

Density-dependent Survival in Seedlings Differs among Woody Life-forms in Tropical Wet Forests of a Caribbean Island

Saara J. DeWalt^{1,3}, Benton N. Taylor², and Kalan Ickes¹

¹ Department of Biological Sciences, Clemson University, Clemson, SC 29634, U.S.A.

² Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, NY 10027, U.S.A.

ABSTRACT

Negative density dependence contributes to seedling dynamics in forested ecosystems, but the relative importance of this factor for different woody plant life-forms is not well-understood. We used 1 yr of seedling survivorship data for woody seedlings in 17 different plots of lower to mid-montane rain forests on the island of Dominica to examine how seedling height, abiotic factors, and biotic factors such as negative density dependence are related to seedling survival of five different life-forms (canopy, midstory, and understory trees; shrubs; and lianas). Across 64 species, taller seedlings in seedling plots with higher canopy openness, greater seedling density, lower relative abundance of conspecific seedlings, and lower relative abundance of conspecific adults generally had a greater probability of surviving. Height was the strongest predictor of seedling survival for all life-forms except lianas. Greater seedling density was positively related to survival for canopy and midstory trees but negatively related to survival for the other life-forms. For trees, the relative abundance of conspecific seedling and adult neighbors had weak and strong negative effects on survival respectively. Neither shrub nor liana seedling survival was affected by the relative abundance of conspecific neighbors. Thus, negative density dependence is confirmed as an important structuring mechanism for tree seedling communities but does not seem to be important for lianas and shrubs in Dominican rain forests. These results represent the first direct assessment of controls on seedling survival of all woody life-forms – an important step in understanding the dynamics and structure of the entire woody plant community.

Key words: Dominica; forest dynamics; Janzen-Connell hypothesis; lianas; light; negative density dependence; shrubs.

MANY OF THE MECHANISMS PROPOSED TO MAINTAIN WOODY PLANT SPECIES DIVERSITY IN FORESTED ECOSYSTEMS—recruitment limitation, environmental filtering, competition, and predation/disease—involve biotic and abiotic processes affecting seedling establishment and survival (Janzen 1970, Connell 1971, Webb & Peart 1999, 2000, Harms *et al.* 2000, 2001, Nathan & Muller-Landau 2000, Wright 2002). Among biotic interactions, competition among seedlings in tropical forests is likely diffuse and weak (Paine *et al.* 2008, Svenning *et al.* 2008). In contrast, negative density-dependence (NDD) involving greater predation and disease at higher densities of seedlings or adults appears to mediate seedling dynamics in many forested ecosystems (Uriarte *et al.* 2005, Queenborough *et al.* 2007, Chen *et al.* 2010, Comita *et al.* 2010, Kobe & Vriesendorp 2011, Lin *et al.* 2012, Paine *et al.* 2012, Xiao *et al.* 2012, Piao *et al.* 2013). High conspecific density may spread or attract specialist pathogens or herbivores, leading to increased mortality (Janzen 1970, Connell 1971).

The influence of NDD may be obscured by environmental filtering – the tendency for conspecific seedlings and adults to co-occur because of similar resource and edaphic requirements (Queenborough *et al.* 2007, Bagchi *et al.* 2011, Bai *et al.* 2012). For example, edaphic factors such as soil water availability and soil nutrients are important regulators of species distributions in

some tropical forests (Engelbrecht *et al.* 2007, John *et al.* 2007), and even small differences in light differentially affect seedlings of species along the shade-tolerance spectrum (Kobe 1999, Montgomery & Chazdon 2002, Poorter & Arets 2003, Baraloto *et al.* 2005). Teasing apart the myriad interactions of biotic and abiotic factors affecting seedling dynamics is important for understanding forest communities because survival through the seedling stage is a critical bottleneck for eventually reaching maturity.

Studies of seedling community dynamics to date have focused on tree life-forms, but lianas and shrubs can compose a substantial fraction of the seedling community (Comita *et al.* 2007). In addition, lianas contribute substantially to the diversity and structure of tropical forests (Schnitzer & Bongers 2002) and have been increasing in abundance over the past few decades (Schnitzer & Bongers 2011). Exclusively focusing on trees in seedling dynamic studies ignores potentially important controls of forest structure mediated by lianas.

Seedlings of different life-forms may differ in their responses to biotic and abiotic factors because of differences in life-history strategies. Negative density-dependence has been found to be more prevalent among tree species that are more shade intolerant possibly because they are less resistant to herbivores and pathogens (Kobe & Vriesendorp 2011). Shrubs tend to be shade-tolerant because of their small stature, whereas lianas are thought to be relatively shade intolerant but may include both shade tolerant and intolerant species (Cai *et al.* 2007, Kitajima *et al.* 2013).

Received 12 August 2014; revision accepted 15 January 2015.

³Corresponding author; e-mail: saarad@clemson.edu

Therefore, shrubs might be less likely and lianas more likely to have high mortality in neighborhoods with more conspecifics (*i.e.*, exhibit NDD). Our understanding of the importance of density-dependent seedling mortality as a mechanism that structures seedling communities will be improved by examining seedlings of all woody life-forms.

