dispersion surrounding any given individual, we calculated the mean

distance to neighbors (MDN) between that individual and all the other individuals in the same seedling plot (i.e., functional neighborhood). This was done for each individual trait and the three orthogonal PCA axes. To measure trait dispersion between one given species and its neighbors, we calculated the mean MDN across all its individuals. The mean MDN reflects the average distance (along a given PCA axis or univariate trait) between all the individuals of a given species and all the individuals of other species that surround them.

Given that MDN can be related to species richness, especially for small communities (Swenson 2014), we used a null model approach to account for the correlation between species richness and MDN values. The null distribution was generated by performing 999 randomizations where the species names were shuffled within the trait matrix. In each iteration, the trait value for the focal individual was kept constant but the trait values for all the neighbors were shuffled. With this information, we calculated the mean null MDN for each focal species for different years and used it to compute a standardized effect size (SES). Standardized effect size was calculated by subtracting the mean MDN null values from the MDN observed values and divided it by the standard deviation of the null distribution. Positive SES values indicate trait dispersion higher than the expected given the number of species in the neighborhoods of that species, and negative values indicate lower dispersion than the expected for the richness of those neighborhoods. In other words, positive SES values indicate species typically surrounded by dissimilar neighborhoods (and probably subject to stronger divergent forces) and negative SES values indicate species typically surrounded by similar neighborhoods (and probably subject to stronger convergent forces).

Statistical analyses

To evaluate the effects of log-transformed seed mass, and species-level canopy openness preferences on SES MDN values, we fit linear models. For all models, the dependent variable was species SES MDN (calculated for each PCA axis or univariate trait) and the fixed effects were the log-transformed seed mass, and median species-level canopy openness. We checked that the

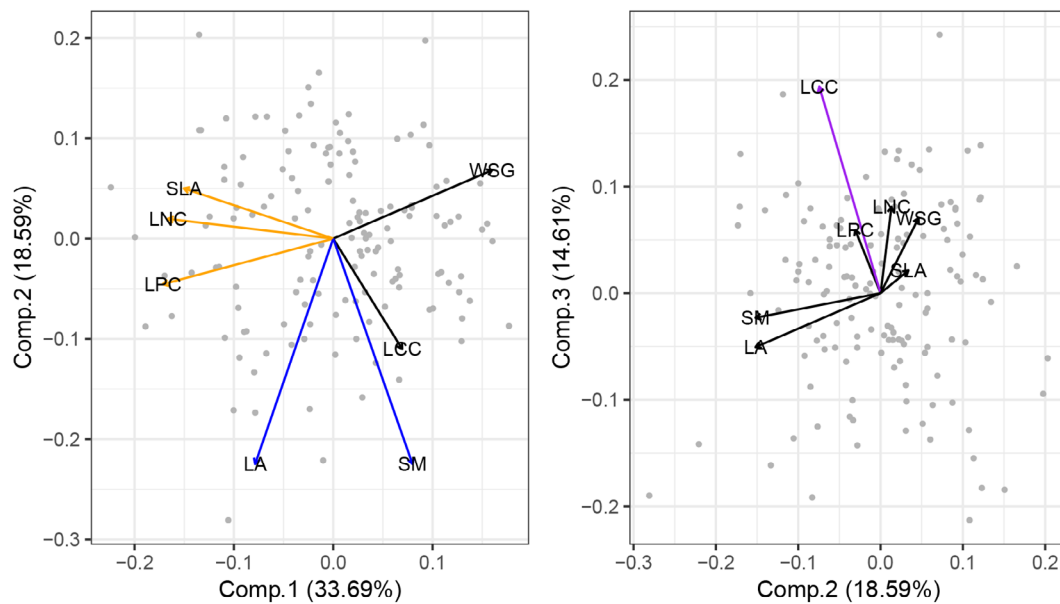


Fig. 1. Principal component analyses of seven functional traits. Vectors show how traits are correlated with each multivariate axis. Orange vectors indicate traits that are more strongly linked to PC1; blue vectors indicate traits that are more strongly linked to PC2; and the purple vector indicates the trait is more strongly linked to PC3. The values in parentheses show the amount of explained variation for each axis. Abbreviations are as follows: LA, leaf area; LCC, leaf carbon content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; SLA, specific leaf area; SM, seed mass; and WSG, wood specific gravity.

residuals conformed the assumptions of the model by plotting residuals against fitted values for each model. Residuals deviated from normality in the seed model (Appendix S1: Fig. S1) so we performed a quantile regression analysis to examine this relationship. Given these limitations, we are cautious when considering this model for further discussion.

