

DISPERSAL SPECIAL FEATURE

Interspecific variation in primary seed dispersal in a tropical forest

Helene C. Muller-Landau^{1,2*}, S. Joseph Wright¹, Osvaldo Calderón¹, Richard Condit¹ and Stephen P. Hubbell^{1,3}

¹Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA; ²Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN 55108, USA; and ³Department of Biology, University of California, Los Angeles, CA, USA

Summary

1. We investigated the relationships of seed size, dispersal mode and other species characteristics to interspecific variation in mean primary seed dispersal distances, mean annual seed production per unit basal area, and clumping of seed deposition among 41 tropical tree species on Barro Colorado Island, Panama.
2. A hierarchical Bayesian model incorporating interannual variation in seed production was used to estimate seed dispersal, seed production, and clumping of seed rain for each species from 19 years of data for 188 seed traps on a 50-ha plot in which all adult trees were censused every 5 years.
3. Seed dispersal was modelled as a two-dimensional Student's *T* distribution with the degrees of freedom parameter fixed at 3, interannual variation in seed production per basal area was modelled as a lognormal, and the clumping of seed rain around its expected value was modelled as a negative binomial distribution.
4. There was wide variation in seed dispersal distances among species sharing the same mode of seed dispersal. Seed dispersal mode did not explain significant variation in seed dispersal distances, but did explain significant variation in clumping: animal-dispersed species showed higher clumping of seed deposition.
5. Among nine wind-dispersed species, the combination of diaspore terminal velocity, tree height and wind speed in the season of peak dispersal explained 40% of variation in dispersal distances. Among 31 animal-dispersed species, 20% of interspecific variation in dispersal distances was explained by seed mass (a negative effect) and tree height (a positive effect).
6. Among all species, seed mass, tree height and dispersal syndrome explained 28% of the variation in mean dispersal distance and seed mass alone explained 45% of the variation in estimated seed production per basal area.
7. *Synthesis.* There is wide variation in patterns of primary seed rain among tropical tree species. Substantial proportions of interspecific variation in seed production, seed dispersal distances, and clumping of seed deposition are explained by relatively easily measured plant traits, especially dispersal mode, seed mass, and tree height. This provides hope for trait-based generalization and modelling of seed dispersal in tropical forests.

Key-words: dispersal mode, dispersal syndrome, fecundity, hierarchical Bayesian model, primary seed dispersal, seed limitation, seed production, seed rain, seed shadow, tropical tree

Introduction

Understanding seed dispersal is critical to understanding plant population and community dynamics (Nathan &

Muller-Landau 2000; Wang & Smith 2002), especially in tropical forests where seed limitation is pervasive (Clark *et al.* 1999; Hubbell *et al.* 1999). In most tropical tree species, seed arrival is sparse and patchy, and thus knowledge of where seeds arrive is a prerequisite for understanding the influences of post-dispersal processes such as seed predation (Wright

*Correspondence author. E-mail: mullerh@si.edu

et al. 2000; Russo 2005), microhabitat requirements for establishment (Svenning 2001), and density-dependent survival (Harms *et al.* 2000; Bell *et al.* 2006). Despite its importance, we know very little about seed dispersal of tropical trees, because it has been studied in only a tiny proportion of the many tropical tree species and because general relationships that might allow dispersal patterns to be predicted from more easily measured species characteristics have yet to emerge.

Fruits and seeds of tropical tree species vary widely in their size and morphology and are dispersed by a broad array of dispersal agents (Levey *et al.* 1994; Muller-Landau & Hardesty 2005). Seed dispersal patterns thus depend on the interaction of the local frugivore community with plant attributes that influence attractiveness to dispersers. Dispersal agents vary in their movement and fruit handling patterns, and therefore in their influences on seed viability and spatial patterns of seed deposition (Howe 1989, 1993; Wenny & Levey 1998; Westcott *et al.* 2005). We thus expect that dispersal syndrome should explain some portion of interspecific variation in dispersal distance, as in other ecosystems (Willson 1993). Indeed, previous studies in tropical forests have found that dispersal syndrome is related to seed deposition patterns around isolated trees (Clark *et al.* 2005) and spatial patterns of trees and saplings (Seidler & Plotkin 2006), albeit in both cases there was considerably more variation within than among dispersal syndromes. Systematic variation with adult tree stature in the proportion of species having different dispersal strategies (Gentry 1983) suggests that there are differences in the efficacy of dispersal strategies in different conditions, and that dispersal agent and adult stature together should explain additional interspecific variation in dispersal distance within any given site.

Among species with the same dispersal syndromes, further variation in fruit and seed characteristics may affect seed dispersal patterns. Among wind-dispersed species, seed dispersal depends on the aerodynamic properties of diaspores (seeds plus wings or other dispersal appendages), such as their terminal velocities, as well as upon tree height (Augspurger 1986; Nathan *et al.* 2001). Among animal-dispersed species, the quantity and quality of pulp, the sizes of seeds, and the chemical composition of pulp and seeds may determine attractiveness to different disperser groups (Howe 1989; Grubb 1998; Tewksbury & Nabhan 2001).