Little is known about the dynamics of tropical forests of Caribbean islands, and particularly those of the Lesser Antilles. The Caribbean is considered the third most important global biodiversity hotspot (Myers *et al.* 2000, Mittermeier *et al.* 2004) with a high number of endemic species (Santiago-Valentin & Olmstead 2004). As oceanic island ecosystems are generally simpler than those on mainland locations (Whittaker & Fernández-Palacios 2007), specialist natural enemies might be less common than generalists (Ribeiro *et al.* 2005, Roderick & Percy 2008). If this is the case, NDD and Janzen-Connell patterns of seedling and sapling distributions may be less prevalent on islands than mainland locations (Hansen *et al.* 2008).

Here, we examine potential mechanisms affecting survivorship of tree, shrub, and liana seedlings in lower- to mid-montane rain forests of Dominica, a hurricane-prone island in the Lesser Antilles. We use seedling survival over 1 yr to explore the relative importance of biotic and abiotic factors on seedling survival for the entire woody plant community: trees, lianas, and shrubs. In particular, we address the prediction that negative effects of conspecific seedling and adult neighbors are stronger for trees and lianas than shrubs, controlling for the effects of environmental factors such as light.

METHODS

STUDY SITE.—The study was carried out in 17 permanent vegetation plots each of 0.25-ha on the island of Dominica in the Lesser Antilles (Fig. S1 in Supporting Information). Plots were located in lower- to mid-montane, old-growth rain forest dominated by *Dacryodes excelsa* Vahl (Burseraceae), *Sloanea caribaea* Krug & Urb. ex Duss (Elaeocarpaceae), *Licania ternatensis* Hook. f. ex Duss (Chrysobalanaceae), *Sterculia caribaea* R. Br. (Sterculiaceae), and sometimes *Amanoa caribaea* Krug & Urb. (Phyllanthaceae; S. J. DeWalt, K. Ickes, and A. James, unpubl. data). Rainfall records are not available for these plots, but we infer that the study plots receive mean annual precipitation between 4000 and 7000 mm/y with no dry season (*i.e.*, months < 100 mm) based on rainfall stations located in the center of the island (D'leau Gommier, Pont Casse, and Emerald Pool) where daily rainfall has been recorded since 1998 (Forestry, Wildlife & Parks Division of Dominica, unpubl. data). We clustered plots in three geographic regions: northeast (NE, 224–389 m asl), northwest (NW, 549–747 m), and southwest (SW, 549–732 m). Sites in the NE were at lower elevations and likely have lower mean annual precipitation. Sites in the SW have been impacted more by hurricanes in the past 30 yr. Plots were established where there was no sign of current or past human activity (*e.g.*, cut stumps), slopes were <45°, and large ravines were absent. Gaps were not avoided. During the study period, annual precipitation at the

three rainfall stations mentioned above was close to average values from the 7 yr prior to the study (Forestry, Wildlife & Parks Division of Dominica, unpubl. data).

PERMANENT VEGETATION PLOTS.—Each 0.25-ha permanent vegetation plot measured 50 m × 50 m and was surveyed into 10 m × 10 m subplots in 2006 or 2007. All trees ≥1 cm diameter at breast height (dbh) and all lianas ≥0.5 cm diameter at 1.3 m along the stem from the last substantial roots were tagged, measured for diameter, and identified using standard Center for Tropical Forest Science methods for trees (Condit 1998) and Liana Working Group methods for lianas (Gerwing *et al.* 2006, Schnitzer *et al.* 2008). These trees and lianas, referred to as adults, were measured a few months before the first seedling survey. Plants were identified to species by comparison of voucher specimens deposited in the national herbarium of Dominica and the University of Puerto Rico-Río Piedras (UPRRP). Several morphotypes were used for species in families that have not been taxonomically well-resolved (*e.g.*, Lauraceae and Myrtaceae). Species names were standardized using the Taxonomic Name Resolution Service, accessed on 9 September 2013 (Boyle *et al.* 2013). A total of 105 angiosperm tree, three tree fern, nine shrub, and 18 liana species in 52 families have been identified in these plots (S. J. DeWalt and K. Ickes, unpubl. data).

SEEDLING PLOTS.—To examine survivorship of seedlings, permanent seedling plots (1 m × 1 m) were established in the approximate center of each 10 m × 10 m subplot for a total of 425 seedling plots. When seedling plots would have been located in a place covered more than 25 percent by rocks, tree basal area, or newly fallen coarse woody debris that precluded seedlings from occurring in the area, the seedling plot was moved slightly. We tagged, identified, and measured every seedling within each seedling plot between 26 May and 16 July 2008 and then measured them again between 23 June and 20 July 2009. Seedlings were defined as free-standing woody stems ≥10 cm tall and <1 cm dbh for trees and <0.5 cm diameter for lianas. Palms and tree ferns were excluded from the seedling census. For each individual in the first census, we measured the length of the longest stem (base of the plant to the apex) as a measurement of initial seedling size. Length is likely a more appropriate measurement of initial size than height perpendicular to the forest floor for prone or leaning plants and is the measurement used in seedling censuses on Barro Colorado Island, Panama and Yasuní, Ecuador (L. Comita, M. Metz, and N. Norden, pers. comm.). Lianas, in particular, may trail along the ground before climbing or standing vertically. We refer to our length measurements as height to be consistent with the term used in other studies (*e.g.*, Comita *et al.* 2007, 2010, Metz *et al.* 2010). Species were classified into one of five life-forms based on architecture and maximum height attained: shrubs (rarely reach >1.0 cm dbh), understory trees (maximum height: 2–10 m), midstory trees (10–20 m), canopy trees (>20 m), and lianas. Liana seedlings were included if they were clearly independently rooted within the subplot. Analyses examining the effect of biotic and abiotic variables on survivor-

ship were conducted on 64 focal species that occurred in at least three seedling plots.

