

Ontogenetic shifts in trait-mediated mechanisms of plant community assembly

JESSE R. LASKY,^{1,2,7} BÉNÉDICTE BACHELOT,² ROBERT MUSCARELLA,² NAOMI SCHWARTZ,² JIMENA FORERO-MONTAÑA,³ CHRISTOPHER J. NYTCH,³ NATHAN G. SWENSON,⁴ JILL THOMPSON,^{5,6} JESS K. ZIMMERMAN,⁶ AND MARÍA URIARTE²

¹Earth Institute, Columbia University, New York, New York 10025 USA

²Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York 10027 USA

³Department of Biology, University of Puerto Rico, Río Piedras Campus, San Juan, Puerto Rico 00931 USA

⁴Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824 USA

⁵Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB United Kingdom

⁶Department of Environmental Sciences, University of Puerto Rico, Río Piedras Campus, San Juan, Puerto Rico 00936 USA

Abstract. Identifying the processes that maintain highly diverse plant communities remains a central goal in ecology. Species variation in growth and survival rates across ontogeny, represented by tree size classes and life history stage-specific niche partitioning, are potentially important mechanisms for promoting forest diversity. However, the role of ontogeny in mediating competitive dynamics and promoting functional diversity is not well understood, particular in high-diversity systems such as tropical forests. The interaction between interspecific functional trait variation and ontogenetic shifts in competitive dynamics may yield insights into the ecophysiological mechanisms promoting community diversity. We investigated how functional trait (seed size, maximum height, SLA, leaf N, and wood density) associations with growth, survival, and response to competing neighbors differ among seedlings and two size classes of trees in a subtropical rain forest in Puerto Rico. We used a hierarchical Bayes model of diameter growth and survival to infer trait relationships with ontogenetic change in competitive dynamics. Traits were more strongly associated with average growth and survival than with neighborhood interactions, and were highly consistent across ontogeny for most traits. The associations between trait values and tree responses to crowding by neighbors showed significant shifts as trees grew. Large trees exhibited greater growth as the difference in species trait values among neighbors increased, suggesting trait-associated niche partitioning was important for the largest size class. Our results identify potential axes of niche partitioning and performance-equalizing functional trade-offs across ontogeny, promoting species coexistence in this diverse forest community.

Key words: competition; intraspecific variation; Luquillo Forest Dynamics Plot; niche differentiation; ontogenetic niche shift; Puerto Rico; size-structured population; subtropical rain forest trees.

INTRODUCTION

Understanding the demographic and ecophysiological drivers of community assembly is a central goal in ecology. There is increasing evidence that variation in the environments that individuals experience and individual responses can affect community assembly (Clark 2010, Bolnick et al. 2011, Miller and Rudolf 2011, Violle et al. 2012). This intraspecific variation is often associated with ontogeny (Werner and Gilliam 1984, Parish and Bazzaz 1985), especially for forest trees (Niinemets 2010). Similarly, interspecific differences in traits that affect community assembly may vary in relevance across ontogenetic stages (Werner and Gilliam 1984, Parish and Bazzaz 1985, Poorter 2007, Muscarella et al. 2013, Spasojevic et al. 2014). Such ontogenetic

differences could promote species coexistence if there are trade-offs in performance across life stages, (i.e., if species with high performance at early life stages have poor performance in later stages) or if species partition niches across life stages (Loreau and Ebenhoh 1994, Moll and Brown 2008). Ontogenetic shifts are often overlooked in studies of diverse communities, which may obscure mechanisms of assembly and coexistence (Moll and Brown 2008, Piao et al. 2013). If community assembly processes are specific to particular ontogenetic stages, then predictive models of community dynamics will require knowledge of those ontogenetic shifts.

Species differences in performance (i.e., vital rates) are a major driver of community turnover, leading to dominance by species with traits that confer the greatest competitive ability. Plant physiological and demographic responses to abiotic stress may differ dramatically across ontogeny (Cavender-Bares and Bazzaz 2000, Wen et al. 2008, Niinemets 2010, Steppe et al. 2011, Kitajima et al. 2013). One hypothesis posits that interspecific variation in seedling survival in shade is a primary driver

Manuscript received 22 September 2014; revised 15 January 2015; accepted 3 February 2015. Corresponding Editor: D. C. Laughlin.

⁷ E-mail: jl3985@columbia.edu

of community change between seedling and sapling stages (Hubbell and Foster 1992, Niinemets 2006) and that this transition represents a major bottleneck in community assembly (Poorter 2007). For trees in closed-canopy forests, light levels associated with canopy position and local tree crowding are a major axis of ontogenetic environmental change (Pacala et al. 1996), yet different traits may confer shade tolerance to seedlings compared with adults (Lusk and Warton 2007, Wright et al. 2010). For example, Lusk and Warton (2007) found a shift in the relationship between specific leaf area (SLA) and shade tolerance in deciduous trees, from negative in seedlings, to positive in saplings. In some cases, studies have found that species with apparently asymmetric competitive abilities frequently co-occur (Kneitel and Chase 2004, Uriarte et al. 2012, Lasky et al. 2014a). This co-occurrence may be facilitated by ecophysiological constraints that generate demographic trade-offs across ontogenetic stages (Wright et al. 2010), e.g., species with relatively good adult growth or survival may perform poorly as seedlings. Such trait-based ontogenetic trade-offs may equalize overall performance and promote coexistence of functionally diverse competitors.

The role of species interactions, such as competition and herbivory, in driving community assembly may also be life-stage specific and thus obscured if ontogeny is overlooked (Werner and Gilliam 1984, Schiffers and Tielbörger 2006, Moll and Brown 2008, Armas and Pugnaire 2009, Piao et al. 2013, Barabás et al. 2014). Niche partitioning along functional trait axes may enable species to coexist, as evidenced by better performance when surrounded by neighbors with divergent trait values (Uriarte et al. 2010, Lasky et al. 2014a). Niche partitioning may have an ontogenetic component; for example, species may stably coexist due to resource niche partitioning at a single life stage despite niche overlap during other stages (Moll and Brown 2008, Barabás et al. 2014). For trees, species that differ in their maximum height may compete weakly as adults if they partition light environment niches, although such effects may not be apparent at the seedling stage. In contrast, the demographic effects of natural enemies and enemy-mediated niche partitioning may be strongest for seedlings, due to their limited stored resources (Janzen 1970, Boege and Marquis 2005). Additionally, the herbivore and parasite species that attack plants may differ across plant ontogeny, as do the traits involved in defense (Boege and Marquis 2005, Barton and Koricheva 2010), creating further potential for ontogenetic change in trait-mediated interactions with neighbors.

While ontogenetic shifts have often been studied in the context of trophic communities, there is much less known about the role of ontogenetic niche shifts in communities of species at the same trophic level (Miller and Rudolf 2011). Published demographic studies of ontogenetic shifts in plant communities have also tended

to focus on a single or few species (e.g., Miriti 2006, Armas and Pugnaire 2009, Soliveres et al. 2010). Scientists have taken steps to study how assembly mechanisms change across tree ontogeny in tropical forests (Webb and Peart 2000, Poorter 2007, Swenson et al. 2007, Swenson and Enquist 2009, Baldeck et al. 2013, Iida et al. 2014), but relatively little is known about these processes in high diversity communities. To address this research need, we develop a process-oriented approach to estimate the demographic effects of ontogenetic shifts for multiple mechanisms of trait-mediated community assembly. We take a spatially explicit approach to modeling variation in the tree neighborhoods of individual stems in order to estimate ontogenetic differences in niche partitioning among neighbors. By viewing species ontogenetic changes through the lens of functional trait variation, we can generate hypotheses about the ecophysiological mechanisms of ontogenetic change (McGill et al. 2006, Webb et al. 2010) and make understanding the high taxonomic diversity in tropical forests more tractable.