In seasonal forests in which weather conditions and fruit availability vary during the year, some variation in dispersal distances among species is likely to be explained by the time of fruiting. We expect dispersal distances of wind-dispersed species to be longer for species that fruit in seasons of higher wind speeds (Nathan *et al.* 1999). For animal-dispersed species, dispersal distances are expected to be longer in species that fruit in times of relative fruit scarcity – that is, low food availability relative to the number of frugivores. At these times, a larger proportion of fruit is likely to be consumed and seeds may be taken farther by frugivores searching longer distances for food (van Schaik *et al.* 1993). By this logic, temporal variation in dispersal success should create selection pressure for animal-

dispersed species to fruit in times of relative fruit scarcity until equal amounts of animal-dispersed fruit are available throughout the year. However, other selective forces may favour fruiting at times when conditions are best for germination and seedling establishment such as the beginning of the wet season (Garwood 1983), and thus maintain seasonal disparities in fruit availability.

Novel analytical techniques now make multi-species studies of seed dispersal feasible. Inverse modelling enables estimation of seed production and seed dispersal from data on seed rain within mapped stands (Ribbens *et al.* 1994; Tufto *et al.* 1997; Clark *et al.* 1998; Clark *et al.* 1999). Information on the mother trees and thus dispersal distances of individual captured seeds is not necessary for reliable reconstruction of the seed shadow (Nathan & Muller-Landau 2000; Bullock *et al.* 2006; Jones & Muller-Landau 2008). Seed trapping studies within multi-species mapped stands can be used to examine seed production and dispersal in many species simultaneously (Clark *et al.* 1998; Clark *et al.* 1999; Clark *et al.* 2004). In contrast, most other methods for studying seed rain focus on one or a few tree species or dispersal agents (Bullock *et al.* 2006). Seed dispersal has been investigated by sampling post-dispersal seed densities around isolated trees (e.g. Dalling *et al.* 1998), quantifying fruit removal and following the movements of animal seed dispersers (e.g. Wenny 2000), labelling seeds of particular trees and tracking their displacements (Vander Wall 1994), or using genetic methods to identify parents of dispersed seeds (Jones *et al.* 2005). These methods have been employed in a number of excellent studies that have elucidated dispersal patterns and/or processes in particular taxa at particular sites, but they do not lend themselves to large-scale studies of many species that might shed light on the community-level importance of seed dispersal and provide scope for generalization to the many unstudied taxa.

In this study, we use a long-term seed rain data set and inverse modelling to investigate seed production and seed dispersal of many co-occurring tree species in a tropical forest. We analyse factors hypothesized to explain interspecific variation in seed production and dispersal distances. Among all species, we expect seed production to vary inversely with seed size. We test relationships of fitted dispersal parameters with dispersal syndrome, seed and fruit characteristics, tree size and season of dispersal. We expect that dispersal distances will be longest in bird-dispersed species and shortest in explosively dispersed species, and that clumping unrelated to dispersal distance will be higher in animal-dispersed species reflecting clumped seed deposition. Among wind-dispersed species, we expect dispersal distances to increase with decreasing seed size, decreasing terminal velocity, increasing tree height, and increasing wind speed in the month of peak dispersal. Among animal-dispersed species, we analyse the relationship of seed and fruit size with dispersal distances, and we test the hypothesis that dispersal distances will be longer for species that have larger tree size (and are thus more attractive to dispersers) and that fruit when few other animal-dispersed species are fruiting.

Methods

STUDY SITE

Barro Colorado Island (9°10' N, 79°51' W), is a 1600-ha island in central Panama, covered in lowland moist tropical forest. The climate is seasonal, with a pronounced dry season approximately from mid-December to the end of April. Annual rainfall averages 2600 mm (Leigh *et al.* 1996; Paton 2007). Wind speeds are consistently higher in the dry season than in the wet season (Paton 2007). This study was conducted in the 50-ha forest dynamics plot located on the central plateau of the island (Hubbell & Foster 1983; Condit 1998) where the soil is a well-weathered, nutrient-poor oxisol (Yavitt 2000). With the exception of a small (< 2 ha) patch of secondary forest < 200 years old, the forest in this area has been little disturbed since at least 1500 years BP (Piperno *et al.* 1990).

BCI has a diverse and essentially intact community of animal seed dispersers. Because of a well-enforced ban on hunting, herbivore and predator densities are comparable with those at much more remote sites (Wright *et al.* 1994). Three frugivorous/granivorous vertebrate species known to have inhabited the area previously, however, are absent: white-lipped peccaries and two species of macaw (all important seed predators, but not seed dispersers). For the purposes of our analyses, we divide frugivorous species into three groups: birds, bats and nonvolant mammals. Leigh (1999) estimates that birds, bats and nonvolant mammals consume 27, 20 and 355 kg dry wt. of fruits and seeds per hectare per year, respectively, on BCI. Eighty-three bird species (27% of resident species) include fruit in their diet with fruit accounting for on average 40% of the diet of these species (Willis 1990). Twenty species of bats also consume fruit (Kalko *et al.* 1996); the Jamaican fruit bat, *Artibeus jamaicensis*, is by far the most common (Handley *et al.* 1991) and accounts for perhaps half of all fruit consumption by bats (Leigh 1999). Among the 24 species of nonvolant mammals known to consume fruit, howler monkeys consume the most: an estimated 122 kg dry wt. per hectare per year, almost a third of all fruit consumption by vertebrates (calculated from Leigh (1999)).

