ABSTRACT

Title of thesis: HEIGHT-BASED SURVIVAL ADVANTAGES AMONG UNDERSTORY SEEDLINGS FOLLOWING HURRICANE MARIA

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Understanding how seedlings succeed or fail during disturbance recovery is fundamental to understanding post-disturbance regeneration in forests. I tracked the recruitment and survival of seedlings in the Luquillo Experimental Forest for just under 2 years, beginning shortly after Hurricane Maria, and assessed the predictors of seedlings' success using a series of Bayesian mixed-effect models. I found that size-based advantages were key in determining survival among established understory seedlings, and that pioneer seedlings, in particular, were reliant on these advantages, especially when seedling densities were high. I also found that, within the first year of canopy-regeneration, there were clear changes in performance for later arriving seedlings which seemed to reflect differing causes of mortality for seedlings at different size classes. In concert, these findings contribute to a larger discussion about disturbance, regeneration, and the role of successional stage in determining seedling responses.

HEIGHT-BASED SURVIVAL ADVANTAGES AMONG UNDERSTORY SEEDLINGS FOLLOWING HURRICANE MARIA

by

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Table of Contents

List of Tables

Due to the length of these tables, both have been appended at the end of the thesis, rather than placed in text. Please find them in Appendix 1 at the following page numbers.

List of Figures

As with tables, all figures have been appended at the end of the text in order to preserve readability of complex elements on multi-panel figures. Please find them in Appendix 2 at the following page numbers.

Introduction

Hurricanes are an important structuring force in tropical forests, especially in the Caribbean (Brokaw & Walker, 1991; Crow, 1980; Tanner, Kapos, & Healey, 1991). As global-change leads to stronger, more frequent hurricanes in the Caribbean (Biasutti, Sobel, Camargo, & Creyts, 2012; Emanuel, 2005), understanding how forests respond to hurricanes is crucial to their long-term management and conservation. While hurricane-related mortality among adult trees is usually low, at least in the immediate aftermath (Frangi & Lugo, 1991; Sidrak & Kapos, 1992; Walker, 1991, 1995), damage to leaves and branches, or the need to re-sprout if toppled, can have growth or reproductive consequences. Moreover, hurricanes can defoliate large swathes of a typically closed-canopy forest (Everham & Brokaw, 1996), strongly altering conditions in the understory. For seedlings on the forest floor, this sudden canopy-opening can present a rare opportunity for rapid growth (Denslow, 1987; Luke, McLaren, & Wilson, 2014; You & Petty, 1991) allowing access to light levels which may be two- to twenty-fold times higher than typical understory levels (Bellingham, Tanner, Rich, & Goodland, 1996; Turton, 1992; Walker, Voltzow, Ackerman, Fernandez, & Fetcher, 1992). However, not all seedlings are equally able to capitalize on this opportunity. For some, the challenges that accompany canopy-opening — including increased density of seedling communities (Comita et al., 2009; Luke et al., 2014; Shiels et al., 2010) and changes in understory temperature or water-availability (González, Lodge, Richardson, & Richardson, 2014; Van Beusekom, González, Stankavich, Zimmerman, & Ramírez, 2020) — may out-weight the benefits. Understanding how seedlings differ in their response to post-hurricane conditions is key to understanding the pathways that post-disturbance regeneration in the seedling community will follow, and ultimately, how that regeneration will feed into the adult community as seedlings mature. Outcomes during the earliest stages of regeneration may be particularly important, as a disproportionate number of the long-term survivors from seedling communities that emerge during canopy-closure recruit during the first two years (Brokaw, 1985, 1987).

There are a number of key changes to understory conditions that follow hurricane disturbance, most of which are linked to the defoliation of the adult canopy. Immediately following a hurricane, defoliation leads to the deposition of large amounts of green, nutrient-rich litter onto the forest floor, which may alter nutrient-availability to seedlings as it decomposes (González et al., 2014; Guzman-Grajales & Walker, 1991; Liu et al., 2018; Lodge, Scatena, Asbury, & Sanchez, 1991). Litter may shelter seedlings from physical disturbances, or, alternatively, bury seedlings, leading to mortality (Guzman-Grajales & Walker, 1991; Shiels et al., 2010). With wide-spread defoliation, light penetrance into the understory can radically increase. Typically, a closed understory receives only a small portion of the total above-canopy irradiance. Depending on the degree of defoliation, post-disturbance light availability can increase up to twenty times above pre-disturbance levels (Bellingham et al., 1996; Turton, 1992; Walker et al., 1992). Understory air temperatures may also increase, or become more variable, due to increased direct sunlight and the loss of the canopy's buffering effect on heat losses. Water availability in the soil is typically similar under closed- or open-canopy conditions, but surface moisture, moisture in litter, and in air at the understory level can decline without the canopy acting as a barrier against water loss (González et al., 2014; Van Beusekom et al., 2020). While all of these effects will fade as the canopy regenerates, initial canopy closure can take several years (Comita et al., 2009), especially when the area of defoliation is large.

These altered conditions trigger, unsurprisingly, a strong biotic response from the seedling community as a whole. Short-term growth and recruitment rates increase well above pre-hurricane norms, and for many species, overall mortality rates decline (Denslow, 1987; Luke et al., 2014; You & Petty, 1991). Germination rates often increase, especially for gap-adapted species whose seeds respond to temperature or spectral cues that signal an open canopy (Tanner et al., 1991). In concert, these responses lead to a period of highly saturated seedling communities, with seedling densities well above pre-hurricane levels. Because of this, a likely secondary effect of canopy defoliation is an increase in the importance of seedling-to-seedling interactions (Comita et al., 2009; Luke et al., 2014), and, perhaps especially, in competition among seedlings for light.

This intensity of seedling interactions during regeneration, along with abiotic conditions which facilitate rapid growth, may be responsible for the disproportionate failure of seedlings which recruit later in the regeneration sequence (Brokaw, 1985, 1987). Specifically, size-asymmetry between established individuals and newly recruiting individuals may pose a strong entry barrier in highly populated seedling communities, especially if larger seedlings are able to shade smaller ones. For the seedlings of pioneer species, early size-advantages may be highly important for maintaining long-term success. Pioneers are poor performers under low-resource conditions (Grime, 1977), and will respond more negatively to shading by neighboring seedlings, in the short term, and by the closing canopy in the longer term (Agyeman, Swaine, & Thompson, 1999). Pioneers may also be less able to handle highly competitive conditions (Luke et al., 2014). Either mechanism poses less of an obstacle for more established pioneer seedlings. Larger, better established individuals are more likely to shade neighbors than be shaded themselves, and thus, their performance is less likely to suffer from light-competition at high seedling densities; they may also be better able to withstand periods of poor performance without experiencing mortality.

Early size-advantages may still be important for non-pioneer species, but are likely less steep, leading to a less severe restriction on the success of less established or later-arriving recruits. Non-pioneer seedlings' ability to capitalize on high light penetrance and achieve very high early growth rates is generally less than that of pioneers (Agyeman et al., 1999), which may make initial size-advantages more difficult to maintain. Shading and crowding are also less likely to pose a strong challenge, at least to survival, as non-pioneer species tend to be more conservative in their growth strategies, and their success is less dependent on light availability. If light-levels are extremely high, some degree of shading may even be beneficial, especially to light-intolerant species which may experience photoinhibition (Agyeman et al., 1999). Primary challenges for the seedlings of late-successional species are more likely to be abiotic, related to light, heat, or water conditions during canopy-closure which may be more difficult for shade-adapted species to cope with (as with the aforementioned photoinhibition), or to local soils or other microclimates.

The following study aimed to empirically test the set of predictions about the role of height-advantages and arrival-timing that is proposed above. For just over a year, following Hurricane Maria, I followed the recruitment and survival of understory seedlings at three locations within Luquillo Experimental Forest (LEF) in Puerto Rico. I also manipulated local recruitment in some seedling plots to delay community formation and create artificially low seedling densities during the mid-census period, when naturally occurring seedling communities were dense and well established. My aims were two-fold. First, to assess initial height-based survival advantages among what I will call early-arriving seedlings—those which were either pre-established at the time of Hurricane Maria, or recruited in the first few months following the event, and thus, form the initial community in the defoliated understory. Second, to assess potential barriers to success among later-arriving seedlings, those which recruited during the census period. Specifically, I asked:

1. Among early-arriving seedlings, did individuals which were better-established (taller) at the start of canopy-regeneration in the LEF experience lower mortality in the first year?
    a. If there were advantages to larger size, were these advantages consistent, or did they differ with the successional stage of an individual, the density of seedlings in an area, or some other plot factor, such as local climatic variation or the degree of canopy defoliation?
2. Did seedlings which recruited later in the regeneration sequence experience higher mortality compared to earlier arrivals?
    a. If so, do increases in mortality appear to be associated with entry barriers posed by an established seedling community, or do other factors, such as canopy closure, reduce the success of later arrivals in the absence of seedling-to-seedling effects?