To assess the relationship between seedling survival and the species-level functional neighborhoods of the species to which they belonged, we fit a generalized linear mixed-effects model (logistic GLMMs with binomial error). Seedling survival was modeled as a function SES MDN based on three orthogonal PCA axes, log-transformed seed mass, and seedling height (scaled). Individuals and plot identity were modeled as random effects, to account for variation across seedlings and space. GLMMs were fitted using the function `glmer` from package `lme4` (Bates et al. 2015) in R version 3.2.1. Confidence intervals were calculated by bootstrapping.

Seedlings have very high mortality rates during their first year, so mortality events were

highly concentrated in that initial time step. To check whether this confounded our overall results, we performed similar analyses for seedlings that were older than one year. These complementary analyses gave largely consistent results and are thus presented in the supplementary materials only (Appendix S1: Tables S3, S4).

RESULTS

Relationship between neighborhood functional dissimilarity and seed mass

For analyses based on univariate traits, we found that dissimilarity in species-level functional neighborhood (SES MDN) based on seed mass decreased for species with larger seeds (Appendix S1: Tables S5, S6). That is, species with larger seeds tend to be surrounded by neighbors with similar seed masses, while smaller-seeded species tend to be surrounded by neighbors of varying seed size. This result needs to be taken with caution because the residuals from the linear model violated the normality assumption, and instead, we used a quantile

regression (using the median; Appendix S1: Fig. S1, Table S5). The result from the quantile regression was consistent with the results obtained with the model showing a negative relationship between SES MDN and species seed mass. The additional results for models using SES MDN based on other univariate traits were not significant (Fig. 2; Appendix S1: Table S6).

For analyses based on multivariate (PCA) axes, we found a significant positive relationship between log-transformed seed mass and SES MDN-PC1 (negatively correlated with the leaf economic traits; LNC, LPC, and SLA; Fig. 2; Appendix S1: Table S6). That is, species with larger seeds tend to be surrounded by neighbors that are dissimilar in leaf economic traits, while species with smaller seeds tend to be surrounded by neighbors that are similar in leaf economic traits. The model for PC1 explained 19% of the variation in SES MDN-PC1 (Appendix S1: Table S6). For PC2 (negatively correlated with leaf area and seed mass), we found that SES MDN was significant and negatively related to log-transformed seed mass (Fig. 2; Appendix S1:

Table S6). That is, species with larger seeds tend to be surrounded by neighbors that are similar in leaf area and seed mass, while species with smaller seeds tend to be surrounded by neighbors that are dissimilar in leaf area and seed mass. The PC2-based model explained 11% of the variation in SES MDN-PC2 (Appendix S1: Table S6). For analyses based on PC3, we found non-significant relationships (Fig. 2; Appendix S1: Table S6).

Relationship between neighborhood functional dissimilarity and species-level light preferences

The species-level canopy openness preferences (measured as the median of canopy openness conditions) never had any significant effect on the functional dissimilarity in the neighborhoods of the different species, regardless of the response variable evaluated (Appendix S1: Table S6).

Relationship between seedling survival and species-level functional neighborhood

Survival models showed that seedling survival decreased with higher functional dispersion at