ABIOTIC FACTORS.—We assessed canopy openness for each seedling plot using hemispherical photographs taken using a Nikon Coolpix 4500 digital camera with a Nikon FC-E8 fisheye lens mounted 0.60 m from the ground on a tripod over the center of each seedling plot. Photographs were taken early in the morning, late in the afternoon, or under uniformly cloudy skies between 7 June and 9 July 2008. We used Sidelook v. 1.1.01 (Nobis & Hunziker 2005) to automatically determine the threshold value of each photo, which determines a binary division in the photo to distinguish between vegetation and sky. We then calculated the percentage of canopy openness using this threshold value in Gap Light Analyzer v. 2.0 (Frazer *et al.* 1999). Values of canopy openness can range from 0 to 100 percent, with 0 percent being completely closed and 100 percent being completely open. One seedling plot in the S2 site was an outlier for canopy openness (very low light level due to being located under a suspended log) and was omitted from all analyses.

Steeper slopes may be associated with wetter or drier soils (Becker *et al.* 1988, Daws *et al.* 2002) and greater disturbance from water runoff and land slips. The percent slope of each 10 m × 10 m subplot was calculated from the elevation measurements generated during the original surveys of the plots.

BIOTIC FACTORS.—We examined how seedling and adult neighbors were associated with seedling survival by calculating, for each focal seedling, the density of seedlings within its seedling plot and the total basal area of woody plants within its 10 m × 10 m subplot. To examine the relative effect of conspecifics, we additionally calculated the percentage of seedlings and the percentage of adults composed by conspecifics as in Lin *et al.* (2012) and Chen *et al.* (2010). By using the percentage of conspecifics rather than the absolute density or basal area of conspecifics, we were able to isolate the effect of conspecifics from positive effects of the habitat that would lead seedling survival of any species to appear to be positively related to seedling density. To examine how relatedness affected the results, we calculated the number of congeneric and confamilial adults and seedlings as well. For five morphospecies that we were able to classify to the level of family but not to genus, we classified the species as a genus not already represented. Basal area of adults was calculated by summing for trees, including tree ferns and palms, ≥1 cm dbh and lianas ≥0.5 cm diameter.

STATISTICAL ANALYSIS.—We used hierarchical generalized linear mixed-effects modeling (GLMM) with binomial errors (Zuur *et al.* 2010) and model selection via the Akaike information criterion corrected for finite sample sizes (AICc) to examine how measured variables were associated with individual seedling survivorship. All variables were standardized before analysis by subtracting the mean value of the variable, as calculated across all individuals in the analysis, and dividing by one standard deviation. We employed standardized variables to be able to compare the

relative importance of these explanatory variables (Gelman & Hill 2006, Comita *et al.* 2009).

All main effects were examined for collinearity before analysis by calculating their Variance Inflation Factor (VIF) and pairwise correlations. All variables had a VIF < 1.3 and Pearson *r* correlation coefficient < 0.32 with any other variable, indicating low collinearity (Zuur *et al.* 2010).

Each GLMM included variables and their interactions that we hypothesized *a priori* might affect seedling fate. Site, seedling plot, and species identity were included as random effects in all models to account for the increased likelihood of seedlings at the same site, in the same seedling plot, and of the same species having similar probabilities of survival. Including the site and seedling plot as random effects in a GLMM is equivalent to imposing a compound symmetrical correlation structure, which allows for spatial correlation between seedlings occurring in the same location (Zuur *et al.* 2010). All analyses were conducted using R v. 3.0.1 with the packages lme4 v. 1.1-7 (function ‘glmer’) and AICcmodavg v. 2.0-1 (function ‘aictab’) (R Development Core Team 2013).

We built models starting with basic variables and then added abiotic or biotic variables, both abiotic and biotic, and then their interactions. Models that had a $\Delta\text{AICc} < 2.0$ were retained at each stage for addition of other variables. The ‘basic’ models contained variables such as region of the site (NE, NW, or SW Dominica), natural log of initial seedling height, life-form, and the interaction between height and life-form (Table S1). We used this first set of models to determine how many life-form categories to use in subsequent models: five (canopy tree, midstory tree, understory tree, shrub, and liana), three (tree, shrub, and liana), or two (liana and not liana). We also examined whether to include region, and whether it should be a fixed or random effect. We expected the NE region to differ from the other two because they are at lower elevation and differ slightly in species composition from the NE region (S. J. DeWalt, K. Ickes, and A. James, unpubl. data). We included the interaction term for life-form and height to determine whether height mediated survivorship of some life-forms and not others. The best-fit basic model included region as a fixed effect, five life forms, height, and the interaction between height and life-form (Table S1). This model was retained for further analysis. Subsequent models (see below) also had substantially better fits when region was included as a fixed rather than random effect.