I hypothesized that initial height advantages among early-arriving seedlings would be strongest for seedlings of pioneer species, for the reasons discussed previously, and strongest when seedling densities were high or abiotic conditions within a plot were stressful. I also hypothesized that growth would be increasingly reduced, and mortality increased, for seedlings recruiting later in the census period; that pioneer seedlings would, again, be most impacted; and that removing the influence of established individuals during highly saturated later censuses would improve outcomes among late-arriving recruits.

Materials and methods

Site description:

Fieldwork for this study was conducted near the El Verde research station, located within the Luquillo Experimental Forest (LEF). The LEF is a subsection of the larger El Yunque National Forest, in northeastern Puerto Rico. The LEF has been designated protected land in one form or another since the 1870s, and has been a National Science Foundation Long-Term Ecological Research site since 1988. Its 11,500 ha of forest spans 5 different subtropical forest types and just under 1,000 meters of elevational change (Brown, Lugo, Silander, & Liegel, 1983), and is home to over 240 species of trees.

On September 20, 2017, Hurricane Maria made landfall in Puerto Rico, massively impacting forests, and infrastructure, across the island. Maria was the strongest storm to hit Puerto Rico since 1928, with sustained wind speeds reaching 210 km/hr (Van Beusekom, Álvarez-Berríos, Gould, Quiñones, & González, 2018), and >1200 mm of rainfall across 48 hrs in some areas (Hall et al., 2020). In the LEF, Maria resulted in as much as 50% of the canopy being opened, due either to leaf-loss, landslides, or tree-fall. The severity of defoliation was greater for parts of the LEF at higher elevations, where wind speeds were greater and sloped soils more vulnerable to landslides (Van Beusekom et al., 2018).

Our study sites were located within five kilometers of each other, at 300, 400 and 500 m.a.s.l. All three were within the tabonuco forest, a subtropical wet forest type that dominates the lower elevations of the LEF. This forest type experiences relatively little seasonality in temperature (mean monthly temperatures ranging from 21˚C in January, to 25˚ C in September) and only slight seasonality in precipitation, receiving approximately 3050 mm of rain per year, with a drier season lasting from December to April. Local averages in annual precipitation increase slightly as one moves upslope, while average temperatures and solar irradiance decrease slightly (Brown et al., 1983; Murphy, Stallard, Scholl, González, & Torres-Sánchez, 2017).

A typical, mature tabonuco forest is closed-canopy, dominated by *Dacryodes excelsa*, *Sloanea berteriana*, and *Manilkara bidentata*, with *Cecropia schreberiana* as the most common pioneer species (Brown et al., 1983; Zimmerman et al., 1994). Each of our sites was heavily defoliated by Maria, becoming primarily open-canopy in the immediate aftermath. Defoliation was most severe at 500m and 400m, and slightly less so at 300m; canopy regeneration across the census period was also slower at the higher two sites (personal observation). These elevational differences among our three sites established a likely gradient in the severity of abiotic changes, and stresses, that understory seedlings experienced following Maria.

Experimental set-up and seedling inventories:

Seedling plots were installed at our 300m, 400m, and 500m study sites in the LEF in January of 2018, about 3 months after Hurricane Maria made landfall. At total of 50 1 meter square seedling plots were installed at each elevation, placed in pairs on an approximately regular grid. Plots within a pair were spaced 1m apart, with approximately 7m separating each pair from its neighbors on the grid. Each pair of plots consisted of one unmanipulated control, and one plot where seedling recruitment was artificially delayed. In plots assigned to the control group, all seedlings > 4 cm in height at the initial census were tagged, measured for initial height, and identified to the species level. Monthly re-surveys of each plot recorded mortality among this initial cohort of early-arrivals, as well as all new recruits into the > 4cm height class, their species and initial heights, and their subsequent mortality.

In plots where recruitment was delayed, all seedlings present at the initial inventory were removed via weeding, after which a fine mesh cloth was tented over the plot in order to exclude incoming seed-rain. From January of 2018 to May of 2018, these plots remained covered, and each month all new recruits, from either the soil seedbank or from seeds which may have escaped the mesh, were removed. Following the May 2018 census, the mesh was removed, and recruitment in the manipulation plots was allowed to proceed uninhibited. From this point on, monthly censuses recorded recruitment and mortality in delay plots following the same procedure as control plots.

In total, the census period lasted from January 2018 to September 2019. Monthly censuses were conducted from January 2018 to January 2019, with two additional censuses completed in May and September of 2019. Seedlings in the control plots were re-measured for height during the January 2019 census, allowing some limited inferences about growth or performance in these plots. However, heights were not re-measured in the recruitment delay plots, due to unavoidable timing constraints during that particular census, and thus, inferences in these plots, or comparisons between control and delay plots, are limited to measures of mortality only.

Survival among early-arriving individuals:

Height-based survival advantages among the early-arriving seedling community were assessed by fitting and comparing a series of hierarchical Bayesian logistic models to the survival of seedlings in the first cohort. This first cohort consists of all seedlings first recorded at the establishing January 2018 census. Seedlings in this cohort ranged from 4 cm to over 30 cm, capturing clear differences in the degree of establishment between individuals, and species of both early and late successional groups were well represented.

I explored four potential explanatory variables in this analysis: two continuous variables (initial seedling height and the number of seedlings in a plot), and two ordinal variables (successional stage, defined as ‘early’,’middle’, or ‘late’ as determined through literature, and elevation, from low to high). During initial analyses, models also considered species and plot identity as random effects. However, neither species nor plot identity yielded significant parameters in fitted models, although they did somewhat improve overall predictive ability, and analyses which included these variables as random effects gave qualitatively identical results to models which did not. For simplicity’s sake, therefore, I have excluded random effects from the analyses as published.

Survival models were distinguished into two primary sets: those which focused on density effects and their interactions with initial height and successional stage, and those which focused on elevational effects and their interactions with height and stage. For all models, the response variable defining survival was the survival of individual seedlings to the final census in September 2019, as a binary outcome. For each of the two model sets, I fit all possible models in which only some combination of initial height, stage, and density or elevation were considered, including all one, two, and three predictor models, and all possible two and three way interactions. This resulted in a total of 24 models fitted to the data, the details of which are summarized in Table 2. A 25th model was then fit, including all significant effects from the best supported models (as determined by WAIC values) in each set.

All model fitting was done using the *rethinking* package in R version 4.0.4. *rethinking* is a wrapper for *rstan* and, like *rstan*, interfaces with the STAN software to perform Monte Carlo operations. Hamiltonian Monte Carlo simulations were run for 3 chains, 8000 iterations, with a warm-up period of 4000 iterations. Trace plots for all fitted models were examined to identify potential problems within the sampling process, and a series of posterior predictive checks was performed as well, which allowed me to visually confirm that models which were preferred based on WAIC comparisons were indeed reasonably predicting the data. Model comparison was based on WAIC values, and the significance of effect parameters within models was assessed based on the 95% credibility interval for a given parameter, where an interval not crossing zero is assumed to be significant.

Success among later recruits:

I separated the question of success and mortality among later-arriving seedlings into three components: first, whether the absolute number of seedlings successfully recruiting into the >4cm height class declined across the census period; second, whether seedlings which did recruit into the study in later censuses experienced higher rates of early failure, which I defined as mortality taking place between a seedling's first and second observation in a study plot; and third, whether later recruits experienced higher rates of mortality once successfully established, which I defined as mortality taking place between a seedling's 5th and 6th observation in a study plot. In concert, these three components may provide a sense of at what life-stage entry barriers to these communities arise for seedlings, ie, in initial establishment or in later success, and how quickly those barriers are established after the initial post-hurricane flush of growth.

I calculated each of these components separately for seedling cohorts found in control plots and seedling cohorts in recruitment delay plots, and again for seedling cohorts made up of pioneers-only and mid/late successional species-only, which included seedlings from both plot-types. I then fit linear regressions to each measure, where the predictors were either treatment or stage, as a categorical, and what I am calling cohort number—ie, all individuals first recorded in the first census become cohort one, all individuals first recorded in the fourth census become cohort 4, and so on. The response variable was either the number of seedlings in the cohort, or the mortality rate of seedlings from that cohort across the relevant interval.

Height-based survival bias among later-arriving seedlings

In addition to calculating the above measures of success, I also assessed whether initial height advantages existed for late-arriving seedlings, as I hypothesized they did for early-arrivals. I did so by examining the initial heights of seedlings that recruited into the study in later censuses. Specifically, I compared the recorded initial heights among survivors in the seedling cohort first recorded in each census to a randomized sample of initial heights drawn from that cohort, containing the same number of 'survivors'. For each cohort, I randomized which seedlings survived 999 times, while keeping the total number of survivors constant, and compared the average initially measured height of the true surviving seedlings to the averages obtained by the randomization. I repeated this procedure for each cohort of seedlings as a whole, and for each cohort subdivided, as above, by either plot treatment or successional stages. Significance in any observed survival-bias was then assigned relative to the 95% confidence envelope within the randomized outcomes.

