

# Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest

Liza S. Comita<sup>1\*</sup>, Maria Uriarte<sup>1</sup>, Jill Thompson<sup>2†</sup>, Inge Jonckheere<sup>3</sup>, Charles D. Canham<sup>4</sup> and Jess K. Zimmerman<sup>2</sup>

<sup>1</sup>Department of Ecology, Evolution and Environmental Biology, Columbia University, 1200 Amsterdam Ave., New York, NY 10027, USA; <sup>2</sup>Institute for Tropical Ecosystem Studies, Universidad de Puerto Rico, PO Box 21910, San Juan, PR 00931-3341, USA; <sup>3</sup>Biosystems Department, Geomatics Group, Katholieke Universiteit Leuven, 3001 Heverlee, Belgium; and <sup>4</sup>Cary Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545, USA

## Summary

1. Many forests experience periodic, large-scale disturbances, such as hurricanes and cyclones, which open the forest canopy, causing dramatic changes in understorey light conditions and seedling densities. Thus, in hurricane-impacted forests, large variations in abiotic and biotic conditions likely shape seedling dynamics, which in turn will contribute to patterns of forest recovery.

2. We monitored 13 836 seedlings of 82 tree and shrub species over 10 years following Hurricane Georges in 1998 in a subtropical, montane forest in Puerto Rico. We quantified changes in the biotic and abiotic environment of the understorey and linked seedling dynamics to changes in canopy openness and seedling density, and to spatial variation in soil type, topography and tree density.

3. Canopy openness was highest when first measured after Hurricane Georges and dropped significantly within *c.* 3 years, while seedling densities remained high for *c.* 5 years post-hurricane. When all species and census intervals were analysed together, generalized linear mixed effects models revealed that canopy openness, seedling and adult tree densities were significant drivers of seedling survival.

4. The relative importance of abiotic and biotic factors changed over time. Separate analyses for each census interval revealed that canopy openness was a significant predictor of survival only for the first census interval, with lower survival at the highest levels of canopy openness. The effect of conspecific seedling density was significant in all intervals except the first, and soil type only in the final census interval.

5. When grouping species into life-history guilds based on adult tree susceptibility to hurricane damage, we found clear differences among guilds in the effects of biotic and abiotic factors on seedling survival. Seedlings of hurricane-susceptible and intermediate guilds were more strongly influenced by canopy openness, while seedlings of the hurricane-resistant group were less affected by conspecific seedling density. Individual species-level analyses for 12 common species, however, showed considerable variation among species within guilds.

6. *Synthesis.* Our results suggest that hurricanes shape species composition by altering understorey conditions that differentially influence the success of seedlings. Thus, predicted increases in the intensity and frequency of hurricanes in the Caribbean will likely alter seedling dynamics and ultimately the species composition in hurricane-impacted forests.

**Key-words:** density dependence, hurricanes, long-term ecological research, Luquillo Forest Dynamics Plot, neighbourhood effects, Puerto Rico, recruitment limitation, regeneration niche, seedling dynamics, tropical forest dynamics

\*Correspondence author. E-mail: lsc2125@columbia.edu

†Present address: Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK.

## Introduction

Biologists have long recognized the importance of disturbance in structuring ecological communities (Sousa 1984; Pickett & White 1985). In forests, much attention has been paid to the role of small-scale disturbance created by branch or tree falls (see special issue in *Ecology* 70(3), 1989). However, many forests throughout the world also experience periodic disturbances that can dramatically alter forest structure on a large scale (Everham & Brokaw 1996; Whitmore & Burslem 1998). In coastal regions in both the tropics and temperate zone, these disturbance events can result from cyclone activity (i.e. hurricanes, typhoons, cyclones and tropical storms; Boose, Foster & Fluet 1994; Everham & Brokaw 1996; Mabry *et al.* 1998; McNab, Greenberg & Berg 2004; Lugo 2008).

Tree species native to hurricane-affected areas are likely to be well adapted to wind-mediated disturbance, and mortality as a result of storm damage is often low (Brokaw & Walker 1991; Tanner, Kapos & Healey 1991; Bellingham *et al.* 1992; Everham & Brokaw 1996; Burslem, Whitmore & Brown 2000). Nonetheless, significant structural damage to the forest often occurs during storms in the form of defoliation, stem snap, branch breakage and tip ups (Brokaw & Walker 1991; Everham & Brokaw 1996). Although large trees are more likely to be directly affected by storm events through increased wind exposure (Everham & Brokaw 1996; Canham, Papaik & Latty 2001; Ostertag, Silver & Lugo 2005), damage to the forest canopy can also have significant effects on plants growing in the understorey. Branch and tree falls and deep leaf litter can directly damage and kill smaller plants (You & Petty 1991), but can also have indirect effects on plants in the understorey. Damage to larger trees opens the forest canopy, dramatically increasing the area of gaps and altering the light regime, microclimate and heterogeneity of the forest floor (Brokaw & Grear 1991; Fernandez & Fetcher 1991; Walker *et al.* 1992; Bellingham *et al.* 1996; Lin *et al.* 2003). These changes in microclimate and understorey light levels are often short-lived (Fernandez & Fetcher 1991; Bellingham *et al.* 1996), and thus hurricanes increase both the spatial and temporal variation in environmental conditions of the understorey.

Plants growing under intact tropical forest canopies are severely light-limited, receiving only a small fraction of overhead light (Chazdon *et al.* 1996). Increases in light levels usually result in increased growth, survival and density of plants in the understorey (Everham, Myster & VandeGenachte 1996; Montgomery & Chazdon 2002; Barberis & Tanner 2005), although increased canopy openness could also result in lower seedling survival through desiccation (Gerhardt 1996). Higher understorey light availability, as well as increased heterogeneity, following hurricane disturbance are therefore expected to have strong impacts on seedling dynamics, with differences among species driven by variation in life-history strategy (Walker *et al.* 2003). While light is typically the most limiting factor, tree seedling dynamics are also driven by the availability of below-ground resources (Burslem, Grubb & Turner 1996; Coomes & Grubb 2000; Lewis & Tanner 2000; Yavitt &

Wright 2008; Comita & Engelbrecht 2009). After hurricanes, the large temporal and spatial variation in light availability may initially override the influence of soil resources on seedling dynamics. Conversely, if light is no longer limiting following disturbance, seedling dynamics may be more strongly driven by other abiotic factors, such as soil moisture or nutrient availability (Coomes & Grubb 2000; Walker *et al.* 2003; Barberis & Tanner 2005).

Studies have also shown that the local biotic neighbourhood (i.e. the density and identity of neighbouring plants) has significant effects on seedling dynamics in both tropical and temperate forests (Webb & Peart 1999; Harms *et al.* 2000; Hille Ris Lambers, Clark & Beckage 2002; Uriarte *et al.* 2005; Queenborough *et al.* 2007; Comita & Hubbell 2009). High densities of conspecific neighbours can result in decreased survival, presumably due to strong intraspecific competition or host-specific natural enemies, such as insect herbivores and pathogens (Janzen 1970; Connell 1971). In addition to effects on abiotic conditions, large-scale natural disturbances likely alter the biotic neighbourhood as well: increased light levels following hurricane disturbance can result in higher seedling densities in the understorey (Walker *et al.* 2003), which may then trigger a subsequent increase in density-dependent mortality over time. At the same time, hurricanes potentially reduce the intensity of competition between neighbours for soil resources since they lead to significant, long-term decreases in fine root biomass (Silver *et al.* 1996). Thus, in hurricane-impacted forests, large variations in both local abiotic and biotic conditions are likely to be important drivers of seedling dynamics.

Understanding the factors influencing seedling dynamics is critical to understanding forest community dynamics because the seedling stage suffers high mortality and, therefore, represents a significant bottleneck in the life cycle of trees (Harper 1977). Processes affecting the spatial and temporal patterns of seedling recruitment and survival are thought to play a significant role in promoting species coexistence in diverse forests (Janzen 1970; Connell 1971; Grubb 1977; Chesson & Warner 1981). In this context, the role of biotic and abiotic conditions has been well-explored in a number of temperate and tropical forests (Nakashizuka 2001; Wright 2002). Few studies, however, have been conducted in hurricane-impacted forests, where understorey conditions fluctuate to a much greater degree than in other forests.

Information on how species respond to variations in understorey conditions are essential for making predictions about how forest communities will respond to both human and natural disturbance. Previous studies that have looked at patterns of seedling survival following hurricane disturbance have been restricted to a handful of species (e.g. Guzman-Grajales & Walker 1991; Walker *et al.* 2003), and attempts to group species based on their seedlings' responses to hurricanes have shown limited success (Walker *et al.* 2003; Uriarte *et al.* 2005). Seedlings of species with differing life-history strategies are expected to respond differently to abiotic and biotic neighbourhood variables. Shade tolerance is often a key trait in determining seedling survival in the forest understorey (Valladares & Niinemets 2008), with a trade-off between a species'

ability to persist at low light levels and to grow quickly under high-light conditions (Kobe *et al.* 1995). Shade-tolerant species are typically less susceptible to pathogen and herbivore attack than light-demanding species, because of differences in the allocation of resources to defence vs. growth (Coley 1980). Shade tolerance should, therefore, be a strong determinant of seedlings' reactions to light levels and neighbour densities following hurricane disturbance. Studies of large trees have found a trade-off between species' susceptibility to damage by hurricanes and their ability to take advantage of increased light availability (Zimmerman *et al.* 1994; Uriarte *et al.* 2004; Ostertag, Silver & Lugo 2005; but see Gleason *et al.* 2008). Thus, species' susceptibility to hurricanes may serve as a proxy for shade-tolerance and may therefore be a useful life-history trait for predicting species' seedling responses to changing environmental conditions after hurricanes (Bellingham, Tanner & Healey 1995; Burslem, Whitmore & Brown 2000; Batista & Platt 2003).