We then compared the basic model with models containing abiotic variables. These ‘abiotic’ models included the variables included in the best-fit basic model, two abiotic variables (canopy openness and slope), and any interactions between basic and abiotic variables we hypothesized *a priori* would affect survival. Next, we compared the best-fit basic models against models with biotic variables including seedling density in the seedling plot, the percentage of seedlings in the seedling plot composed by conspecific species, and the percentage of basal area in the 10 m × 10 m subplot composed by conspecific adults. Finally, we compared the best-fitting ‘biotic’ and best-fitting ‘abiotic’ models against models including interactions between biotic and abiotic variables

to determine top-ranked models. Six models provided fits with $\Delta AICc < 2.0$. For simplicity, we used parameter coefficients and standard errors only from the top-ranked model to present in figures in the text, but we discuss the results of the other five top-ranked models and present figures using parameters from them in Supporting Information (Tables S3–S7; Figs. S2 and S3). Model averaging was not possible because parameter estimates of main effects differ substantially among models when interactions among main effects are included or excluded.

We examined the relative effect of the parameters included in the top model for all life-forms (Table 2) and then for each life-form separately (Fig. 1). For the models for each life-form, we calculated standardized variables using only those seedlings within each life-form as the range and mean of the variables differed by life-form (Table S8). To examine whether NDD is related to the relative abundance of close relatives besides conspecifics, we conducted the model selection process with the percentage of conspecific seedlings and basal area replaced with the percentage of congeneric species or confamilial species.

RESULTS

SEEDLING COMMUNITY STRUCTURE.—In the 424 seedling plots, we recorded 6562 seedlings of which 83 percent were trees, 10 percent shrubs, and 6 percent lianas (Table 1). We were unable to identify 47 seedlings (<1% of individuals). A total of 90 species belonging to 74 unique genera and 42 families were found across the sites (Table S2). Canopy and midstory tree species were the most common seedlings (Table 1), while midstory and understory

TABLE 1. Number of focal species individuals (and total individuals), number of species, and 1-yr survival of each life-form included in the individual-level seedling analyses on the island of Dominica. Focal species were present in at least three seedling plots across the 17 sites. Sample sizes and percent survival of each species are presented in Table S2.

Life-form	No. of individuals	No. of species	% survival
Canopy tree	2648 (2668)	12 (18)	80.4
Midstory tree	1428 (1437)	20 (25)	89.1
Understory tree	1339 (1350)	20 (27)	90.0
Shrub	676 (682)	3 (8)	93.9
Liana	375 (378)	9 (12)	89.9
Unidentified	0 (47)	–	55.3
Total	6466 (6562)	64 (90)	86.0

trees had the most species (30% and 28% of species respectively). Of the focal seedlings used in the statistical analysis, there were 6466 individuals and 64 species (Table 1).

The most common seedling species included six canopy trees, two midstory trees, two understory trees, one shrub, and one liana and composed 76 percent of the seedlings in the study and 77 percent of the focal seedlings. *Amanoa caribaea*, a near endemic found only on the islands of Guadeloupe and Dominica, was the most abundant seedling species, but was absent from half of the sites (Table S2). The understory tree *Faramea occidentalis* (L.) A. Rich. (Rubiaceae) and the shrub *Psychotria urbaniana* Steyererm. (Rubiaceae) were present in all 17 sites, and the canopy trees *Dacryodes excelsa* and *Licania ternatensis* were present in all but one site.

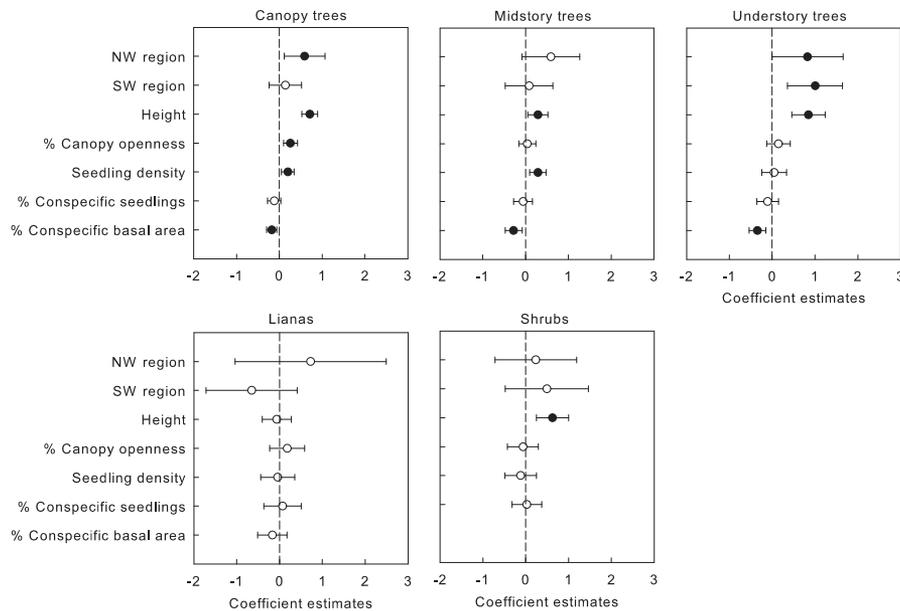


FIGURE 1. For each of the five life-forms, estimates of the slope (± 2 SE) of biotic and abiotic model parameters from the top-ranked model following model selection. Estimates were derived from standardized variables to compare relative effect sizes. Filled circles denote that the 95% confidence intervals do not overlap with 0. The baseline region was NE Dominica. Percent conspecific basal area was not examined for shrubs because, by our definition, shrubs did not have basal area.