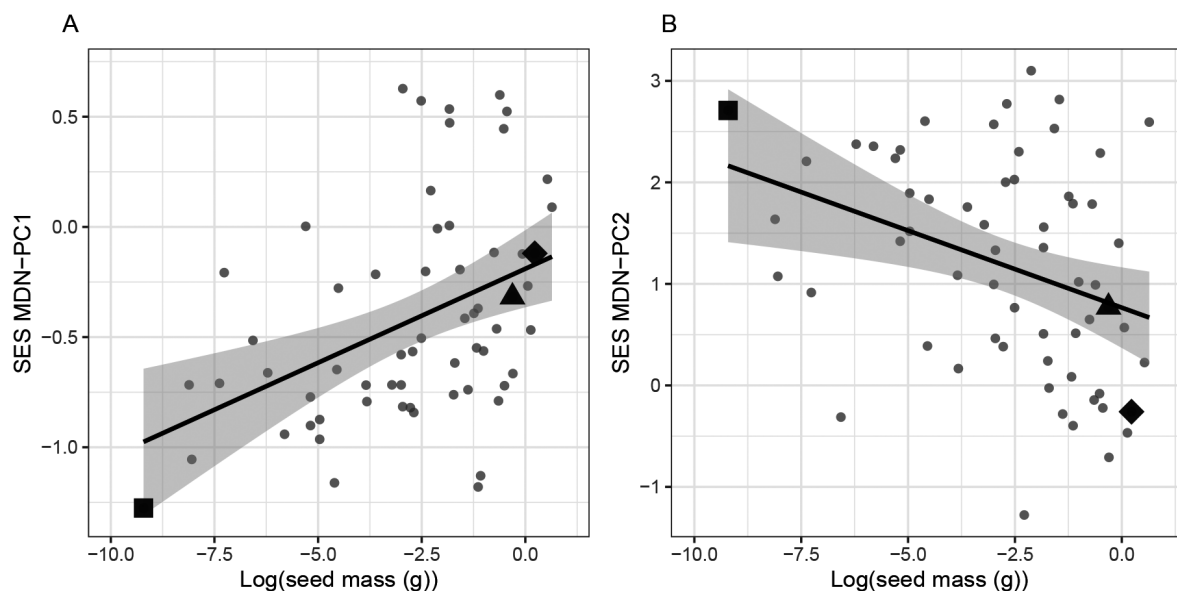


Fig. 2. Standardized mean distance to neighbors (MDN), a measure of functional dispersion in species-level neighborhoods, as a function of log-transformed seed mass values. (A) Standardized effect size (SES) MDN based on PC1 values. (B) SES MDN based on PC2 values. The shaded area shows the 95% confidence intervals for the slope estimate. *Piper blattarum* (squares) has a small seed and is a species of secondary forests. *Dacryodes excelsa* (diamonds) is a common species in the Luquillo Forest Dynamics Plot (LFDP) and is a late successional species. *Prestoea acuminata* (triangles) is a palm and the most common species in the LFDP forest.

the neighborhood (i.e., higher SES MDN values) for the three trait PCs and increased for species with large seed mass (Fig. 3; Appendix S1: Table S7).

DISCUSSION

In this study, we sought to investigate (1) whether convergent/divergent forces driving communities at a local scale (1×1 m) vary for the typical neighborhoods of the different species in the assemblage, (2) whether this variation relates to seed mass and/or to canopy openness preferences of the target species, and (3) how that correlates with demographic performance of the individuals of the different species. We found that small- and large-seeded species associate with functionally contrasting neighbors, suggesting that the role of convergent/divergent forces varies across the sub-assemblages surrounding the different species. These differences were significantly related to seedling survival, with species that associate with functional similar neighborhoods having higher survival rates. These results have important implications for understanding the diversity of processes driving

community structure in seedling communities. A detailed discussion of our results is presented below.

Functional dispersion in neighborhoods varies with species seed mass and correlates with seedling survival

Our results based on univariate traits showed that the trait dispersion between the individuals of one species and its neighbors does not significantly relate to species seed mass of that species, except for seed mass itself. However, such relationship was significant for the two first PCA axes and these results were congruent with the results obtained using only seed mass. This suggests that biotic interactions at the scale of 1×1 m (neighborhoods) are related to species ecological strategies that can be expressed in terms of combinations of different traits (multivariate trait axes), more than univariate traits. Similar results have been reported in previous studies, in which niche differences of plant species were best described by multivariate trait axes (Kraft et al. 2015).

