

# Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees

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## Summary

**1** We used inverse modelling to parameterize spatially-explicit seedling recruitment functions for nine canopy tree species in the Luquillo Forest Dynamics Plot (LFDP), Puerto Rico. We modelled the observed spatial variation in seedling recruitment following Hurricane Georges as a function of the potential number of seedlings at a given location (based on local source trees and the potential contribution of parents from outside of the mapped area) and of light levels and density-dependent mortality during establishment. We adopted the model comparison paradigm and compared the performance of increasingly complex models against a null model that assumes uniform seedling distribution across the plot.

**2** Our data supported a model in which parents must reach a threshold size before any seedling production will occur. Once parents attain that size, the relationship between tree diameter and the number of seedlings produced is fairly flat for the majority of species. These results contradict previous analyses that simply assumed a linear relationship between biomass and seedling production and a uniform size threshold for seedling production across species.

**3** The majority of species tested supported models that included at least one of a bath term (contribution from non-local trees), conspecific density dependence and light availability after the hurricane. Density dependence shifted the mode of the effective dispersal kernel away from potential parent trees and significantly reduced the number of seedlings established near parent trees. Recruitment from non-local sources accounted for 6–81% of observed seedling recruitment depending upon the tree species. Light availability appeared to divide species into three groups that showed more successful seedling establishment at low (< 5% of full sun), intermediate or high light levels (> 30% full sun).

**4** Differences between individual species in the importance of local vs. bath recruitment and the intensity of density dependence suggest the existence of distinct recruitment syndromes that go beyond the traditional focus of tropical tree life histories. Understanding these syndromes will provide valuable insights into the spatial distribution of tropical tree species and the maintenance of tropical forest diversity.

*Key-words:* inverse modelling, Luquillo experimental forest, Puerto Rico, tropical forest dynamics

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## Introduction

A series of hurricanes in the Caribbean in the past two decades have stimulated much research on the effects of wind disturbance on tropical forests (Walker *et al.* 1991; Zimmerman *et al.* 1994). One lesson is that the post-hurricane response of some tropical forests can be swift, with 'recovery' of many aspects of ecosystem function occurring over months to a few years. This suggests that hurricanes may represent a relatively minor perturbation to the long-term dynamics of Caribbean tropical forests. Despite the vast literature generated in the wake of these storms (see special issue in *Biotropica* 23, 1991), the long-term implications of disturbance frequency and severity for the structure and dynamics of Caribbean tropical forests are still open to debate.

Seedling recruitment is a bottleneck in the population dynamics of many species of trees (Swaine 1996). Recruitment reflects not only seed production but also the compound filtering effects of seed dispersal and seedling establishment. Seedlings may fail to occupy a particular site either because seeds do not arrive at the site (dispersal limitation) or because the site is not a suitable environment for establishment (establishment limitation) (Grubb 1977; Clark *et al.* 1998; Nathan & Muller-Landau 2000). In general, supply processes such as fecundity of parent trees, together with the factors that affect seedling establishment, are the major determinants of local abundance and diversity of adult trees (Tilman 1994; Hurtt & Pacala 1995; Dalling *et al.* 1998). Although an absence of density-dependent processes leads to seedling and adult tree abundances being tightly linked in many stable, mature forests, negative density-dependent processes from conspecifics due to host-specialized pests (e.g. Janzen-Connell effects, Janzen 1970; Connell 1971), particularly those acting at the seedling stage, can uncouple the abundance of seedlings from that of adults (Warner & Hughes 1988). Moreover, large-scale disturbance can uncouple seedling and adult abundance during the building phase when light-demanding taxa dominate the canopy but fail to recruit in the understorey.

The effect of hurricane damage on tree seedling recruitment remains one of the least understood aspects of the dynamics of Caribbean forests. Hurricanes can alter many of the processes that may determine the number of seedlings that recruit into a given area. Hurricane damage to tree crowns often decreases or delays seed production in the short term (Walker & Neris 1993; Wunderle 1999; Zimmerman, unpublished data). Hurricanes also affect conditions at the forest floor, with both positive and negative effects on seedling establishment (e.g. Guzmán-Grajales & Walker 1991; Lodge & McDowell 1991; Carlton & Bazzaz 1998; Walker *et al.* 2003). Negative effects are caused by the increased litter inputs during a hurricane, which may kill seedlings already present, inhibit germination by covering seeds and prevent seedling establishment,

as deep litter may be difficult for seedling roots to penetrate. Moreover, increased light penetration through the damaged canopy to the soil surface may both kill seeds before germination and desiccate existing seedlings. Conversely, positive effects may accrue as increased light stimulates seed germination and the growth of seedlings present in the seedling bank, while litter inputs also enhance nutrient supply (Lomascolo & Aide 2001; Walker *et al.* 2003).

By uncoupling the spatial distribution of adults from that of new seedling recruits, hurricanes may be expected to lead to weaker density-dependent effects of adults on seedling survival, with significant implications for both seedling survival and species coexistence (Vandermeer *et al.* 1996). Disturbance in general, and hurricanes in particular, increase the size and prevalence of canopy gaps and dramatically alter the light environment (Fernández & Fetcher 1991; Bellingham *et al.* 1996). The resulting community is highly dynamic and, often, density-dependent competitive thinning of saplings recruited through advanced regeneration plays a pivotal role in re-structuring the community to a new state (Uriarte *et al.* 2004a). Episodic recruitment into gaps after a hurricane could also alter density-dependent interactions among seedlings, but the effects of disturbance on seedling recruitment remain poorly understood (Walker *et al.* 2003). Understanding how disturbance influences recruitment is essential to predict the long-term effects of natural disturbance on tropical forest dynamics and species richness.

The forests of Puerto Rico experience one of the highest frequencies of hurricanes of any island in the Caribbean (Boose *et al.* 2004). In September 1989, Hurricane Hugo struck the Luquillo forest in Puerto Rico with maximum sustained winds of 166 kph and gusts to 194 kph (Scatena & Larsen 1991), significantly damaging about 25% and completely defoliating 56% of the trees (Walker *et al.* 1991; Zimmerman *et al.* 1994). Recovery from Hurricane Hugo has been extensively documented (Walker *et al.* 1991). The forest canopy in the Luquillo forest was returning to pre-Hugo height and evenness when it was severely damaged by Hurricane Georges in September 1998 (Brokaw *et al.* 2004). Hurricanes of Hugo's severity affect Puerto Rico every 50–60 years on average (Scatena & Larsen 1991). Hurricane damage to a forest canopy varies considerably across the forest area, depending upon the local strength of the winds, topography and species composition, and is highly variable within and among different hurricanes (Boose *et al.* 2004).

Tree species in Puerto Rican forests differ in both their adult susceptibility to wind damage and in the nature of their response to the overall effects of hurricane disturbance in ways that are readily interpretable in terms of species life history (Zimmerman *et al.* 1994; Uriarte *et al.* 2004a; C. D. Canham *et al.*, unpublished data). These differences account, at least in part, for the distribution and abundance of adult trees in these forests. In contrast, although species-specific seedling

responses to the heterogeneous patterns of light, nutrients and organic debris generated in the wake of a hurricane may contribute to substantial variation among species in rates of subsequent seedling recruitment, these patterns have been difficult to interpret in relation to tree life histories (Walker *et al.* 2003).

We used a spatially explicit analysis to develop models that explain the observed spatial variation in seedling recruitment following Hurricane Georges for nine canopy tree species in the Luquillo Forest Dynamics Plot (LFDP) as a function of two types of processes: (i) those that generate a potential number of seedlings at a given location based on the spatial distribution of local source trees and background, 'bath' recruitment (i.e. where a uniform number of seedlings is present regardless of the local distribution of conspecific adults, probably reflecting contributions from non-local parent trees); and (ii) two factors that may influence seedling recruitment after a hurricane, light levels and density-dependent mortality during the period between seed germination and seedling establishment. The nine species represent a range of life histories and responses to both hurricane damage and resource availability (Zimmerman *et al.* 1994; Uriarte *et al.* 2004a; C. D. Canham *et al.*, unpublished data). We use maximum-likelihood methods to compare models that represent alternate hypotheses about the factors we believe may determine the abundance and spatial distribution of seedlings following a hurricane.

## Materials and methods

### STUDY AREA AND SPECIES

The Luquillo Forest Dynamics Plot (LFDP), previously known as the Hurricane Recovery Plot (Zimmerman *et al.* 1994), is a 16-ha forest plot (SW corner 18°20' N, 65°49' W) located near El Verde Field Station in the Luquillo Mountains of north-eastern Puerto Rico (Thompson *et al.* 2004). The plot is 500 m N-S and

320 m E-W and is divided into 400 20 × 20 m quadrats. Vegetation and topography of this research area is typical of the tabonuco (*Dacryodes excelsa*) forest zone. The forest is classified as subtropical wet in the Holdridge life zone system (Ewel & Whitmore 1973) and tropical montane in Walsh's (1996) tropical climate system. Rainfall averages 3500 mm year<sup>-1</sup>. Elevation ranges from 333 m to 428 m a.s.l. All of the soils are formed from volcaniclastic rock (Soil Survey Staff 1995).