Here, we studied ontogenetic change in the relationship between species functional traits, demography, and responses to neighbors. We focused on interspecific variation in five traits measured on adult trees: SLA, leaf N, wood density, seed mass, and maximum height. Based on previous findings in the literature (e.g., Kitajima 1994, Poorter and Rose 2005, Valladares and Niinemets 2008), we predicted specific ontogenetic shifts in the role of each trait (Table 1) and evaluated our predictions using data from a subtropical wet forest in the Luquillo Experimental Forest of Puerto Rico. We ask the following three central questions.

1. *Do relationships between species' adult functional traits and their average performance (growth and survival) change with ontogeny?*—If so, do trait–performance relationships reverse with ontogenetic stage, e.g., from positive to negative, suggesting ontogenetic trade-offs associated with trait variation? We predict traits associated with tissue conservation (low SLA), early nutrient stores (high seed mass), and low palatability (low leaf N) will be positively associated with seedling survival rates because of the importance of carbon limitation and herbivore impacts on seedlings compared to adults (Table 1). As trees become larger, we expect that maximum height, which is associated with adult light niche, will be a strong predictor of average growth, and that wood density, which is associated with structural integrity, will be a strong predictor of adult survival.

2. *Does the relationship between a species' trait values and its response to neighborhood crowding change with ontogeny, indicating stage-specific responses to resource gradients?*—We predict that smaller trees will show greater declines in growth and survival due to resource competition (e.g., for light) associated with crowding by (potentially larger) neighbors, and that acquisitive strategies characterized by high SLA will be associated

TABLE 1. Hypothesized relationships between traits and stage-specific average performance (i.e., growth or survival), response to crowding by neighbors, and niche differences for two size classes (small and large) of trees in a subtropical rain forest in Puerto Rico.

Trait	Average performance		Response to crowding		Niche differences		Comments
	Small	Large	Small	Large	Small	Large	
Leaf N	+G,-S	+G					High leaf N is associated with palatability to herbivores, which is particularly important for seedlings (Coley and Barone 1996, Poorter et al. 2004).
Max. height		+		+		+	Species reaching the canopy may have greater access to light (King et al. 2005). Emergent species are not sensitive to crowding (Loehle 2000), but species of differing maximum heights may have weak competitive effects on each other (Kohyama et al. 2003).
Seed size	+		+				Large seeds provide resources for seedlings (Foster 1986, Westoby et al. 1992) and are associated with shade tolerance (Poorter and Rose 2005).
SLA	+G,-S	+G	-	-	+	+	High SLA is associated with susceptibility to herbivory (Coley et al. 1985) and shade intolerance (Markestijn and Poorter 2009), but species of differing SLA may have weak negative effects on each other (Lasky et al. 2014a).
Wood density	-G,+S	-G,+S	+				Wood density provides structural support and resistance to pests (Kitajima 1994, Chave et al. 2009) and shade tolerance (Augsburger 1984, Valladares and Niinemets 2008).

Notes: Each cell in the table represents a combination of assembly mechanism, trait, and size class (i.e., small or large). Positive (+) or negative (-) relationships are shown between each trait and assembly mechanism, which may be specific to growth (G) or survival (S). Niche differences are evidenced by greater performance as neighbor trait differences increase. SLA is specific leaf area.

with greater declines in survival under crowding. We expect weaker crowding effects for large trees, although we expect high SLA will also be associated with sensitivity to crowding among large trees.

3. *Do trait differences with neighbors correspond to greater performance, indicating local niche partitioning associated with functional trait variation?*—If so, do such effects change with ontogeny, suggesting the existence of stage-specific niche partitioning? We expect that maximum height will be associated with niche differences and that species with different maximum height will show weaker competition when compared to competition among species with similar maximum heights. Furthermore, we expect SLA will be associated with niche differences, most strongly among small trees that are likely light-limited, and SLA variation may be associated with resource use niche variation.

METHODS

Study site

The Luquillo Forest Dynamics Plot (LFDP) is a 16-ha permanent plot located in subtropical wet forest of northeast Puerto Rico (18°20' N, 65°49' W, Thompson et al. 2002; see Plate 1). Mean annual rainfall in the LFDP is ~3500 mm/yr and elevation ranges from 333 m to 428 m above sea level (Thompson et al. 2002). Soils are formed from volcanoclastic rock (Soil Survey Staff 1995).

Census data

Tree censuses have been conducted in the LFDP approximately every five years since 1990. All free-standing woody stems with dbh \geq 1 cm (diameter at breast height 1.3 m from the ground) were tagged, identified to species, mapped, and measured (Thompson et al. 2002). We calculated absolute diameter growth and stem survival between censuses in 2005 to 2010. We focused on a single stem from each (potentially multi-stemmed) individual, typically the largest stem, designated as the main stem when the individual was first censused. Growth values that were greater than five standard deviations above a species mean for each size class were considered likely measurement errors and excluded from analyses. Palm and tree fern allometry differs from other species in that height growth is weakly related to diameter growth; thus we modeled their survival but did not model their growth.

The LFDP has 213 1 \times 2 m seedling plots distributed across the whole 16-ha plot. We used seedling censuses from 2004, 2007, 2008, 2009, and 2010 when all seedlings with height \geq 10 cm and dbh < 1 cm in these plots were counted, tagged, and identified to species. Seedlings that grew to be at least 1 cm dbh entered the census of all plot stems. Root collar diameter was measured during each census for each tagged individual. We modeled seedling survival but not growth because seedling growth is subject to high observation error, e.g., as stems break, different stems may be subsequently measured on each

individual. Despite the potential error in growth measurements, we included root collar diameter as a predictor of survival due to the rapid change in survival as seedling grow (Comita et al. 2009). We modeled the survival of each seedling between each pair of subsequent censuses. A total of 108 species were included in this study: 68 species were present in both the 2005 census having stems at least 1 cm dbh and in seedling plots; 35 species were present as stems at least 1 cm dbh but not as seedlings; five species were present as seedlings but not as larger stems (Appendix: Table A1).

Functional traits

We collected trait data for all woody species present in the LFDP using standard protocols with minor exceptions noted below (Cornelissen et al. 2003, Swenson et al. 2012). We selected five functional traits that are believed to represent fundamental functional trade-offs in life-history differentiation among tree species (Wright et al. 2010). We measured leaf N (percentage N of oven-dry mass), specific leaf area (SLA, cm^2/g), wood density (g/cm^3), maximum height (m), and seed dry mass (g). For each species, leaf traits were measured on sun-exposed leaves (where possible) or leaves from the crowns of large individuals (Swenson et al. 2012). For most species, we measured wood density using an increment borer in trees 10–20 cm in diameter at 1 m off the ground. For species that did not reach this size, we measured wood density using branch material (Swenson et al. 2012). Four of these traits (SLA, leaf N, wood density, and seed mass) possibly vary across size classes within species, potentially limiting our ability to learn about community assembly via adult traits. Nevertheless, interspecific variation in traits may be largely consistent across ontogeny (Iida et al. 2014, Spasojevic et al. 2014), and traits measured on adults often correspond to major axes of niche, demographic history, and life history variation among species (Kraft et al. 2010, Uriarte et al. 2010, Wright et al. 2010, Rüger et al. 2012, Lasky et al. 2013, 2014a). Here we focus on adult traits as predictors of demography across different life stages. The mean trait value for each species was used in all analyses below. Leaf N and SLA were positively correlated (Spearman's rank correlation, $\rho = 0.48$) while all other traits showed weaker correlations (all $|\rho| < 0.38$, Appendix: Table A2). We did not have trait data for one species (*Cyathea arborea*) comprising 151 stems that was assigned the mean of all species at Luquillo for its species trait values.