Of the 299 free-standing woody plant species that have been recorded on the 50 ha plot for which we have dispersal syndrome information, 72% are dispersed by animals, 11% by wind, 4% by explosion (ballistically), and just one species by water (Muller-Landau & Hardesty 2005). Of the animal-dispersed species, most are known to be dispersed by more than one group: 90% by nonvolant mammals, 88% by birds, and 18% by bats. There are systematic differences in dispersal syndrome frequency among life forms; in particular, wind dispersal is much more common among canopy tree species (25%) than among mid-storey (7%) and understorey (2%) tree species. Similar patterns hold when calculations are done by basal area (Muller-Landau & Hardesty 2005). There is strong seasonal variation in the availability of ripe fruits and seeds of animal-dispersed species; fruiting peaks in the late dry season and is at its lowest in the late wet season (Wright *et al.* 1999).

TREE AND SEED CENSUS DATA

All free-standing woody plants over 1 cm in diameter in the Forest Dynamics Plot were censused in 1982–83, 1985, 1990, 1995, 2000 and 2005. In each census, stems new to the census are permanently tagged, identified to species, and mapped to within 0.5 m, and the diameters of all living stems (new and old) are measured at 1.3 m height (Condit 1998). The complete tree census data set is available at <<http://www.ctfs.si.edu/doc/datasets.html>>.

Seed rain has been censused weekly since January 1987, using 200 seed traps set along 2.7 km of trails within the plot (Wright & Calderón 1995; Wright *et al.* 1999). Each seed trap consists of a square, 0.5 m² PVC frame supporting a shallow, open-topped, 1-mm nylon-mesh bag, suspended 0.8 m above the ground on four PVC posts. All seeds, fruits, seed-bearing fruit fragments, flowers, capsules, and other reproductive parts of plants that fall into the traps are identified to species and recorded. Fruits are categorized as aborted, immature, damaged, fragments and mature. Because the seed traps are located above the ground, they capture fruits and seeds falling directly from trees, as well as those spat or defecated by birds, bats and arboreal mammals; they do not, however, record secondary dispersal by rodents and other terrestrial animals. Data from the 12 traps within 20 m of the edge of the plot were excluded because these traps could be strongly influenced by uncensused trees outside the plot.

Seed data collected in the 188 traps more than 20 m from the edge of the plot between 1 January 1987 and 1 January 2007 were employed for the analyses here (Fig. 1). For each species, we used the month of minimum seedfall into the traps to define the start and end of the phenological fruiting year for that species (Zimmerman *et al.* 2007). The minimum monthly fruitfall was zero for most species, and just one species, *Hyeronima alchorneoides*, fruits more than once a year (Zimmerman *et al.* 2007). For example, for *Dipteryx oleifera* whose fruit production peaks in February, the phenological year starts July 15. To avoid having data for any partial fruiting season in the analyses, we used only data collected in the nineteen complete phenological years of each species falling during the census interval.

Seed production and dispersal models were fitted to tree species that met the following conditions: (i) its seeds are greater than the mesh size of the traps and are reliably identified to species (this excludes taxa whose seeds or fruits are too small or similar among congeners to be consistently captured and identified to species, specifically species in the genera *Alseis*, *Casearia*, *Conostegia*, *Ficus*, *Inga* with the exception of *Inga marginata*, *Hyeronima*, *Miconia* and *Zanthoxylum* with the exception of *Zanthoxylum ekmanii*); (ii) its seeds and/or fruits reached 10 or more traps during the study period; (iii) all potentially reproductive individuals within the plot are recorded in the tree census (this excludes shrubs and small trees that can reproduce below 1 cm in diameter, as well as lianas, which are not included in the plot census); (iv) at least one adult tree was present on the plot. A total of 107 species met these criteria. For each species, the number of fruits was multiplied by the species-specific average seed-to-fruit ratio and added to the number of simple seeds to obtain total counts of seed equivalents falling into each trap. For all these species, we fit models to the total seed equivalents falling into the traps. For nine wind-dispersed species whose fruit are capsules which hold multiple diaspores, we also fit models to the total seeds alone; this allowed us to relate diaspore dispersal distances to diaspore characteristics among all wind-dispersed species combined.

PLANT SPECIES TRAIT DATA

Species diaspore, seed and fruit masses as well as seed : fruit ratios were from measurements by S. J. Wright, supplemented in some cases by literature data (Augsburger 1986; Kitajima 1992; Daws *et al.* 2005). The diaspore was defined as the dispersal unit, encompassing wings in the case of wind-dispersed species. Dry weights were taken after drying at 60 °C for at least 48 h. Terminal velocities of wind-dispersed diaspores were from Augspurger (1986). Mature heights of tree species were based on measurements at this site, extrapolated to additional individuals via allometric relationships with diameter (O'Brien *et al.* 1995; Bohlman & O'Brien 2006).