The LFDP contains 89 species of trees with stems ≥ 10 cm d.b.h. distributed across 72 genera and 38 families (Thompson *et al.* 2002). Forty-five of these species are rare (< 1 stem ≥ 10 cm d.b.h. ha<sup>-1</sup>) and over 75% of species have fewer than five stems ha<sup>-1</sup>. We limited our analyses of seedling recruitment to a group of nine species for which we had sufficient numbers of seedlings, that represent a broad range of life histories and account for 69% of adult stems in the plot: *Casearia arborea* (Rich.) Urb., *Dacryodes excelsa* Vahl, *Guarea guidonia* (L.) Sleumer, *Inga laurina* (Sw.) Willd. Ex L., *Manilkara bidentata* (A. DC.) A. Chev., *Prestoea acuminata* (Willd.) H.E. Moore, *Schefflera morototoni* (Aubl.) Maguire, Steyerl. & Frodin, *Sloanea berteriana* Choisy, and *Tabebuia heterophylla* (DC.) Britton (Table 1).

All free-standing individuals greater than 10 cm d.b.h. are tagged, mapped within the LFDP, identified to species and measured for diameter at 130 cm from the ground (d.b.h.). Trees < 10 cm are assigned to a 5 × 5 m quadrat but not mapped exactly within the plot. Trees are identified by sight in the field or from voucher specimens. Nomenclature follows Liogier (1985, 1988, 1994, 1995, 1997). For these analyses, we used data from stems mapped in the 1995 census to identify potential parent trees for the seedlings of the nine species. For the analyses we included all trees that were larger than 8 cm d.b.h. in 1995 as potential sources of new seedlings following Hurricane Georges. For source trees < 10 cm and > 8 cm in d.b.h. coordinates within the 5 × 5 m quadrat were assigned at random.

**Table 1** Number of adult stems (<sup>3</sup> 8 cm d.b.h. in 1995), maximum diameter (cm), seed weight, dispersers, number of seedlings sampled, and successional status of nine common species at the LFDP. Successional status determined from Thompson *et al.* (2002), and Zimmerman *et al.* (1994). Seed weights and dispersers determined from Devoe (1989)<sup>1</sup>, Zimmerman *et al.* (2000)<sup>2</sup>, Francis (1982)<sup>3</sup> and Foster (1982)<sup>4</sup>. Dry seed weights unless indicated otherwise.

Species (family)	Number of adult stems	Maximum diameter	Number of seedlings	Seed weight (g)	Dispersers	Successional status
<i>Casearia arborea</i> (Flacourtiaceae)	1099	49	109	0.001–0.1 <sup>4</sup>	Bats, birds, gravity	Secondary
<i>Dacryodes excelsa</i> (Bursaceae)	1428	82	163	1.24 <sup>2</sup>	Birds, bats, gravity	Late
<i>Guarea guidonia</i> (Meliaceae)	372	96	1299	0.40 <sup>2</sup>	Birds, gravity	Late
<i>Inga laurina</i> (Fabaceae)	592	78	330	1.68 <sup>3</sup>	Birds, bats, gravity	Secondary
<i>Manilkara bidentata</i> (Sapotaceae)	975	79	69	0.56 <sup>1</sup>	Bats, gravity	Late
<i>Prestoea acuminata</i> (Arecaceae)	9332	42	2585	0.97 <sup>2</sup>	Bats, birds, gravity	Secondary
<i>Schefflera morototoni</i> (Araliaceae)	209	66	167	0.03 <sup>1</sup>	Bats, birds, gravity	Pioneer
<i>Sloanea berteriana</i> (Elaeocarpaceae)	779	93	47	3.56 <sup>1</sup>	Birds, bats, gravity	Late
<i>Tabebuia heterophylla</i> (Bignoniaceae)	417	69	880	0.01 <sup>2</sup>	Wind, gravity	Secondary

## SEEDLING CENSUSES

In March 1999, approximately 6 months after Hurricane Georges, we established six transects orientated north–south within the plot, separated by 60 m. On each transect, 2 × 2 m quadrats were established every 20 m, for a total of 150 quadrats, with the first quadrat 10 m from the LFDP edge. We counted and tagged all seedlings of the selected species that were ≥ 10 cm in height at this time and, based upon their visible condition, allocated them to one of two groups, depending on whether they were likely to have been present before the hurricane. If the seedling looked contorted and its stem was marked with leaf scars, if there was evidence of breaking and re-sprouting, or if leaves were covered with epiphyllis, the seedling was assigned to the pre-hurricane class, whereas unscarred stems and the presence of the first set of leaves or cotyledons were considered indicators of post-hurricane establishment.

Optimal light levels for establishment vary greatly among tree species. To assess light conditions in the seedling quadrats and the amount of canopy opening caused by Hurricane Georges we took a digital photograph with a fisheye lens at a height of 1 m above the middle of each seedling quadrat during March–April 1999 and calculated the gap light index (GLI, cf. Canham 1988). GLI indicates the percentage of photosynthetically active radiation (PAR) that reaches a point in the understorey. The seedling quadrats were censused again between June and July of 2002 and all seedlings < 10 cm in height were counted while seedlings ≥ 10 cm height were tagged and measured. During this census we also estimated the fraction of the area in each quadrat that consisted of live wood or rock. We considered these areas unsuitable for seedling establishment and therefore adjusted the quadrat area to exclude the unsuitable portion when calculating seedling density. We calculated the net, post-hurricane seedling recruitment as the total number of seedlings in the 2002 census minus the number we estimated in 1999 to have been present before the hurricane. Seedling densities are expressed m<sup>-2</sup> of quadrat suitable for seedling establishment.

## LIKELIHOOD ESTIMATION OF SEEDLING DISPERSAL FUNCTIONS

We used maximum-likelihood methods (Ribbens *et al.* 1994; LePage *et al.* 2000) to predict seedling recruitment (number m<sup>-2</sup>) in each sampled quadrat *i* as a function of five components: (i) the potential number of recruits produced by a local parent tree of a given size; (ii) the shape of the dispersal function; (iii) ‘bath’ recruitment, i.e. the contribution of long-distance dispersal events from parent trees outside the mapped area; (iv) seedling plot light levels in 1999; and (v) density-dependent mortality during the period between seed germination and seedling establishment. The first three components determine the potential number of seedlings based on the distribution of local source trees and bath

recruitment, while the second two components act to influence seedling recruitment as a function of processes that act locally within a quadrat.

We adopted the model comparison paradigm (Burnham & Anderson 2002; Johnson & Omland 2004) to test the importance of bath recruitment, light and density dependence in producing the observed patterns of seedling abundance in 2002. For each target species analysed, we first tested whether including the effects of any combination of these three factors improved the predictive ability of the model. Following the principle of parsimony, we dropped terms if the added complexity did not improve the likelihood of the model.

As with previous studies (Ribbens *et al.* 1994), we assume that the potential total number of seedlings produced by a tree over a specified period of time is a function of stem diameter (*D*)

$$\#recruits \text{ per tree} = STR \left( \frac{D}{30} \right)^\alpha \quad \text{eqn 1}$$

where STR is the potential number of seedlings produced by a tree with a 30-cm stem diameter. Most previous analyses have assumed that fecundity is proportional to biomass (i.e. *D*<sup>2</sup>), and have treated  $\alpha$  as constant fixed at a value of 2 (Ribbens *et al.* 1994; Clark *et al.* 1998). Recent analyses suggest that this assumption is not well supported for many species (C. D. Canham & M. Uriarte, unpublished data). Thus, we allow  $\alpha$  to vary, and estimate its maximum likelihood value. Previous studies have also used a fixed minimum d.b.h. representing size at first reproduction. In our analysis, we estimate an additional parameter (*D*<sub>min</sub>) to determine the size at which potential parents become reproductive.

We tested two alternate forms for the shape of the seedling dispersal function. Most previous studies (Ribbens *et al.* 1994; Clark *et al.* 1998; LePage *et al.* 2000) have used a Weibull function of the form

$$f(d) = \frac{1}{\eta} \exp^{-Bd^\beta} \quad \text{eqn 2}$$

where *d* is the distance from a quadrat to a parent tree, *B* and  $\beta$  are estimated parameters, and  $\eta$  is a normalization constant equal to the arwise integration of the dispersal kernel. Previous analyses have also arbitrarily fixed  $\beta$  at a value ranging from 1 to 3, but our analyses allow this parameter to vary and let the data determine the appropriate shape. Greene *et al.* (2004) argued that a lognormal function is actually more appropriate for both wind- and animal-dispersed seeds and often fits empirical data as well as or better than Weibull functions, including the ‘2Dt’ dispersal function developed by Clark *et al.* (1999). The lognormal also has an easy mechanistic interpretation (e.g. prevalent wind movement for wind-dispersed seeds or average seed passage time through the stomach for animal-dispersed seeds) (Greene & Johnson 1992; Nathan *et al.* 2002; Tackenberg

2003). Therefore, in addition to the Weibull function described above, we also tested a lognormal dispersal function with the form

$$f(d) = \frac{1}{\eta} \exp^{-\frac{1}{2} \left( \frac{\ln(d/X_0)}{X_b} \right)^2} \quad \text{eqn 3}$$

where  $X_0$  is the distance at which maximum recruitment occurs (i.e. the mode of the dispersal kernel), and  $X_b$  determines the breadth or spread of the dispersal kernel. For both the lognormal and Weibull dispersal kernels, we assumed that the shape of the dispersal kernel was isotropic, i.e. that seeds are equally likely to disperse in any direction from the parent tree.