Results

Recruitment rates and seedling survival across the study period:

A total of 2,856 individual seedlings, comprising 63 species, 58 genera, and 39 families, were tagged during the census period from January of 2018 to September of 2019 (Table 1). Of these, 1,041 seedlings were early-arrivals, present in the initial cohort in Jan. 2018. The remaining 1815 seedlings recruited into the study during later censuses. Pioneer seedlings strongly outnumbered the seedlings of other successional groups throughout the census period, making up 52% of the initial cohort, and just under 50% of all subsequent recruits. While all three elevations saw significant numbers of new seedlings, recruitment was generally greater at 300 m than at either of the two high elevations, with an initial cohort nearly double the size of the other sites', as well as higher recruitment rates in later censuses.

New seedling recruitment was highest early in the study . A full quarter of all new seedlings that were tagged in control plots across the 21-month study period were tagged during the second census (312 new seedlings, of the 1243 that were added across the entire period); by the 5th census, over half of the total recruitment that would be seen in control plots had occurred. Seedling densities in the control plots increased rapidly during this time, climbing from an initial average of 14 seedlings per meter-square plot to peak at 24 seedlings/plot during September 2018, a full year after Hurricane Maria, and 9-months after our plots were installed. While seedling density did decline somewhat following this peak, it remained generally high.

A total of 571 seedlings were tagged in the recruitment delay treatment between June of 2018 and the final censuses. New seedling recruitment into the delay plots following the removal of netting was initially very low, but did accelerate over time, resulting in recruitment rates during the final censuses that were equivalent to, or slightly higher than, those in the control plots over the same interval. However, the extremely high recruitment rates seen during earlier censuses in control plots were never observed in recruitment delay plots, and seedling densities consequently remained very low, peaking at the final survey, after 18 months of censusing, at just under 6 seedlings per meter squared plot.

Seedling mortality across the entire study period was about 38%, with the majority of seedling deaths occurring during the latter portion of the study, as seedling densities began to decline and communities thinned out. Where a full quarter of recruitment was observed between the first and second months, a full quarter of recorded seedling deaths occurred in the 4 months between the final two censuses, May to September of 2019 (28% of deaths, or 302 of a total 1084). In general, mortality appeared slightly higher for seedlings at the 400 and 500m study sites than at the 300m site, slightly higher for seedlings in the recruitment delay plots than for seedlings in the controls, and slightly higher for pioneer species than for mid-or late successional species.

Survival, height advantages, and plot conditions among the initial seedling cohort:

Among the set of models which targeted the effects of seedling height, successional stage, and seedling density on survival, I found strong support for a positive relationship between survivorship and initial height among established seedlings (Figure 2B), as well as a complex set of interactions between height, seedling density and successional stage which suggested that pioneer seedlings, in particular, were reliant on height advantages when plots were densely crowded (Figures 2B, 2C & 3). The best performing model in this set was among the most complex, which included all possible individual effects, two-way interactions between stage-height and stage-density, and a three-way interaction between height, stage, and density (Table 3). Save for the interaction between height and crowding, which was narrowly non-significant, all parameter estimates in the fitted model were significant at the 95% credibility level (Figure 1A). These estimates indicated, in summary:

1. A positive overall effect of later successional stage, such that pioneers had a lower average survival than mid and late stage species. (Figure 2A)
2. A positive overall effect of initial height on survival, and a negative interaction between later successional stage and height, such that height advantages were less steep for mid and late successional seedlings than for pioneers (Figure 2B).
3. A negative overall effect of density, and a positive interaction between later successional stage and density, such that mid and late successional seedlings had less depressed survival under the most crowded conditions (Figure 2C).
4. A negative three-way interaction between density, height, and later successional stage, such that small pioneer seedlings experienced greater survival depression in the most crowded plot conditions than mid or late successional seedlings of the same height (Figure 3).

Elevation had fewer significant effects on survival than seedling density. Among models which targeted elevational effects, the best supported model included initial height, successional stage, and elevation as individual effects, a two-way interaction between stage and height, and a two-way interaction between stage and elevation (Table

3). However, only the two-way interaction between elevation and stage remained significant once density effects were accounted for. This negative interaction was such that late successional seedlings had lower mortality than pioneers at the lowest elevation, but higher mortality at the highest elevation (Figure 2D). This interaction was incorporated into the final model, which was used to generate the predicted survival curves shown in Figures 2 and 3, while all other elevation effects from this analysis were not. It seems likely that elevation in this study co-varied with density or community composition in some way, leading to indirect effects that become non-significant when those co-variates are accounted for more directly.

Seedling outcomes in later cohorts:

In the control plots, the size of seedling cohorts declined sharply across the study period, as predicted (Fig. 4A; P=0.0076, linear model). Early-stage mortality, between a seedling's first and second months in the census, also declined for later arrivals in the control plots (Fig. 4B; P= 0.0025). This decline is, notably, non-linear in its shape, with clear peaks and troughs throughout the year, although the broad trend is towards lower mortality (see Fig 4A). Peaks in early mortality were approximately 6 months apart, occurring during the March/April and August/September intervals between censusing; new seedling mortality in the control plots during these intervals was 7% and 4.3%, respectively. Troughs in early mortality correspond approximately to the June/July and October/November intervals. Later-stage mortality, between a seedling's 5th and 6th months, increased for later cohorts of seedlings(Figure 4C; P=0.035); some non-linearity may also be present in this response, although to a much lesser degree.

In contrast to the control plots, cohort sizes in the recruitment delay plots were much lower overall, but slightly increased across the study period (P=0.002, linear model with treatment effect and interaction; Figure 5A). Early mortality appeared to be higher on average in the recruitment delay treatment, and to increase across the period, again in contrast to behavior in the control plots (P= 0.06, Figure 5B). The overall model which describes these effects is narrowly non-significant, although the P-values for the parameters themselves within the model are significant (P=0.02 and 0.45 for effect intercept and interaction, respectively); while not conclusive, this may suggest that non-significance here is a result of small sample sizes (6 cohorts for which we have 1st-2nd month mortality data in the delay plots) rather than a true non-effect.

We found no differences in later-stage mortality across the study period between the control and recruitment delay plots (parameter P-values = 0.1 and 0.34 for effect intercept and interaction; Fig 5C). While this too could have resulted from the small number of recruitment delay cohorts for which the 5-6th month interval had been recorded (N=4), the visual trend in the data was less suggestive, and neither the overall linear model nor any parameters within it were significant.

We also found no differences between pioneer and non-pioneer seedlings in any of the three responses across the study period (separate linear models, P>0.1 for all effects related to stage; Figure 6).

While the average initial heights of seedlings did decline across the study period, height-based survival bias was not present in any cohort excepting the first (Figure 7), including the first cohort to establish in the recruitment delay plots, where no pre-established seedlings were present.

Discussion

Height-advantages in post-disturbance seedling success:

Among the initial cohort, a seedling's initial height was the single strongest predictor of its mortality, with clear survival advantages for taller seedlings. This is, in itself, not particularly surprising. Mortality among trees is usually assumed to be highest among the smallest individuals and the largest (Fridman & Ståhl, 2001; Holzwarth, Kahl, Bauhus, & Wirth, 2013; Lines, Coomes, & Purves, 2010), although this is more often referenced among adult trees than seedlings. Smaller seedlings are more likely to suffer from shading by neighboring seedlings or by large herbaceous species, such as *Heliconia,* which are common in the LEF. Mortality due to abiotic stresses or physical damage, such as loss of leaf tissue (Kitajima, 2003), is also potentially important to the small seedlings. The results likely support shading, rather than other vulnerabilities, as a cause for small seedling mortality at the LEF. Overall mortality was increased, and height-advantages intensified for light-demanding pioneers, by crowded plot conditions, suggesting a biotic influence. Density influences might also be attributable to competition for space, or some other resource, but light seems likely, given that height *per se* provides a clear advantage in light-competition.

Pioneer seedlings were the most dependent on initial height-advantages for success, as I had initially predicted, and were also disproportionately reliant on height-advantages when plot conditions were crowded. These two results dove-tail nicely with observations and theory that suggest pioneers are less equipped to handle intense competition, particularly for light, than later successional species. Because pioneer species tend to have high maximum photosynthetic rates, and thus a high capacity for rapid growth (Agyeman et al., 1999), a pioneer seedling with sufficient access to light may be able to maintain primacy even under very crowded conditions, simply by moving into larger height-classes very quickly and intercepting enough light to suppress the growth of neighboring seedling competitors. In our study plots, we observed multiple pioneer seedlings, especially of *Cecropia schreberiana,* attain heights over two meters within a year. This was especially common at the higher two sites, where initial canopy damage was intense and canopy closure slow. These rapid-growing individuals were able to dominate the local light-environment and, most likely, strongly influence the success of smaller seedlings in their plots.