To explore the effects of biotic and abiotic conditions on seedling survival in a hurricane-impacted forest, we used data on 13 836 seedlings of 82 tree and shrub species from a subtropical forest in northeastern Puerto Rico. Puerto Rico experiences major (F3 damage) hurricanes every 50–60 years on average (Boose, Serrano & Foster 2004), but suffered severe hurricanes in 1989 and 1998 that caused significant damage to the forest (Walker 1991; Zimmerman *et al.* 1994; Ostertag, Silver & Lugo 2005). Following Hurricane Georges in 1998, we monitored the seedling population over a 10-year period and related seedling community dynamics to changes in canopy openness and seedling densities, and to spatial variation in soil type and topography. Specifically, we ask: (i) Are abiotic factors more important drivers of seedling survival than the local biotic neighbourhood? (ii) After hurricane disturbance, does the relative importance of abiotic and biotic neighbourhood variables for seedling survival change over time? (iii) Can a species' life-history strategy be used to predict which factors are most important for seedling survival?

## Materials and methods

### STUDY SITE

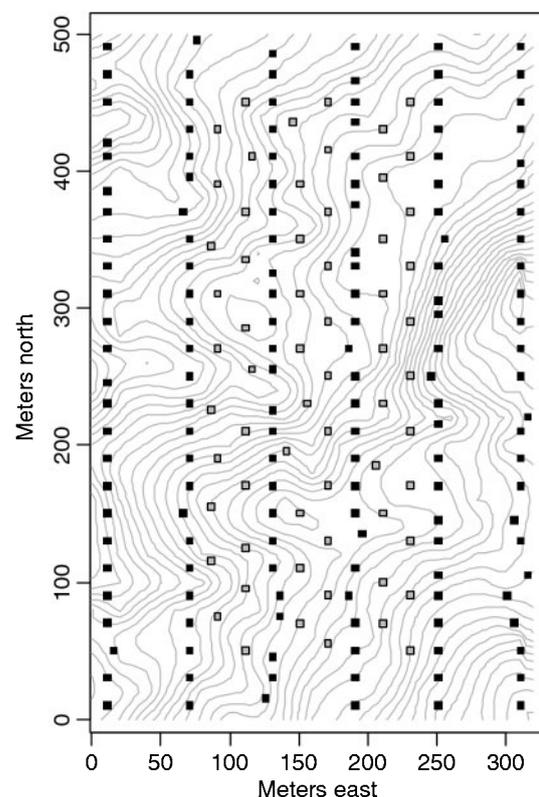
The study was carried out in the 16-ha Luquillo Forest Dynamics Plot (LFDP; 18°20'N, 65°49'W) in the Luquillo Mountains of north-eastern Puerto Rico (Thompson *et al.* 2004). The LFDP (320 × 500 m) is located within the Luquillo Experimental Forest and is part of the Luquillo Experimental Forest Long-Term Ecological Research (LTER) program and the Center for Tropical Forest Science (CTFS) network of forest plots. With a mean annual rainfall of 3500 mm, forest in the LFDP is classified as 'subtropical wet' in the Holdridge life zone system (Ewel & Whitmore 1973) and 'tropical montane' in Walsh's (1996) tropical climate system. The LFDP consists of a mix of primary and secondary forest that has been free from human disturbance since the 1940s (Thompson *et al.* 2002).

The LFDP was established in June 1990, when a professional survey team began gridding the plot into 20 × 20 m quadrats. These quadrats were later divided into 16 5 × 5 m subquadrats. At approximately 5-year intervals since 1990, all free-standing woody stems

≥ 1 cm d.b.h. (diameter at 1.3 m above ground) in the LFDP have been tagged, mapped, identified to species and measured (see Thompson *et al.* 2002 for protocols). Individuals were identified in the field or using voucher specimens, with nomenclature following Liogier (1985, 1988, 1994, 1995, 1997). A total of 145 species of 47 families have been identified in the plot, with an average of 73.3 species per ha (Thompson *et al.* 2004). The most recent major hurricane to impact the forest of the LFDP was Hurricane Georges, which struck Puerto Rico on 21 September 1998. A category 3 storm with sustained winds of 184 km h<sup>-1</sup> and gusts up to 241 km h<sup>-1</sup>, Georges caused considerable damage to trees in the Luquillo Forest (Ostertag, Scatena & Silver 2003; Ostertag, Silver & Lugo 2005).

### SEEDLING CENSUSES

To study seedling regeneration following hurricane damage, 150 seedling plots (2 × 1 m) were established in the LFDP in March 1999 (Uriarte *et al.* 2005), *c.* 6 months after Hurricane Georges. The seedling plots were located at 20-m intervals (in the centre of each 20 × 20 m quadrat) along six north–south running transects spaced 60 m apart (Fig. 1). Where seedling plots at the centre of a 20 × 20 m quadrat would have landed on an established trail or in a stream, the seedling plot was located in a nearby 5 × 5 m subplot within the same 20 × 20 m quadrat. An additional 63 plots were added between the second and fifth transects in 2004 to increase sample sizes in the interior of the plot. These were established in the centre of the 20 × 20 m quadrats and were therefore usually at least 20 m from any other seedling plot (Fig. 1).



**Fig. 1.** Topography and location of seedling plots (2 × 1 m) in the 16-ha Luquillo Forest Dynamics Plot, Puerto Rico. Black squares correspond to 150 seedling plots established in 1999, while grey squares denote seedling plots established in 2004.

The first seedling census took place from 6 March to 24 April 2000. All free-standing woody seedlings  $\geq 10$  cm tall and  $< 1$  cm d.b.h. within the seedling plots were tagged, identified to species and measured for height and basal diameter. Palm seedlings were included if their newest frond arose less than 1.3 m from the ground and were therefore too small to be recorded in the main tree census. Liana seedlings were not included, but ferns were tagged and identified to species in the seedling plots. Ferns that have a stoloniferous habit were tagged as individuals, where each clump of fronds arose on a stolon, to give a better indication of the fern density in the plot. Seedling censuses were also carried out in 2002 (17 April–17 July), 2004 (5 August–14 October), 2007 (20 February–16 March) and 2008 (17 January–22 February).

### *Biotic factors*

To quantify the local biotic neighbourhood in which each seedling was growing, we calculated the density ( $\text{m}^{-2}$ ) of conspecific and heterospecific seedlings in each seedling plot. Ferns were not included as focal individuals in our analysis, but were included in the calculation of heterospecific seedling densities for each plot. As a measure of the effect of larger saplings and trees, we summed the basal area ( $\text{m}^2$ ) of all stems  $\geq 1$  cm d.b.h. within 10 m from the centre of the seedling plot. Preliminary analyses showed that including neighbour information for trees beyond 10 m did not improve model fit. When analysing seedling survival up to 2004, we used data on basal area from the tree census that started in 2000, and for seedling survival after 2004, we used data from the tree census that started in 2005.

### *Abiotic factors*

**Canopy openness:** To assess light conditions in the understorey following Hurricane Georges, hemispherical photographs were taken using a fisheye lens (Nikkor; Nikon Inc., Tokyo, Japan) mounted on a Nikon camera body (Nikon Inc.) at a height of 1 m over the centre of each seedling plot during March–April 1999. Photographs were taken again over each seedling plot during the censuses in 2002, 2004 and 2007. We analysed the colour hemispherical photos using an automatic thresholding program that classifies RGB photographs into binary images, where pixels in black represent vegetation and pixels in white represent sky. The algorithm uses an automatic global thresholding algorithm combined with a local thresholding algorithm to correct for local light anomalies (e.g. sun flecks, underexposure, etc.) in the photographs (Jonckheere *et al.* 2005, 2006). This method ensures objective and repeatable results since no operator is involved in the thresholding step. Following this analysis, the picture was divided in 60 azimuth and five zenith rings, and the proportion of pixels classified as sky was calculated for each resulting segment. The segments were weighted according to the portion of the hemisphere that they represent and then grouped to calculate the percent canopy openness for the entire image.

**Soils:** Soils in the LFDP are formed from volcanoclastic sandstone (Soil Survey Staff 1995). Each  $5 \times 5$  m subquadrat of the LFDP was assigned to one of five soil types based on a survey conducted by the U.S. Department of Agriculture. In order of increasing wetness and poor drainage, the soil types are Zarzal, Cristal, Prieto, Colosa and Fluvaquents (Soil Survey Staff 1995). Zarzal, Cristal and Prieto are deep clays, while Coloso and Fluvaquents are formed from alluvium in the stream channels. Zarzal has low fertility, Cristal and Colosa low to moderate, Prieto moderate and Fluvaquents moderate to high (Soil Survey Staff 1995). However, differences in wetness among soil types typically override effects of soil fertility at our study site due to

low oxygen content in water-logged soils (Silver, Lugo & Keller 1999).