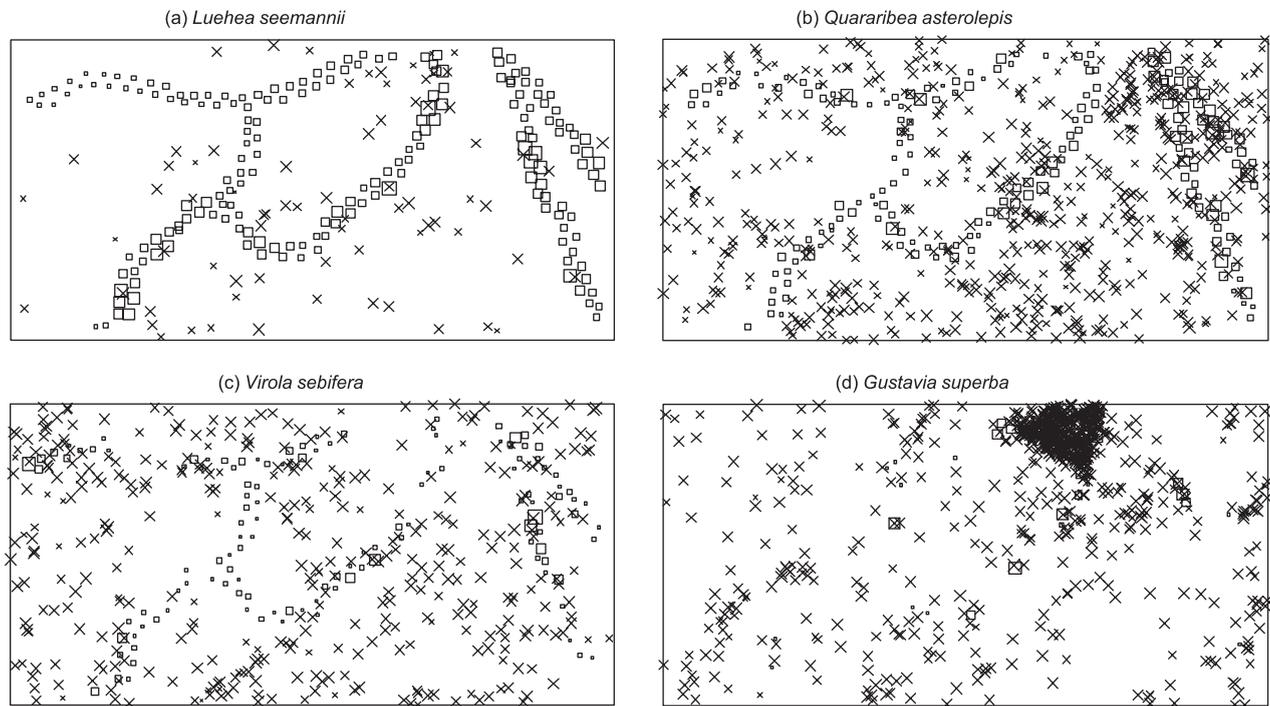


Fig. 1. Maps of adult trees and seed trap contents for four species varying in seed dispersal, seed production and abundance. Traps capturing seeds of the species are represented by boxes, with box size scaled to the number of seed equivalents captured. Adult trees are represented by crosses, with size scaled to their diameters. All 200 traps captured seeds of *Luehea seemannii* (a); traps missing from the remaining panels captured zero seeds of the named species.

Dispersal mode, dispersal syndrome, and known animal disperser groups were assigned to each species based on fruit morphology and published and unpublished observations of fruit consumption. Fruit morphology was the basis for classifying species as dispersed by wind, explosion or animals (Croat 1978). Published records for Central Panama (particularly Croat 1978) and unpublished observations made by O. Calderon, B. DeLeon and S. J. Wright since 1983 for animal-dispersed species and by the late Charles O. Handley Jr for bat-dispersed species were used to further classify each species as dispersed or not by each of the three major disperser groups we consider: bats, nonvolant mammals and birds. As stated above, each group encompasses over 20 animal species. We lack the data to reliably make finer distinctions, because many dispersal agents of individual plant species have yet to be identified in this species-rich forest. Despite the use of such broad categories, 85 of 89 of the animal-dispersed species treated here had dispersal agents from two of the animal-dispersed categories. This confirms the frequent observation that tropical seed-dispersal agent relationships are 'flexible/loose' (Howe & Smallwood 1982; Levey *et al.* 1994; Muller-Landau & Hardesty 2005). We assigned a predominant dispersal syndrome of mammal or bird on the basis of fruit and seed traits for plant species with dispersal agents from multiple animal-dispersed categories (Janson 1983).

SEED SHADOW MODELS AND ESTIMATION

We used a hierarchical Bayesian approach to estimate seed shadows for each species from the location of and number of seeds in seed traps and the sizes and locations of adults within the forest dynamics plot (Clark *et al.* 2004). The general approach is to start with

functions for the probability of seed arrival as a function of distance from an adult tree and for fecundity as a function of tree size, and then to calculate expected seed rain into each trap as the sum of contributions from every conspecific adult tree on the plot, with those contributions determined by their distances from the trap and their sizes, according to the functions. We then searched for functions that produced the best fit to the observed seed rain, with the fit evaluated by maximum likelihood methods (Ribbens *et al.* 1994; Tufto *et al.* 1997; Clark *et al.* 1998).

The seed shadow models we explored present a simplified picture of seed dispersal, in which expected seed density declines monotonically with distance from source tree, and is affected only by distance. All trees in a species are assumed to have the same seed dispersal kernel – that is, the same probability density function specifying the probability a particular seed will land at various positions relative to a source tree. Thus, in the fitted model, dispersal kernels do not vary depending on direction relative to the source tree, local habitat (e.g. the presence of gaps or of trees in which monkeys regularly sleep), or any other factors except species identity. All additional variation is unexplained, and becomes part of the error term. It is possible to construct more complicated and potentially more realistic models of dispersal, but such models have additional parameters and require additional data.