Combining the first three components of the model, the potential number of new recruits ( $S_i$ ) in quadrat  $i$  over a specified period of time is then

$$S_i = bath + STR \sum_{k=1}^n \left( \frac{D_k}{30} \right)^\alpha f(d_{ik}) \quad \text{eqn 4}$$

where  $D_k$  is the diameter of  $k = 1 \dots n$  trees with diameter greater than  $D_{min}$  within a distance of 50 m,  $d_{ik}$  is the distance from quadrat  $i$  to tree  $k$ , and  $bath$  is the contribution of potential parents from outside the mapped area (in recruits  $m^{-2}$ ). We selected 50 m for our analyses after testing a range of potential radii of influence. A distance of 50 m consistently produced models with greater likelihood than smaller radii. The 58 outermost quadrats were < 50 m from the edge of the mapped stand. In order to estimate the potential contribution from trees outside the mapped stand, we created a 40-m buffer zone around the plot that contained a population of parent trees with a density and diameter size distribution identical to that of the trees present in the two permanent  $20 \times 20$  m quadrats closest to the edge of the plot at that point. This allowed us to use a radius of 50 m around the 'edge' plots (40 m buffer plus 10 m from the seedling plots to the edge of the LFDP). The exact spatial location of the trees within each of the  $20 \times 20$  m quadrats in the buffer zone was determined at random. The buffer therefore maintained spatial structure in the tree populations, at least at the scale of these quadrats. However, parent trees are likely to be spatially aggregated at a smaller spatial scale (Condit *et al.* 2000) and we do not have an understanding of their spatial structure at that scale. Therefore, we did not attempt to replicate exactly the clumped spatial pattern for parent trees in the buffer zone. In future analyses, however, we will explore the recruitment implications of assuming a spatial structure in parents outside the plot parallel to that of parents inside the plot.

The effect of light on seedling recruitment is calculated as a function of three estimated parameters.  $L_{opt}$  determines the light level (GLI) at which maximum recruitment occurs for a given focal species.  $L_{lo}$  determines the slope of the relationship at light levels <  $L_{opt}$ , while  $L_{hi}$  determines the slope of the decrease in

recruitment for quadrats with GLI greater than the optimal light ( $L_{opt}$ ).

$$m(GLI) = \begin{cases} \text{if } GLI < L_{opt}, m(GLI) = 1 - \{L_{lo}(L_{opt} - GLI)\} \\ \text{if } GLI = L_{opt}, m(GLI) = 1 & 0 \leq m(GLI) \leq 1 \\ \text{if } GLI > L_{opt}, m(GLI) = 1 - \{L_{hi}(GLI - L_{opt})\} \end{cases} \quad \text{eqn 5}$$

Seed rain at any given location is typically assumed to be a simple, additive function of the seed input from local parent trees. Once seeds arrive, however, there are a number of processes that may act in a density-dependent manner to alter the probability that a seed survives predation and pathogens to germinate and become an established seedling. In addition, once seeds germinate several processes, including conspecific competition, predation and, particularly, pathogens, cause seedling mortality resulting in negative density dependence. To test for the potential effects of density-dependent mortality, we examined models that included a function for density-dependent survival rate (a fraction that ranges from 0 to 1) as a function of the predicted potential number of new recruits ( $S$ ) (equation 4) (i.e. 'bath' input from long-distance dispersal in addition to local input from trees within the mapped stand):

$$g(S) = \exp^{-cS^\delta} \quad \text{eqn 6}$$

where  $c$  and  $\delta$  are estimated parameters.

The full function then takes the form

$$R_i = S_i m(GLI_i) g(S_i) \quad \text{eqn 7}$$

where  $R_i$  is the expected density of seedling recruitment (number  $m^{-2}$ ) in quadrat  $i$ .

As in Ribbens *et al.* (1994) and LePage *et al.* (2000), we used likelihood estimation and assumed that the expected density of recruits in a quadrat follows a Poisson distribution in which the mean of the distribution is given by equation 7. Clark *et al.* (1998) have recommended the use of a negative binomial distribution to fit dispersal functions for heavy, animal-dispersed seeds for which there is a high degree of clumping. The negative binomial requires estimation of one additional parameter (a 'clumping' parameter) that allows the variance to vary as a function of the mean. We have done extensive comparisons of the Poisson vs. negative binomial distribution, and find that the negative binomial often produces models with higher likelihood, in part because it can treat occasional extreme values as more likely than under a Poisson process. However, for the same reason, the negative binomial is very sensitive to the effects of even a few outliers (i.e. anomalously large numbers of seedlings in just one or a few quadrats). Thus, we have assumed a Poisson error structure in all of our analyses. We used simulated annealing, a global optimization algorithm (Goffe *et al.* 1994), to find the parameter values that maximized the

likelihood of observing the observed recruitment densities. For each species included in the analyses, we used the principle of parsimony and Akaike's information criterion corrected for small sample size ( $AIC_c$ ) to compare the performance of increasingly complex models against a null model that assumes a uniform seedling distribution across the plot. We selected the model with the lowest  $AIC_c$  with the added condition that bias, as reflected by the slope of the regression of observed vs. predicted, ranged from 0.9 to 1.1 (an unbiased model has a slope of 1). We also compared the best fit model with null models that assume that seed rain was uniform across the plot. Recall that we are comparing two dispersal kernels (lognormal vs. Weibull) as well as competing models that contain various degrees of complexity (bath, light and/or density dependence). We calculated goodness of fit of observed vs. predicted seedling densities (Pearson's  $r^2$ ) for the most parsimonious model. For the goodness of fit calculations, seedling densities were log transformed as  $\log(\text{seedling number} + 1)$  to reduce deviation from normality (Zar 1996).

## Results

The maximum likelihood model produced good to excellent fits ( $r^2 = 0.17\text{--}0.65$ ) for eight of the nine species included in the analysis but only fair to poor fit ( $r^2 = 0.11$ ) for the pioneer species *Schefflera morototoni* (Table 2). The best fit was observed for *Tabebuia heterophylla*, the only wind-dispersed species included in our analyses. The most parsimonious model, i.e. the unbiased model with the lowest  $AIC_c$ , for *Guarea guidonia*, *Manilkara bidentata*, *Prestoea acuminata*, *Sloanea berteriana* and *Tabebuia heterophylla* assumed a Weibull dispersal kernel (equation 2) while the remaining species, *Casearia arborea*, *Dacryodes excelsa*, *Inga laurina* and *S. morototoni*, supported a lognormal kernel (equation 3) (Tables 2 and 3, Fig. 1). For the majority of species, models that included light level, seedling density dependence, a bath term or a parameter that estimated minimum size at reproduction for potential source trees, had greater likelihood than simpler,

alternate models (Table 3). Nevertheless, not all species supported the most complex model. For instance, *S. berteriana* supported a model that only included a bath term and size at minimum reproduction.

Estimated parameters indicated strikingly different seedling recruitment patterns for the nine focal species (Table 2, Fig. 1). The potential standardized number of recruits (STR) produced per individual was highly variable. In general, species with lighter seeds (*Casearia arborea*, *Tabebuia heterophylla* and *Schefflera morototoni*) had greater STR than those with heavier seeds (*Dacryodes excelsa*, *Inga laurina* and *Sloanea berteriana*) (Tables 1 and 2, regression of log transformed seed mass vs. STR  $r^2 = 0.43$ ,  $P = 0.05$ ).

To explore the potential of diameter size thresholds for reproduction, we estimated an additional parameter to specify a minimum size ( $DBH_{min}$ ) below which trees are assumed to be non-reproductive. With the exception of *D. excelsa*, our data supported a model in which parents must reach a threshold size before any seed production will occur (Tables 2 and 3, Fig. 2). The estimated minimum reproductive size ranged from 9 to 48 cm d.b.h. (Table 2).