Ontogenetic classes

In order to make inferences about the importance of ontogeny, we made ontogenetic comparisons, i.e., smaller individuals of a species were compared with larger individuals of that same species (Spasojevic et al. 2014). By contrast, dividing individuals into size classes that are invariant across species would result in comparisons of individuals of small-statured species

with individuals of large-statured species, which is not an ontogenetic comparison. To assess the implications of size class approaches, we conducted parallel analyses where the same size class thresholds (8.3 and 5.7 cm dbh for survival and growth, respectively) were used for all species (Appendix: Fig. A6).

For trees in the 2005 census that had at least one stem with $\text{dbh} \geq 1$ cm, we divided the individuals of each species evenly (or as close as possible when the number of individuals was not a multiple of two) into two species-specific size classes based upon the main stem of each individual and on the quantiles of dbh measurements for each species (Appendix: Figs. A1 and A2). Because each species was divided evenly among size classes, species composition and their respective abundances were approximately equivalent for all size classes, i.e., community composition did not vary with size class. Size class cutoffs for stems with $\text{dbh} \geq 1$ cm were calculated separately for the growth and survival data sets (i.e., live stems in 2005 that were dead in 2010 were not included in defining quantiles for the growth data set). Seedlings (woody stems ≥ 10 cm in height with $\text{dbh} < 1$ cm) present in the seedling plots between 2004 and 2009 were our smallest size class and were used in survival analyses.

Modeling ontogenetic shifts in trait-mediated assembly

We built hierarchical Bayes models of stem growth and survival that we separately fit to each size class and trait combination. For each ontogenetic stage-specific model, we included parameters that described the effect of three different mechanisms by which interspecific trait variation can be associated with community assembly (Lasky et al. 2014a). In order to answer the questions posed in the *Introduction*, we focus on changes in the estimated parameter values for these processes across size classes. Our model structure, implementation, and prior specification followed that of Lasky et al. (2014a) with three exceptions: (1) we stratified the analyses by size class, (2) we did not include effects of hierarchical (i.e., signed) neighborhood trait differences, as we found them to be weak in our previous study (Lasky et al. 2014a), and (3) we included dbh interactions with crowding, as sensitivity to crowding may change as trees grow larger (Niinemets 2010).

Our model of growth took the form:

$$E(\log(g_{si})) = \beta_{1s} + \beta_{2s}\log(\text{NCI}_{si}) + \beta_{3s}\log(\text{NCIS}_{si}) \\ + \beta_{4s}\log(\text{size}_{si}) + \beta_{5s}\log(\text{size}_{si}) \\ \times \log(\text{NCI}_{si}) \quad (1)$$

where $E(\log(g_{si}))$ is the expected log growth of stem i of species s . Our stem survival model followed a similar form except that we used logistic regression. Hereafter, when discussing covariates (e.g., NCI) in the text, we drop subscripts to improve readability. The latter four terms in Eq. 1 include covariates corresponding to crowding in the neighborhood surrounding the stem

(NCI; Uriarte et al. 2004), trait differences with neighbors (NCIS: NCI weighted by trait similarity), stem size (root collar diameter for seedlings, dbh for stems ≥ 1 cm dbh), and the interaction between crowding and stem size, respectively. For stems with dbh ≥ 1 cm (i.e., not seedlings), we defined the neighborhood crowding index (NCI) for each stem i based on the size and distance of its neighbors

$$NCI_{si} = \sum_{j=1, i \neq j}^J \frac{dbh_j^2}{d_{ij}^2} \tag{2}$$

where d_{ij} is the distance between stem i and neighbor j of which there are J total neighbors within a radius of 20 m (Uriarte et al. 2004). Note that we did not stratify neighbors by size class, i.e., neighbors J included stems of all size classes at least 1 cm dbh regardless of the size of focal stem i . To avoid edge effects, we did not model growth and survival of stems less than 20 m from plot boundaries. For seedlings, NCI was replaced by a seedling crowding index calculated as the total number of seedlings present in the 1×2 m seedling plot p at time t , i.e., NCI was not size- and distant-dependent for seedlings because specific locations of seedlings within plots were not available. Additionally, for seedlings, we did not include an interaction term between size and crowding due to the variation in seedling size measurements that changed when stems broke, and variation in root collar diameter measurement locations that was driven by changes in leaf litter depth. We modeled survival of each seedling across each census interval, including an individual random effect in seedling survival models to account for repeated observations of the same individual. As seedling census intervals varied, we used time as a covariate in seedling survival models.

Ontogenetic change in trait relationships with average demographic rates.—To address question 1 in the *Introduction*, we modeled how species traits affect species average growth or survival, β_{1s} , in a second-level, i.e., species-level, regression:

$$\beta_{1s} = \beta_{1,0} + F_s \beta_1 + \varepsilon_{1s} \tag{3}$$

where β_1 determines the effect of functional trait F_s , ε_{1s} is the normally distributed random effect of species s , and $\beta_{1,0}$ is the intercept for all species. High values of $|\beta_1|$ indicate a close link between interspecific trait variation and average growth or survival, independent of neighborhood variation. We determined if traits were associated with ontogenetic trade-offs by comparing the sign of β_1 for each trait in different size classes; significant but opposite signs (e.g., significant negative β_1 for seedlings vs. significant positive β_1 for large trees) were considered evidence of a tradeoff.

Ontogenetic change in trait associations with response to crowding.—To address question 2 in the *Introduction*, we modeled how a focal tree’s traits mediate its response to crowding, β_{2s} (see Eq. 1), in an additional second-level regression:

$$\beta_{2s} = \beta_{2,0} + F_s \beta_2 + \varepsilon_{2s} \tag{4}$$

where β_2 determines the influence of functional trait F_s on species response to NCI. High values of $|\beta_2|$ indicate an association between a trait and species response to crowding.

Ontogenetic change in trait-mediated niche differences.—To address question 3 in the *Introduction*, we estimated whether crowding effects were mediated by absolute trait differences between focal stem i and neighbors j (of J_k neighbors of species k) as follows:

$$NCIS_{si} = \sum_{k=1}^S \left[|\lambda_{sk}| \sum_{j=1, i \neq j}^{J_k} \frac{dbh_j^2}{d_{ij}^2} \right] \tag{5}$$

where s is the focal species and S the total number of species in the neighborhood. The effect of crowding by each neighboring stem j is mediated by the absolute value of species trait difference λ_{sk} , which is calculated as $\lambda_{sk} = F_s - F_k$, where F_s and F_k are the traits of focal species s and neighboring species k , respectively (Uriarte et al. 2010). $NCIS = 0$ for conspecific neighbors (i.e., $s = k$). For seedlings, we used the sum of the differences between the value of the species mean traits of the focal seedling i and the species traits of all of the other seedlings present in the seedling plot p at time t :

$$NCIS_{ptsi} = \sum_{k=1}^S [|\lambda_{sk}| n_k] \tag{6}$$

where n_k represents the abundance of the neighboring seedling species k in the plot p at time t . The effect of NCIS is determined by the sign of the β_{3s} coefficient (Eq. 1), with positive values indicating that greater trait differences with neighbors are associated with greater growth or survival.