In the absence of specific information on the reproductive status of each adult tree in each year (or even its sex in the case of dioecious species), our model of individual tree fecundity is similarly simplified. We assume that expected seed production is a function of expected basal area for trees above species-specific minimum size thresholds for reproduction. Tests with simulated data showed that the fitted seed shadows are very sensitive to the omission of reproductive

trees, but not particularly sensitive to the inclusion of non-reproductive trees (H. C. Muller-Landau, unpublished analyses); thus we chose low thresholds for reproduction representing the minimum (not average) size for onset of reproduction. Based on data for 16 species, we used diameter cutoffs that were two-third of the unpublished species-specific average diameters at onset of reproduction estimated by Robin Foster (Wright *et al.* 2005a). Adult diameter data from the 1985, 1990, 1995, 2000 and 2005 censuses were used, as appropriate. Expected basal area of a tree in a phenological year was calculated as the probability an adult tree was alive in the midpoint of the phenological year times its conditional basal area at that time. Conditional basal areas were interpolated between census dates of individual trees using cubic splines and linearly extrapolated beyond the final census in which a tree was alive (implemented with the *R* function *splinefun* with method = 'natural' in *R* 2.50). The probability a tree was alive was linearly extrapolated between the last census it was recorded alive and the first census it was recorded dead (implemented with the *R* function *approxfun* with method = 'linear' and rule = 2).

We accommodated interannual variation in population-level seed production by fitting hierarchical models for each species incorporating lognormal variation in the fecundity parameter among years (Clark 2007). For each species, we fit annual fecundity parameters for each phenological year constrained by hyperparameters for the mean and SD of the lognormal distribution of fecundities across years. That is, the total likelihood of the model was the likelihood of the data given the dispersal parameters, error parameter, and individual year fecundity parameters times the likelihood of the individual year fecundity parameters given the fecundity hyperparameters (Clark *et al.* 2004). The lognormal distribution of fecundities was chosen based on previous analyses (Wright *et al.* 2005b).

Together, the seed dispersal and fecundity models predict expected seed rain for each trap in each phenological year given the distances to conspecific adult trees and their expected sizes (basal areas) in that year. We calculate the expected total seed rain in year y to trap j , \hat{S}_{jy} , as the sum of contributions from each tree, i , on the plot in year y plus the contribution of trees off the plot. The contribution of a given tree i in a given phenological year y depends on its expected basal area in that year, b_{iy} , as well as the distance between the trap and the tree, r_{ij} :

$$\hat{S}_{jy} = x \left[\sum_{\text{trees } i} Q_y(b_{iy}) F(r_{ij}) + \frac{\sum Q_y(b_{iy})}{a} \iint_{\text{area off plot}} F(r_j) \right] \quad \text{eqn 1}$$

where x is the area of the trap (to convert the total from seeds per unit area to seeds per trap), $Q_y(b_{iy})$ is fecundity as a function of basal area in year y , $F(r_{ij})$ is the two-dimensional dispersal kernel (probability of seed arrival per unit area as a function of distance), and a is the area of the plot on which trees were mapped. The second term represents annual contributions to seed rain from unknown trees off the plot. Assuming an equivalent uniform density of seed production per unit area off the plot, these contributions were estimated as the product of the average seed production per unit area on the plot in that year (the fraction), with seed input weighted by distance (the double integral).

Here we report and compare among species fits obtained for the model that provided the best fit for the most species. We modelled dispersal as a two-dimensional T distribution (Clark *et al.* 1999) in which the degrees of freedom parameter was set to 3,

$$F(r_{ij}) = \frac{1}{\pi \exp(\alpha) \left(1 + \frac{r_{ij}^2}{\exp(\alpha)}\right)^2} \quad \text{eqn 2}$$

(Clark *et al.* 2004). Expected seed production was modelled as proportional to expected basal area,

$$Q_y(b_{iy}) = \exp(\beta_y) b_{iy} \quad \text{eqn 3}$$

(as in Ribbens *et al.* 1994; Clark *et al.* 1998; Clark *et al.* 1999), with the annual fecundity parameters for a species normally distributed with estimated hyperparameters mean μ and SD σ (note that this is equivalent to having the fecundity per basal area lognormally distributed). And finally, actual seed rain in each trap in each year, S_{jy} , was assumed to be distributed around expected seed rain \hat{S}_{jy} according to a negative binomial distribution with clumping parameter κ (Hilborn & Mangel 1997; Clark *et al.* 1998). We assumed uniform (flat, non-informative) priors on all relevant parameters (α , μ , σ and κ). Thus the joint posterior distribution is

$$\begin{aligned} p(\alpha, \beta, \mu, \kappa | S, b, r, x, a, \dots) = & \prod_{\text{traps years}} \text{NegBinom}(S_{jy} | b, r, x, a, \alpha, \beta, \kappa) \\ & \times \prod_{\text{years}} \text{Normal}(\beta_y | \mu, \sigma) \\ & \times \text{Unif}(\alpha | -100, +100) \\ & \times \text{Unif}(\mu | -100, +100) \\ & \times \text{Unif}(\sigma | -100, +100) \\ & \times \text{Unif}(\kappa | -100, +100) \end{aligned} \quad \text{eqn 4}$$