In agreement with our predictions, we found that the degree of trait dispersion in

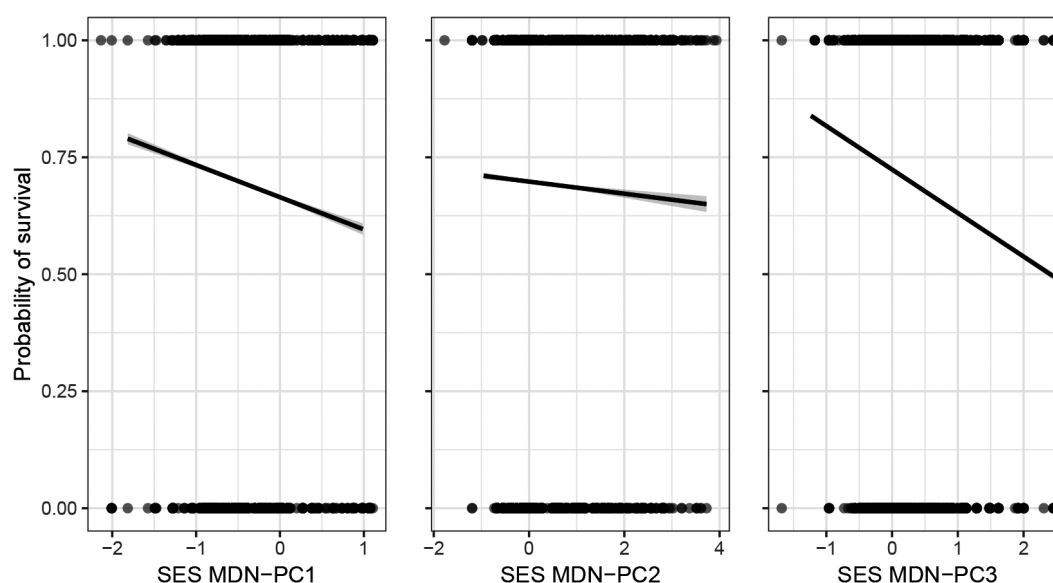


Fig. 3. Seedling survival responses to standardized effect size (SES) mean distance to neighbor (MDN) based on the first three axes from a functional principal component analysis (PCA). Black regression lines show significant effects, and shaded area (extremely narrow and almost invisible) shows the 95% confidence intervals for the slope.

neighborhoods based on seed mass as well as multivariate axes PC1 (leaf economic axis) and PC2 (leaf area–seed axis) varied across species with different seed mass. However, the sign of relationship between seed mass and neighborhood trait dispersion changed depending on the trait axis used. That is, large-seeded species were surrounded by species dissimilar in traits related to the leaf economic spectrum (PC1), but similar for the leaf area–seed axis (PC2), while small-seeded species were surrounded by species similar in leaf economic traits, but dissimilar for leaf area–seed axis (Fig. 2). The leaf economic spectrum axis (leaf phosphorus, leaf nitrogen, and SLA) represents a range of strategies that go from fast to slow carbon assimilation rates (Reich et al. 1998, Wright et al. 2004). Thus, our results show that species with large seed mass germinate and establish in neighborhoods with diverse carbon processing strategies, while small-seeded species tend to grow in functional neighborhoods that have similar carbon processing strategies to them. On the other hand, results for the leaf area–seed axis showed an opposite relationship with seed mass; large-seeded species tend to be surrounded by more similar neighbors than small-seeded species. Given that the leaf area–seed axis reflects differences in structural and reproductive traits, these results indicate that small-seeded species tend to diverge from their neighbors in terms of display to capture light and stress tolerance strategies, while large-seeded species do not.

Discrepancies in patterns of trait dispersion for different traits have been previously found in several studies for community-level analyses and suggest that distinct ecological processes may operate simultaneously on species leading to patterns of functional over- and under-dispersion depending on the trait (Swenson and Enquist 2009, Herben and Goldberg 2014, Umaña et al. 2016). Our analyses go one step further by suggesting that trait dispersion varies not only according to the trait analyzed but is also dependent on the species—more specifically, their life-history strategies (in this case, related to seed mass). In agreement with this, a recent study found that seed mass relates to the strength of positive and negative interactions among species (Zepeda and Martorell 2019). Thus, small- and large-seeded species differ in the balance between

negative and positive interactions. If true, it is possible that the observed contrasting functional neighborhood composition between species with distant ecological strategies (e.g., small and large seed masses) could be the outcome of differences in the interplay of positive and negative interactions. However, inferring differences in species interactions is not possible with the data used in this study and future work should test for this.