**Topography:** Elevation measurements were taken at the corner of each  $20 \times 20$  m quadrat in the 16-ha grid and ranged from 333 to 428 m a.s.l. Elevation values for the  $20 \times 20$  m quadrats were interpolated to calculate the elevation of the corners of the  $5 \times 5$  m subquadrats. These values were then used to calculate percent slope for each subquadrat. In addition, each subquadrat was assigned to one of four topographic classes (slope, ridge, valley and bench) based on observations in the field during the 2005 tree census. The slope category corresponds to subquadrats with  $> 15\%$  slope, while benches are relatively flat areas not associated with ridge tops or valleys. Soil moisture often varies with topographic unit in tropical forests (Becker *et al.* 1988; Daws *et al.* 2002), and percent slope is important as seedlings in steeper areas are more likely to be damaged by water runoff or land slips (Daws *et al.* 2005).

### STATISTICAL ANALYSIS

We modelled the probability of an individual seedling surviving a census interval as a function of the abiotic and biotic neighbourhood variables described above, using generalized linear mixed-effects models with binomial errors. Biotic variables included conspecific and heterospecific seedling density and tree basal area within 10 m of the seedling plot. For abiotic variables, we included soil type, topography and canopy openness. For canopy openness, we incorporated terms for both absolute and squared canopy openness, to allow for a nonlinear effect of light on survival (e.g. a hump-shaped curve), as has been observed in other tropical forests (Kobe 1999). For topography, we included both topographic category (slope, ridge, valley and bench) and percent slope. We assigned to each seedling the canopy openness of the seedling plot at the start of the census interval and the soil type, topographic category and percent slope of the  $5 \times 5$  m subquadrat in which it was located. All biotic and abiotic variables as well as log-transformed initial seedling height entered the model as fixed effects. For all continuous explanatory variables (seedling height, seedling density, tree basal area, canopy openness and percent slope), values were standardized by subtracting the mean value of the variable (across all individuals in the analysis) and dividing by 1 standard deviation. This allows for a direct comparison of the relative importance of the explanatory variables (Gelman & Hill 2006). The mean and range of all explanatory variables used in the analysis are listed in Appendix S1.

Seedlings within the same seedling plot are likely to have probabilities of survival that are more similar than those of seedlings in different plots, even when accounting for local biotic and abiotic conditions. To account for this spatial autocorrelation in survival, we included seedling plot as a random effect in the model. Including a plot effect should be sufficient, since all seedling plots are spaced at least 10 m apart, and previous studies have found that spatial autocorrelation in tropical seedling survival is negligible at distances  $> 5$  m (Queenborough *et al.* 2007).

Seedling survival was analysed at several different taxonomic and temporal scales. First, we included observations of all seedlings over all census intervals together in a single community-level analysis, with the survival of each seedling through each census interval as a separate observation. In this analysis all species were analysed together, therefore, we included species as a random effect. We also included seedling individual as a random effect because we had multiple observations of some individuals that survived multiple intervals. Since the time between censuses varied, we also included census interval length as a fixed effect in this analysis.

**Table 1.** Focal species used in species-level analyses of seedling survival, grouped by life-history guild based on susceptibility to damage during hurricanes. *n* is the number of seedlings encountered over the course of the study

Species	Code	Family	Hurricane susceptibility	Growth form	<i>n</i>
<i>Piper glabrescens</i>	PIPGLA	Piperaceae	–	Shrub	303
<i>Psychotria berteriana</i>	PSYBER	Rubiaceae	–	Shrub	351
<i>Psychotria brachiata</i>	PSYBRA	Rubiaceae	–	Shrub	170
<i>Inga laurina</i>	INGLAU	Fabaceae	Susceptible	Tree	906
<i>Sapium laurocerasus</i>	SAPLAU	Euphorbiaceae	Susceptible	Tree	143
<i>Schefflera morototoni</i>	SCHMOR	Araliaceae	Susceptible	Tree	142
<i>Guarea guidonia</i>	GUAGUI	Meliaceae	Intermediate	Tree	2764
<i>Ocotea leucoxydon</i>	OCOLEU	Lauraceae	Intermediate	Tree	218
<i>Tabebuia heterophylla</i>	TABHET	Bignoniaceae	Intermediate	Tree	219
<i>Dacryodes excelsa</i>	DACEXC	Burseraceae	Resistant	Tree	659
<i>Prestoea acuminata</i> var. <i>montana</i>	PREMON	Arecaceae	Resistant	Palm	5627
<i>Trichilia pallida</i>	TRIPAL	Meliaceae	Resistant	Tree	177

Secondly, to determine how the relative importance of biotic and abiotic factors changed over time after the hurricane, we analysed community-level survival patterns for each census interval separately. In this analysis, we included species, but not individual, as a random effect since we only had one observation per individual over each census interval. Covariates were standardized as described above, but calculated separately for each census interval (i.e. using the mean and standard deviation of values from only that interval).

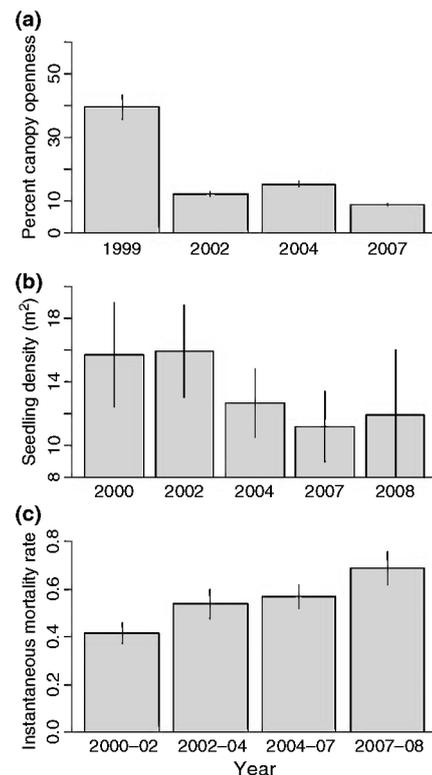
Next, we assessed the effect of species life-history strategy by dividing species into different life-history guilds and analysing each guild separately. Previous studies in Puerto Rico have found that hurricane damage is related to species shade tolerance in that fast-growing, pioneer species suffer greater damage than slower-growing, non-pioneer species (Zimmerman *et al.* 1994; Uriarte *et al.* 2004; Ostertag, Silver & Lugo 2005; Ogle *et al.* 2006). We therefore used data on the percent of adult trees ( $\geq 10$  cm d.b.h.) with broken stems caused by Hurricane Hugo (J. Zimmerman, unpublished data) to classify tree species (with  $\geq 10$  observations of damage status) into three guilds that reflect species' reactions to hurricanes, in terms of both susceptibility to damage during a hurricane and ability to respond to the high light levels afterwards. Tree species with  $< 6\%$  broken stems were classified as hurricane-resistant (14 species), with 6–10% broken stems as intermediate (15 species), and with  $\geq 10\%$  as hurricane-susceptible (14 species). Shrub species were not assessed for damage after Hurricane Hugo, and so we examined these species as a separate group.

In addition to the analyses examining all species in each life-history guild together, we performed separate species-level analyses for the three most abundant species in each guild, as well as the three most common shrub species in the plot (Table 1). These focal species had  $> 175$  observations of seedling survival over all census periods and were encountered in at least 50 seedling plots. For both guild- and species-level analyses, we analysed all observations (each record of an individual seedling surviving across each census interval) together, since there were not sufficient data to analyse each census interval separately. We did not include individual as a random effect in these analyses, since many species did not have enough repeated observations to estimate this effect, and for those species that did, the amount of variance explained was minimal. For analyses of guilds and focal species, we again standardized the continuous explanatory variables as described above, but used the mean and standard deviation of all observations, not only of the focal group or species being analysed. This allowed us to compare effects across species and guilds. All analyses were carried out in R version 2.7.1 (R Development Core Team 2008), using the 'lme4' package (Bates & Maechler 2009).

## Results

### CHANGES IN THE FOREST UNDERSTOREY OVER TIME

Both canopy openness and seedling density varied significantly among censuses (Fig. 2). Canopy openness was nearly four



**Fig. 2.** Mean percent canopy openness (a), seedling densities (b) and seedling mortality rates (c) in the understory of the Luquillo forest over 10 years of recovery following Hurricane Georges, which occurred in September 1998. Bars represent mean values ( $\pm 2$  SE) for each census over all seedling plots. Instantaneous mortality rates were calculated as  $\ln(n/S)/\text{time}$ , where *n* is the total number of seedlings at the start of the census interval and *S* is the number that survived to the next census.

times higher in March 1999, 6 months after Hurricane Georges, than in subsequent seedling censuses 3–9 years later (Fig. 2a). Seedling densities were noticeably higher in the first two censuses (in 2000 and 2002) after Hurricane Georges compared to subsequent censuses (in 2004, 2007, 2008; Fig. 2b). Seedling mortality recorded over each census interval increased steadily over time, with mortality rates significantly lower over the first census interval (2000–02) and higher over the final census interval (2007–08) compared to other intervals (Fig. 2c).

#### ABIOTIC AND BIOTIC DRIVERS OF SEEDLING SURVIVAL

Overall, we found significant effects of individual-level, biotic and abiotic factors on seedling survival in the Luquillo forest (Fig. 3). As expected, taller seedlings showed an increased probability of survival, while survival decreased as length of the census interval increased. Of the abiotic and biotic variables assessed, canopy openness had the strongest impact on survival (Fig. 3) and its effect was nonlinear: the probability of survival increased with increasing canopy openness up to *c.* 70% openness, then decreased slightly at levels > 70% (Fig. 4). In contrast to the strong effect of canopy openness, we found little evidence that survival was influenced by soil type, topographic category or percent slope (all  $P < 0.05$ ).