This was but one of a wide variety of models we tested. The other dispersal kernels we fitted included the Gaussian (Clark *et al.* 1998), one-dimensional exponential (Turchin 1998), two-dimensional exponential, exponential family (Ribbens *et al.* 1994), Bessel function (Turchin 1998), full 2DT (Clark *et al.* 1999), lognormal (Greene *et al.* 2004), and Weibull functions (Tufto *et al.* 1997). Fits of dispersal kernels with more than one parameter were highly unstable for many species, with large parameter correlations, large confidence intervals on parameters, and sometimes unreasonable best-fit parameter values, and thus these models were excluded. Of the one-parameter models, the one-parameter version of the two-dimensional T distribution performed best for the most species, though no single dispersal kernel was preferred (had the highest likelihood) for all species. While estimated mean dispersal distances varied systematically with respect to dispersal kernel among the one-parameter dispersal models, interspecific patterns were consistent (that is, species that had the highest dispersal distances in one model were also highest in others, and so forth). The other fecundity models we fitted were proportional to diameter, proportional to diameter cubed, and constant. Both fitted dispersal parameters and estimated population-level seed production were relatively unaffected by the choice of fecundity model.

Parameter values and their credible intervals were estimated for each species using a Gibbs sampler with Metropolis-Hastings steps implemented in *R* 2.50 (The *R* Foundation for Statistical Computing, <www.r-project.org>). For each species, the full dispersal model and the null model were first run for 1000 iterations with adaptive changes in the step sizes of each parameter to determine the appropriate step size, and then run for three chains of 5000 iterations each with a fixed step size. The non-spatial null model assumed seed dispersal was uniform/global, and retained parameters for annual fecundities, fecundity hyperparameters, and the negative binomial clumping parameter. Species were included in the analysis of

interspecific differences in dispersal if (i) the probability distributions of the parameters converged appropriately, (ii) the deviance information criterion (DIC) calculated for the seed shadow model presented above was lower than for the corresponding null model without spatial variation in seed deposition, (iii) the final effective sample size for each parameter was above 200 after accounting for autocorrelation (Gelman *et al.* 2006), and (iv) posterior credible intervals on the fitted dispersal parameters were sufficiently narrow that the posterior median could be said to adequately represent the dispersal strategy of the species. We used the posterior median as our best estimate of each parameter, and conducted subsequent analyses that relied on single values per species based on these parameters.

We analysed interspecific variation in estimated mean seed dispersal distance (henceforth referred to as the mean dispersal distance), the mean seed production per adult basal area per year (henceforth referred to as mean fecundity), and the κ parameter of the negative binomial error distribution (henceforth referred to as the dispersion parameter). For the fitted dispersal kernel, the mean dispersal distance is calculated as $\Gamma(3/2)\Gamma(1/2)\sqrt{[\exp(\alpha)]}$ (which is approximately equal to $0.6366\sqrt{[\exp(\alpha)]}$). Note that for the dispersal kernel we use, the q th quantile of the dispersal distance distribution is calculated as $\sqrt{\{[1/(1-q)] - 1\}[\exp(\alpha)]}$, and thus all quantiles of the distribution are linearly related to the mean dispersal distance. For our fecundity model, the mean fecundity is calculated as $(\mu + 0.5\sigma^2)$ (because the annual seed production parameter β , is the log of seed production per basal area, and thus the normal hyperdistribution of this parameter translates to a lognormal distribution of seed production per basal area). Finally, smaller values of the dispersion parameter reflect more clumped distributions of seeds across trap-years relative to that expected under the best-fit seed dispersal and fecundity model, while larger values reflect greater dispersion of seeds among trap-years.

INTERSPECIFIC ANALYSES

We tested for differences in seed dispersal as captured by the estimated mean dispersal distance and the dispersion parameter κ . We analysed variation in estimated mean dispersal distance and the dispersion parameter with respect to different gross dispersal modes (abiotic vs. biotic, and wind vs. explosive vs. animal) and predominant dispersal syndromes (wind, explosive, bird and mammal) using one-way Analyses of Variance (ANOVAS) on the log-transformed mean dispersal distance.

We used linear regressions, ANOVA and ANCOVA to test for the influences of other factors within dispersal syndromes and for all species combined. Among wind-dispersed species, we tested for relationships between the log-transformed mean diaspore dispersal distance and log-transformed values of fresh diaspore mass, dry diaspore mass, diaspore terminal velocity, tree height and mean wind speed in the month of peak fruiting. We also tested the relationship of dispersal distance to an integrated measure of these predictors, specifically a crude, quasi-mechanistic estimate of predicted dispersal distance calculated as the product of the average time it is expected to take a seed to fall to the ground and the average wind speed expected to be encountered. The fall time was calculated simply as tree height divided by terminal velocity, and the average wind speed was calculated assuming a linear decrease in wind speed from the ground to the top of the canopy 40 m above-ground.

Among animal-dispersed species, we tested for relationships of dispersal distance with log-transformed fresh and dry seed mass, fresh and dry fruit mass, mature tree height, and the number of animal-dispersed species fruiting in the peak fruiting month. We then performed a multiple regression of dispersal distance on dry seed

mass, dry fruit mass, mature tree height, and number of co-fruiting species.

For all species combined, we tested the relationship of mean dispersal distance to combinations of seed mass, tree height and dispersal syndrome using linear models.