Species-specific size-dependent differences in growth and survival within each size class were modeled via the dbh parameter (β_{4s}), which was not dependent on species trait values. For the seedling survival model, dbh was replaced by the root collar diameter of the seedling. Species-specific differences in the interaction between size and crowding were modeled as β_{5s} , which was not dependent on species trait values. For regression purposes, NCI and NCIS were transformed by adding 1 and taking the log because metrics were highly right-skewed. We standardized $\log(\text{dbh})$ values within size classes, for each species, in addition to seedling root collar diameter for each species, to mean zero and unit standard deviation. We similarly standardized other covariates (species-level trait values, $\log(\text{NCI})$ and $\log(\text{NCIS})$) within each size class. Growth values were scaled to unit standard deviation for each size class in order to facilitate comparisons of parameter effects among size classes.

Interspecific variation in trait-mediated crowding and dbh coefficients were modeled such that species-specific parameters β_{3s} , β_{4s} , and β_{5s} were drawn from normal hyper-distributions with means β_3 , β_4 , and β_5 , respec-

tively. We also incorporated random effects at the plot, census and individual levels in the seedling survival model because the data included multiple seedling censuses, although we modeled survival between each pair of consecutive censuses.

We fit separate models for each size class and trait combination. All parameters were given proper, diffuse priors and posterior sampling was conducted via Markov chain Monte Carlo (MCMC; details in the Appendix). We fitted survival models for trees with dbh ≥ 1 cm and growth models using Gibbs sampling in JAGS software (*available online*)⁸. For seedling survival models, Gibbs sampling resulted in poor model convergence, thus we used Hamiltonian Monte Carlo implemented in Stan software (Stan Development Team 2014), which resulted in rapid convergence. Convergence of MCMC was verified using the diagnostic of Gelman and Rubin (1992; Appendix: Table A3).

Parameters were considered significantly different from 0 when 95% CIs excluded 0. We also sought to compare parameters for models of small vs. large trees for the same trait. To do so, we converted each parameter back to its previous, non-standardized scale, because covariate means and standard deviations (used to standardize within size class) differed among size classes. We then randomly sampled posteriors of each parameter and calculated the 2.5 and 97.5 percentile of differences between parameter samples to obtain a 95% CI on parameter differences. Parameters at different size classes were considered significantly different if the 95% CI excluded zero. We did not test for differences between seedling survival parameters and parameters for trees with dbh ≥ 1 cm due to differences in data collection and models.

RESULTS

Ontogenetic change in demographic rates of the average species

Average species dbh growth increments were greater in the larger size class of stems at least 1 cm dbh (Appendix: Fig. A3). Within both non-seedling size classes larger dbh trees had significantly greater absolute growth, although the dbh effect was weaker for larger trees (Appendix: Fig. A3). Higher neighborhood crowding was associated with reduced growth, although this effect was slightly diminished for larger size classes (Appendix: Fig. A3). Interactions between dbh and crowding were mostly non-significant in the smaller tree size class (Appendix: Fig. A3). However, the interaction was significantly positive in larger classes, indicating larger trees showed less sensitivity to crowding.

Average survival across species was greatest in the larger size-class of tree stems (at least 1 cm dbh) (Appendix: Fig. A4). Seedlings with larger root collar diameter had higher survival and stems with larger dbh within the smaller size class of tree stems had higher

survival. However, the dbh effect disappeared in the largest size class (Appendix: Fig. A4). Averaged across species, seedlings showed greater survival in plots with greater seedling crowding, i.e., plots with more seedlings. On the contrary, for tree stems, survival was only weakly related to crowding by other stems, and focal tree dbh interactions with crowding were weakly related to survival (Appendix: Fig. A4).

Ontogenetic change in trait associations with average performance.—Contrary to our expectations (Table 1), relationships between interspecific trait variation and species average growth and survival (i.e., β_{1s} parameters, averaged across individuals, independent of neighborhood and dbh variation) within each size class were largely consistent across size classes (Fig. 1a, b). For example, high species maximum height was associated with significantly greater growth while high wood density was associated with significantly less growth in both dbh size classes (Appendix: Fig. A5). Additionally, high wood density was always associated with high species survival (Fig. 2c). We show examples of traits (wood density, SLA, and maximum height) with distinct ontogenetic patterns in the relationships between species traits and average survival in Fig. 2. In contrast to wood density, SLA was not associated with survival in seedlings but was negatively related to survival for both size classes with dbh ≥ 1 cm (Fig. 2b). Alternatively, species maximum height (Fig. 2a) and seed mass were the only traits for which there were both significant positive and negative relationships with species survival within different size classes, suggesting these traits were associated with ontogenetic trade-offs. Seedlings of species with low maximum height had significantly higher survival in the seedling stage, while for the largest stem size class species with higher maximum height had significantly higher survival. Additionally, trees in the largest size class showed a significantly more positive relationship between survival and maximum height than trees in the smaller size class (Fig. 1b). For example, seedlings of *Dacryodes excelsa* (species maximum height ~ 30 m, seed mass 1.255 g), and *Guarea guidonia* (species maximum height ~ 23 m, seed mass 0.2508 g) survived between seedling censuses only 16% and 44% of the time, while tree stems in the largest size class had survival of 99% and 97%, respectively. On the other hand, *Psychotria brachiata* (maximum height ~ 5 m, seed mass 0.005 g) and *Miconia prasina* (maximum height ~ 8 m, seed mass 0.00032 g) survived between seedling censuses 74% and 68% of the time, while tree stems in the largest size class had survival of only 49% and 63%, respectively.

Ontogenetic change in trait associations with response to crowding.—In contrast to trait associations with species average growth and survival among individuals (β_1), trait associations with species response to crowding (β_2) were often size-class specific and showed significant ontogenetic changes for both growth and survival (Fig. 1c, d). Traits were more strongly related to growth response to crowding for trees in the smaller dbh size