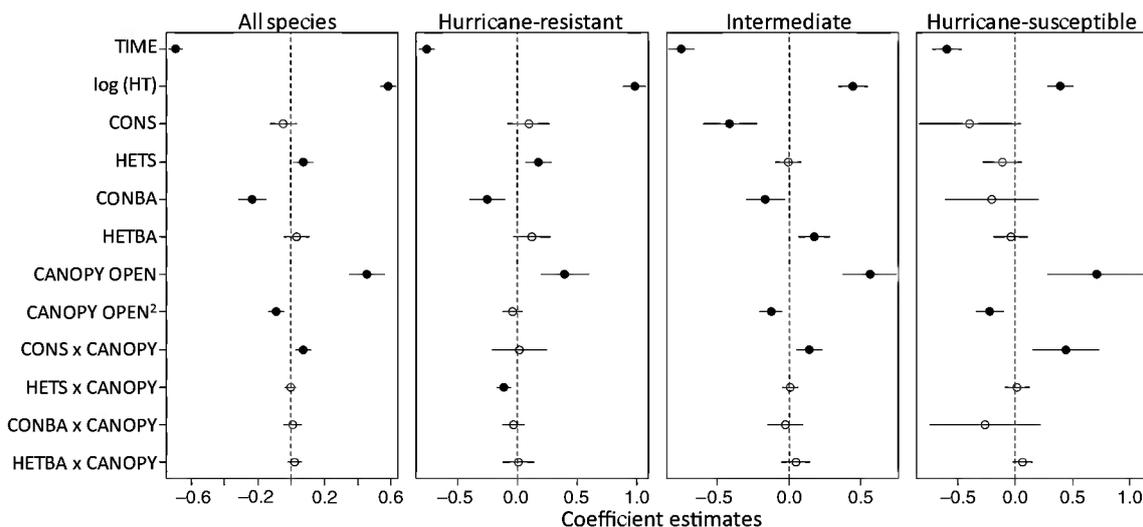
Both the density of seedling neighbours and basal area of trees within 10 m significantly influenced seedling survival, with conspecific neighbours tending to have a negative effect. Conversely, the effect of heterospecific seedling density was slightly positive, while heterospecific adult basal area did not have a significant effect. There was a significant interaction between canopy openness and conspecific seedling density (Fig. 3). At low to medium canopy openness, higher conspecific seedling density reduced the probability of survival. As canopy openness increased, the effect of conspecific seedling

neighbours weakened, becoming negligible at values above *c.* 50% (Fig. 5).

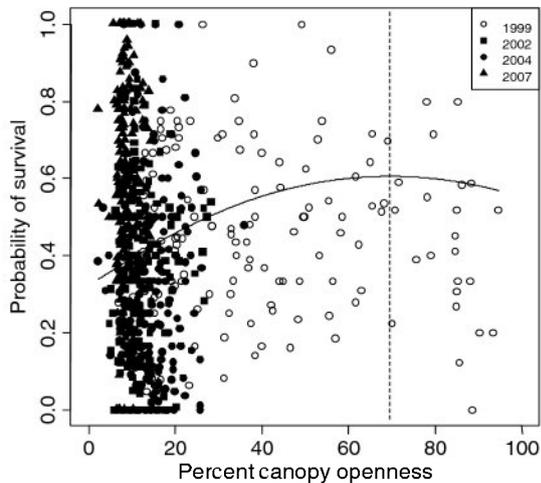
#### CHANGES IN THE RELATIVE IMPORTANCE OF ABIOTIC AND BIOTIC FACTORS OVER TIME

When analysing each census interval separately, we observed that the relative importance of factors influencing seedling survival changed over time after the hurricane. Canopy openness was a significant predictor of seedling survival during the first census interval (2000–02), showing a hump-shaped response with survival declining at higher levels (Figs 4 and 6). In subsequent intervals, when mean canopy openness was significantly lower and less variable across the LFDP (Fig. 2), we detected no significant effects of canopy openness on seedling survival (Fig. 6). Conversely, the effect of conspecific seedling density on survival was not significant for the first census interval, but was for subsequent intervals (Fig. 6). Interestingly, the effect of conspecific seedling neighbours was negative in the second and third census intervals (2002–04 and 2004–07 respectively), but positive in the final census interval (2007–08). Significant interactions between seedling density and canopy openness were only found in the second census interval, 5–6 years after Hurricane Georges. Contrary to the pattern found when analysing all intervals together, both conspecific and heterospecific seedling neighbours tended to have an increasingly negative effect on seedling survival as canopy openness increased (Fig. 6).

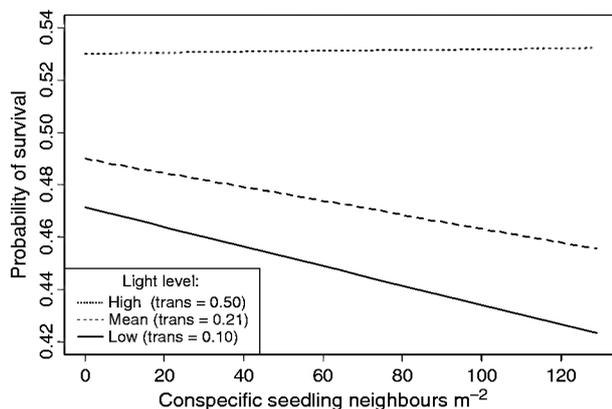
Despite differences among census intervals in the effects of canopy openness and seedling neighbour density, there were some consistent patterns across all intervals. The probability of seedling survival increased with seedling height and decreased with conspecific tree basal area in all census intervals (Fig. 6). As in the analysis of all intervals combined, there was little evidence for significant effects of soil type or topography on seedling survival. However, for the final census interval (2007–08), there was significantly lower survival in the Prieto



**Fig. 3.** Estimated effects ( $\pm 2$  SE) of individual-level, abiotic and biotic variables on seedling survival in the Luquillo forest for all species combined, and separately for each of three life-history guilds based on susceptibility to hurricanes. Filled circles indicate significant effects ( $P < 0.05$ ). Effects of topographic category, soil type and percent slope were not significant and are not shown. Note difference in *x*-axis ranges.



**Fig. 4.** Effect of percent canopy openness on seedling survival in the Luquillo Forest Dynamics Plot. Points represent mean survival in each seedling plot in each census interval plotted as a function of canopy openness measurements taken at the start of the interval (see legend). Curve represents predicted relationship based on the generalized linear mixed-effect model including all observations (see Materials and methods for details).



**Fig. 5.** Effect of conspecific seedling density on the probability of survival for seedlings in the Luquillo forest. The strength of the effect depended on percent canopy openness, with stronger negative effects of conspecific neighbour density at lower canopy openness levels.

soil type, of moderate soil wetness, compared to the better drained Zarzal soil type (the baseline in the model).

#### DIFFERENCES AMONG LIFE-HISTORY GUILDS AND SPECIES

There were several interesting differences among the three life-history guilds (hurricane-susceptible, intermediate and hurricane-resistant, using 43 species total) in the relative importance of abiotic and biotic variables for seedling survival. Canopy openness had a significant positive effect on survival for all three guilds. As expected, the strength of this effect was greatest for the hurricane-susceptible group, followed by the intermediate and then the hurricane-resistant group, although differences among groups were not statistically significant

(Fig. 3). For both the intermediate and hurricane-susceptible groups, the effect of conspecific seedling density was negative, and there was a significant positive interaction between conspecific seedling density and canopy openness. For the hurricane-resistant group, there was no significant effect of conspecific seedling density on survival, but there was a significant positive effect of heterospecific seedling density and also a significant negative interaction between heterospecific seedling density and canopy openness, indicating a more negative effect of heterospecifics at higher levels of canopy openness (Fig. 3).

When looking at the three most common species within each life-history guild, the patterns were not as clear (Table 2). A strong, positive effect of canopy openness on seedling survival was found for only one of the three hurricane-susceptible species (*Inga laurina*; Fig. 7). The term for canopy openness squared was significantly negative for another hurricane-susceptible species (*Schefflera morototoni*), indicating a declining probability of seedling survival with increasing light (Fig. 7). Two out of the three focal species in both the hurricane-resistant group (*Prestoea acuminata* var. *montana* Henderson, *Trichilia pallida*) and the intermediate group (*Guarea guidonia*, *Tabebuia heterophylla*) showed a significant effect of canopy openness on seedling survival (Table 2). For those species, the effect of canopy openness was positive with survival increasing up to an intermediate level of canopy openness, and then levelling off or declining slightly (Fig. 7). One exception was the palm species *P. acuminata* which showed little evidence of levelling off at higher values of canopy openness (Fig. 7). Like trees, the three focal shrub species showed a variety of relationships between seedling survival and canopy openness, although canopy openness was only a significant predictor of survival for one shrub species (*Psychotria berteriana*; Fig. 7).