Finally, we also examined the relationship of estimated fecundity to seed mass, using type 1 and type 2 linear regression on log-transformed parameters.

Throughout, relationships with dry masses were very similar to relationships with fresh masses for the same species. Thus, because we had data on dry masses for more species, we report only relationships with dry masses in the results.

Results

Forty-four species met the convergence, effective sample size, and predicted deviance criteria for analyses, and of those 40 had reasonably narrow confidence intervals on the dispersal parameter for seed equivalent fits, and one additional species met criteria for analyses for diaspore only fits. The species that failed to meet criteria for analyses had highly significantly fewer traps hit by seeds than those that met the criteria (an average of 35 vs. 93; $F_{1,101} = 50.9$, $P < 0.0001$), but did not differ significantly in adult abundance, dispersal syndrome, or seed : fruit ratio. Mean seed equivalent dispersal distances among the 40 well-fit species varied over two orders of magnitude while mean fecundity varied over five orders of magnitude (Table 1). There was no correlation between the log of fecundity and the log of mean dispersal distance among species ($r = 0.03$, $P = 0.84$).

Of those wind-dispersed species for which separate models were fit for diaspores and for seed equivalents, three species were well-fit in both cases and did not differ significantly in parameter values, five species did not meet criteria for analyses in either case, and a single species, *Luehea seemannii*, met criteria for analyses for the diaspore fits but not for the seed equivalent fits (the data set for *Luehea* includes comparable numbers of seed equivalents from fruits as from seeds). In our interspecific analyses, we used seed equivalent fits in all cases except for the analyses of predictors of diaspore dispersal distances by wind, where we use diaspore fits.

Dispersal mode and dispersal syndrome explained very little of the interspecific variation in dispersal distances. Instead, there was wide variation in dispersal distances within each grouping, with the exception of explosive dispersal where the single fitted species exhibited very short dispersal distances (Fig. 2). ANOVAS on log-transformed mean dispersal distances found no significant difference between species dispersed by abiotic and biotic means ($F_{1,38} = 0.02$, $P = 0.89$), or between wind, explosively, and animal dispersed species ($F_{2,37} = 1.93$, $P = 0.16$). There was also no significant difference in dispersal distances between animal-dispersed species thought to be dispersed predominantly by mammals vs. those dispersed predominantly by birds ($F_{1,29} = 0.54$, $P = 0.47$).

Clumping of seed deposition did vary significantly among dispersal syndromes, with wind-dispersed species showing less clumping (Fig. 3). All the same analyses were done for this parameter as for mean dispersal distances, and in every