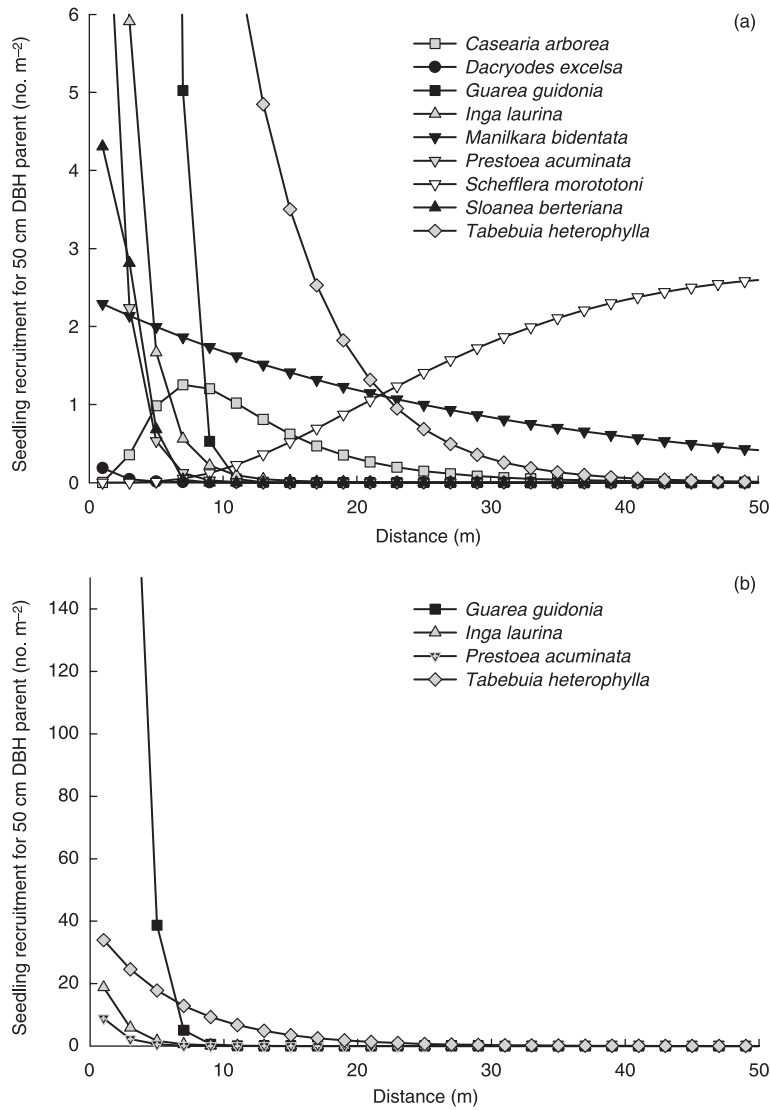
Unlike previous studies that assumed a fixed relationship between tree size (d.b.h.) and seedling production (Ribbens *et al.* 1994; Clark *et al.* 1998), we estimated  $\alpha$  in equation 2, the coefficient that relates tree diameter to seedling production. We allowed  $\alpha$  to vary from 0 to 4, and maximum likelihood estimates for the nine different species varied from 0.1 to 3.22 (Table 2). The highest estimated value for  $\alpha$  occurred in the relatively fast-growing, short-lived pioneer tree species, *S. morototoni*. For this species, seedling production appears to vary significantly with tree diameter once the trees are above the minimum estimated reproductive size (9.61 cm d.b.h.). Otherwise, there appeared to be no relationship between species life history and the estimated value of  $\alpha$  (equation 2). Estimated values for  $\alpha$  were fairly low for most species, indicating a weak relationship between parent size and seedling production once size at minimum reproduction is included as a factor (Table 2, Fig. 2).

**Table 2** Percentage of variance explained by the most parsimonious model (Pearson's  $r^2$ ). Seedling count data were transformed (seedling number + 1) to reduce deviations from normality. Dispersal kernel supported by the data and estimated values for bath term (in number of recruits  $m^{-2}$ ), standard number of recruits produced by a 30-cm DBH parent, coefficient of the relationship between parent size and seedling production ( $\alpha$ ) and minimum size at reproduction for the most parsimonious model. NA indicates that model comparison did not warrant the inclusion of the factor.

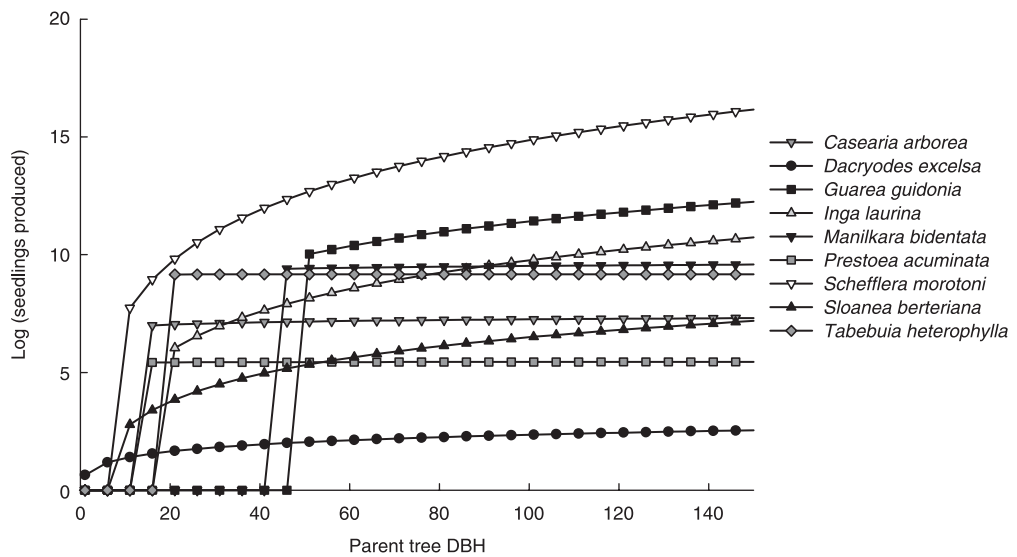
Species	$r^2$	Dispersal Kernel	Bath (recruits $m^{-2}$ )	STR	$\alpha$	Size
<i>Casearia arborea</i>	0.17	Lognormal	NA	1192	0.14	13.7
<i>Dacryodes excelsa</i>	0.29	Lognormal	0.19	5	0.51	NA
<i>Guarea guidonia</i>	0.21	Weibull	3.52	7650	2.06	48.13
<i>Inga laurina</i>	0.31	Lognormal	0.10	983	2.38	16.39
<i>Manilkara bidentata</i>	0.23	Weibull	0.06	227	0.01	44.04
<i>Prestoea acuminata</i>	0.21	Weibull	2.11	11384	0.15	13.89
<i>Schefflera morototoni</i>	0.11	Lognormal	NA	58255	3.22	9.61
<i>Sloanea berteriana</i>	0.39	Weibull	0.02	84	1.7	11.06
<i>Tabebuia heterophylla</i>	0.65	Weibull	0.20	9512	0.01	20.93

**Table 3** AIC and slope for model used to analyse seedling abundance of nine species in Table 1. The most parsimonious model is the one with lowest AIC<sub>c</sub>. To avoid bias we excluded from consideration all models with a slope > 1.10 or < 0.90. DD = density dependence. Size = size threshold included in the analyses. NULL = uniform seedling distribution across the plot. Most parsimonious model indicated in bold.