⁸ <http://mcmc-jags.sourceforge.net/>

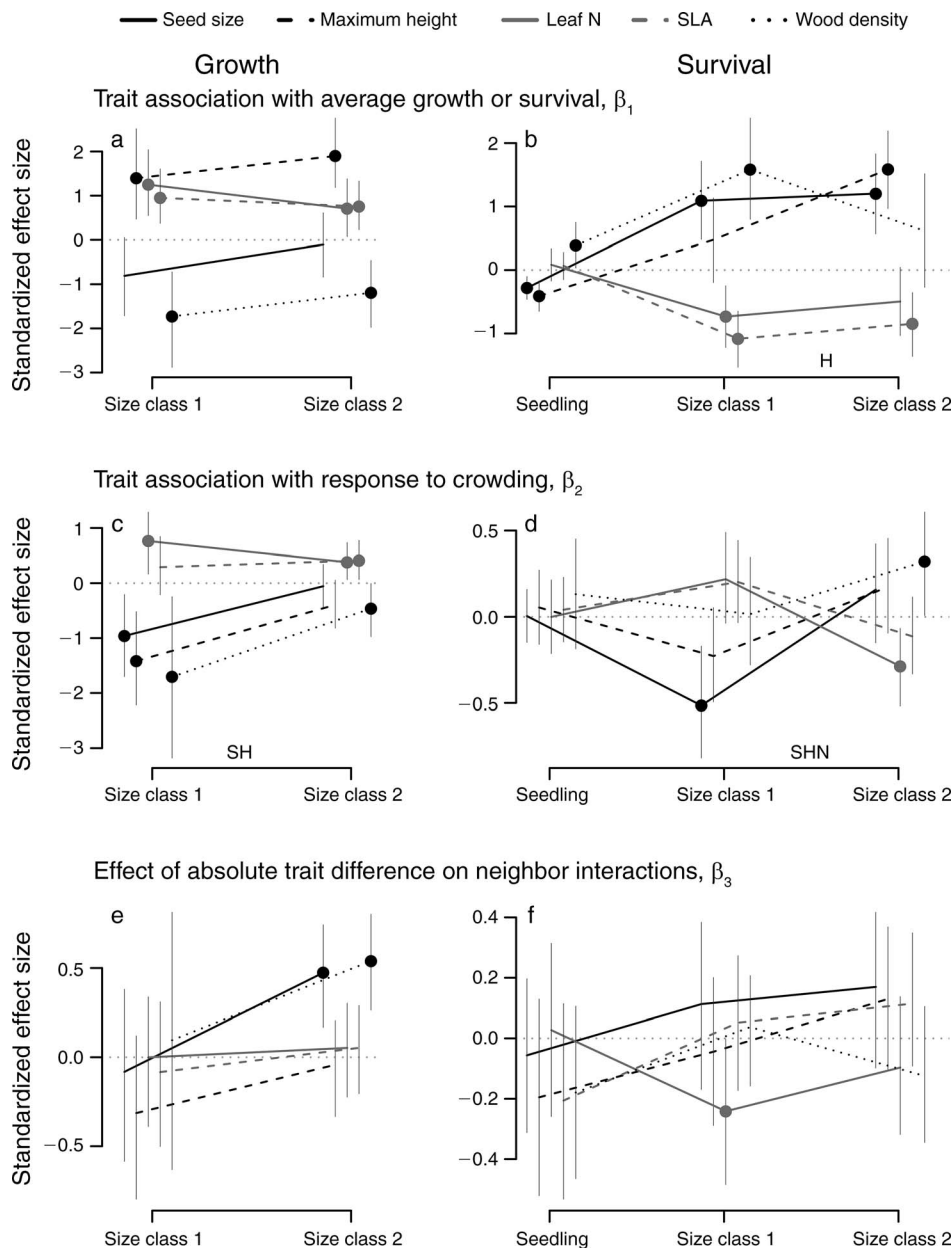


FIG. 1. Changes in trait associations with (a, c, e) growth and (b, d, f) survival across tree ontogeny, where standardized effect size estimates are shown to allow comparison among traits. Lines connect parameter estimates for the same trait across different size classes. Significant effects are indicated as solid circles. Capital letters indicate traits (seed size, S; maximum height, H; leaf N, N) where parameters significantly differ (based on 95% CI) between size class 1 and size class 2 on a nonstandardized (i.e., raw) scale. Vertical bars indicate 95% credible intervals (CIs). (e, f) Note that β_3 is the mean of a hyperdistribution of species-specific parameters for trait associations with niche differences. Positive standardized effect sizes for β indicate greater growth or survival with increasing values of the covariate. For example, (a) positive growth β_1 for SLA (all size classes) indicates species with greater SLA had greater growth, independent of crowding variation. (d) Positive survival β_2 for wood density (largest size class) indicates species with greater wood density were less sensitive to crowding effects (NCI) on survival. (e) Positive growth β_3 for wood density (largest size class) indicates greater growth for focal trees with high absolute wood density differences with neighbors (NCIS). Note that seedling survival is measured at 1–2-year intervals, while stems in size classes 1–2 are measured across 5-year intervals.

class, with species with high leaf N, low wood density, low seed size, and low maximum height showing less sensitivity to crowding. By contrast, in the largest size class, the relationship between crowding response and maximum height and seed size was significantly more

positive, i.e., species with high maximum height and seed size were not significantly more sensitive to crowding.

Trait relationships with survival responses to crowding also showed ontogenetic shifts. Survival of trees in the largest size class was significantly lower for species