For seedlings ≥ 10 cm in height, we found a range in density per seedling plot of 0 to 99 seedlings/m² and a maximum species richness of 16. The mean (mode) density and species richness were 15.4 (7.9) seedlings/m² and 6.5 (4.8) species respectively. For seedlings ≥ 20 cm in height, the maximum density and species richness were 46 seedlings/m² and 12 species respectively. Mean (mode) density and richness were 5.0 (0.4) seedlings/m² and 2.6 (0.15) species. Seedlings ≥ 10 cm in height tended to be more abundant and species rich in the NE (19.1 seedlings, 6.8 species/m²) and SW (14.9, 7.0) than the NW (10.7, 5.2) region. Seedlings ≥ 20 cm in height showed the same regional pattern.

DETERMINANTS OF FOCAL-SEEDLING SURVIVORSHIP.—Exactly 917 seedlings (14%) died between 2008 and 2009. Survivorship was lowest for canopy and midstory trees (Table 1). Individuals growing in the NW region of Dominica had higher survivorship than seedlings growing either in the NE or SW.

Following hierarchical model selection, there were six top-ranked models with $\Delta AICc < 2$ (Table S1). All of these models included main effects of basic (region, seedling height, life-form), abiotic (canopy openness), and biotic variables (seedling density, percentage of seedlings composed by conspecific species, percentage of basal area composed by conspecific species) as well as interactions between life-form and seedling height and between life-form and number of seedlings in the seedling plot (Table S1). Only one of the six top models included total adult basal area within the 10 m \times 10 m subplot. Slope was not included in any of them. The top-ranked models differed in whether interactions were included between life-form and canopy openness (2 models), canopy openness and percent of seedlings composed by conspecifics (2), and canopy openness and percent of adult basal area composed by conspecifics (1).

The relative effects of the six basic, abiotic, and biotic variables included in the top-ranked model differed among the five life-forms (Fig. 1). For all life-forms except lianas, initial seedling height had the strongest effect of all the variables on seedling survivorship (Fig. 1). The positive effect of height was particularly strong for canopy trees (Table 2; Fig. 1). Canopy trees were predicted to have only a 66 percent chance of survival at the minimum seedling height of 10 cm, whereas other life-forms had an 82–87 percent chance of 1-yr survival at this height (Fig. 2A).

Greater canopy openness generally conferred greater survival to seedlings even within the small range of light levels found in the understory (4.6–10.8% canopy openness; Fig. 2B). Two of the top six models suggested that life-forms differed in their response to canopy openness, with canopy trees showing a stronger, more positive relationship to canopy openness, than the other life-forms (Fig. S2).

The direction of the effect of seedling density, irrespective of species identity, differed among life-forms (Table 2; Fig. 2C). Canopy and midstory trees had greater survivorship in areas with greater seedling density, but survivorship of understory trees, lianas, and shrubs was unrelated to or was lower in areas of high seedling density (Fig. 1).

TABLE 2. Parameter estimates for the top-ranked model predicting survivorship of seedlings over 1 yr across 17 permanent plots in Dominica. Estimates were derived from standardized variables. The baseline life-form and region are canopy tree and NE Dominica respectively. Life-forms were determined by observations in the field (C = canopy tree, M = midstory tree, U = understory tree, S = shrub, and L = liana).

Parameter	Estimate	± 2 SE
(Intercept)	1.733	0.446*
Life-form L	-0.205	0.835
Life-form M	0.550	0.601
Life-form S	0.709	1.023
Life-form U	0.925	0.646*
Region NW	0.653	0.336*
Region SW	0.197	0.270
Log (height)	0.852	0.221*
Canopy openness (CO)	0.172	0.121*
Log (seedling density)	0.238	0.143*
Percent conspecific seedlings (PerConSdl)	-0.111	0.102*
Percent conspecific basal area (PerConBa)	-0.179	0.086*
Life-form L \times log (height)	-0.875	0.420*
Life-form M \times log (height)	-0.539	0.331*
Life-form S \times log (height)	-0.301	0.394
Life-form U \times log (height)	-0.153	0.378
Life-form L \times log (seedling density)	-0.301	0.372
Life-form M \times log (seedling density)	0.054	0.230
Life-form S \times log (seedling density)	-0.446	0.416*
Life-form U \times log (seedling density)	-0.260	0.233*

*95% confidence interval of the coefficient does not overlap with 0.

Both conspecific adult and seedling neighbors negatively affected seedling survivorship (Table 2; Fig. 2), but conspecific seedling neighbors had less of an effect than adults (Fig. 1). Seedling survival of lianas and shrubs, in particular, appeared unrelated to the percentage of seedlings composed by conspecifics given the large variance associated with the parameter estimates for these life-forms (Fig. 1). The percentage of adult basal area composed by conspecifics had a strongly negative effect on trees but little effect on lianas (Fig. 1).