Species		CASARB	DACEXC	GUAGUI	INGLAU	MANBID	PREACU	SCHMOR	SLOBER	TABHET
Lognormal dispersal kernel										
BASIC	AICc	407.18	537.38	1611.75	650.84	307.03	2424.28	643.65	132.09	1379.52
	Slope	0.75	0.90	0.81	1.12	0.99	0.85	0.73	1.12	0.82
BASIC + BATH	AICc	393.49	504.94	1275.24	648.04	309.16	2315.14	619.80	134.28	1361.31
	Slope	0.88	0.91	1.04	1.12	0.96	0.89	0.89	1.15	0.84
BASIC + LIGHT	AICc	390.95	511.17	1596.53	570.80	299.42	2457.33	593.58	134.97	1291.98
	Slope	0.90	0.92	0.82	1.12	0.97	0.97	0.86	1.14	0.84
BASIC + SIZE	AICc	388.17	539.30	1613.66	640.25	309.57	2191.66	632.02	167.93	1304.57
	Slope	0.75	0.90	0.80	1.15	0.96	0.91	0.77	1.06	0.87
SIZE + DD	AICc	395.26	532.59	1497.39	513.11	308.53	2171.66	599.16	172.80	1154.29
	Slope	0.99	0.99	0.94	1.25	1.04	0.95	0.91	1.15	1.01
SIZE + BATH	AICc	399.62	520.03	1210.60	632.59	299.88	2098.74	597.10	171.55	1234.58
	Slope	0.95	1.02	1.06	1.10	1.02	0.95	1.00	1.10	0.90
SIZE + LIGHT	AICc	379.72	544.16	1598.13	798.73	302.05	2104.98	616.53	166.64	1232.33
	Slope	0.81	0.89	0.82	1.17	0.96	0.92	0.81	1.01	0.90
BATH + SIZE + DD	AICc	373.44	525.08	1663.90	509.04	303.43	2096.81	590.00	175.60	1109.48
	Slope	0.96	1.00	0.99	1.22	1.10	0.98	0.96	1.12	0.96
LIGHT + SIZE + DD	AICc	<b>365.34</b>	537.10	1499.78	493.44	295.72	2089.62	<b>572.12</b>	160.78	1041.21
	Slope	<b>0.98</b>	0.95	0.95	1.22	0.99	1.00	<b>0.98</b>	1.04	0.97
LIGHT + BATH + SIZE	AICc	376.96	519.11	1198.67	<b>609.66</b>	292.63	2022.26	597.69	169.31	1052.73
	Slope	0.80	1.00	1.03	<b>1.10</b>	1.06	0.97	1.02	1.05	0.84
BATH + LIGHT	AICc	400.87	504.94	1603.00	779.05	301.53	2485.25	594.90	135.41	1355.51
	Slope	0.88	0.97	0.86	1.22	1.01	0.96	0.87	1.19	0.81
BASIC + DD	AICc	407.17	537.20	1611.75	650.84	306.48	2424.28	643.64	132.08	1379.54
	Slope	0.75	0.90	0.81	1.12	0.98	0.85	0.73	1.14	0.82
BATH + DD	AICc	379.10	<b>491.38</b>	1239.98	549.14	2345.11	2270.85	594.09	138.50	1150.21
	Slope	1.00	<b>0.99</b>	1.06	1.23	6634615.38	0.97	0.93	1.20	1.02
LIGHT + DD	AICc	390.01	504.19	1498.75	574.82	281.26	2611.77	588.05	139.98	1065.38
	Slope	0.96	1.00	0.94	1.11	1.12	0.93	0.95	1.22	1.07
BATH + LIGHT + DD	AICc	391.89	506.23	1509.12	783.71	298.12	2656.75	590.99	141.74	1301.71
	Slope	0.91	0.99	1.00	1.20	1.15	0.94	1.01	1.47	1.15
BATH + LIGHT + DD + SIZE	AICc	407.17	537.20	1611.75	650.84	306.48	2424.28	643.64	132.08	1379.54
	Slope	0.75	0.90	0.81	1.12	0.98	0.85	0.73	1.14	0.82
Weibull dispersal kernel										
BASIC	AICc	407.29	537.41	1647.25	698.10	309.25	2511.71	657.67	139.53	1433.0242
	Slope	0.78	0.89	0.79	1.11	0.94	0.87	0.70	1.09	0.73
BASIC + BATH	AICc	394.07	516.15	1318.89	682.53	311.28	2317.86	633.14	134.84	1423.05
	Slope	0.90	0.84	1.05	1.07	0.94	0.90	0.96	1.05	0.74
BASIC + LIGHT	AICc	399.68	542.17	1632.91	826.69	302.08	2400.82	661.03	136.63	1422.7987
	Slope	0.76	0.88	0.79	1.13	0.98	0.90	0.75	1.11	0.72
BASIC + SIZE	AICc	389.51	539.39	1649.29	688.31	309.86	2255.54	642.55	139.46	1349.31
	Slope	0.75	0.89	0.79	1.14	0.93	0.90	0.75	1.04	0.81
SIZE + DD	AICc	401.46	513.77	1290.31	657.92	304.40	2238.58	627.95	138.56	1330.33
	Slope	0.89	0.89	1.06	1.05	0.97	0.90	0.95	1.11	0.77
SIZE + BATH	AICc	407.18	537.40	1647.27	698.15	309.36	2511.73	657.68	<b>131.68</b>	1433.05
	Slope	0.77	0.90	0.79	1.12	0.95	0.87	0.70	<b>1.08</b>	0.73
SIZE + LIGHT	AICc	382.22	496.58	1264.11	687.12	307.99	2276.91	604.28	139.12	1208.67
	Slope	0.96	0.95	1.04	1.07	1.10	0.97	0.95	1.06	1.00
BATH + SIZE + DD	AICc	382.08	534.96	1516.71	680.04	289.62	2379.28	595.88	140.76	1100.74
	Slope	0.93	0.98	0.94	1.14	1.12	0.94	0.97	1.20	1.10
LIGHT + SIZE + DD	AICc	373.24	532.73	1514.12	692.51	303.82	2246.58	612.64	144.77	1196.96
	Slope	0.93	0.99	0.96	1.15	1.01	0.95	0.97	1.17	1.03
LIGHT + BATH + SIZE	AICc	383.90	513.24	1270.28	663.47	298.35	2088.69	597.09	137.71	1280.56
	Slope	0.88	0.91	1.08	1.05	0.97	0.94	1.00	1.07	0.84
BATH + LIGHT	AICc	383.08	549.81	1635.14	825.52	316.01	2161.52	625.84	142.72	1268.86
	Slope	0.75	0.89	0.82	1.19	0.95	0.92	0.81	1.04	0.83
BASIC + DD	AICc	399.70	497.26	1194.82	636.22	287.97	2082.70	601.10	235.86	1142.72
	Slope	0.98	0.96	1.00	1.10	1.09	0.98	1.01	0.99	0.97
BATH + DD	AICc	368.70	537.12	1518.09	674.92	295.53	2163.13	588.27	148.05	1086.75
	Slope	0.91	0.97	0.93	1.19	1.06	0.96	1.01	1.17	1.11
LIGHT + DD	AICc	379.76	521.65	1244.64	642.72	319.49	2018.27	593.39	137.71	1106.67
	Slope	0.82	0.94	1.07	1.08	0.98	0.95	1.01	1.07	0.77
BATH + LIGHT + DD	AICc	378.33	501.38	1270.78	663.58	307.36	2205.72	579.33	143.46	1184.09
	Slope	0.99	0.95	1.09	1.11	1.11	0.96	0.96	1.02	0.98
BATH + LIGHT + DD + SIZE	AICc	371.04	495.38	<b>1189.81</b>	627.26	<b>275.30</b>	<b>2009.86</b>	583.06	140.84	<b>1020.69</b>
	Slope	0.99	0.96	<b>1.03</b>	1.15	<b>1.07</b>	<b>0.99</b>	1.00	1.22	<b>0.98</b>
NULL MODEL	AICc	416.17	593.87	1652.45	1191.63	342.57	2725.62	625.14	222.82	2569.12
	Slope	1.00	0.98	1.01	0.96	1.04	0.95	0.96	0.97	0.99

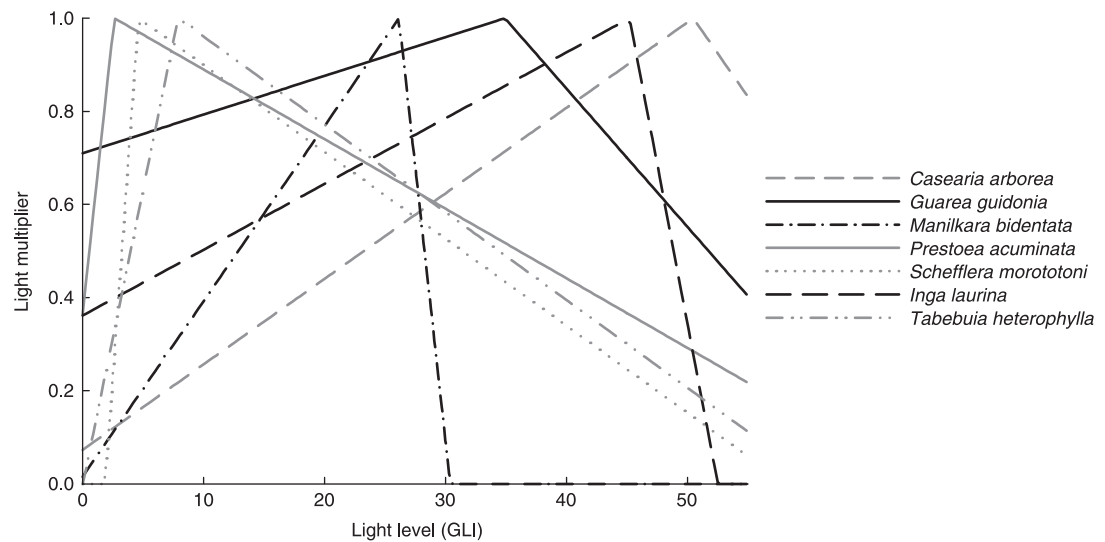


**Fig. 1** (a) Predicted seedling densities (per m<sup>2</sup>, per 50 cm d.b.h. trees), as a function of distance from parent trees. Colour code: early successional species = white; mid-successional = grey; and late-successional = black. (b) Species with large number of seedlings produced. *Guarea guidonia* reaches a maximum seedling production of 982 seedlings (not shown).



**Fig. 2** Predicted seedling production as a function of parent size. Early successional species = white; mid-successional = grey; and late-successional = black.





**Fig. 3** Effect of light availability (GLI) on seedling recruitment of species that supported a model that included light. Effect was calculated using three estimated parameters:  $L_{opt}$  determines the light level (GLI) at which maximum recruitment occurs for a given focal species;  $L_{low}$  determines the slope of the relationship between GLI and the scaling factor;  $L_{high}$  determines the slope of the decrease in recruitment for quadrats with GLI greater than the optimal light ( $L_{opt}$ ).

Bath recruitment, light limitation and density-dependent mortality all influenced patterns of seedling recruitment (Table 3). With the exception of *Casearia arborea* and *Schefflera morototoni*, the estimated bath term (number of seedlings  $m^{-2}$  from sources outside the 50-m radius neighbourhood) was greater than zero (Tables 2 and 3). Bath recruitment ranged from less than one seedling recruit  $m^{-2}$  to more than three and accounted for 6% to 81% of observed mean seedling density of a given species (Tables 1 and 2).