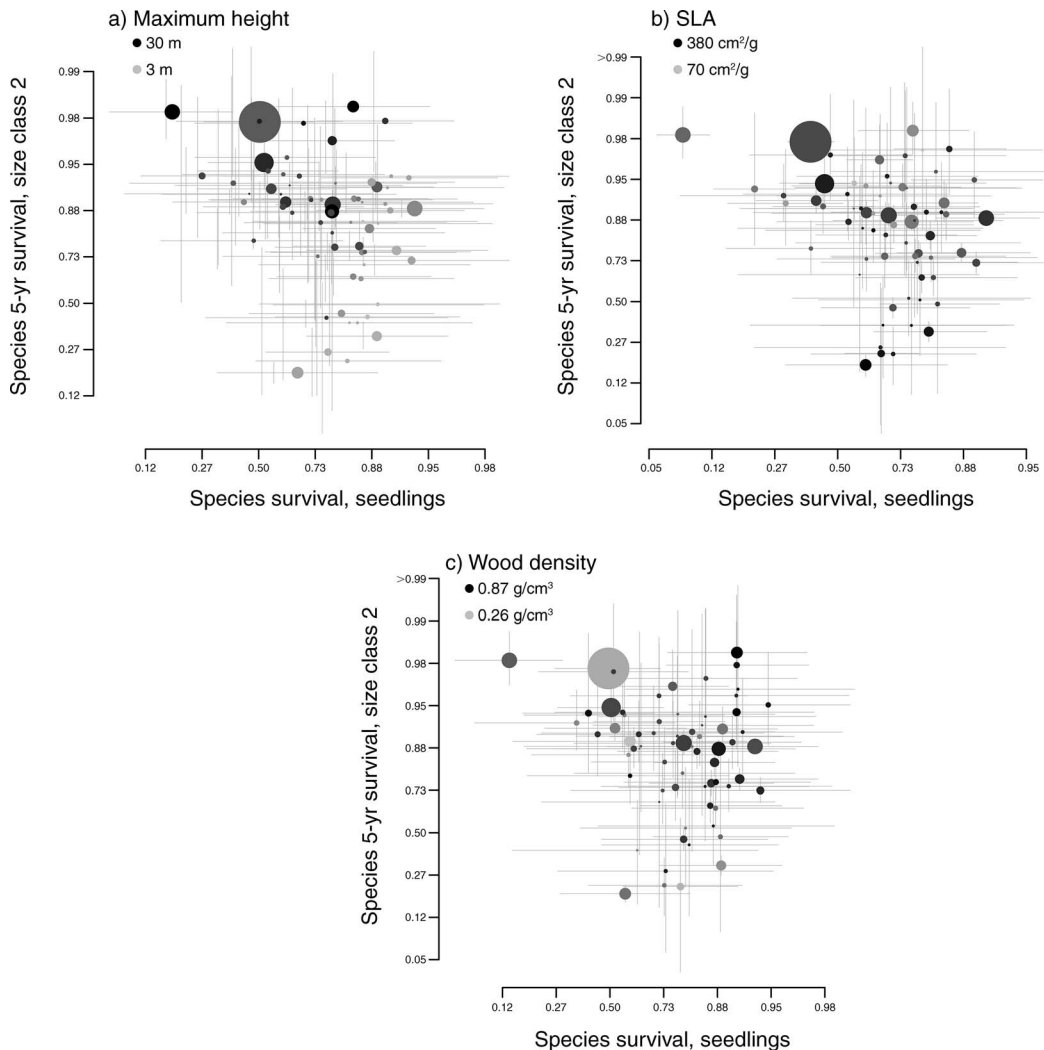


FIG. 2. Estimated species average survival rates as seedlings vs. survival in the largest dbh size class, with species trait values color-coded by the quantitative gray scale; keys in each panel indicate minimum (lightest gray) and maximum (black) trait values. Circle size is proportional to the square root of mean species relative abundance, averaged across the seedling and largest dbh size classes. Three largely uncorrelated traits with distinct ontogenetic relationships with survival are shown in the different panels. (a) Maximum height showed a significant trade-off, being negatively related to seedling survival but positively related to survival among the largest trees. (b) SLA was unrelated to seedling survival, but negatively related to survival among the largest trees. (c) Wood density was positively associated with species survival as seedlings and large trees. Gray lines represent 95% CIs. Note y -axis scaling differs slightly among panels.

with high leaf N and low wood density as crowding increased, but these relationships were not significant for the smaller size class with dbh ≥ 1 cm. Seed size, leaf N, and maximum height all showed significant ontogenetic shifts from smaller to larger trees with dbh ≥ 1 cm (Fig. 1d). For example, *Sloanea berteriana* (wood density 0.77 g/cm³, leaf N content 1.3%) had higher survival under high neighborhood crowding when in the largest size class but reduced growth under crowding in the smaller dbh size class, while *Schefflera morototoni* (wood density 0.42 g/cm³, leaf N content 2.2%) had lower survival under high crowding when in the largest size class but

little change in growth under crowding in the smaller size class.

Ontogenetic change in demographic relationships with neighborhood trait differences.—Species trait differences with neighbors had the most significant and positive relationships (β_3) with growth in the largest size class, although differences between size classes were not significant (Fig. 1e). In the largest size class, growth significantly increased as seed size and wood density differences with neighbors increased. Unexpectedly, seedlings tended to have higher survival as trait differences with neighboring seedlings decreased, although these effects were not significant (Fig. 1f). For

trees at least 1 cm dbh, trait difference relationships with survival were non-significant, except for the smaller size class of trees at least 1 cm dbh where increased difference in leaf N with neighbors was associated with significantly lower survival.

DISCUSSION

Identifying changes in community assembly across ontogenetic stages may suggest potential life history and ecophysiological mechanisms driving community turnover or promoting species coexistence (McGill et al. 2006, Adler et al. 2013). Ontogenetic changes in tree physiology and environment are extensive (Thomas and Winner 2002, Niinemets 2006, Rozendall et al. 2006, Barthélémy and Caraglio 2007, Wen et al. 2008, Niinemets 2010, Martin and Thomas 2013), but the consequences of ontogenetic differences for the assembly of diverse communities are less well known. Here, we used a process-oriented approach, linking interspecific functional trait variation with demography, in order to study ontogenetic differences in tree performance and response to neighbors. Overall, functional traits showed consistent associations with average growth and survival, i.e., trait associations with average demography did not reverse with ontogeny (which would indicate an ontogenetic tradeoff), largely consistent with previous empirical results (Wright et al. 2010, Iida et al. 2014). However, we found evidence for some trait-mediated ontogenetic trade-offs that might equalize performance across ontogeny (i.e., equalize per capita population growth rates), and therefore promote species coexistence (Loreau and Ebenhoh 1994, Chesson 2000, Adler et al. 2007). Positive growth in association with neighborhood functional differences was significant among larger trees, suggesting that local niche partitioning associated with wood density and seed size variation was important at later ontogenetic stages.

Ontogeny and trait associations with performance

Our results were partly consistent with our hypotheses about associations between traits and average performance, as we found less evidence for ontogenetic shifts than expected. First, high species SLA and leaf N were not associated with lower seedling survival as expected, but for both size classes of tree stems at least 1 cm dbh, SLA and leaf N were associated with lower survival. This may indicate that species with fast growth strategies and low herbivore defenses are relatively vulnerable to mortality throughout their lives (Wright et al. 2004). In contrast, Wright et al. (2010) found that the relationship between SLA and performance weakened for large trees in a Panamanian forest that has a much stronger dry season than our study site. We also found positive relationships between survival and wood density across size classes, likely because higher wood density confers greater resistance to damage (Kitajima 1994, Chave et al. 2009) or because high wood density is broadly associated with a conservative, slow life history with

high survival (Wright et al. 2010, Reich 2014). Future research efforts that collect trait data on individuals of different sizes that occupy different environments will help shed additional light on this question (Iida et al. 2014, Lasky et al. 2014c).

Ontogenetic trade-offs in the association between traits and performance may equalize the performance of functionally distinct species, promoting coexistence and functional diversity (Loreau and Ebenhoh 1994, Chesson 2000). Consistent with this hypothesis, we observed ontogenetic trade-offs from significant negative to significant positive associations between species average survival, and species maximum height and seed size (Fig. 2a). On the one hand, seedlings of species with short maximum height and small seed size had greater survival; on the other hand, species with tall maximum height and large seed size had greater survival as large stems. As a result, differences in survival across the whole life cycle may be small among species that differ in maximum height and seed size, thus promoting greater community diversity of maximum tree height and seed size (HilleRisLambers et al. 2012, Adler et al. 2013). Similarly, Iida et al. (2014) found a reversal in the relationship between mortality and leaf area from small to large diameter trees in a subtropical forest in Taiwan. In our study, the relative survival of species with tall maximum height may be greatest for large dbh individuals because they are likely to be higher in the canopy with greater access to light (Poorter et al. 2008). In contrast, shrubby short taxa such as species of *Psychotria*, *Piper*, and some *Miconia* in the Luquillo forest have rapid life histories and high mortality as canopy gaps close above them. The relationship between maximum height and survival may also explain the greater survival of the species with larger seed size in large dbh size classes (Moles and Westoby 2006). However, we know of no clear physiological mechanism to explain why species with high maximum heights and large seed size, such as *Dacryodes excelsa* and *Guarea guidonia*, should be at a disadvantage as seedlings compared with short, small-seeded taxa such as *Casearia* species. In fact, previous work at our site suggested that seed size is positively related to the probability of transition from seed to seedling, albeit across a slightly different study period from 2007 to 2012 when the forest canopy was less open (Muscarella et al. 2013). In a meta-analysis, Rose and Poorter (2003) found that in high light, seed size had little relation to seedling survival. Thus high light levels in the understory at Luquillo due to frequent hurricane disturbance might reduce the mortality of small-seeded seedling species in the understory. Finally, the relationship between seed size and adult survival, and maximum height and seedling survival may be driven by some correlated but unmeasured traits that affected survival. For example, the rapid growth of species with high maximum height, even when in smaller tree size classes (Figs. 1a and A5), may involve



PLATE 1. Luquillo Forest Dynamics Plot, in northeast Puerto Rico, with the common palm *Prestoea acuminata* in the foreground. Photo credit: J. R. Lasky.

a tradeoff with herbivore defense such that these species are more vulnerable as seedlings. Future research could resolve this question by directly quantifying defense mechanisms and incorporating these into demographic models.