We suggest that the opposed trends for the leaf economic axis and the leaf area–seed axis provide evidence of alternative strategies to succeed in the Luquillo forest. Given that the ultimate goal of a given plant is to maximize performance and persist in the neighborhood, seedling species in the LFDP might either diverge in carbon assimilation strategies (from their neighbors), while preserving similar architectural display to capture light and similar seed mass, or species might diverge in their architectural design and seed mass while preserving similar carbon assimilation rates. We examined this possibility by relating seedling survival (i.e., demographic performance) and species functional neighborhood. We found that seedling survival increases at greater trait similarity in the neighborhood based on any of the three functional PCA axes and the effect was stronger for the functional neighborhood based on the leaf economic axis (PC1) and PC3. This indicates that species that associate with neighborhoods that exhibit similar leaf carbon processing (PC1) and leaf C content (PC3) have lower mortality rates. However, seedling demographic performance might be balanced for species that diverge in leaf economic functional neighborhood (PC1) but converge in leaf area–seed functional neighborhood (PC2), given that survival was also negatively associated with SES MDN-PC2. This suggests that alternative functional configurations might be equivalent solutions for the environment in the LFDP. An example of similar compensatory strategies across traits is described by Valladares et al. (2002) who found that tree species in a lowland tropical forest in Panama exhibit alternative arrangement of morphological and architectural traits of crowns to achieve similar light use efficiencies. In our case, the compensatory strategies are evidenced at the neighborhood scale influencing interactions between a focal individual and its neighbors.

Species-level preferences to canopy openness do not relate to species-level functional neighborhoods

Our results show non-significant relationships between species-level understory light conditions and the functional dissimilarity in the species-level neighborhoods. This lack of relationship could be accentuated by species that were widely distributed across the different light conditions within the plot but had contrasting functional neighborhoods. For example, *P. acuminata* and *Piper blattarum* can be found across a broad range of light understory conditions. Indeed, previous studies have shown that tropical pioneer species, such as *P. blattarum*, are often found across different microsites that include gaps, gap edges, and forests interior (Hubbell and Foster 1986). However, both species exhibited divergent functional neighborhoods (Fig. 2): *P. acuminata* tends to have neighbors that are dissimilar along the leaf economics spectrum but similar in leaf area and seed mass traits, while *P. blattarum* tends to have neighbors similar along the leaf economics spectrum but dissimilar in leaf area and seed mass. Thus, despite the substantial differences in functional neighborhoods among species, many of these species showed weak associations with light conditions and were widespread in the LFDP. In support of the weak light species-specific associations, a recent study on the same site showed that although light has a positive effect on seedling survival at the whole-community level, about two-thirds of species studied showed non-significant effects (Uriarte et al. 2018).

Caveats

Our analyses were based on seedlings of tree species and did not consider co-occurring seedlings of liana species (which, at that ontogenetic stage, typically have the form of small trees similar to tree seedlings). Lianas constitute an important component of Neotropical forests (Schnitzer and Bongers 2002, 2011, Umaña et al. 2019) and are particularly abundant in the seedling community of the LFDP (Umaña et al. 2019). Although trait data for lianas are scarce, previous studies have suggested that lianas exhibit a similar range of life-history strategies than tree species (Gilbert et al. 2006). In particular, at early stages, lianas and trees do not exhibit clear differences in morphological and photosynthetic traits

(van der Sande et al. 2013). Although lianas differ from trees in hydraulic traits (van der Sande et al. 2019), these water-use-related traits are more relevant in the adult stage when lianas have thin stems carrying water for tens if not hundreds of meters. Overall, we expect that by expanding our dataset and including trait information of lianas, the trends of functional dispersion should be consistent with the patterns found for the tree seedling community. Integrating physiological and trait information of lianas should be a priority for future studies on seedling communities in tropical forests.

CONCLUSIONS

In this study, we show that the functional composition of species neighborhoods varies importantly across species suggesting that the strength of convergent/divergent forces structuring plant communities does not operate homogeneously within forest assemblages in the tropics. Given that seed mass variation is ubiquitous in communities from temperate to tropical regions, we should expect to find similar trends for forests in different regions and biomes. In particular, seedling species tend to associate with different species in their neighborhoods depending on intrinsic characteristics associated with life-history strategies (related to seed mass). These results indicate that there is not a single mechanism that influences all species equally at the seedling stage. Instead, species might be differentially affected by ecological forces that result in different functional neighborhood configurations. Not accounting for these differences might mask differences in species responses to local conditions and lead to inaccurate inferences of ecological mechanisms shaping natural communities.