Without the existing height-advantage needed to secure sufficient light, however, the seedlings of pioneer species likely experience crowding, and particularly light competition, much more negatively than mid- or late-successional species. Crowding does not, in itself, necessitate that seedlings will experience shading by other seedlings, but it does make it more likely that at least one neighbor will be sufficiently large to cause a problem for a given seedling. Pioneers are, as a group, relatively shade-intolerant, and, although most are reasonably good competitors under high light, they quickly become less so when light is limited. Thus, the potential for neighbor-shading in crowded seedling communities may be a very strong barrier to the success of small pioneer seedlings, explaining the strong effects we saw on these small pioneers in the highest density plots.

In contrast to the very clear effect that crowding had in this study, elevation had a fairly mild influence on survival among the initial cohort of seedlings, or on the intensity of height-advantages they experienced. The sole effect of elevation that was significant, once other predictors had been accounted for, was an interaction between elevation and successional stage. Late successional seedlings had increased success at the lowest elevation, and reduced success at the highest. This would appear to reflect the degree of canopy opening at each elevation after Maria, with the lowest elevation being the most intact and the quickest to start to close. Because late successional seedlings tend to be more shade-tolerant, it is likely that they were at an advantage in this relatively shaded site. On the other hand, at the highest elevation sites, where canopy opening remained almost 100% well into the study period, light-demanding pioneers were able to fully capitalize on increased light levels and dominate the local seedling community.

Changes in seedling outcomes across early regeneration:

Regeneration in the understory and canopy following a disturbance on the scale of Hurricane Maria can lead to clear, rapid changes in conditions. Across the span of this study, we saw clear, accompanying changes in the success of seedlings which recruited during different periods of the regeneration sequence.

In the first few months of seedling censuses, the degree of canopy opening was extremely high, and seedling communities underwent a period of rapid recruitment. During this time, we saw many seedlings entering the >4cm height class (Fig. 5A), but also the highest rates of early seedling mortality. These high rates of early mortality are likely associated with abiotic, rather than biotic, challenges faced by seedlings in these early cohorts. There was a clear seasonal signal in this early mortality, which suggests that month-to-month changes in, e.g., temperature or precipitation averages, influence the early success of seedlings. ‘Peaks’ in mortality appeared to correspond with a period of drought in March and April of 2018, and a period of relatively high precipitation in August.

The smallest size-classes of seedlings are intensely vulnerable to fluctuations in short-term abiotic conditions, because they lack many of the structures—such as an established root system—that allow larger seedlings to endure periods of water- or heat-stress. Ordinarily, a closed-canopy will moderate understory temperatures and soil-surface water availability; however, early-arriving seedling cohorts experienced a fully opened canopy, in many places, exposing them to a greater-than-normal degree of potentially fatal of heat- or water-stress. Later-arriving seedlings, which we found to have lower rates of early mortality, would have been better protected from these conditions by the recovering adult canopy. The increased presence of large, well-established seedlings, which may form a local understory canopy, may also have helped to mediate temperature or moisture fluctuations for later arrivals.

Later-stage mortality in this study increased for seedlings which recruited during later censuses. This increase seems likely to be associated with biotic causes, unlike early mortality. Seedling plots became highly saturated during the latter half of the study period, and large, well established seedlings became increasingly common. However, in the recruitment delay treatment, where these biotic factors were removed for late-arriving seedlings, we didn’t see a clear reduction in later-stage mortality relative to the controls. There was a slight decrease in the average later-stage mortality rate, but it was not statistically significant, and only apparent for the first two cohorts which established in the delayed plots. This could suggest a number of things. We might be looking at an alternative, non-biotic driver of late-mortality among the seedlings. It could also be that established seedlings compete, and can drive mortality in others, on a larger spatial scale than anticipated. While seedling densities in the delayed plots remained low, it’s possible that neighboring seedlings outside the bounds of our meter-squared area influenced the seedlings in these plots in a way that was not accounted for.

The delayed plots did differ from the controls in both their cohort sizes, which were smaller on average, and their early-mortality rates, which appeared to increase for later establishing cohorts. The difference in cohort size most likely reflected the nature of the treatment itself—by excluding seed-rain and weeding out recruits during the delay period, the existing soil seedbank in these plots was depleted. Subsequent recruitment, especially in the first few censuses following the nettings' removal, would have depended heavily on seed-rain, unlike the control plots, both germination from the seedbank and recruitment by existing < 4 cm seedlings were additional, viable pathways for seedlings to enter the study.

The increase in cohort sizes in the delay plots during later censuses may be partially attributable to this latter pathway, as this pool of < 4 cm seedlings would not exist during the first several censuses of the weeded delay plots. I would argue, though, that the lack of an existing community to shade or compete with new recruits also contributed, as I had hypothesized initially. By the final censuses, cohort sizes in the delayed plots were slightly larger than those in the controls, which could reflect a lack of early entry barriers associated with the lower density and, on average, smaller size of seedlings in these plots. There was also some evidence of bias in these plots towards pioneer recruits (about 60% of total recruitment was pioneers, as opposed to 40% during the same interval in the controls), which would support the hypothesis that these entry barriers are stronger for the less shade-tolerant pioneer species.

Conclusions and significance

Post-hurricane understory conditions can be dramatically different from those in an intact, closed-canopy forest. Understanding seedling outcomes a following disturbance is important to both ongoing protection and management in hurricane-driven tropical forests, and to predicting how these diverse communities will respond to future disturbances. While many studies have investigated both post-disturbance conditions and pioneer vs. non-pioneer responses in understory regeneration, few, to my knowledge, have specifically addressed the question of height advantages in this sense. Brokaw observed that long-term survivors among seedlings in light gaps tend to establish early, especially among pioneer species (Brokaw, 1985, 1987); others have observed that survival or size-accumulation curves among tree species, in general, are steepest for pioneers (Klopcic, Simoncic, & Boncina, 2014); and many have noted that pioneer and non-pioneer species differ in their ability to tolerate low-light conditions. This study extends and synthesizes these earlier observations to consider, specifically, the ways in which initial degrees of defoliation, initial height differences, and high seedling densities, can lead to early-establishment advantages which differ across successional stages. The results obtained, therefore, serve as a natural extension to those reported in the earlier literature.

I suggest two specific conclusions. First, that the differences in performance which lead to the types of pattern seen by Brokaw, and others, emerge very early, within the first 2 years after canopy opening. Within 24 months of Hurricane Maria, I was able to detect strong height-based survival differences among the initial seedling community, as well as rising mortality rates among seedlings recruiting into the established community. Second, that understanding pioneer responses to post-hurricane conditions, and potentially their responses more generally, may benefit from a consideration of more complex interactions between factors of interest. Of the relationships which were important to understanding both survival and outcomes for later seedlings, an overwhelming number involved steeper responses to one or more conditions by pioneers, detectable only when considering two- or three-way interactions between variables. While this may not be entirely generalizable, it does emphasize the importance of considering these types of interactions when attempting to understand seedling outcomes.

Appendix 1: Tables

Table 1: (continues through page 33) Table of species present in the seedling plots. A dash in the successional stage column denotes a lack of information, or a lack of consensus in the literature, for that species' successional stage. The right-most three columns provide the total number of seedlings of that species recorded in the study, the number of seedlings of that species which were counted among the first cohort, and the number of seedlings of that species counted in plots belonging to the recruitment delay treatment.

Family	Species	Growth form	Successional stage	Total tagged	First cohort	Recruitment delay treatment
Moraceae	Cecropia schreberiana	Tree	Early	355	163	49
Rubiaceae	Psychotria berteroana	Shrub	Early	292	76	65
Meliaceae	Guarea guidonia	Tree	Late	226	127	39
Araliaceae	Schefflera morototoni	Tree	Early	158	68	24
Connaraceae	Rourea surinamensis	Liana	Mid	128	85	3
Meliaceae	Swietenia macrophylla	Tree	Early	105	83	11
Arecaceae	Roystonea borinquena	Palm	Mid	103	14	29
Araliaceae	Dendropanax arboreus	Tree	Mid	101	26	12
Euphorbiaceae	Sapium laurocerasus	Tree	Mid	99	4	7
Burseraceae	Dacryodes excelsa	Tree	Late	96	44	29
Malvaceae	Hibiscus rosa-sinensis	Shrub	-	84	2	21
Euphorbiaceae	Alchorneopsis floribunda	Tree	Early	77	31	0
Fabaceae	Dalbergia monetaria	Liana	Early	76	59	4
Meliaceae	Trichilia pallida	Small tree	Late	74	29	6
Lauraceae	Ocotea leucoxylon	Tree	Mid	71	27	2
Rubiaceae	Gonzalagunia spicata	Shrub	Early	70	2	46
Anacardiaceae	Spondias mombin	Tree	Early	59	3	15
Arecaceae	Prestoea acuminata	Palm	Late	55	14	10
Celastraceae	Hippocratea volubilis	Liana	Mid	47	29	3
Melastomatacea	Miconia racemosa	Shrub	Early	45	0	42
Elaeocarpaceae	Sloanea berteroana	Tree	Late	45	22	6
Euphorbiaceae	Alchorneopsis latifolia	Tree	Early	41	19	5
Lauraceae	Ocotea sintensis	Tree	Early	37	16	9
-	No ID	-	-	37	3	14
Piperaceae	Piper glabrescens	Shrub	Early	36	1	2
Euphorbiaceae	Drypetes glauca	Small tree	Late	31	12	3
Vitaceae	Cissus verticillate	Liana	Early	29	2	16