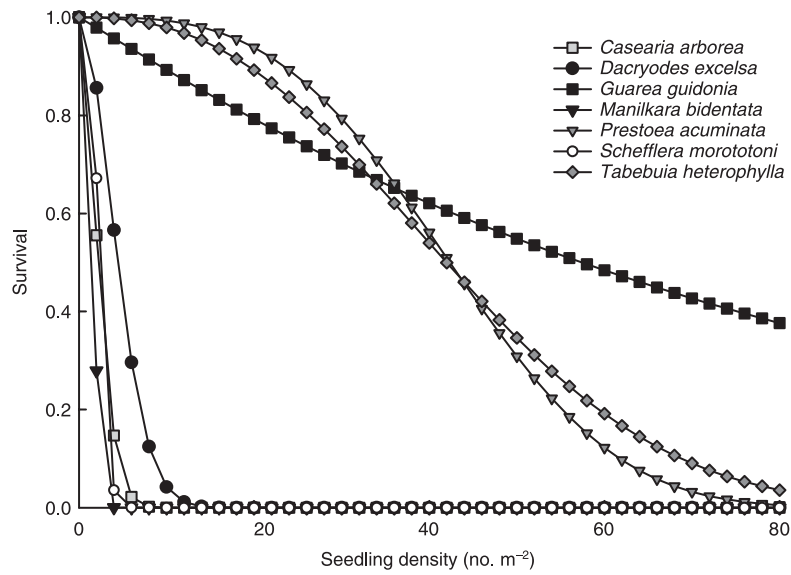
Light levels measured with the fish eye lens at 1-m height above the seedling quadrats 6 months after Hurricane Georges, ranged from 1 to 55% of full sun. This range of light levels influenced seedling recruitment for seven of the nine species included in the analyses (Fig. 3), but did not affect two shade-tolerant, late successional species: *Dacryodes excelsa* and *Sloanea berteriana* (Table 3).  $L_{opt}$ , the parameter that estimates the light level (GLI) at which maximum recruitment occurs for a given species, ranged from 2.64% for *Prestoea acuminata* to 50.49% for *Casearia arborea* (Fig. 3). Contrary to expectation, the pioneer *Schefflera morototoni* had a very low value of  $L_{opt}$  (Fig. 3) suggesting that these seedlings were able to establish in low light levels. Establishment declined sharply for most species at light levels away from the optimum ( $L_{opt}$ ) for that species (Fig. 3).

For most species, seedling abundances appear to reflect not only parental seed production and a favourable light environment but also the effects of conspecific seedling density on seedling survival (Table 3, Fig. 4). Incorporating an explicit term for density dependence in the model changed the shape of the estimated seedling dispersal kernel. Including the density term shifted the mode of the pre-density dependence dispersal kernel closer to potential parent trees, and therefore increased the number of recruits close to the potential

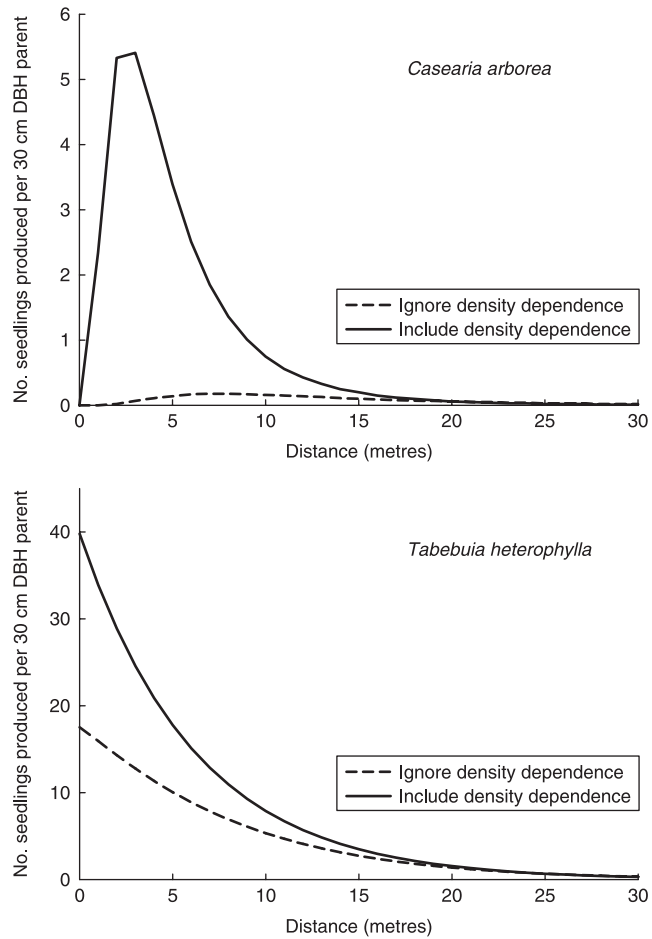
parent trees (Fig. 5). Presumably, density dependence effects due to con-specific seedlings act to reduce seedling establishment near parent trees. For example, a model that failed to account for the effect of density-dependent mortality in *Casearia arborea* would have estimated the mode of the lognormal seed dispersal kernel at 7.6 m away from the parent tree, with a peak density of only 0.18  $m^{-2}$  established seedlings. In contrast, a model that included the possibility that density-dependent mortality may have reduced seedling density near the parent tree, resulted in an estimated modal dispersal distance of only 2.5 m from parent trees, with a maximum potential recruitment of 5.61 seedlings  $m^{-2}$ . In effect, density-dependent mortality shifted the effective peak dispersion of seedlings away from parent trees by over 5 m, while dramatically reducing the maximum potential seedling density (Fig. 5a). A similar shift was observed for species that supported a Weibull dispersal kernel such as *Tabebuia heterophylla* (Fig. 5b).

## Discussion

The use of inverse modelling to understand patterns of recruitment and seedling establishment in the Luquillo Forest Dynamics Plot shows great promise. Our ability to explain patterns of seedling abundance in the LFDP is equal to, or better than, that of other studies that have used a similar method to understand seedling establishment in other forests (Ribbens *et al.* 1994; LePage *et al.* 2000). Our results indicate that, for most species, seedling recruitment reflects the interactions between a suite of processes. Distance from potential parent trees, parent size, bath recruitment, light availability in the understorey and density-dependent effects from conspecific seedlings all influenced



**Fig. 4** Effect of density dependence on seedling survival calculated using ML estimates of parameters in equation 3 for the most parsimonious model. Early successional species = white; mid-successional = grey; and late-successional = black. Only species that supported a model that included density dependence are shown.



**Fig. 5** Shape of estimated dispersal kernels for *Casearia arborea* (lognormal kernel) and *Tabebuia heterophylla* (Weibull kernel). Estimated parameters from most parsimonious model were used to calculate the kernel. Continuous lines represent the dispersal kernel of a model that includes density dependence prior to any density effects of seedling density. Actual recruitment would be reduced by density-dependent processes. Dotted lines represent a model that does not include density dependence.

seedling recruitment in the 3 years following Hurricane Georges.

Neighbourhood analyses using inverse modelling are one of several potential methods for estimating the parameters of dispersal functions (or 'kernels'), based on measurements of seed rain or seedling abundance at a set of sample locations and a map of the spatial distribution and sizes of potential parent trees in the vicinities of the sample locations (e.g. Ribbens *et al.* 1994; Clark *et al.* 1998, 1999; LePage *et al.* 2000). Although powerful, our approach is not without methodological challenges (C. D. Canham & M. Uriarte, unpublished data). Perhaps the most serious challenge is the need to develop a sampling scheme that overcomes two limitations of inverse modelling: censored data and the potential for parameter trade-offs. Clearly, sample locations should be located far enough from plot edges to avoid omitting a large percentage of unknown potential parent trees. In this study we attempted to compensate for the plot edge effect by creating a 40-m buffer of potential adults around the plot (see Methods). The most effective means of avoiding parameter trade-offs is to make sure that the sampling effort is distributed across a gradient of neighbourhood conditions that include an appropriate range of potential parent tree diameter, distances from parent to measured seedlings and seedling densities.

The appropriate shape for the empirical dispersal kernel has received much attention (see review in Greene *et al.* 2004). Most previous studies (Ribbens *et al.* 1994; Clark *et al.* 1998; LePage *et al.* 2000) have used a two-parameter Weibull dispersal kernel. Clark *et al.* (1999) have argued that only the 2Dt function has the right shape to accommodate both short- and long-distance dispersal. For many species of trees, particularly wind-dispersed species, the asymptote of the dispersal function is non-zero, and some portions of the seeds disperse long distances (Nathan & Muller-Landau 2000). However, Greene *et al.* (2004) argued that a lognormal dispersal kernel is more amenable to a mechanistic interpretation. The peak of the lognormal can be interpreted as the median distance travelled by seeds released from a single tree. Furthermore, we can assume that most seeds will fall some distance away from the centre of the bole of the parent tree rather than directly below the hypothetical centre of the stem (Greene & Calogeropoulos 2002). In fact, Greene *et al.* (2004) compared lognormal, 2Dt and two-parameter Weibull dispersal functions and found that the performance of the three dispersal terms was species specific. Our results also show that the shape of the dispersal kernel may reflect the life-history traits and dispersal syndromes of individual species. However, there appears to be no strong relationship of dispersal kernel with species life history or dispersal type. For example, both the pioneer *Schefflera morototoni* and the late-successional species *Dacryodes excelsa*, whose seed weights differ by almost two orders of magnitude, were classified as having a lognormal dispersal kernel. The

wind-dispersed species *Tabebuia heterophylla* and the bat-dispersed *Manilkara bidentata* both exhibited a Weibull dispersal kernel.