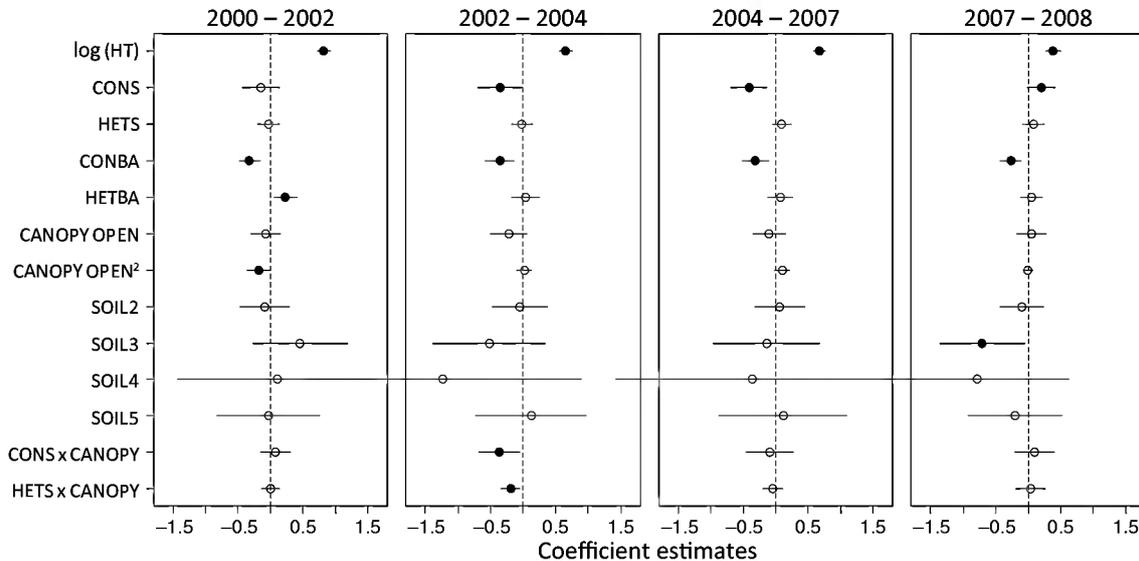
As with canopy openness, the effects of neighbours varied widely among species (Table 2). Conspecific seedling density had a neutral or positive effect on survival for the three hurricane-resistant species as found in the guild-level analysis. For all three shrub species, however, the effect of conspecific seedling density was negative, although not significant. In contrast, negative effects were found for only three out of the nine focal tree species (Table 2).

We detected significant effects of topographic or soil variables for only three of the 12 focal species (Table 2). The shrub species *Piper glabra* had significantly lower survival in valleys compared to ridges, slopes and benches. Survival of *Schefflera morototoni* seedlings increased with percent slope, and *Guarea guidonia* had significantly lower survival in the Cristal soil type.

## Discussion

### HURRICANE EFFECTS ON UNDERSTOREY CONDITIONS

As expected, when canopy openness was measured in March 1999, 6 months after Hurricane Georges, we found high canopy openness due to the widespread forest canopy damage that occurred in the Luquillo forest during the hurricane (Ostertag, Silver & Lugo 2005; Canham *et al.* in press). Within 3 years,



**Fig. 6.** Estimated effects ( $\pm 2$  SE) of seedling height, abiotic and biotic neighbourhood variables on seedling survival in the Luquillo forest in each census interval. Filled circles indicate significant effects ( $P < 0.05$ ). Variables that were not significant in any interval are not shown.

however, the canopy had closed substantially and canopy openness levels remained low when measured during subsequent censuses (Fig. 2a), demonstrating that increases in understorey light availability following hurricane damage are short-lived. This is consistent with studies that reported rapid recovery of the forest structure following hurricanes through refoliation and resprouting (Walker 1991; Zimmerman *et al.* 1994). For example, after the Luquillo forest had been defoliated by Hurricane Hugo, 70% of trees had produced new leaves after only 7 weeks (Walker *et al.* 1992). Rapid growth and sprouting of the understorey (i.e. shrubs and saplings) was also observed following Hurricane Georges, and this, in addition to regrowth of the forest canopy, likely contributed to decreased light availability for seedlings (Angulo-Sandoval *et al.* 2004).

In contrast to canopy openness, seedling densities remained high for *c.* 5 years following Hurricane Georges (Fig. 2b). This pattern differed slightly from observations of seedling densities following Hurricane Hugo, which damaged the forest 10 years before Georges. Seedling density peaked 1 year after Hurricane Hugo and remained high for only 3 years before declining rapidly (Scatena *et al.* 1996). This difference may be because Hurricane Hugo caused more damage to canopy trees, and there was a greater recruitment of pioneer species, such as *Cecropia scherberiana* (J. Thompson, unpublished data), that persist for shorter periods of time in the understorey than more shade-tolerant species. Increases in seedling density following hurricane disturbance likely result from overall higher seed germination and seedling establishment, triggered by increased light and litter (Everham & Brokaw 1996).

#### ABIOTIC AND BIOTIC FACTORS DRIVING SEEDLING SURVIVAL

We found significant effects of both abiotic and biotic neighbourhood variables on seedling survival in the Luquillo forest.

Canopy openness had the strongest effect overall, increasing survival at low to medium levels and decreasing survival slightly at high levels ( $> 70\%$ ). The negative effect of high light on seedling survival was likely caused directly by sunscald and photoinhibition, or indirectly by reduced humidity and soil moisture as a result of the loss of forest canopy (Brown 1993). Leaf damage due to high levels of post-hurricane irradiation has been reported for several species at our study site (Guzman-Grajales & Walker 1991; You & Petty 1991).

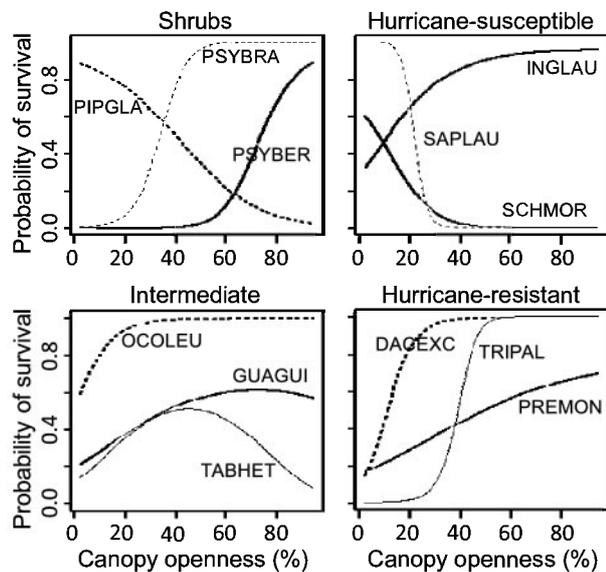
The density and identity of neighbouring plants also had significant effects on seedling survival. Our results show that both conspecific seedling and adult neighbours tended to have a negative impact on seedling survival. Negative conspecific density-dependent mortality at the seedling stage has been observed in a number of tropical and temperate forest communities (Webb & Peart 1999; Harms *et al.* 2000; Hille Ris Lambers, Clark & Beckage 2002; Uriarte *et al.* 2005; Queenborough *et al.* 2007; Comita & Hubbell 2009) and is hypothesized to play a role in the maintenance of diversity, particularly in species-rich tropical forests (Janzen 1970; Connell 1971). These negative effects of related neighbours are often the result of host-specific natural enemies, including pathogens and insect herbivores that respond in a density or distance-dependent manner (Augspurger 1984; Wong *et al.* 1990; Gilbert, Hubbell & Foster 1994).

We found a significant interaction between canopy openness and conspecific seedling density, with the effect of conspecific neighbours declining as canopy openness increased. A similar result was found in Panama where lower pathogen-mediated seedling mortality occurred in light gaps compared to the shaded understorey, despite higher seedling densities in gap sites (Augspurger 1984). Seedlings growing under higher light levels may be better able to survive herbivore or pathogen attack compared to those growing in the shade (Norghauer, Malcolm & Zimmerman 2008) because they have more resources available for defence and the replacement of dam-

Table 2. Coefficients from species-level analyses of seedling survival in the 16-ha Luquillo Forest Dynamics Plot, Puerto Rico. See Table 1 for species names