Table 1: (continued)

Family	Species	Growth form	Successional stage	Total tagged	First cohort	Recruitment delay treatment
Clusiaceae	Garcinia portoricensis	Small tree	Mid	29	2	27
Sapindaceae	Paullinia pinnata	Liana	Late	26	22	1
Bignoniaceae	Tabebiua heterophylla	Tree	Mid	21	5	5
Sapindaceae	Matayba domingensis	Tree	Late	18	0	9
Clusiaceae	Calophyllum antillanum	Tree	-	17	2	14
Sapotaceae	Manilkara bidentata	Tree	Late	17	11	0
Dioscoreaceae	Dioscorea polygonoides	Liana or forb	-	13	1	2
Ulmaceae	Trema micrantha	Small tree	Early	13	0	9
Boraginaceae	Cordia borinquensis	Small tree	Mid	12	2	6
Rubiaceae	Psychotria brachiata	Shrub	Early	12	3	3
Myrtaceae	Syzygium jambos	Small tree	Mid	12	7	1
Rutaceae	Zanthoxylum martinicense	Tree	Early	12	2	5
Chrysobalanace	Hirtella rugosa	Small tree	Late	10	1	3
Polygalaceae	Securidaca virgate	Liana	-	8	2	2
Euphorbiaceae	Croton poecilanthus	Tree	Mid	7	3	0
Rubiaceae	Palicourea riperia	Shrub	Early	6	3	2
Rubiaceae	Faramea occidentalis	Small tree	Late	5	1	0
Dilleniaceae	Pinzona coriacea	Liana	Early	5	0	4
Smilacaceae	Smilax coriacea	Liana	-	4	1	0
Burseraceae	Tetragastris balsamifera	Tree	Late	4	2	1
Urticaceae	Urera baccifera	Shrub	Early	4	0	0
Melastomatacea	Miconia impetiolaris	Shrub	Early	3	3	0
Melastomatacea	Micona prasina	Shrub	Early	3	1	2
Rubiaceae	Psychotria grandis	Shrub	-	3	0	1
Malpighiaceae	Byrsonima wadsworthii	Tree	-	2	0	0
Flacourtiaceae	Casearia arborea	Tree	Mid	2	1	0
Simaroubaceae	Simarouba amara	Tree	Mid	2	1	0
Flacourtiaceae	Casearia sylvestris	Small tree	Mid	1	0	0
Oleaceae	Chionanthus domingensis	Tree	Early	1	0	0
Myrtaceae	Eugenia stahlii	Tree	Late	1	1	0
Melastomatacea	Henriettea fascicularis	Small tree	-	1	0	1
Malpighiaceae	Heteropterys laurifolia	Liana	-	1	1	0
Fabaceae	Inga Laurina	Tree	Late	1	0	1
Sapotaceae	Micropholis garciniifolia	Tree	-	1	1	0
Myrtaceae	Myrcia leptoclada	Small tree	Late	1	1	0
Solanaceae	Solanum torvum	Shrub	Early	1	0	0

Table 2: Complete model specifications and comparison for models of initial cohort survival. WAIC is the widely available information criterion, with lower WAICs indicating better predictive ability. The final, combined model is not listed here, and is excluded from the ranking system, which was used to select the parameters which were kept in it. That model contained all 4 predictors, with individual effects on height, stage, and density, all 2-way interactions involving stage, and the three-way interaction between height, stage, and density. Is WAIC was 1266, performing slightly better than the best uncombined model below.

Predictor variables			**2 way interactions**			**3 way interaction**	**WAIC**	**Model rank**
height	*stage*	*density*	*ht*stage*	*ht*density*	*stage*density*	*ht*stage*density*		
YES	YES	YES	YES	YES	YES	YES	1270	1
YES	YES	YES	YES	YES		YES	1275	3
YES	YES	YES		YES	YES	YES	1277	4
YES	YES	YES	YES		YES	YES	1272	2
YES	YES	YES	YES	YES	YES		1279	5
YES	YES	YES	YES	YES			1285	7
YES	YES	YES		YES	YES		1289	9
YES	YES	YES	YES		YES		1280	6
YES	YES	YES	YES				1285	8
YES	YES	YES		YES			1295	11
YES	YES	YES			YES		1292	10
YES	YES		YES				1321	22
	YES	YES			YES		1311	13
YES		YES		YES			1310	12
YES	YES						1333	32
	YES	YES					1333	33
YES		YES					1312	14
YES							1351	36
	YES						1353	37
		YES					1329	28

Predictor variables			**2 way interactions**			**3 way interaction**	**WAIC**	**Model rank**
height	*stage*	*elevation*	*ht*stage*	*ht*elevation*	*stage*elevation*	*ht*stage*density*		
YES	YES	YES	YES	YES	YES	YES	1316.7	16
YES	YES	YES	YES	YES		YES	1317.9	20
YES	YES	YES		YES	YES	YES	1325.5	27
YES	YES	YES	YES		YES	YES	1316.9	17
YES	YES	YES	YES	YES	YES		1317.8	19
YES	YES	YES	YES	YES			1318.7	21
YES	YES	YES		YES	YES		1324.1	25
YES	YES	YES	YES		YES		1314.9	15
YES	YES	YES	YES				1316.9	18
YES	YES	YES		YES			1324.4	26
YES	YES	YES			YES		1322.6	24
YES	YES		YES				1321	23
	YES	YES			YES		1333.1	34
YES		YES		YES			1331.8	31
	YES	YES					1331.5	30
YES		YES					1329.9	29
		YES					1335.07	35

Appendix 2: Figures

Figure 1: Parameter estimates for the best supported model of initial cohort survival. Open circles represent the mean parameter estimate, with bars demonstrating the 95% credibility interval. A positive parameter value indicates a positive impact on survival. Parameters denote, from top to bottom: global average survival (a), effect of successional stage (bs), effect of seedling initial height (bh), interaction effect between height and successional stage (bhs), interaction between seedling density and stage (bcs), three-way interaction between height, stage, and density (bhsc), effect of seedling density alone (bc), and the interaction between elevation and successional stage (bes).

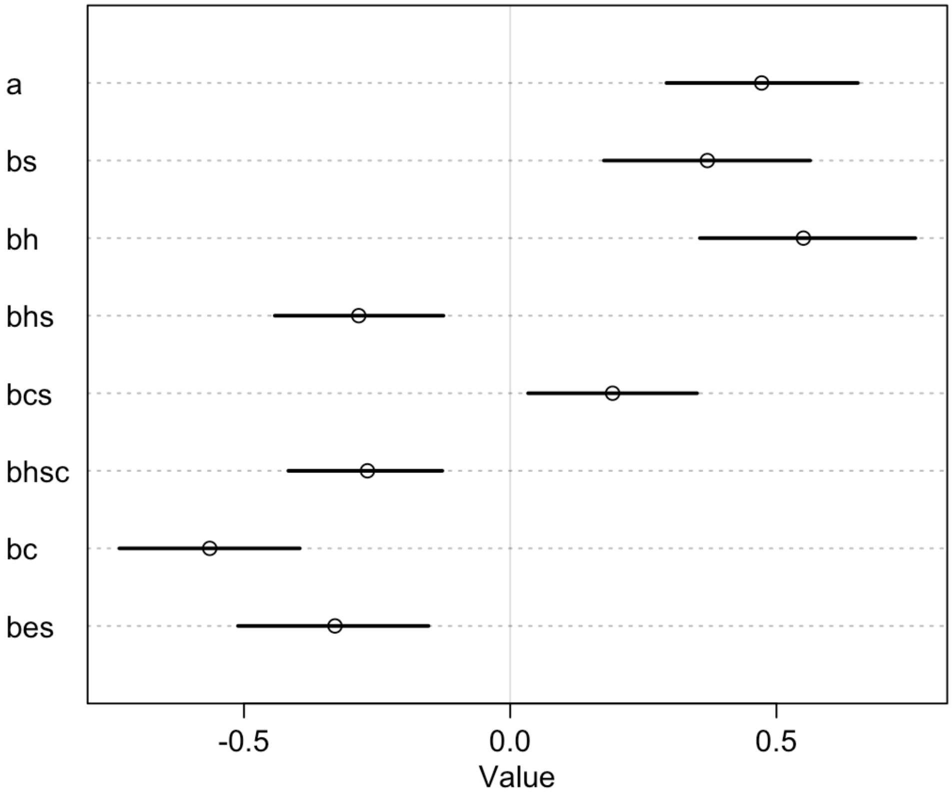


Figure 2: Individual effects and 2-way interactions in the best supported model of initial seedling survival. Data shown are simulated based on fitted model parameters, for illustrative purposes, rather than real data. All values other than those shown on axes or legends are held constant at the average. Shaded intervals represent the 95% highest posterior density interval in the simulated samples. A: Late successional seedlings had better survival than pioneers at low elevations, but worse at high elevations. B: For pioneers and, to a lesser degree, mid-successional seedlings, predicted survival probability increases with increasing initial height. C: Predicted seedling survival decreases in plots with higher than average crowding conditions, most severely for pioneers relative to mid- or late-successional seedlings.