Our analyses of data for seedling dispersion extend previous inverse modelling exercises by estimating two additional parameters related to seedling production. First, we estimated a parameter to specify a minimum size (d.b.h.) below which trees are assumed to be non-reproductive. There was striking variation in the estimated d.b.h. for first reproduction. The estimated minimum reproductive size ranged from the smallest size included in the analyses (8 cm) to 48 cm d.b.h. for the different species analysed. Secondly, we estimated the parameter  $\alpha$  (equation 2), rather than fixing it at a value of 2, to allow for the possibility that seedling production may not be linearly related to parent biomass (i.e. that  $\alpha < > 2$ ). The highest estimated value for  $\alpha$  occurred in a fast-growing, relatively short-lived pioneer tree species, *Schefflera morototoni*. For this species, successful seedling production appears to vary significantly with tree size once the trees are above the minimum reproductive size estimated in the analyses (9.61 cm d.b.h.). *S. morototoni* can flower when small if it has sufficient light, but in closed canopy situations it must be tall enough to reach the canopy in order to flower. Shade-tolerant species generally flower when they are larger as they rarely reach the canopy to obtain sufficient light when they are small. However, Fig. 2 clearly shows that, for the majority of species, seedling production reaches a plateau after trees attain a minimum reproductive size. It is worth noting that none of the recently published analyses allow for functional relationships that are either asymptotic or in which the number of seedlings that a tree successfully produces actually declines with increasing tree size.

Variation in understorey light levels after Hurricane Georges had a significant effect on seedling establishment for seven of the nine species (Table 3, Fig. 3). The seven species that responded to light availability fell into three groups: group one establish better in low light, group two in medium light and group three in high light. Some of these results are surprising; for example both the pioneer *S. morototoni* and the secondary species *T. heterophylla* appear to establish best in low light. This may reflect the specific conditions of deep litter and soil surface drying in the large gaps after Hurricane Georges, which prevented successful establishment of these small seeded, light-demanding species. *P. acuminata*, with relatively large seeds, is generally considered a medium light demanding species but is also in group one and its apparent preference for low light in this analysis may also be a result of drought and increased herbivory in the more open canopy areas. Species in groups two and three conform more to our expectations. The more shade-tolerant primary forest species *G. guidonia* and *M. bidentata* in group two, show a preference for mid-range light levels and experience a steep decline in establishment success as light levels increase. This may reflect the effect of

chronic photo-inhibition and damage to shade-tolerant leaves in open canopy areas. *C. arborea* and *I. laurina* are in group three and establish better at the highest light levels as might be expected from species that typically colonize secondary forest and disturbed areas.

The different abilities of species to emerge through litter debris, coupled with the species response to increased light availability, may determine the fate of the seedlings after a hurricane. For example, shade-tolerant, large seeded species can easily germinate through litter but are highly susceptible to mortality by sun-scald (Guzmán-Grajales & Walker 1991). Other studies suggest that seeds germinate with increased light levels after the hurricane, but that herbivory, litter debris or diseases may have limited seedling establishment (Martínez-Ramos *et al.* 1989; Schupp *et al.* 1989; Lomascolo & Aide 2001; Walker *et al.* 2003). Our analyses corroborate studies by Walker *et al.* (2003) and indicate that, in contrast to the responses of adults (Zimmerman *et al.* 1994), seedlings respond to hurricane damage in a species-specific manner that does not necessarily conform to our current understanding of species life-history characteristics.

However, there is an alternative interpretation of the low light required for recruitment of the pioneer species *S. morototoni*. In all likelihood Hurricane Georges damaged a non-negligible portion of potential parent trees, particularly for light-wooded pioneer species, and these therefore cannot reasonably be considered to contribute to post-hurricane seedling recruitment. Zimmerman *et al.* (1994) showed that *C. arborea* was prone to tip-up during Hurricane Hugo and low density wood pioneer species such as *S. morototoni* were also likely to suffer damage. This may account for the fact that the goodness of fit for the model is lowest for pioneer species. For similar reasons, sites with highest GLI after the hurricane may have been those that suffered the highest amount of defoliation. Pioneer trees are most susceptible to damage during hurricanes, and it would appear that their seedlings fail to recruit in the sites with highest GLI. Unfortunately, we only have an estimate of damage for a small subset of potential parent trees but we can use these data to estimate the probability that individual adults may have been killed or heavily damaged by the hurricane as a function of tree size and taxonomic identity (cf Canham *et al.* 2001). A sample reanalysis, excluding potential parents based upon the probability that they may have sustained damage during Hurricane Georges, showed that our original analyses underestimated the number of seedlings produced per tree (STR in equation 1, Table 2). Other parameters were only slightly affected. The GLI at which maximum recruitment occurred was only slightly altered for pioneer species. Clearly, the dynamic nature of light availability at the forest floor following a hurricane is difficult to capture with just a few measures of light availability.

The hypothesis that host-specific seed and seedling predators are responsible for maintaining tropical

tree diversity by causing density- and frequency-dependence mortality, through an interaction between local seed dispersal and density-dependent seed and seedling predation (Janzen 1970; Connell 1971), has been an important theme in the debate over tropical tree diversity (Clark & Clark 1984; Hubbell & Foster 1986). Notwithstanding criticisms of the importance of these effects in the maintenance of diversity in tropical forests (Clark & Clark 1984), there is ample evidence that density-dependent effects are common, particularly at the seedling stage (Connell & Green 2000; Harms *et al.* 2000). Studies that use seedling plots with long intervals between censuses may fail to uncover density-dependent effects if predators or pathogens act swiftly to kill potential new recruits or if mortality occurs before seeds germinate or seedlings reach measurable size classes (Schupp *et al.* 1989). By allowing for this possibility, our analyses uncovered potential density-dependent effects in the majority of species. The density dependence term allowed us to estimate the displacement of the mean dispersal distance from potential parent trees as density dependence reduced the number of seedlings that established near parent trees. Failure to include a density-dependent term could mislead us into believing that the majority of seeds disperse further than they do, and that the number of seedlings produced per tree is lower than it is. Density-dependent effects were strong even though, *a priori*, one might expect that the damage to adult canopies, increased light availability and increased heterogeneity in light availability (Fernández & Fetcher 1991; Walker *et al.* 2003) might have obscured any relationship between adults and seedling recruitment. If anything, the high levels of seedling recruitment that followed Hurricane Georges appeared to magnify these effects.

Traditionally, ecologists have hypothesized that frequent disturbances will reduce the strength and importance of density-dependent interactions in tropical forests. Nevertheless, such a statement must be qualified to include both the severity of a disturbance and variation among species in their response to it. Comparative analyses of this disturbed Luquillo forest, and the less disturbed forest at Barro Colorado Island (BCI), Panama, have demonstrated that the prevalence and importance of density-dependent interactions are greater in Luquillo than BCI (Uriarte *et al.* 2004a,b). An alternate explanation is that the lower species pool in the flora of Puerto Rico generates greater spatial aggregation of conspecifics and hence potentially greater conspecific density-dependent effects.

Assessing the degree to which density dependence at the seedling stage contributes to the maintenance of tropical forest diversity represents an open challenge (Harms *et al.* 2000). Use of inverse modelling to understand the long-term fate of seedlings as they reach sapling size is one promising avenue that appears to have been successful in the analyses presented here. We hypothesize that including a density dependence term in similar analyses from other sites and for sapling

distribution will show sapling distributions strongly repelled from potential parent trees. Furthermore, the distance between potential parent trees and offspring is likely to be greater for saplings than for seedlings. The highly dynamic Luquillo forest, which is still undergoing high stem mortality and turnover as a result of Hurricane Georges, when compared with other tropical forests, provides a promising data set to test this hypothesis.

Species in the Luquillo forest appear to represent three different recruitment 'syndromes': (i) local dispersal processes account for the majority of seedling recruits; (ii) 'bath' recruitment from non-local sources dominates recruitment; and (iii) density-dependent processes act to reduce recruitment from local sources. In turn these three syndromes result in aggregated (local dispersal), uniform (no spatial pattern) and repelled (as density dependence weakens clustering) spatial distributions. *Sloanea berteriana*, with heavy seeds, a low bath term, low dispersal distance and no density dependence, represents the local dispersal syndrome. *Guarea guidonia*, with a large bath term, short dispersal distance and weak density dependence, represents the bath syndrome. *Casearia arborea*, with a lognormal kernel, relatively large dispersal distance and strong density dependence, represents the repelled distribution syndrome. Linking dispersal syndromes to density-dependent processes provides an important link between seed and seedling stages that goes beyond the usual focus of tropical tree life histories (Swaine & Whitmore 1988) and has the potential to provide useful insights into the spatial distribution of tree populations (Nathan & Muller-Landau 2000; Svenning 2001).