The lack of significant ontogenetic trade-offs for other traits we studied does not preclude the existence of additional performance-equalizing trade-offs (Uriarte et al. 2012). Our results suggest that, to a large degree, plant functional traits measured on adults (i.e., our approach) correspond to general ecological strategies and are strong indicators of interspecific variation in average vital rates and physiology across ontogeny (Reich 2014). However, trait associations with response to crowding were much more specific to size classes and less predictable, indicating that more complex mechanisms may link traits with resource limitation. In particular, we found significant ontogenetic shifts indicating species with high maximum height, large seed size, and low leaf N were less sensitive to crowding when they had large diameter when compared to smaller stems. These shifts may correspond to trade-offs in response to crowding that equalize performance across the whole life cycle under high crowding conditions, promoting greater community diversity of these traits. Our results suggest that scientists using a functional

traits approach to model community demography (Rüger et al. 2012, Lasky et al. 2013, 2014a) might reasonably assume consistent trait relationships with average demography, but should include size-stage-specific responses to local environments.

Ontogenetic change in effects of neighborhood trait differences

The effects of competition for resources and niche overlap can change with ontogenetic stages, e.g., as trees grow larger, allowing for additional axes of niche partitioning beyond those possible for organisms with simple life cycles. We found significant evidence for trait-mediated niche differences primarily among the larger tree size classes, suggesting that niche partitioning is important even at a life stage when trees are likely to have crowns in the canopy and the greatest access to light resources. Furthermore, the strong niche partitioning among large individuals may result in niche partitioning effects on ecosystem functioning, in which large trees may play an outside role. Our findings suggest a potential for neighborhood trait diversity to enhance productivity and carbon storage among large trees due to niche complementarity (Lasky et al. 2014b). Uriarte et al. (2010) found evidence in the LFDP data that trait differences with neighbors were associated with greater growth or survival for 14 of the most common species. However, Uriarte et al. (2010) also found that stems that died between censuses tended to be surrounded by more functionally and phylogenetically diverse neighbors, suggesting that ecological filtering plays an important role in assembly at our study plot. Here we found significant negative relationships between leaf N differences with neighbors and survival among smaller trees at least 1 cm dbh. Our results suggest that ecological filtering effects associated with leaf N of smaller trees are more important than local niche partitioning for the traits considered here. However, note that local niche partitioning may also be driven by interactions among traits (Kraft et al. 2015), thus we cannot rule out additional complex axes of niche partitioning. The higher survival we observed for species of smaller trees surrounded by neighbors with similar leaf N may be partly driven by a positive relationship between conspecific tree density and survival (Comita et al. 2009). While hypotheses (Janzen 1970) and empirical results from the Luquillo forest (Comita et al. 2009) have identified negative effects of conspecific frequency as a stabilizing mechanism of coexistence at early life stages of tropical trees, our results for the five traits that we chose suggest that these effects on seedlings did not extend across species that have similar functional traits.

Previous findings for other tropical forests have been mixed with respect to whether species niche differences are manifested mostly among juveniles or adults (Webb and Peart 2000, Poorter 2007, Swenson et al. 2007, Swenson and Enquist 2009, Baldeck et al. 2013, Iida et al. 2014). For example, Swenson and Enquist (2009)

inferred no clear ontogenetic pattern in the effects of niche differences on tree distributions across a tropical dry forest plot. However, Swenson et al. (2007) found that across four tropical forest plots including the LFDP, phylogenetic overdispersion indicative of niche differences was stronger among larger size classes, consistent with our finding that larger size classes had better performance when surrounded by functionally diverse neighbors. In contrast, Baldeck et al. (2013) found little change in the relationship between environmental variables and community composition across size classes in several large tropical forest plots. However, studies of static distributional data (e.g., Webb and Peart 2000, Poorter 2007, Swenson and Enquist 2009, Baldeck et al. 2013) may be limited in their ability to distinguish between ontogenetic changes in assembly mechanisms vs. the accumulated effects of consistent mechanisms acting across ontogeny. Our approach is notable for using species-specific size classes, which allowed us to compare assembly processes for the same assemblages across size classes. We acknowledge that our results do not necessarily represent all potential ontogenetic niche shifts that affect tree community assembly, as other traits that we have not measured or analyzed here are also likely to affect tree community dynamics.

Conclusion

Understanding the empirical importance of ontogenetic ecological shifts in promoting diversity of species is a goal that deserves increased research attention (Miller and Rudolf 2011). Here, we revealed that commonly investigated plant functional traits are likely to be associated with ontogenetic stage-specific effects on community assembly, yielding mechanisms that potentially promote species coexistence. Seedling stages are often considered to be the most important in community assembly, because of the high mortality and potential for rapid change in species relative abundances (Poorter 2007). Our findings suggest that local niche partitioning may also play a major role in community dynamics for large trees. Long-term forest plots are essential systems for understanding ontogenetic change and community assembly because ontogenetic environment shifts (e.g., light environments) are dramatic and individuals can be followed across ontogeny. Our approach to identifying the functional basis of ontogenetic shifts in community assembly may be applied to additional systems where interspecific differences in demography can be related to functional traits.

ACKNOWLEDGMENTS

We thank all of the volunteers and Luquillo LTER technicians for their major contributions to the tree and seedling censuses. This work was supported by U.S. National Science Foundation (NSF) grants DEB-1050957 to MU, DEB-0516066, which supported tree censuses, respectively, and BSR-8811902, DEB-9411973, DEB-0080538, DEB-0218039, DEB-0620910 and DEB-0963447 to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, working with

the International Institute of Tropical Forestry (USDA Forest Service), for the Luquillo Long-Term Ecological Research Program. The U.S. Forest Service and the University of Puerto Rico and the Smithsonian Institution provided additional support.

LITERATURE CITED

- Adler, P. B., A. Fajardo, A. R. Kleinhesselink, and N. J. B. Kraft. 2013. Trait-based tests of coexistence mechanisms. *Ecology Letters* 16:1294–1306.
- Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- Armas, C., and F. I. Pugnaire. 2009. Ontogenetic shifts in interactions of two dominant shrub species in a semi-arid coastal sand dune system. *Journal of Vegetation Science* 20: 535–546.
- Augsburger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72:777–795.
- Baldeck, C. A., et al. 2013. Habitat filtering across tree life stages in tropical forest communities. *Proceedings of the Royal Society* 280:20130548.
- Barabás, G., G. Meszéna, and A. Ostling. 2014. Fixed point sensitivity analysis of interacting structured populations. *Theoretical Population Biology* 92:97–106.
- Barthélémy, D., and Y. Caraglio. 2007. Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany* 99:375–407.
- Barton, K. E., and J. Koricheva. 2010. The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. *American Naturalist* 175:481–493.
- Boege, K., and R. J. Marquis. 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology and Evolution* 20:441–448.
- Bolnick, D. I., et al. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26:183–192.
- Cavender-Bares, J., and F. A. Bazzaz. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* 124:8–18.
- 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.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Clark, J. S. 2010. Individuals and the variation needed for high species diversity in forest trees. *Science* 327:1129–1132.
- Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305–335.
- Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–899.
- Comita, L. S., M. Uriarte, J. Thompson, I. Jonckheere, C. D. Canham, and J. K. Zimmerman. 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *Journal of Ecology* 97:1346–1359.
- 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.
- Foster, S. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review* 52:260–299.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 457–472.
- HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking community assembly