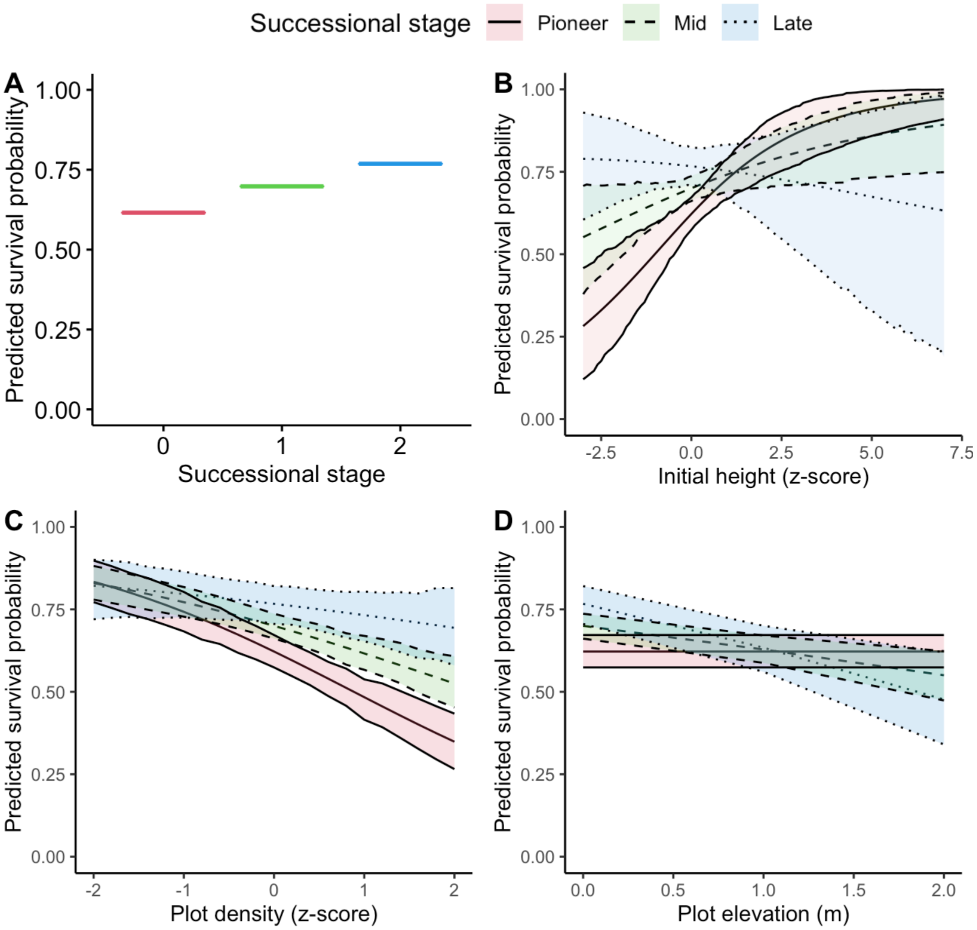


Figure 3: Predicted topography of the 3-way interaction between height, successional stage, and plot density, and observed topography of the same. Increasingly light areas represent conditions of better survival for a given successional group. A: As in Figure 2, data shown are simulated predictions, rather than real data, for visual clarity. All values other than those shown on axes or legends are held constant. Ranges of the relationships shown are slightly constricted from the full ranges of seeding height and density, as real coverage in the interaction space becomes relatively sparse at the extremes. B: Approximate true topography in the data, constructed by binning outcomes for individuals across the parameter space. Color scale as in A, red text superimposed on each cell gives the sampling depth in that region (number of seedlings).

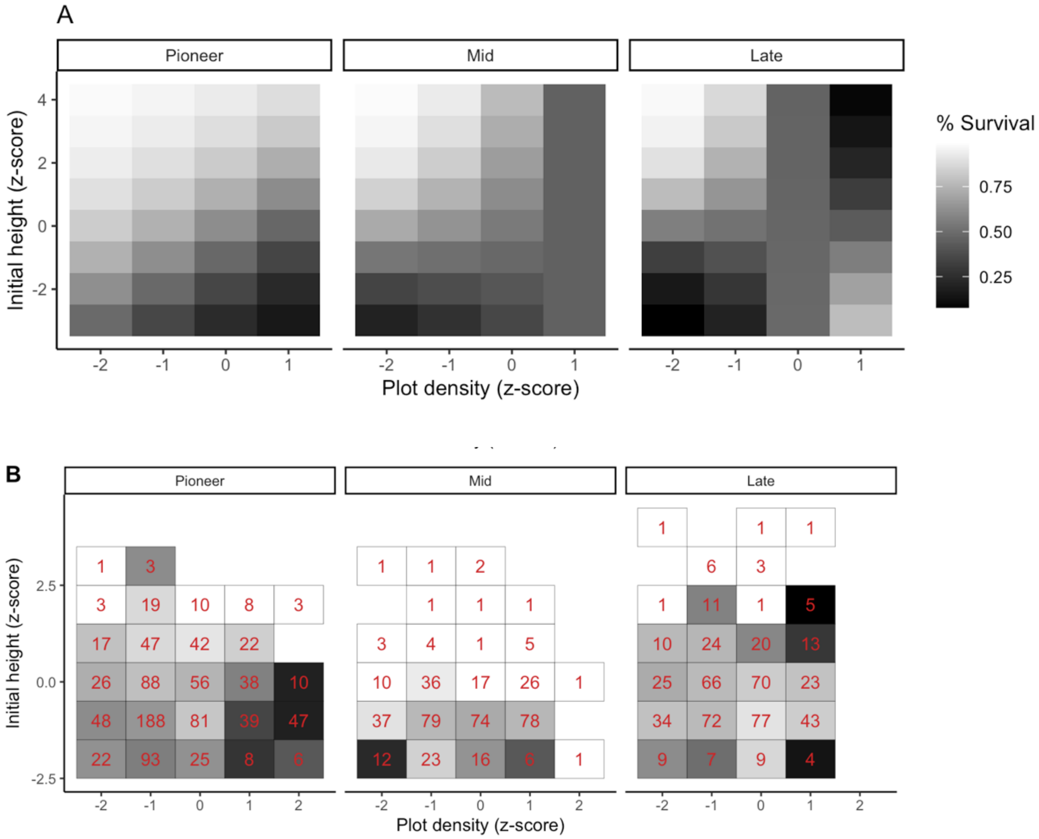


Figure 4: Seedling outcomes across the survey period among later recruits. Overall, cohort size decreased over the study period, and mortality at later life stages increased. Early mortality, between the first and second month, generally decreased across the study period, in contrast to what was predicted. However, this behavior appears to be more cyclical than linear, suggesting a likely seasonal pattern in early mortality.

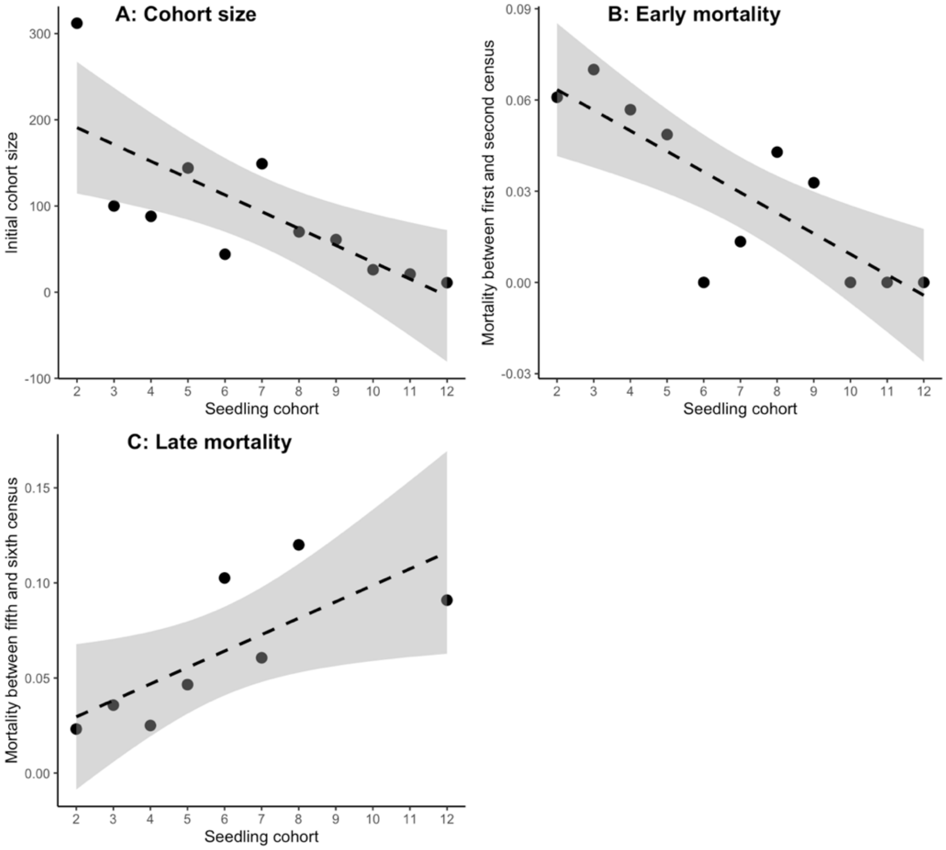


Figure 5: Seedling outcomes across the survey period in recruitment delay plots. Cohort sizes in recruitment delay plots were relatively steady, their early mortality may have increased across the period, and their late mortality increased. Note that there are relatively few cohorts in these delayed plots where mortality was available, particularly over the longer interval, and the sample sizes of individual seedlings were very small.