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### References

- Bellingham, P.J., Bellingham, E.V., Tanner, J., Rich, P.M. & Goodland, T.C.R. (1996) Changes in light below the canopy of a Jamaican rainforest after a hurricane. *Journal of Tropical Ecology*, **12**, 699–722.

- Boose, E.R., Serrano, M.I. & Foster, D.R. (2004) Landscape and regional impacts of hurricanes in Puerto Rico. *Ecological Monographs*, **74**, 335–352.
- Brokaw, N., Fraver, S., Grear, J.S., Thompson, J., Zimmerman, J.K., Waide, R.B. *et al.* (2004) Disturbance and canopy structure in two tropical forests. *Tropical Forest Diversity and Dynamism* (eds E. Losos, R. Condit & J. La Frankie). Center for Tropical Forest Science, Smithsonian Institution, Washington, DC.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Canham, C.D. (1988) An index for understory light levels in and around canopy gaps. *Ecology*, **69**, 1634–1638.
- 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 species. *Canadian Journal of Forest Research*, **31**, 1–10.
- Carlton, G.C. & Bazzaz, F.A. (1998) Regeneration of three sympatric birch species on experimental hurricane blow-down microsites. *Ecological Monographs*, **68**, 99–120.
- Clark, D.A. & Clark, D.B. (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist*, **124**, 769–788.
- Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, **68**, 213–235.
- Clark, J.S., Silman, M., Kern, R., Macklin, E. & HilleRis-Lambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N. *et al.* (2000) Spatial patterns in the distribution of tropical tree species. *Science*, **288**, 1414–1418.
- 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.
- Connell, J.H. & Green, P.T. (2000) Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology*, **81**, 568–584.
- Dalling, J.W., Hubbell, S.P. & Silveira, K. (1998) Seed dispersal, seedling establishment, and gap partitioning among pioneer trees. *Journal of Ecology*, **86**, 674–689.
- Devoe, N.N. (1989) Differential seeding and regeneration in openings and beneath closed canopy in sub-tropical wet forest. Dissertation, Yale University School of Forestry and Environmental Studies, New Haven, CT.
- 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.
- Fernández, D.S. & Fetcher, N. (1991) Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica*, **23**, 393–399.
- Foster, R.B. (1982) The seasonal rhythm of fruitfall on Barro Colorado Island. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes* (eds E.G. Leigh Jr, A.S. Rand & D.M. Windsor), pp. 151–172. Smithsonian Institution Press, Washington, DC.
- Francis, J.K. (1993) *Alchornea latifolia* SW. SO-ITF-SM-60 (pamphlet). International Institute of Tropical Forestry, Río Piedras, Puerto Rico.
- Goffe, W.L., Ferrier, G.D. & Rogers, J. (1994) Global optimization of statistical functions with simulated annealing. *Journal of Econometrics*, **60**, 65–99.
- Greene, D.F. & Calogeropoulos, C. (2002) Measuring and modeling seed dispersal in terrestrial plants. *Dispersal Ecology* (eds J. Bullock, R. Kenward & R. Hails), pp. 3–23. Blackwell Scientific, Oxford.

- Greene, D.F. Canham, C.D. Coates, K.D. & LePage, P.T. (2004) An evaluation of alternative dispersal functions for trees. *Journal of Ecology*, **92**, 758–766.
- Greene, D.F. & Johnson, E.A. (1992) Can the variation in samara mass and terminal velocity on an individual plant affect the distribution of dispersal distances? *American Naturalist*, **139**, 825–838.
- Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.
- Guzmán-Grajales, S. & Walker, L.R. (1991) Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest in Puerto Rico. *Biotropica*, **23**, 407–413.
- Harms, K.E. Wright, J.S. Calderón, O. Hernández, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in tropical forests. *Nature*, **404**, 493–495.
- Hubbell, S.P. & Foster, R.B. (1986) Biology, chance and history and the structure of tropical rain forest tree communities. *Community Ecology* (eds J.M. Diamond & T.J. Case), pp. 314–329. Harper & Row, New York.
- Hurttt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1–12.
- Janzen, D. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.
- Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.
- LePage, P.T. Canham, C.D. Coates, K.D. & Bartemucci, P. (2000) Seed source versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. *Canadian Journal of Forest Research*, **30**, 415–427.
- Liogier, H.A. (1985, 1988, 1994, 1995, 1997) *Descriptive Flora of Puerto Rico and Adjacent Islands. Volumes I–V*. Editorial de la Universidad de Puerto Rico, Rio Piedras, Puerto Rico.
- Lodge, D.J. & McDowell, W.H. (1991) Summary of ecosystem-level effects of Caribbean hurricanes. *Biotropica*, **23**, 373–385.
- Lomascolo, T. & Aide, T.M. (2001) Seed and seedling bank dynamics in secondary forests following Hurricane Georges in Puerto Rico. *Caribbean Journal of Science*, **37**, 259–270.
- Martinez-Ramos, M. Alvarez-Buylla, E. & Sarukhan, J. (1989) Tree demography and gap dynamics in a tropical rain forest. *Ecology*, **70**, 336–342.
- Nathan, R. Horn, H.S. Chave, J. & Levin, S.A. (2002) Mechanistic models for tree seed dispersal by wind in dense forest and open landscapes. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 69–82. CAB International Press, Wallingford, Oxfordshire.
- Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.
- Ribbens, E. Silander, J.A. Jr & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.
- Scatena, F.N. & Larsen, M.C. (1991) Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica*, **23**, 317–323.
- Schupp, E.W. Howe, H.F. Augspurger, C.K. & Levey, D. (1989) Arrival and survival in tropical treefall gaps. *Ecology*, **70**, 562–564.
- Soil Survey Staff. (1995) *Order 1 Soil Survey of the Luquillo Long-Term Ecological Research Grid, Puerto Rico*. United States Department of Agriculture, Natural Resources Conservation Service, Lincoln, Nebraska.
- Svenning, J.C. (2001) Environmental heterogeneity, recruitment limitation and the mesoscale distribution of palms in a tropical montane rain forest (Maquipucuna, Ecuador). *Journal of Tropical Ecology*, **17**, 97–113.
- Swaine, M.D. (1996) *The Ecology of Tropical Forest Tree Seedlings*. Parthenon, New York.
- Swaine, M.D. & Whitmore, T.C. (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio*, **75**, 81–86.
- Tackenberg, O. (2003) Modelling long-distance dispersal of plant diaspores by wind. *Ecological Monographs*, **73**, 173–189.
- 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, Jr), pp. 540–550. University of Chicago Press, Chicago, Illinois.
- Thompson, J., Brokaw, N., Zimmerman, J.K., Waide, R.B., Everham, E.M. III, Lodge, D.J. et al. (2002) Land use history, environment, and tree composition in a tropical forest. *Ecological Applications*, **12**, 1344–1363.
- Tilman, D. (1994) Competition and biodiversity in spatially-structured habitats. *Ecology*, **75**, 2–16.
- Uriarte, M., Canham, C.D., Thompson, J. & Zimmerman, J.K. (2004a) A maximum-likelihood, neighborhood analysis of tree growth and survival in a tropical forest. *Ecological Monographs*, **74**, 591–614.
- Uriarte, M., Condit, R., Canham, C.D. & Hubbell, S.P. (2004b) A spatially-explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology*, **92**, 348–360.
- Vandermeer, J., Boucher, D., Perfecto, I. & Granzow de la Cerda, I. (1996) A theory of disturbance and species diversity: evidence from Nicaragua after Hurricane Joan. *Biotropica*, **28**, 600–613.
- Walker, L.R., Brokaw, N.V.L., Lodge, D.J. & Waide, R.B. (1991) Ecosystem plant and animal responses to hurricanes in the Caribbean. *Biotropica*, **23** (Special issue).
- Walker, L.R., Lodge, D.J., Guzmán-Grajales, S.M. & Fetcher, N. (2003) Species-specific seedling responses to hurricane disturbance in a Puerto Rican rain forest. *Biotropica*, **35**, 472–485.
- Walker, L.R. & Neris, L.E. (1993) Posthurricane seed rain dynamics in Puerto Rico. *Biotropica*, **25**, 408–418.
- Walsh, R.P.D. (1996) *Climate. The Tropical Rainforest: an Ecological Study*, 2nd edn (ed. P.W. Richards), pp. 159–205. Cambridge University Press, Cambridge.
- Warner, R.R. & Hughes, T.P. (1988) The population dynamics of reef fishes. *Proceedings of the 6th International Coral Reef Symposium*, **1**, 149–155.
- Wunderlee, J.M. Jr (1999) Pre- and post-hurricane fruit availability: implications for Puerto Rican parrots in the Luquillo mountains. *Caribbean Journal of Science*, **35**, 249–264.
- Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, New Jersey.
- Zimmerman, J.K., Everham, E.M., 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., Pascarella, J.B. & Aide, T.M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology*, **8**, 350–360.

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