Two of the top models for all life-forms also included an interaction term between canopy openness and percent conspecific seedlings (Tables S5 and S6). When canopy openness was low, survival was low regardless of the relative abundance of conspecific seedlings. In contrast, survival declined more rapidly with increasing conspecific seedling abundance when canopy openness was greater (Fig. S3A). One model included an interaction between canopy openness and percent conspecific adult basal area that suggested that NDD was partially alleviated at higher light levels (Table S7; Fig. S3B).

The results of the model selection process using congeners or confamilials were very similar to those using conspecifics; *i.e.*, the same variables and interaction terms were included in the top models (data not shown). The model with percent seedling and

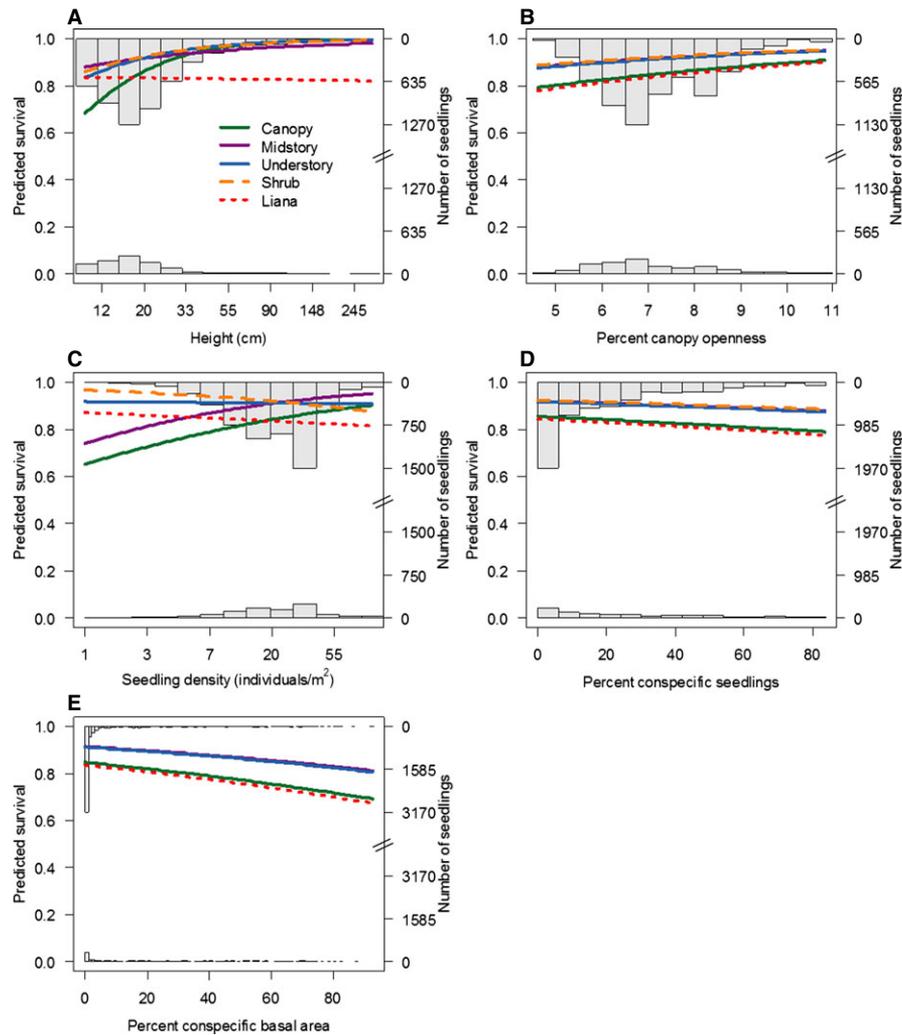


FIGURE 2. Predicted probabilities of individual seedling survival over 1 yr in rain forest of the island of Dominica in relation to (A) initial seedling height, (B) percent of canopy openness, (C) the number of seedlings in the seedling plot, (D) percent conspecific seedlings, and (E) percent conspecific basal area. The predicted probabilities are from parameter estimates from the top-ranked model (Table 2) and holding all other variables in the model at their median values. In all panels, the histograms represent the actual number of seedlings that died ($y = 0$) or survived ($y = 1$) in the range of the predictor variable plotted on the x -axis. Longer bars represent a greater number of seedlings found in that range of the predictor variable. Interaction terms for life-form and seedling height (A) and density (C) were included in the top-ranked model, and therefore different slopes are plotted for different life-forms in those two panels.

percent adult abundance composed by congeneric species had a similar AICc and weight as the model using percentages of conspecifics, and the parameter estimates for those two variables were the same or only slightly different (-0.111 compared to -0.111 ; -0.176 compared to -0.179 respectively). In contrast, the model with percent confamilial seedlings and adults fit substantially worse than the model with conspecifics ($\Delta\text{AICc} > 5$) and had substantially smaller parameter estimates for those variables (-0.093 and -0.166 respectively). Thus, the effects of conspecific and congeneric neighbors on seedling survival were similar but the effect of confamilials was not as strong, and the model containing confamilials did not fit the data as well as the ones identifying more closely related species.