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LITERATURE CITED

- Ågren, G. I., and T. Fagerström. 1984. Limiting dissimilarity in plants: Randomness prevents exclusion of species with similar competitive abilities. *Oikos* 43:369–375.
- Anderson-Teixeira, K. J., et al. 2015. CTFS-ForestGEO: A worldwide network monitoring forests in an era of global change. *Global Change Biology* 21:528–549.
- Baraloto, C., et al. 2012. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology* 100:690–701.
- Bates, D., M. Maechler, B. M. Bolker, and S. Walker. 2015. lme4: linear mixed-effects models using Eigen and S4. Version 1.1-12. <https://cran.r-project.org/web/packages/lme4/lme4.pdf>
- Canham, C. D. 1988. An index for understory light levels in and around canopy gaps. *Ecology* 69:1634–1638.
- Chapin III, F. S. 1991. Integrated responses of plants to stress. *BioScience* 41:29–36.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Condit, R., S. P. Hubbell, R. B. Foster, H. Stephen, and R. B. Foster. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a Neotropical forest. *American Naturalist* 140:261–286.
- Coomes, D. A., and P. J. Grubb. 2003. Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology and Evolution* 18:283–291.
- Cornelissen, J. H. C., et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335–380.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12:47–55.
- Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18:431–451.
- Díaz, S., et al. 2015. The global spectrum of plant form and function. *Nature* 529:1–17.
- Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service Research, Institute for Tropical Forestry, Rio Piedras, Puerto Rico.
- Foster, D. R., M. Fluet, and E. R. Boose. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological Applications* 9:555–572.
- Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53:77–88.
- Gilbert, B., S. J. Wright, H. C. Muller-Landau, K. Kitajima, and A. Hernández. 2006. Life history trade-offs in tropical trees and lianas. *Ecology* 87:1281–1288.
- Goldberg, D. E., and K. Landa. 1991. Competitive effect and response – Hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* 79:1013–1030.
- Guzman-Grajales, S. M., and L. R. Walker. 1991. Differential seedling responses to litter after hurricane Hugo in the Luquillo experimental forest, Puerto Rico. *Biotropica* 23:407–413.
- Harper, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.
- Henery, M. L., and M. Westoby. 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* 92:479–490.
- Herben, T., and D. E. Goldberg. 2014. Community assembly by limiting similarity vs. competitive hierarchies: testing the consequences of dispersion of individual traits. *Journal of Ecology* 102:156–166.
- Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19:166–172.
- Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314–329 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Keddy, P. A., and B. Shipley. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54:234–241.

- Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences USA* 112:797–802.
- Kraft, N. J. B. B., R. Valencia, and D. D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322:580–582.
- Kunstler, G., S. S. Lavergne, B. B. Courbaud, W. Thuiller, G. Vieilledent, N. E. Zimmermann, J. Kattge, and D. A. Coomes. 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters* 15:831–840.
- Larson, J., and J. L. Funk. 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology* 104:1284–1298.
- Lebrija-Trejos, E., P. B. Reich, A. Hernández, and S. J. Wright. 2016. Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest. *Ecology Letters* 19:1071–1080.
- Leishman, M. R., I. J. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pages 31–58 in M. Fenner, editor. *Seeds: the ecology of regeneration in plant communities*. CABI Publishing, Wallingford, UK.
- Lugo, A. E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190:145–161.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- Moles, A. T. 2018. Being John Harper: using evolutionary ideas to improve understanding of global patterns in plant traits. *Journal of Ecology* 106:1–18.
- Moles, A. T., M. Westoby, A. T. Moles, M. Westoby, and M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92:372–383.
- Muller-Landau, H. C. 2010. The tolerance – fecundity trade-off and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences USA* 107:4242–4247.
- Muller-Landau, H. C., S. J. Wright, O. Calderón, R. Condit, and S. P. Hubbell. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology* 96:653–667.
- Niinemets, Ü. 2007. Photosynthesis and resource distribution through plant canopies. *Plant Cell and Environment* 30:1052–1071.
- Paine, C. E. T., C. Baraloto, J. Chave, and B. Hérault. 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* 120:720–727.
- Poorter, L., and D. M. A. Rozendaal. 2008. Leaf size and leaf display of thirty-eight tropical tree species. *Oecologia* 158:35–46.
- Rees, M. 1995. Community structure in sand dune annuals: Is seed weight a key quantity? *Journal of Ecology* 83:857–863.
- Reich, P. B., D. S. Ellsworth, and M. B. Walters. 1998. Leaf structure (specific leaf area) modulates photosynthesis – nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology* 12:948–958.
- Ridler, T. W., and S. Calvard. 1978. Picture thresholding using an iterative selection methods. *IEEE Transactions on Systems, Man, and Cybernetics* 8:630–632.
- Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. *Trends in Ecology & Evolution* 17:223–230.
- Schnitzer, S. A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* 14:397–406.
- Swenson, N. G. 2014. *Functional and phylogenetic ecology in R*. Springer, New York, New York, USA.
- Swenson, N. G., and B. J. Enquist. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology* 90:2161–2170.
- Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, D. J. Lodge, C. M. Taylor, D. García-Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12:1344–1363.
- Turnbull, L. A., M. Rees, M. J. Crawley, and J. Crawley. 1999. Seed mass and the competition/colonization: a sowing experiment. *Journal of Ecology* 87:899–912.
- Umaña, M. N., J. Forero-Montaña, R. Muscarella, C. J. C. J. Nytch, J. Thompson, M. Uriarte, J. Zimmerman, and N. G. Swenson. 2016. Interspecific functional convergence and divergence and intraspecific negative density dependence underlie the seed-to-seedling transition in tropical trees. *American Naturalist* 187:99–109.
- Umaña, M. N., J. Forero-Montaña, C. J. Nytch, J. Thompson, M. Uriarte, J. K. Zimmerman, and N. G. Swenson. 2019. Dry conditions and disturbance promote liana seedling survival and abundance. *Ecology* 100:e02745.
- Umaña, M. N., C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2015. Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. *Ecology Letters* 18:1329–1337.

- Umaña, M. N., C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2017. A core-transient framework for trait-based community ecology: an example from a tropical tree seedling community. *Ecology Letters* 20:619–628.
- Uriarte, M., S. P. Hubbell, R. John, R. Condit, and C. D. Canham. 2005. Neighbourhood effects on sapling growth and survival in a neotropical forest and the ecological equivalence hypothesis. Pages 89–106 in D. Burslem, M. Pinard, and S. Hartley, editors. *Biotic interactions in the tropics: their role in the maintenance of species diversity*. Cambridge University Press, Cambridge, UK.
- Uriarte, M., R. Muscarella, and J. K. Zimmerman. 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change Biology* 24:e692–e704.
- Uriarte, M., N. G. Swenson, R. L. Chazdon, L. S. Comita, W. John Kress, D. Erickson, J. Forero-Montaña, J. K. Zimmerman, and J. Thompson. 2010. Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecology Letters* 13:1503–1514.
- Valladares, F., J. Skillman, and R. W. Pearcy. 2002. Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architecture: a case of morphological compensation. *American Journal of Botany* 89:1275–1284.
- van der Sande, M. T., L. Poorter, S. A. Schnitzer, B. M. J. Engelbrecht, and L. Markesteijn. 2019. The hydraulic efficiency–safety trade-off differs between lianas and trees. *Ecology* 1000:e02666.
- van der Sande, M. T., L. Poorter, S. A. Schnitzer, and L. Markesteijn. 2013. Are lianas more drought-tolerant than trees? A test for the role of hydraulic architecture and other stem and leaf traits. *Oecologia* 172:961–972.
- Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos* 74:159–164.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33:125–159.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Zepeda, V., and C. Martorell. 2019. Seed mass equalises the strength of positive and negative plant–plant interactions in a semi-arid grassland. *Oecologia* 190:287–296.
- Zimmerman, J. K., E. M. Everham, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto-Rico – Implications for tropical tree life- histories. *Journal of Ecology* 82:911–922.

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