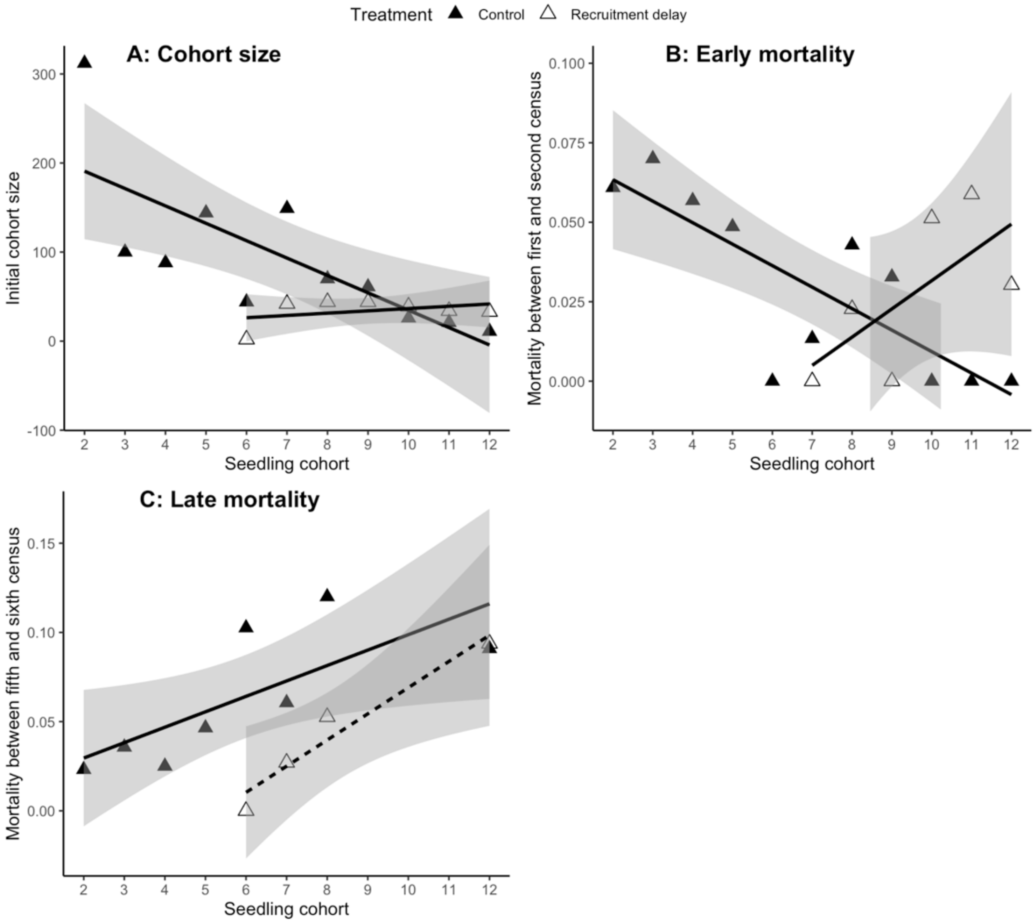


Figure 6: Equivalent seedling outcomes across the survey period among differing successional stages. We found no strong differences between pioneer and non-pioneer seedling for any of the three measures shown here.

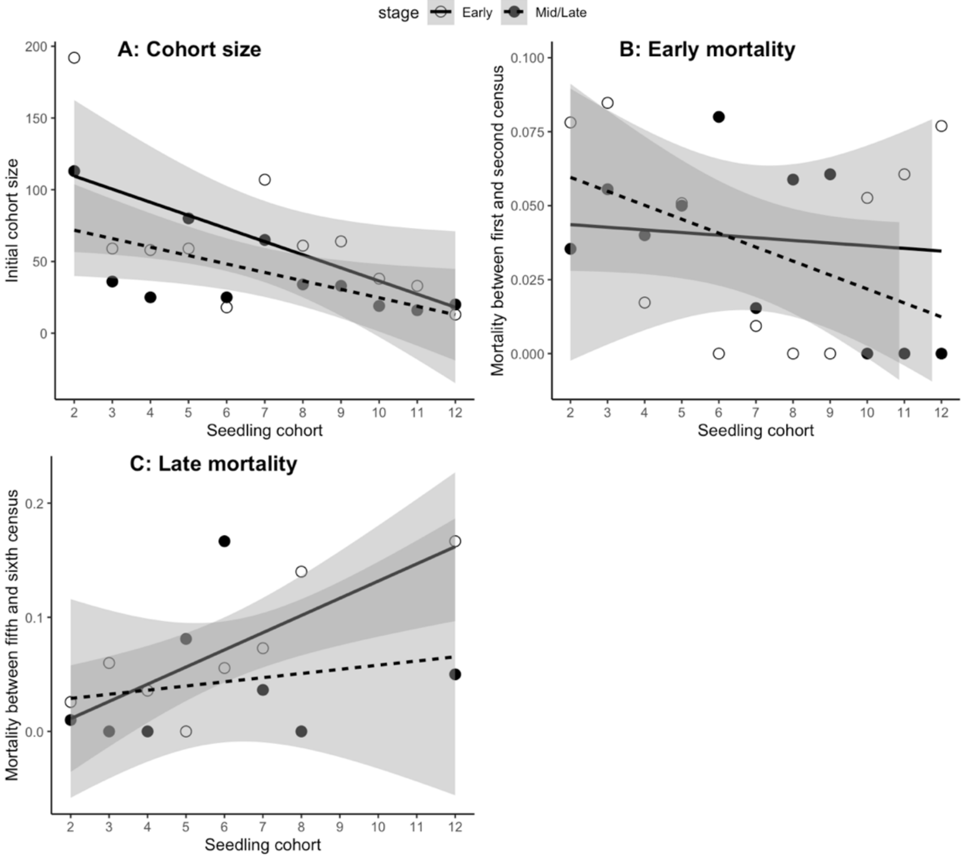
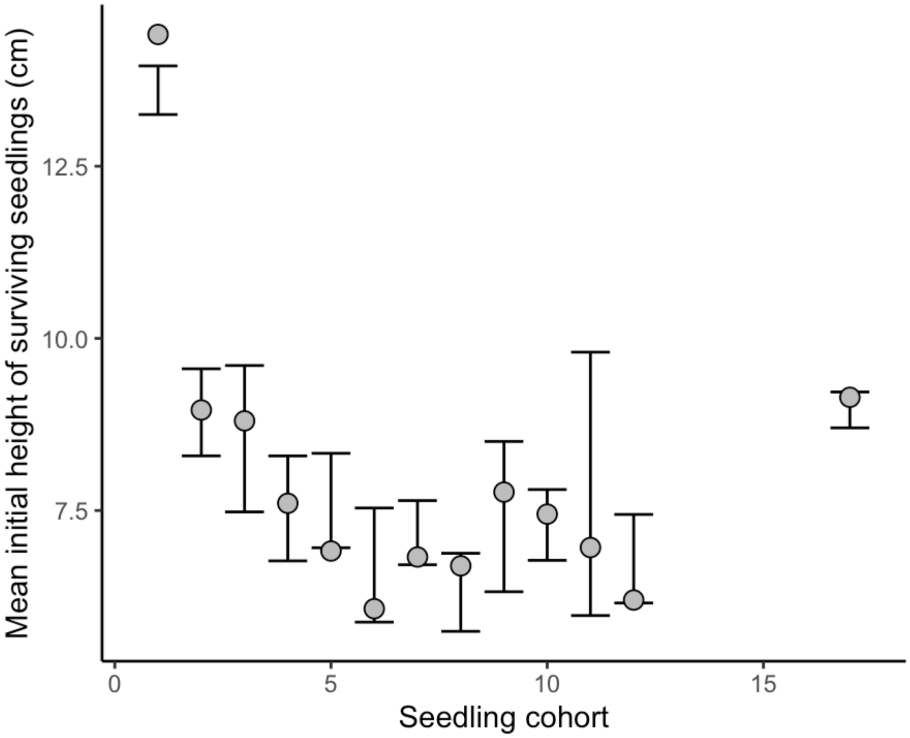


Figure 7: Absence of height-based survival bias in later cohorts. Survivorship among later seedling cohorts was unrelated to their measured initial height. Filled points represent the average height at initial measurement of seedlings which survived to the September survey from each seedling cohort. Capped bars represent a 95% confidence envelope for unbiased survivorship, constructed from 999 random draws from each cohort of the same number of survivors. Only the first cohort falls clearly outside of the null expectation. This general result holds true for both entire cohorts, as shown here, and for the divided cohorts for pioneers only/non-pioneers only and control only/recruitment delay only.