DISCUSSION

In low-light understory conditions of Dominican rain forest, seedling survival of woody plants depends on both the local and abiotic conditions. Across the 64 tree, shrub, and liana species in this study, taller seedlings in seedling plots with greater canopy openness, fewer conspecific seedlings, and lower conspecific adult abundance had a greater chance of surviving. Although our study ran for only 1 yr, and we must therefore be cautious in our conclusions, our results of a strong, negative effect of conspecific adult abundance and a weak effect of conspecific seedlings on tree seedling survival are consistent with longer term dynamics seen in rain forest in Puerto Rico including directly after a

hurricane (Comita *et al.* 2009), in subtropical forest and seasonal rain forest in China (Chen *et al.* 2010, Lin *et al.* 2012), and rain forest of Ecuador (Metz *et al.* 2010). In addition, the patterns of survivorship for tree seedlings in forests of Dominica generally corresponded to those found in other Caribbean wet forests in the absence of a recent hurricane (Comita *et al.* 2009, Luke *et al.* 2014) and other tropical rain forests in general (Webb & Peart 1999, Queenborough *et al.* 2007, Comita & Hubbell 2009, Comita *et al.* 2010, Metz *et al.* 2010). Our results therefore substantiate the now-widespread finding that tree seedling communities display negative density dependence when considering conspecific adult abundance and suggest that NDD is as prevalent in lower-diversity island forests as it is in higher-diversity mainland forests.

SEEDLING AND ADULT NEIGHBORHOOD EFFECTS.—NDD is hypothesized to maintain diversity by thinning conspecifics either because of intraspecific competition for resources or because of predation or disease (Janzen 1970, Connell 1971, Chesson 2000, Wright 2002). In this study, survivorship declined with increasing percentages of conspecific/congeneric adult basal area and, to a lesser extent, conspecific/congeneric seedling density. Replacing conspecifics with confamilials in the analysis substantially reduced the magnitude of the effect, suggesting that the causal mechanisms of NDD are species- or genus-specific rather than family specific. It is not surprising that conspecifics and congeners were equivalent in their effects because most species in the Dominican plots (82%) were in different genera. If NDD is caused by natural enemies, then it appears that specialist predators and pathogens play a strong role in structuring seedling communities in these lower-diversity island forests as they do in higher-diversity mainland locations (Hansen *et al.* 2008). Without experimental studies, however, we cannot determine whether NDD is caused by competition or predation/disease.

Disentangling whether NDD is mediated more strongly by seedling or adult neighbors is difficult with an observational study; areas with high conspecific adult abundance are generally also areas with high numbers of conspecific seedlings. Nonetheless, our results suggest that NDD is driven more by conspecific adults than conspecific seedlings because the percentage of adult basal area composed by conspecific species had a stronger, more negative effect than the percentage of seedlings composed by conspecific species. Stronger or more consistently negative effects of adult abundance compared to seedling abundance are found in other forests as well (Comita *et al.* 2009, 2010, Metz *et al.* 2010, Lin *et al.* 2012 but see Paine *et al.* 2012). For example, the average negative effect on tree seedling survival was greater for conspecific adult basal area than conspecific seedling density in tropical forests of Yasuní, Ecuador (Metz *et al.* 2010) and Barro Colorado Island (BCI), Panama (calculated from supplementary materials in Comita *et al.* 2010). Nevertheless, experimental studies isolating the two would be needed to determine the relative strength of adult and seedling conspecific abundance on seedling survival.

Among tree seedlings in Dominica, NDD appears to be mediated slightly by the light environment. Survival of tree seed-

lings was low when canopy openness was *ca* 5 percent regardless of the percentage of seedlings being conspecifics, but conspecific seedlings had a more pronounced negative effect on survivorship when canopy openness was closer to 10 percent. The weak negative effect of conspecific seedlings on survival appears, therefore, to be detectable only when understory light levels are relatively high.

In contrast, the negative effect of conspecific adult abundance was greater when canopy openness was lower. Herbivores and pathogens that are more common where conspecific adults are present may be more abundant or have exacerbated effects on seedlings in low light versus high light even along this short light gradient, as has been found in other experiments (*e.g.*, Augspurger & Kelly 1984). Some fungal pathogens have detrimental effects on seedlings primarily in wetter conditions, which would be found at lower light levels (Hersh *et al.* 2012, Swinfield *et al.* 2012). Small increases in light levels may therefore reduce the risk of natural-enemy-related mortality such that, in higher – yet still understory – light conditions, natural enemies have less of an effect on seedling survival.

The positive relationship between seedling density and seedling survivorship for midstory and canopy trees in Dominica supports the previous findings of weak competition among tropical tree seedlings and suggests that there is positive density dependence (PDD) among heterospecific tree seedlings (Paine *et al.* 2008, Svenning *et al.* 2008). Positive effects of seedling density and specifically of heterospecific, distantly related or functionally distinct seedlings in the seedling neighborhood are generally found on seedling survival (Comita *et al.* 2009, 2010, Paine *et al.* 2012, Luke *et al.* 2014). PDD could arise because of facilitation or because favorable microsites increase seedling density and survivorship concomitantly. We controlled for the effect of light availability at 0.60 m above the ground by including canopy openness in the models, but most seedlings were not this tall (see distribution of seedling heights in Fig. 2A). Favorable microsites could be areas with higher light levels at lower heights, areas with lower density of the common herbaceous lycophyte *Selaginella flabellata* (L.) Spring, higher concentrations of limiting nutrients, or more stable soil. Indirect facilitation among seedlings could also result from the reduced probability of species-specific pests encountering a host in areas of greater heterospecific density, as posited by the species herd-immunity hypothesis (Wills 1996).