Species	Shrubs				Hurricane-susceptible				Intermediate				Hurricane-resistant			
	PSYBRA	PIPGLA	PSYBER	SAPLAU	SCHMOR	INGLAU	TABHET	OCOLEU	GUAGUI	TRIPAL	DACEXC	PREMON				
Intercept	-2.59	1.11	-10.09**	0.48	-1.32	0.66	-0.60	2.74	-0.51**	-3.98	1.75	-0.88**				
Time	-0.15	-0.49**	-0.46	-1.43	-1.55**	-0.67**	-0.95**	-0.5**	-0.91**	-0.29	-0.87**	-0.82**				
Logsize	0.47**	0.48**	0.38**	1.07**	0.57**	0.19*	0.42*	0.20	0.45**	0.71**	0.47	1.1*				
CONS	-5.57	-0.16	-2.99	1.4	5.94	-0.35	-2.01	5.54	-0.37**	1.98	7.61	0.2*				
HETS	0.15	-0.06	0.04	0.67*	0.07	-0.27	-0.29	0.18	-0.06	0.21	0.19	0.19**				
CONBA	2.0	1.29	-8.16**	0.51	-5.4	0.14	0.4	-2.42	-0.18*	-5.97	0.13	-0.33**				
HETBA	0.20	0.10	0.02	0.24	-0.04	0.04	0.35	0.11	0.18*	-0.12	0.54	0.26*				
Canopy open	3.64	-1.06	4.83**	-8.21	-2.19	1.32**	0.98	2.39	0.73**	3.24	3.37	0.68**				
Canopy open <sup>2</sup>	0.08	-0.06	-0.43**	-0.33	-0.38*	-0.18	-0.38*	-0.12	-0.14*	0.98*	-0.37	-0.06				
Slope	0.23	-0.24	0.04	-0.39	0.96*	-0.01	-0.13	0.05	-0.1	0.37	0.07	0.05				
Soiltype 2	0.33	0.52	-0.35	-1.07	-0.68	0.46	0.04	-0.14	-0.47**	-0.02	0.02	-0.15				
Soiltype 3	-0.41	-0.26	-13.86	0.35	-14.43	1.00	-0.23	1.31	-0.41	-1.47	-0.47	0.10				
Soiltype 4	-	-	-	-16.88	-16.04	-	-	-	-	-	-13.47	-0.45				
Soiltype 5	-	-0.72	-14.7	-16.2	1.48	-0.32	2.15	-0.5	0.15	-0.62	1.52	0.19				
TOPO: ridge	3.16	0.98	-0.87	0.69	0.24	11.85	0.15	-0.23	-0.17	0.25	-1.14	0.75				
TOPO: slope	1.12	0.18	-0.63	-0.12	-0.64	-0.17	0.45	-0.38	-0.21	0.61	-0.42	0.19				
TOPO: valley	-14.44	-1.62*	-1.34	-0.09	-0.63	0.28	1.9	0	-0.31	-0.7	-0.63	-0.12				
CONS × Canopy	0.58	1.56	0.76	-13.11	-7.38	0.57**	0.79	-5.04	0.08	-11.05	5.72	0.19				
HETS × Canopy	0.02	0.03	-0.04	0.03	0.06	0.03	0.13	-0.08	0.05	-0.64*	-0.22	-0.02				
CONBA × Canopy	3.43	-1.92	3.24*	-2.09	0.93	0.58	-0.2	5.18	0	11.27	0.71	-0.03				
HETBA × Canopy	-0.19	-0.03	0.11	-0.18	0.05	0.88*	0.35	0.24	0.03	-0.07	0.8	0.27**				

\* $P < 0.05$  level.\*\* $P < 0.01$  level.



**Fig. 7.** Effect of canopy openness on seedling survival for the three most abundant species of shrubs and of hurricane-susceptible, intermediate and hurricane-resistant trees. Solid line signifies a significant effect of canopy openness on survival for the species ( $P < 0.05$ ), while a dashed line means the effect was not significant. See Table 1 for full species names.

aged tissue (Shure & Wilson 1993). In addition, pathogen abundance may be lower in light gaps due to lower humidity and soil moisture (Augspurger 1984).

In contrast to conspecific neighbours, the effect of heterospecific neighbour density on seedling survival tended to be positive. This is consistent with the species-herd hypothesis (Wills 1996; Peters 2003), which posits that increasing density of unrelated individuals slows the rate or reduces the chance of natural enemies encountering susceptible individuals. Alternatively, the increase in the probability of survival with increasing heterospecific seedling density may simply be because high-density patches correspond to microsites that are good for seedling establishment and continued survival (Comita & Hubbell 2009). Although we included canopy openness, soil type and topographic variables in the model, there may be other environmental factors at a microsite scale (e.g. nutrient availability) that affect seedling densities, and it is the sum of all these factors that influences site suitability.

#### RELATIVE IMPORTANCE OF ABIOTIC AND BIOTIC FACTORS OVER TIME

The results of analyses for each census interval separately revealed significant changes in the relative importance of abiotic and biotic variables over time after the hurricane. Canopy openness had a significant effect on seedling survival in the first census interval following Hurricane Georges (2000–02), but not in subsequent census intervals. Only the effect of the canopy openness squared term, which governed the decline in survival at higher levels, was significant, however. This suggests that the strong positive effect of canopy openness detected when all intervals were combined for analysis was driven pre-

dominantly by the difference in light conditions between the first census interval and subsequent intervals. The deposition of leaves and branches during hurricanes contributes to large nutrient pulses that occur in tandem with increases in light availability (Lodge *et al.* 1991; Silver *et al.* 1996), but at the same time, hurricane-generated coarse woody debris can lead to nutrient immobilization (Zimmerman *et al.* 1995). Thus, it is difficult to distinguish the effect of increased light availability during the first census interval from potential effects of nutrient fluxes. However, Silver *et al.* (1996) reported that many of the changes in nutrient cycling following hurricane disturbance at the Luquillo forest occurred within the first year and were often not distinguishable beyond that period. Our initial seedling census took place 1.5 years after Hurricane Georges, thus, it is likely that the elevated survival during our first census interval was due to higher light levels rather than elevated nutrient availability.

The significant decline in survival at higher levels of canopy openness during the first census interval suggests that light levels were high enough to negatively impact seedlings only during the first few years after the hurricane (Fig. 4). A negative effect of high light caused by photoinhibition and leaf burn would have a greater effect on seedlings that had established in the dark understorey and were present before the hurricane. Seeds that germinated or seedlings that grew new leaves after the hurricane would have leaves that were better acclimated to the high light levels (Wen, Fetcher & Zimmerman 2008).

In contrast to light, conspecific seedling density did not have a significant effect on seedling survival during the first census interval following Hurricane Georges, but did significantly influence survival across subsequent census intervals. The lack of a significant effect of seedling density during the first interval, despite high seedling densities during that time, could be due to lower density-dependent mortality at higher light levels, as discussed above. Alternatively, the abundance or activity of herbivores and pathogens may have been reduced by hurricane disturbance. Angulo-Sandoval *et al.* (2004) found significantly lower levels of herbivore damage following Hurricane Georges compared to pre-hurricane herbivory levels. Willig & Camilo (1991) reported significant decreases in the densities of two walking stick (order Phasmatodea) and three snail species following Hurricane Hugo, suggesting that reductions in herbivory may be due to declines in invertebrate populations.

Over the second and third census intervals, the effect of conspecific seedling density was negative, while in the final census interval, there was a significant positive effect of conspecific seedling density on seedling survival. Our interpretation of this pattern is that soon after the hurricane, seedlings were encountering conspecific neighbours at densities high enough to cause density-dependent patterns of mortality. By 2007, however, seedling densities had thinned sufficiently, such that species' habitat preferences played a stronger role in driving survival than density-dependent natural enemies, resulting in a positive relationship between survival and conspecific seedling density. The significant effect of soil type in the final census interval, but not in other intervals, is consis-

tent with this idea that the relative importance of the soil environment increased over time. Conspecific tree basal area, on the other hand, had a consistent, significant negative effect on seedling survival across all census intervals, indicating that seedlings near conspecific adult trees were unable to fully escape density-dependence even when light levels were high, as in the first interval, or seedling densities were low, as in the final interval.

Significant interactions between canopy openness and seedling density were only detected in the second census interval. In this case, we found a significant negative interaction between canopy openness and both conspecific and heterospecific seedling densities, suggesting a stronger effect of seedling neighbours at high light levels. This may be due to increased competition among all species for below-ground resources in patches where seedling density was high and light was not limiting.

#### VARIATION AMONG SHADE-TOLERANCE GUILDS AND SPECIES

Tree species in this forest exhibit a trade-off between ability to resist wind damage and sapling mortality in the shade, with light-loving species being more vulnerable to damage than shade-tolerant ones (cf. Fig 1, Uriarte *et al.* 2004). For our analysis of life-history guilds, we grouped species based on the degree of hurricane damage adult trees suffered, which we expected would serve as a proxy for species shade tolerance. As expected, we found clear differences among the life-history guilds, with the strength of the canopy openness effect increasing from hurricane-resistant to intermediate to hurricane-susceptible species. Thus, species whose adult trees were most likely to be damaged by hurricanes appear to be those who, through increased seedling survival, are also most able to take advantage of elevated light levels. This trade-off between damage susceptibility and seedling light response may be a significant component of species life-history strategies that contributes to species coexistence (Loehle 2000; Uriarte *et al.* 2004; Hughes *et al.* 2007).

There were also differences in the response of guilds to the biotic neighbourhood. The intermediate and hurricane-susceptible groups were negatively affected by conspecific seedling density, and both exhibited a significant positive interaction between conspecific seedling density and canopy openness. This is consistent with the idea that more light-demanding species devote fewer resources to defence than shade-tolerant species (Coley 1980). However, light-demanding species are able to overcome density-dependent mortality when growing in light gaps (Augsburger 1984). The hurricane-resistant group, on the other hand, appears to suffer more from the overall density of seedling neighbours when growing at high light, as indicated by a significant negative interaction between heterospecific seedling density and canopy openness. This suggests that shade-tolerant, hurricane-resistant species lose out to light-demanding, hurricane-susceptible species when there is strong competition between seedlings in light gaps.

While differences among hurricane susceptibility guilds met with our expectations, analyses of focal species from each guild showed a much wider variety of responses to abiotic and biotic variables. Only one of the three hurricane-susceptible species, *Inga laurina*, showed a significant, positive relationship between seedling survival and canopy openness. Seedling survival of *Schefflera morototoni*, another hurricane-susceptible species, was negatively impacted by high canopy openness levels. This is consistent with a related study in the Luquillo plot (Uriarte *et al.* 2005), in which *Schefflera morototoni* was found to have lower recruitment at high light levels. Although this species is generally considered to be a light-demanding pioneer species that is also susceptible to hurricane damage, its seedlings do not appear to be able to take advantage of the high light levels that follow hurricane disturbance.