Literature Cited

Agyeman, V. K., Swaine, M. D., & Thompson, J. (1999). Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology*. https://doi.org/10.1046/j.1365-2745.1999.00400.x

Bellingham, P. J., Tanner, E. V. J., Rich, P. M., & Goodland, T. C. R. (1996). Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. *Journal of Tropical Ecology*. https://doi.org/10.1017/S0266467400009883

Biasutti, M., Sobel, A. H., Camargo, S. J., & Creyts, T. T. (2012). Projected changes in the physical climate of the Gulf Coast and Caribbean. *Climatic Change*. https://doi.org/10.1007/s10584-011-0254-y

Brokaw, N. (1985). Gap-phase regeneration in a tropical forest. *Ecology*. https://doi.org/10.2307/1940529

Brokaw, N. (1987). Gap-Phase Regeneration of Three Pioneer Tree Species in a Tropical Forest. *The Journal of Ecology*. https://doi.org/10.2307/2260533

Brokaw, N. V. L., & Walker, L. R. (1991). Summary of the Effects of Caribbean Hurricanes on Vegetation. *Biotropica*. https://doi.org/10.2307/2388264

Brown, S., Lugo, A. E., Silander, S., & Liegel, L. (1983). Research history and opportunities in the Luquillo Experimental Forest. *U.S.D.A. Forest Service, General Technical Report SO-44*, Southern Forest Experiment Station, New Orleans.

Comita, L. S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C. D., & Zimmerman, J. K. (2009). Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *Journal of Ecology*. https://doi.org/10.1111/j.1365-

2745.2009.01551.x

Crow, T. R. (1980). A Rainforest Chronicle: A 30-Year Record of Change in Structure and Composition at El Verde, Puerto Rico. *Biotropica*. https://doi.org/10.2307/2387772

Denslow, J. S. (1987). Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics. Vol. 18*. https://doi.org/10.1146/annurev.ecolsys.18.1.431

Emanuel, K. (2005). Increasing destructiveness of tropical cyclones over the past 30 years. *Nature*. https://doi.org/10.1038/nature03906

Everham, E. M., & Brokaw, N. V. L. (1996). Forest Damage and Recovery from Catastrophic Wind. *Botanical Review*. https://doi.org/10.1007/BF02857920

Frangi, J. L., & Lugo, A. E. (1991). Hurricane Damage to a Flood Plain Forest in the Luquillo Mountains of Puerto Rico. *Biotropica*. https://doi.org/10.2307/2388248

Fridman, J., & Ståhl, G. (2001). A three-step approach for modelling tree mortality in Swedish forests. *Scandinavian Journal of Forest Research*. https://doi.org/10.1080/02827580152632856

Gelman, A., Hwang, J., & Vehtari, A. (2014). Understanding predictive information criteria for Bayesian models. *Statistics and Computing*. https://doi.org/10.1007/s11222-013-9416-2

González, G., Lodge, D. J., Richardson, B. A., & Richardson, M. J. (2014). A canopy trimming experiment in Puerto Rico: The response of litter decomposition and nutrient release to canopy opening and debris deposition in a subtropical wet forest. *Forest Ecology and Management*. https://doi.org/10.1016/j.foreco.2014.06.024

Grime, J. P. (1977). Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist*. https://doi.org/10.1086/283244

Guzman-Grajales, S. M., & Walker, L. R. (1991). Differential Seedling Responses to Litter After Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*. https://doi.org/10.2307/2388259

Hall, J., Muscarella, R., Quebbeman, A., Arellano, G., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2020). Hurricane-Induced Rainfall is a Stronger Predictor of Tropical Forest Damage in Puerto Rico Than Maximum Wind Speeds. *Scientific Reports*. https://doi.org/10.1038/s41598-020-61164-2

Holzwarth, F., Kahl, A., Bauhus, J., & Wirth, C. (2013). Many ways to die - partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.12015

Kitajima, K. (2003). Impact of Cotyledon and Leaf Removal on Seedling Survival in Three Tree Species with Contrasting Cotyledon Functions. *Biotropica*. https://doi.org/10.1111/j.1744-7429.2003.tb00597.x

Klopcic, M., Simoncic, T., & Boncina, A. (2014). Comparison of regeneration and recruitment of shade-tolerant and light-demanding tree species in mixed uneven-aged forests: Experiences from the Dinaric region. *Forestry*. https://doi.org/10.1093/forestry/cpv021

Lines, E. R., Coomes, D. A., & Purves, D. W. (2010). Influences of forest structure, climate and species composition on tree mortality across the Eastern US. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0013212

Liu, X., Zeng, X., Zou, X., González, G., Wang, C., & Yang, S. (2018). Litterfall production prior to and during Hurricanes Irma and Maria in four puerto Rican forests. *Forests*. https://doi.org/10.3390/f9060367

Lodge, D. J., Scatena, F. N., Asbury, C. E., & Sanchez, M. J. (1991). Fine Litterfall and Related Nutrient Inputs Resulting From Hurricane Hugo in Subtropical Wet and Lower Montane Rain Forests of Puerto Rico. *Biotropica*. https://doi.org/10.2307/2388249

Luke, D., McLaren, K., & Wilson, B. (2014). The effects of a hurricane on seedling dynamics and abiotic interactions in a tropical lower montane wet forest. *Journal of Tropical Ecology*. https://doi.org/10.1017/S0266467413000734

Murphy, S. F., Stallard, R. F., Scholl, M. A., González, G., & Torres-Sánchez, A. J. (2017). Reassessing rainfall in the Luquillo Mountains, Puerto Rico: Local and global ecohydrological implications. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0180987

Ruiz-Benito, P., Lines, E. R., Gómez-Aparicio, L., Zavala, M. A., & Coomes, D. A. (2013). Patterns and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0056843

Shiels, A. B., Zimmerman, J. K., García-Montiel, D. C., Jonckheere, I., Holm, J., Horton, D., & Brokaw, N. (2010). Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *Journal of Ecology*. https://doi.org/10.1111/j.1365-2745.2010.01646.x

Sidrak, G., & Kapos, V. (1992). Hurricanes need not cause high mortality: The effects of hurricane gilbert on forests in jamaica. *Journal of Tropical Ecology*. https://doi.org/10.1017/S0266467400006386

Tanner, E. V. J., Kapos, V., & Healey, J. R. (1991). Hurricane Effects on Forest Ecosystems in the Caribbean. *Biotropica*. https://doi.org/10.2307/2388274

Turton, S. M. (1992). Understorey light environments in a north-east Australian rain forest before and after a tropical cyclone. *Journal of Tropical Ecology*. https://doi.org/10.1017/S0266467400006453

Van Beusekom, A. E., álvarez-Berríos, N. L., Gould, W. A., Quiñones, M., & González, G. (2018). Hurricane Maria in the U.S. Caribbean: Disturbance forces, variation of effects, and implications for future storms. *Remote Sensing*. https://doi.org/10.3390/rs10091386

Van Beusekom, A. E., González, G., Stankavich, S., Zimmerman, J. K., & Ramírez, A. (2020). Understanding tropical forest abiotic response to hurricanes using experimental manipulations, field observations, and satellite data. *Biogeosciences*. https://doi.org/10.5194/bg-17-3149-2020

Walker, L. R. (1991). Tree Damage and Recovery From Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica*. https://doi.org/10.2307/2388255

Walker, L. R. (1995). Timing of Post-Hurricane Tree Mortality in Puerto Rico. *Journal of Tropical Ecology*. https://doi.org/10.1017/S0266467400008786

Walker, L. R., Voltzow, J., Ackerman, J. D., Fernandez, D. S., & Fetcher, N. (1992). Immediate Impact of Hurricance Hugo on a Puerto Rican Rain Forest. *Ecology*. https://doi.org/10.2307/1940775

You, C., & Petty, W. H. (1991). Effects of Hurricane Hugo on Manilkara bidentata, a

Primary Tree Species in the Luqillo Experimental Forest of Puerto Rico. *Biotropica*. https://doi.org/10.2307/2388258

Zimmerman, J. K., III, E. M. E., Waide, R. B., Lodge, D. J., Taylor, C. M., & Brokaw, N. V. L. (1994). Responses of Tree Species to Hurricane Winds in Subtropical Wet Forest in Puerto Rico: Implications for Tropical Tree Life Histories. *The Journal of Ecology*. https://doi.org/10.2307/2261454