LIFE-FORM EFFECTS.—Our study provides some of the first evidence that shrub and liana seedling survival are not affected by the biotic and abiotic factors that structure tree communities. Shrub seedling survival was only related to initial seedling height, and liana seedling survival was unrelated to any variable in our study. Strong NDD related to adult neighbors was found for tree life-forms but not for lianas, and NDD related to conspecific seedlings were weak and only found for trees. Thus, we did not find support for our predictions that lianas would experience greater NDD, but we did find that shrubs appeared to experience less NDD than trees. However, we note that on Dominica, there were few shrub and liana species, and our analyses for

these life-forms are based only on three species of shrubs and nine species of lianas.

Examining the effect of adult abundance for the liana life-form also presents various challenges. If we assume that foliar pathogens raining down from adults are the cause of the majority of NDD, then liana basal area within the subplot may not be the best measure of adult abundance for two reasons. First, liana basal area scales differently with leaf area than it does for trees, such that liana basal area will be a small percentage of the total basal area but may compose a much larger percentage of the vegetative biomass. Using liana density might be a better measure of adult abundance than basal area, but tree abundance measured as density has less of an effect on seedling survivorship than basal area (Comita & Hubbell 2009). In fact, we would have missed finding the NDD due to adult abundance for trees had we used density as a measure (data not shown). Second, liana crowns may be far from the point of rooting (Putz 1984), such that conspecific liana basal area measured in the surrounding 10 m × 10 m subplot of a focal seedling may be a poor indicator of how many leaves are above the seedling. A more accurate measure of adult abundance would include only those conspecifics with liana crowns within the subplot of the focal liana seedling.

To our knowledge, NDD has never explicitly been examined for liana seedlings other than in our study, likely because adult lianas have been surveyed in few permanent plots with ongoing seedling studies. However, two other studies also point to a limited role for NDD for lianas (Muscarella *et al.* 2013, Ledo & Schnitzer 2014). Conspecific seed density had a negative effect on trees but not lianas in a study comparing lianas to trees in the seed-to-seedling transition in the Luquillo Forest Dynamics Plot in Puerto Rico (Muscarella *et al.* 2013). In addition, there was evidence for NDD, measured as spatial overdispersion, among tree but not liana saplings in relation to adult conspecifics on BCI, where both adult trees and lianas have been surveyed (Ledo & Schnitzer 2014). Based on the results of these two studies and ours, NDD appears to play a relatively minor role for liana communities.

CONCLUSIONS

Our study of liana, tree, and shrub survival across 17 rain forest plots of Dominica provides evidence that seedlings of different life-forms respond differently to some biotic and abiotic variables. Density-dependent effects, both positive and negative, appear important in structuring the seedling layer of trees but not lianas or shrubs. Density-dependent effects may be caused by biotic interactions, such as competition or predation/disease for NDD and facilitation for PDD. Our study is the first to directly compare seedling dynamics of trees, lianas, and shrubs; future experiments that test which specific mechanisms drive density dependence and determine how abiotic factors mediate density-dependent effects for all woody life-forms will help elucidate drivers of seedling dynamics for the entire woody plant community.

ACKNOWLEDGMENTS

We thank D. Zoellner-Kelly, C. Woods, E. Stedman, B. McGill, C. Riley, A. Martin, and E. Quinn for help with field work; L. Comita and M. Metz for advice on seedling survey methods and data analysis; C.E.T. Paine, W. P. Carson, D. Zoellner-Kelly, C. Woods, M. Uriarte, R. Muscarella, N. Schwartz, J. Lasky, B. Bachelot, and several anonymous reviewers for comments on previous versions of the manuscript; F. Axelrod and R. Graveson for help identifying species; A. James, R. Charles, and S. Durand for help with obtaining permits and locating sites for plots in Dominica; and N. Osler and the Archbold Tropical Research and Education Center for substantial logistical help. Funding for the project was provided by Clemson University and gifts from the Bay and Paul Foundations and the SeaWorld and Busch Gardens Conservation Fund.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Candidate models used in hierarchical model selection procedures.*

TABLE S2. *Seedling life-form, abundance, frequency, and percent survival of all woody species encountered in seedling plots in 17 different permanent plots on the island of Dominica.*

TABLES S3–S7. *Parameter estimates for the second-ranked through to sixth-ranked model predicting survivorship of seedlings across 17 permanent plots in Dominica.*

TABLE S8. *Range and mean (± 1 S.D.) values of predictor variables for seedlings in the five life-forms.*

FIGURE S1. Map of study sites on the island of Dominica, eastern Caribbean.

FIGURE S2. Effects on survival of canopy openness by life-form.

FIGURE S3. Effects on survival of canopy openness and (A) percent of seedlings composed by conspecifics and (B) percent of basal area (BA) composed by conspecifics.

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