Five other focal tree species in this study of seedling survival showed similar patterns to those reported by Uriarte *et al.* (2005) for light availability and seedling recruitment between 2000 and 2002 in the LFDP. One exception was the palm species *P. acuminata*, which showed a peak in recruitment at low light levels in the study of Uriarte *et al.* (2005), but here showed a consistent increase in seedling survival at higher light levels (Fig. 7). This suggests that low light levels favour *P. acuminata* seed germination and seedling establishment, but once established, the seedlings are able to take advantage of high light levels after a hurricane. *Prestoea acuminata* has the most adult trees in the LFDP and is the most common species in the seedling census; its dominance may be due in part to its ability to both establish under shady conditions and take advantage of high light following hurricane disturbance (Zimmerman & Covich 2007; A. Sabat, personal communication).

The differences among species in response to their environment we report here are consistent with the different responses to abiotic variables reported for experiments conducted at Luquillo by Everham & Brokaw (1996) and Walker *et al.* (2003). In these studies, based on five and six species, respectively, the authors found such considerable variation among species that they were not able to place the species into clear life-history groups. Our guild-level results based on 43 species, however, suggest that the major drivers of seedling survival do vary as expected among life-history guilds based on hurricane susceptibility, although there is still considerable variation among species within these groups at the seedling stage.

#### IMPLICATIONS FOR REGENERATION PATHWAYS IN HURRICANE DRIVEN FORESTS

We found clear effects of both canopy openness and conspecific neighbours on seedling survival in the Luquillo forest. These effects on seedling survival appear to be driven largely by hurricane disturbance, which temporarily opens the forest canopy, increasing understorey light levels and seedling densities. Thus, hurricanes may alter species composition not only through differential mortality and resprouting ability of trees (Zimmerman *et al.* 1994), but also through indirect effects on

understorey conditions that influence the relative success of seedlings of different species.

Increases in the intensity and frequency of hurricanes are predicted for the Caribbean as a result of global climate change (Emanuel 2005; Webster *et al.* 2005; Holland & Webster 2007). Studies like the one presented here contribute to efforts to predict the possible responses and potential fate of tropical forests to changes in the hurricane disturbance regime. Our results indicate that hurricanes have a profound impact on patterns of seedling survival and dynamics through their effect on the spatial and temporal variation in understorey conditions. If hurricanes increase in frequency and intensity, changes in patterns of seedling dynamics are likely to result and may ultimately alter forest composition and diversity.

## Acknowledgements

We thank the founders of the LFDP: R. B. Waide, D. J. Lodge, C. M. Taylor and E. M. Everham III. J. Thomlinson helped prepare the tree maps. This work was supported by NSF grants DEB-9906713, DEB-0087214 and DEB-0516066 to C.D.C., J.T. and M.U. and grants from NSF to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, working with the International Institute of Tropical Forestry (USDA Forest Service), for the Luquillo Long-Term Ecological Research Program. The seedling censuses were supported by the Andrew W. Mellon Foundation, the Center for Tropical Forest Science, and NSF grant DEB-0614659. The US Forest Service and University of Puerto Rico provided additional support. L.S.C. acknowledges the support of an Earth Institute Fellowship from Columbia University. Special thanks to the LTER and LFDP technicians and the 100+ volunteer assistants who worked so hard on the tree and seedling censuses.

## References

- Angulo-Sandoval, P., Fernandez-Marin, H., Zimmerman, J.K. & Aide, T.M. (2004) Changes in patterns of understorey leaf phenology and herbivory following hurricane damage. *Biotropica*, **36**, 60–67.
- Augsburger, C.K. (1984) Seedling survival of tropical tree species – interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, **65**, 1705–1712.
- Barberis, I.M. & Tanner, E.V.J. (2005) Gaps and root trenching increase tree seedling growth in Panamanian semi-evergreen forest. *Ecology*, **86**, 667–674.
- Bates, D. & Maechler, M. (2009) *Lme4: Linear mixed-effects models using eigen and QR*. R package version 0.999375-31.
- Batista, W.B. & Platt, W.J. (2003) Tree population responses to hurricane disturbance: Syndromes in a south-eastern USA old-growth forest. *Journal of Ecology*, **91**, 197–212.
- Becker, P., Rabenold, P.E., Idol, J.R. & Smith, A.P. (1988) Water potential gradients for gaps and slopes in a Panamanian tropical moist forests dry season. *Journal of Tropical Ecology*, **4**, 173–184.
- Bellingham, P.J., Tanner, E.V.J. & Healey, J.R. (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology*, **76**, 2562–2580.
- Bellingham, P.J., Kapos, V., Varty, N., Healey, J.R., Tanner, E.V.J., Kelly, D.L., Dalling, J.W., Burns, L.S., Lee, D. & Sidrak, G. (1992) Hurricanes need not cause high mortality – the effects of Hurricane Gilbert on forests in Jamaica. *Journal of Tropical Ecology*, **8**, 217–223.
- 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*, **12**, 699–722.
- Boose, E.R., Foster, D.R. & Fluet, M. (1994) Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs*, **64**, 369–400.
- Boose, E.R., Serrano, M.I. & Foster, D. (2004) Landscape and regional impacts of hurricanes in Puerto Rico. *Ecological Monographs*, **74**, 335–352.
- Brokaw, N.V.L. & Grear, J.S. (1991) Forest structure before and after Hurricane Hugo at 3 elevations in the Luquillo Mountains, Puerto Rico. *Biotropica*, **23**, 386–392.
- Brokaw, N.V.L. & Walker, L.R. (1991) Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica*, **23**, 442–447.
- Brown, N. (1993) The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *Journal of Tropical Ecology*, **9**, 153–168.
- Burslem, D.F.R.P., Grubb, P.J. & Turner, I.M. (1996) Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica*, **28**, 636–648.
- Burslem, D.F.R.P., Whitmore, T.C. & Brown, G.C. (2000) Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *Journal of Ecology*, **88**, 1063–1078.
- Canham, C.D., Papaik, M.J. & Latty, E.F. (2001) Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **31**, 1–10.
- Canham, C. D., Thompson, J., Zimmerman, J. K. & Uriarte, M. (2009) Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica*, in press.
- Chazdon, R.L., Pearcy, R.W., Lee, D.W. & Fetcher, N. (1996) Photosynthetic responses of tropical forest plants to contrasting light environments. *Tropical Forest Plant Ecophysiology* (eds S. S. Mulkey, R. L. Chazdon & A. P. Smith), pp. 5–55. Chapman and Hall, New York.
- Chesson, P.L. & Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive-systems. *American Naturalist*, **117**, 923–943.
- Coley, P.D. (1980) Effects of leaf age and plant life-history patterns on herbivory. *Nature*, **284**, 545–546.
- Comita, L.S. & Engelbrecht, B.M.J. (2009) Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology*, in press.
- Comita, L.S. & Hubbell, S.P. (2009) Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology*, **90**, 328–334.
- Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations* (eds P. J. den Boer & G. R. Gradwell), pp. 298–312. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs*, **70**, 171–207.
- Daws, M.I., Mullins, C.E., Burslem, D., Paton, S.R. & Dalling, J.W. (2002) Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil*, **238**, 79–90.
- Daws, M.I., Pearson, T.R.H., Burslem, D., Mullins, C.E. & Dalling, J.W. (2005) Effects of topographic position, leaf litter and seed size on seedling demography in a semi-deciduous tropical forest in Panama. *Plant Ecology*, **179**, 93–105.
- Emanuel, K. (2005) Increasing destructiveness of tropical cyclones over the past 30 years. *Nature*, **436**, 686–688.
- Everham, E.M. III & Brokaw, N.V.L. (1996) Forest damage and recovery from catastrophic wind. *Botanical Review*, **62**, 113–185.
- Everham, E.M. III, Myster, R.W. & VandeGenachte, E. (1996) Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany*, **83**, 1063–1068.
- Ewel, J.J. & Whitmore, J.L. (1973) *The ecological life zones of Puerto Rico and the United States Virgin Islands. Forest Service Research Papers ITF-18*, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico.
- Fernandez, D.S. & Fetcher, N. (1991) Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica*, **23**, 393–399.
- Gelman, A. & Hill, J. (2006) *Data Analysis Using Regression and Multilevel/Hierarchical Models*, Cambridge University Press, Cambridge, UK.
- Gerhardt, K. (1996) Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management*, **82**, 33–48.
- Gilbert, G.S., Hubbell, S.P. & Foster, R.B. (1994) Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. *Oecologia*, **98**, 100–108.
- Gleason, S.M., Williams, L.J., Read, J., Metcalfe, D.J. & Baker, P.J. (2008) Cyclone effects on the structure and production of a tropical upland rainforest: Implications for life-history tradeoffs. *Ecosystems*, **11**, 1277–1290.
- Grubb, P.J. (1977) Maintenance of species-richness in plant communities – importance of regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, **52**, 107–145.