- through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* 43:227–248.
- Hubbell, S. P., and R. B. Foster. 1992. Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* 63:48–61.
- Iida, Y., T. S. Kohyama, N. G. Swenson, S.-H. Su, C.-T. Chen, J.-M. Chiang, and I.-F. Sun. 2014. Linking functional traits and demographic rates in a subtropical tree community: the importance of size dependency. *Journal of Ecology* 102:641–650.
- Janzen, D. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- King, D. A., S. J. Davies, M. N. N. Supardi, and S. Tan. 2005. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology* 19:445–453.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.
- Kitajima, K., R. A. Cordero, and S. J. Wright. 2013. Leaf life span spectrum of tropical woody seedlings: effects of light and ontogeny and consequences for survival. *Annals of Botany* 112:685–699.
- Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7:69–80.
- Kohyama, T., E. Suzuki, T. Partomihardjo, T. Yamada, and T. Kubo. 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. *Journal of Ecology* 91:797–806.
- 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., M. R. Metz, R. S. Condit, and J. Chave. 2010. The relationship between wood density and mortality in a global tropical forest data set. *New Phytologist* 188:1124–1136.
- Lasky, J. R., I.-F. Sun, S.-H. Su, Z.-S. Chen, and T. H. Keitt. 2013. Trait-mediated effects of environmental filtering on tree community dynamics. *Journal of Ecology* 101:722–733.
- Lasky, J. R., M. Uriarte, V. Boukili, and R. L. Chazdon. 2014a. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proceedings of the National Academy of Sciences USA* 111:5616–5621.
- Lasky, J. R., M. Uriarte, V. K. Boukili, D. L. Erickson, W. John Kress, and R. L. Chazdon. 2014b. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters* 17:1158–1167.
- Lasky, J. R., J. Yang, G. Zhang, M. Cao, Y. Tang, and T. H. Keitt. 2014c. The role of functional traits and individual variation in the co-occurrence of *Ficus* species. *Ecology* 95:978–990.
- Loehle, C. 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *American Naturalist* 156:14–33.
- Loreau, M., and W. Ebenhoeh. 1994. Competitive exclusion and coexistence of species with complex life cycles. *Theoretical Population Biology* 46:58–77.
- Lusk, C. H., and D. I. Warton. 2007. Global meta-analysis shows that relationships of leaf mass per area with species shade tolerance depend on leaf habit and ontogeny. *New Phytologist* 176:764–774.
- Markestijn, L., and L. Poorter. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* 97:311–325.
- Martin, A. R., and S. C. Thomas. 2013. Size-dependent changes in leaf and wood chemical traits in two Caribbean rainforest trees. *Tree Physiology* 33:1338–1353.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- Miller, T. E. X., and V. H. W. Rudolf. 2011. Thinking inside the box: community-level consequences of stage-structured populations. *Trends in Ecology and Evolution* 26:457–466.
- Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology* 94:973–979.
- Moles, A. T., and M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113:91–105.
- Moll, J. D., and J. S. Brown. 2008. Competition and coexistence with multiple life-history stages. *American Naturalist* 171:839–843.
- Muscarella, R., M. Uriarte, J. Forero-Montaña, L. S. Comita, N. G. Swenson, J. Thompson, C. J. Nytych, I. Jonckheere, and J. K. Zimmerman. 2013. Life-history trade-offs during the seed-to-seedling transition in a subtropical wet forest community. *Journal of Ecology* 101:171–182.
- Niinemets, Ü. 2006. The controversy over traits conferring shade-tolerance in trees: ontogenetic changes revisited. *Journal of Ecology* 94:464–470.
- Niinemets, Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management* 260:1623–1639.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66:1–43.
- Parish, J. A. D., and F. A. Bazzaz. 1985. Ontogenetic niche shifts in old-field annuals. *Ecology* 66:1296–1302.
- Piao, T., L. Comita, G. Jin, and J. Kim. 2013. Density dependence across multiple life stages in a temperate old-growth forest of northeast China. *Oecologia* 172:207–217.
- Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? *American Naturalist* 169:433–442.
- Poorter, L., and S. Rose. 2005. Light-dependent changes in the relationship between seed mass and seedling traits: a meta-analysis for rain forest tree species. *Oecologia* 142:378–387.
- Poorter, L., M. van de Plassche, S. Willems, and R. G. A. Boot. 2004. Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biology* 6:746–754.
- Poorter, L., et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* 89:1908–1920.
- Reich, P. B. 2014. The world-wide “fast–slow” plant economics spectrum: a traits manifesto. *Journal of Ecology* 102:275–301.
- Rose, S., and L. Poorter. 2003. The importance of seed mass for early regeneration in tropical forest: a review. Long-term changes in tropical tree diversity: studies from the Guiana Shield, Africa, Borneo and Melanesia. Tropenbos International, Wageningen, Netherlands.
- Rozendall, D. M. A., V. H. Hurtado, and L. Poorter. 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology* 20:207–216.
- Rüger, N., C. Wirth, S. J. Wright, and R. Condit. 2012. Functional traits explain light and size response of growth rates in tropical tree species. *Ecology* 93:2626–2636.
- Schiffers, K., and K. Tielbörger. 2006. Ontogenetic shifts in interactions among annual plants. *Journal of Ecology* 94:336–341.
- Soil Survey Staff. 1995. Order 1 soil survey of the Luquillo long-term ecological research grid, Puerto Rico. USDA, Natural Resources Conservation Service, Lincoln, Nebraska, USA.

- Soliveres, S., L. DeSoto, F. T. Maestre, and J. M. Olano. 2010. Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspectives in Plant Ecology, Evolution and Systematics* 12:227–234.
- Spasojevic, M. J., E. A. Yablon, B. Oberle, and J. A. Myers. 2014. Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* 5: art129.
- Stan Development Team. 2014. Stan: a C++ library for probability and sampling, Version 2.5.0.
- Steppe, K., Ü. Niinemets, and R. Teskey. 2011. Tree size- and age-related changes in leaf physiology and their influence on carbon gain. Pages 235–253 in F. C. Meinzer, B. Lachenbruch, and T. E. Dawson, editors. *Size- and age-related changes in tree structure and function*. Springer, Dordrecht, The Netherlands.
- 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.
- Swenson, N. G., B. J. Enquist, J. Thompson, and J. K. Zimmerman. 2007. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88:1770–1780.
- Swenson, N. G., et al. 2012. Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. *Ecology* 93:490–499.
- Thomas, S. C., and W. E. Winner. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiology* 22:117–127.
- Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, D. J. Lodge, C. M. Taylor, D. Garcia-Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12:1344–1363.
- Uriarte, M., J. S. Clark, J. K. Zimmerman, L. S. Comita, J. Forero-Montaña, and J. Thompson. 2012. Multidimensional trade-offs in species responses to disturbance: implications for diversity in a subtropical forest. *Ecology* 93:191–205.
- Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology* 92:348–360.
- 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., and Ü. Niinemets. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics* 39:237–257.
- Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* 27:244–252.
- Webb, C. O., and D. R. Peart. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88:464–478.
- Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* 13:267–283.
- Wen, S., N. Fetcher, and J. K. Zimmerman. 2008. Acclimation of tropical tree species to hurricane disturbance: ontogenetic differences. *Tree Physiology* 28:935–946.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Westoby, M., E. Jurado, and M. Leishman. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution* 7:368–372.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Wright, S. J., et al. 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91:3664–3674.

SUPPLEMENTARY MATERIAL

Ecological Archives

The Appendix and the Supplement are available online: <http://dx.doi.org/10.1890/14-1809.1.sm>