- Guzman-Grajales, S.M. & Walker, L.R. (1991) Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **23**, 407–413.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, **404**, 493–495.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, New York.
- Hille Ris Lambers, J., Clark, J.S. & Beckage, B. (2002) Density-dependent mortality and the latitudinal gradient in species diversity. *Nature*, **417**, 732–735.
- Holland, G.J. & Webster, P.J. (2007) Heightened tropical cyclone activity in the north Atlantic: natural variability or climate trend? *Philosophical Transactions of the Royal Society A*, **365**, 2695–2716.
- Hughes, A.R., Byrnes, J.E., Kimbro, D.L. & Stachowicz, J.J. (2007) Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters*, **10**, 849–864.
- Janzen, D.H. (1970) Herbivores and number of tree species in tropical forests. *American Naturalist*, **104**, 501.
- Jonckheere, I., Nackaerts, K., Muys, B. & Coppin, P. (2005) Assessment of automatic gap fraction estimation of forests from digital hemispherical photography. *Agricultural and Forest Meteorology*, **132**, 96–114.
- Jonckheere, I., Nackaerts, K., Muys, B., van Aardt, J. & Coppin, P. (2006) A fractal dimension-based modelling approach for studying the effect of leaf distribution on LAI retrieval in forest canopies. *Ecological Modelling*, **197**, 179–195.
- Kobe, R.K. (1999) Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology*, **80**, 187–201.
- Kobe, R.K., Pacala, S.W., Silander, J.A. & Canham, C.D. (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, **5**, 517–532.
- Lewis, S.L. & Tanner, E.V.J. (2000) Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology*, **81**, 2525–2538.
- Lin, C.H., Hamburg, S.P., Hsia, Y.J., Lin, T.T., King, H.B., Wang, L.J. & Lin, K.C. (2003) Influence of typhoon disturbances on the understorey light regime and stand dynamics of a subtropical rain forest in north-eastern Taiwan. *Journal of Forest Research*, **8**, 139–145.
- Liogier, H.A. (1985, 1988, 1994, 1995, 1997) *Descriptive Flora of Puerto Rico and Adjacent Islands*. Editorial de la Universidad de Puerto Rico, Rio Piedras, Puerto Rico.
- 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*, **23**, 336–342.
- Loehle, C. (2000) Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *American Naturalist*, **156**, 14–33.
- Lugo, A.E. (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology*, **33**, 368–398.
- Mabry, C.M., Hamburg, S.P., Lin, T.C., Horng, F.W., King, H.B. & Hsia, Y.J. (1998) Typhoon disturbance and stand-level damage patterns at a subtropical forest in Taiwan. *Biotropica*, **30**, 238–250.
- McNab, W.H., Greenberg, C.H. & Berg, E.C. (2004) Landscape distribution and characteristics of large hurricane-related canopy gaps in a southern Appalachian watershed. *Forest Ecology and Management*, **196**, 435–447.
- Montgomery, R.A. & Chazdon, R.L. (2002) Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia*, **131**, 165–174.
- Nakashizuka, T. (2001) Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology & Evolution*, **16**, 205–210.
- Norghauer, J.M., Malcolm, J.R. & Zimmerman, B.L. (2008) Canopy cover mediates interactions between a specialist caterpillar and seedlings of a Neotropical tree. *Journal of Ecology*, **96**, 103–113.
- Ogle, K., Uriarte, M., Thompson, J., Johnstone, J., Jones, F.A., Lin, Y., McIntire, E. & Zimmerman, J. (2006) Implications of vulnerability to hurricane damage for long-term survival of tropical tree species: a Bayesian hierarchical analysis. *Hierarchical Modeling for the Environmental Sciences: Statistical Methods and Applications* (eds J.S. Clark & A.E. Gelfand), pp. 98–117. Oxford University Press, Oxford.
- Ostertag, R., Scatena, F.N. & Silver, W.L. (2003) Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. *Ecosystems*, **6**, 261–273.
- Ostertag, R., Silver, W.L. & Lugo, A.E. (2005) Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica*, **37**, 16–24.
- Peters, H.A. (2003) Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters*, **6**, 757–765.
- Pickett, S.T.A. & White, P.S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, FL.
- Queenborough, S.A., Burslem, D., Garwood, N.C. & Valencia, R. (2007) Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology*, **88**, 2248–2258.
- R Development Core Team. (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at URL: <http://www.R-project.org>.
- Scatena, F.N., Moya, S., Estrada, C. & Chinea, J.D. (1996) The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley experimental watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **28**, 424–440.
- Shure, D.J. & Wilson, L.A. (1993) Patch-size effects on plant phenolics in successional openings of the southern Appalachians. *Ecology*, **74**, 55–67.
- Silver, W.L., Lugo, A.E. & Keller, M. (1999) Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry*, **44**, 301–328.
- Silver, W.L., Scatena, F.N., Johnson, A.H., Sicama, T.G. & Watt, F. (1996) At what temporal scales does disturbance affect belowground nutrient pools? *Biotropica*, **28**, 441–457.
- Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, **15**, 353–391.
- Soil Survey Staff. (1995) *Order 1 Soil Survey of the Luquillo Long-Term Ecological Research Grid, Puerto Rico*. USDA, Natural Resources Conservation Services, Lincoln, Nebraska.
- Tanner, E.V.J., Kapos, V. & Healey, J.R. (1991) Hurricane effects on forest ecosystems in the Caribbean. *Biotropica*, **23**, 513–521.
- Thompson, J., Brokaw, N., Zimmerman, J.K., Waide, R.B., Everham, E.M. III, Lodge, D.J., Taylor, C.M., Garcia-Montiel, D. & Fluet, M. (2002) Land use history, environment, and tree composition in a tropical forest. *Ecological Applications*, **12**, 1344–1363.
- Thompson, J., Brokaw, N., Zimmerman, J.K., Waide, R.B., Everham, E.M. III & Schaefer, D.A. (2004) Luquillo Forest Dynamics Plot, Puerto Rico, United States. *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network* (eds E. Losos & E. G. Leigh), pp. 540–550. University of Chicago Press, Chicago.
- Uriarte, M., Canham, C.D., Thompson, J. & Zimmerman, J.K. (2004) A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecological Monographs*, **74**, 591–614.
- Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K. & Brokaw, N. (2005) Seedling recruitment in a hurricane-driven tropical forest: Light limitation, density-dependence and the spatial distribution of parent trees. *Journal of Ecology*, **93**, 291–304.
- Valladares, F. & Niinemets, U. (2008) Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology Evolution and Systematics*, **39**, 237–257.
- Walker, L.R. (1991) Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **23**, 379–385.
- Walker, L.R., Voltzow, J., Ackerman, J.D., Fernandez, D.S. & Fetcher, N. (1992) Immediate impact of Hurricane Hugo on a Puerto Rican rain-forest. *Ecology*, **73**, 691–694.
- Walker, L.R., Lodge, D.J., Guzman-Grajales, S.M. & Fetcher, N. (2003) Species-specific seedling responses to hurricane disturbance in a Puerto Rican rain forest. *Biotropica*, **35**, 472–485.
- Walsh, R.P.D. (1996) *Climate. The Tropical Rainforest: An Ecological Study* (ed. P. W. Richards), pp. 159–205. Cambridge University Press, Cambridge, UK.
- Webb, C.O. & Peart, D.R. (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology*, **80**, 2006–2017.
- Webster, P.J., Holland, G.J., Curry, J.A. & Chang, H.R. (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science*, **309**, 1844–1846.
- Wen, S.Y., Fetcher, N. & Zimmerman, J.K. (2008) Acclimation of tropical tree species to hurricane disturbance: ontogenetic differences. *Tree Physiology*, **28**, 935–946.
- Whitmore, T.C. & Burslem, D.F.R.P. (1998) Major disturbances in tropical rainforests. *Dynamics of Tropical Communities* (eds D. M. Newbery, H. H. T. Prins & N. D. Brown), pp. 549–565. Blackwell Science Ltd, Oxford.
- Willig, M.R. & Camilo, G.R. (1991) The effect of Hurricane Hugo on 6 invertebrate species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, **23**, 455–461.

- Wills, C. (1996) Safety in diversity. *New Scientist*, **149**, 38–42.
- Wong, M., Wright, S.J., Hubbell, S.P. & Foster, R.B. (1990) The spatial pattern and reproductive consequences of outbreak defoliation in *Quararibea asterolepis*, a tropical tree. *Journal of Ecology*, **78**, 579–588.
- Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1–14.
- Yavitt, J.B. & Wright, S.J. (2008) Seedling growth responses to water and nutrient augmentation in the understorey of a lowland moist forest, Panama. *Journal of Tropical Ecology*, **24**, 19–26.
- You, C.X. & Petty, W.H. (1991) Effects of Hurricane Hugo on *Manikara bidentata*, a primary tree species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica*, **23**, 400–406.
- Zimmerman, J.K.H. & Covich, A.P. (2007) Damage and recovery of riparian Sierra palms after Hurricane Georges: influence of topography and biotic characteristics. *Biotropica*, **39**, 43–49.
- Zimmerman, J.K., Everham, E.M. III, 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. *Journal of Ecology*, **82**, 911–922.
- Zimmerman, J.K., Pulliam, W.M., Lodge, D.J., Quinonesorfil, V., Fetcher, N., Guzmangrajales, S., Parrotta, J.A., Asbury, C.E., Walker, L.R. & Waide, R.B. (1995) Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. *Oikos*, **72**, 314–322.

Received 15 April 2009; accepted 1 July 2009

Handling Editor: Matthew Turnbull

## Supporting Information

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

**Appendix S1.** Explanatory variables included in the analysis of seedling survival.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.