Table 1. Species, dispersal modes, sample sizes and fitted parameters

| Species | Dispersers | SF ratio | Rdbh (cm) | Seeds | Fruits | Traps | Adults | α | μ | σ | κ |
|--------------------------------|------------|----------|-----------|----------|--------|-------|--------|-------------------|----------------------|-------------------|----------------------|
| <i>Anacardium excelsum</i> | Mam, bat | 1 | 40 | 132 | 590 | 38 | 22 | 4.9 (4.27, 5.33) | -5.64 (-6.13, -5.07) | 0.79 (0.48, 1.28) | 0.131 (0.101, 0.174) |
| <i>Beilschmiedia pendula</i> | Mam, bird | 1 | 20 | 481 | 985 | 82 | 211 | 3.84 (3.49, 4.16) | -5.39 (-6.4, -4.45) | 1.86 (1.24, 2.93) | 0.211 (0.172, 0.261) |
| <i>Calophyllum longifolium</i> | Bat, mam | 1 | 20 | 69 | 54 | 43 | 26 | 7.06 (6.09, 8.04) | -5.69 (-6.52, -4.9) | 1.05 (0.37, 2.11) | 0.024 (0.015, 0.038) |
| <i>Chrysophyllum cainito</i> | Bird, mam | 1.5 | 20 | 878 | 139 | 92 | 19 | 5.6 (4.78, 6.15) | -3.65 (-4.63, -2.64) | 1.83 (1.25, 2.88) | 0.058 (0.047, 0.072) |
| <i>Cordia bicolor</i> | Bird, mam | 1 | 10.7 | 2 218 | 2 454 | 133 | 419 | 4.55 (4.17, 4.88) | -2.6 (-3.12, -2.04) | 1.03 (0.7, 1.59) | 0.067 (0.058, 0.076) |
| <i>Coussarea curvigemma</i> | Bird, mam | 1 | 2 | 542 | 282 | 65 | 1737 | 5.15 (4.57, 5.73) | -4.71 (-6.05, -3.56) | 2.4 (1.58, 3.77) | 0.073 (0.057, 0.093) |
| <i>Croton billbergianus</i> | Exp | 3 | 3.3 | 75 | 38 | 12 | 700 | 2.33 (1.2, 3.11) | -5.5 (-7.77, -4.13) | 2.36 (1.01, 4.72) | 0.21 (0.094, 0.478) |
| <i>Cupania rufescens</i> | Bird, mam | 2.4 | 13.3 | 38 | 0 | 22 | 7 | 6.51 (5.53, 7.45) | -3.38 (-4.46, -2.52) | 1.23 (0.55, 2.4) | 0.283 (0.073, 4.504) |
| <i>Dendropanax arboreus</i> | Bird, mam | 5.3 | 20 | 2 845 | 514 | 147 | 79 | 5.73 (5.27, 6.11) | -1.77 (-2.26, -1.23) | 0.87 (0.59, 1.35) | 0.061 (0.054, 0.068) |
| <i>Dipteryx oleifera</i> | Bat, mam | 1 | 20 | 143 | 697 | 59 | 32 | 4.74 (4.33, 5.1) | -5 (-5.44, -4.59) | 0.67 (0.39, 1.08) | 0.27 (0.208, 0.352) |
| <i>Drypetes standleyi</i> | Bat, mam | 1 | 13.3 | 340 | 297 | 49 | 241 | 4.61 (3.55, 5.34) | -5.09 (-6.36, -3.96) | 2.11 (1.34, 3.58) | 0.055 (0.039, 0.079) |
| <i>Eugenia oerstediana</i> | bird, mam | 1 | 13.3 | 1 353 | 438 | 157 | 194 | 6.85 (6.35, 7.69) | -2.53 (-3.24, -1.83) | 1.42 (1.02, 2.14) | 0.066 (0.058, 0.076) |
| <i>Guarea guidonia</i> | Mam, bird | 1 | 2.7 | 994 | 53 | 118 | 1332 | 5.33 (4.97, 5.69) | -5.46 (-6.47, -4.52) | 2.03 (1.41, 3.09) | 0.163 (0.134, 0.195) |
| <i>Guatteria dumetorum</i> | Mam, bird | 1 | 20 | 729 | 244 | 130 | 159 | 6.33 (6.09, 6.56) | -4.23 (-4.55, -3.94) | 0.56 (0.37, 0.87) | 0.204 (0.169, 0.245) |
| <i>Guapira standleyana</i> | Mam, bird | 1 | 20 | 549 | 257 | 87 | 72 | 6.47 (5.96, 6.99) | -4.86 (-5.8, -4.01) | 1.68 (1.14, 2.47) | 0.043 (0.035, 0.054) |
| <i>Gustavia superba</i> | Bird, mam | 7 | 6.7 | 109 | 63 | 33 | 761 | 2.33 (1.59, 3) | -4.9 (-5.51, -4.2) | 0.82 (0.41, 1.5) | 0.054 (0.041, 0.069) |
| <i>Hasseltia floribunda</i> | Mam, bird | 1.2 | 5.3 | 933 | 1540 | 99 | 579 | 3.48 (2.82, 3.99) | -1.96 (-2.53, -1.34) | 0.8 (0.4, 1.39) | 0.033 (0.027, 0.039) |
| <i>Heisteria concinna</i> | Bird, mam | 1 | 10 | 352 | 470 | 102 | 350 | 5.17 (4.77, 5.57) | -4.42 (-5.11, -3.75) | 1.32 (0.9, 2.1) | 0.077 (0.063, 0.095) |
| <i>Hirtella triandra</i> | Bird, mam | 1 | 5.3 | 398 | 283 | 93 | 1766 | 4.18 (3.84, 4.53) | -5.08 (-5.54, -4.64) | 0.89 (0.61, 1.34) | 0.135 (0.11, 0.166) |
| <i>Jacaranda copaia</i> | Wind | 245.4 | 20 | 89 498 | 107 | 188 | 241 | 5.59 (5.46, 5.71) | -1.63 (-3.03, -0.29) | 3 (2.18, 4.49) | 0.548 (0.517, 0.578) |
| <i>Jacaranda copaia*</i> | Wind | 245.4 | 20 | 89 498 | (107) | 188 | 241 | 5.8 (5.69, 5.92) | -1.92 (-3.34, -0.54) | 2.93 (2.11, 4.48) | 0.697 (0.656, 0.74) |
| <i>Luehea seemannii*</i> | Wind | 43.1 | 20 | 1 00 207 | (1931) | 188 | 73 | 5.67 (5.54, 5.78) | 0.06 (-0.54, 0.64) | 1.24 (0.9, 1.8) | 0.698 (0.662, 0.734) |
| <i>Oenocarpus mapora</i> | Bird, mam | 1 | 5.3 | 682 | 960 | 119 | 2102 | 3.06 (2.7, 3.39) | -3.41 (-3.75, -3.08) | 0.82 (0.56, 0.89) | 0.082 (0.07, 0.096) |
| <i>Platygodium elegans</i> | Wind | 1 | 20 | 3 | 574 | 51 | 36 | 4.96 (4.47, 5.38) | -6.17 (-7.81, -4.89) | 2.76 (1.73, 4.66) | 0.182 (0.14, 0.238) |
| <i>Platymiscium pinnatum</i> | Wind | 1 | 20 | 28 | 317 | 45 | 50 | 4.5 (3.81, 5.02) | -5.96 (-7.06, -4.98) | 1.9 (1.27, 3.14) | 0.285 (0.195, 0.414) |
| <i>Poulsenia armata</i> | Bat, mam | 1 | 20 | 222 | 47 | 46 | 293 | 5.15 (4.48, 5.72) | -5.67 (-6.34, -5.08) | 0.97 (0.51, 1.71) | 0.048 (0.034, 0.066) |
| <i>Porteria reticulata</i> | Bird, mam | 1 | 20 | 392 | 85 | 84 | 149 | 5.2 (4.44, 5.81) | -5.51 (-6.62, -4.48) | 1.94 (1.28, 3.21) | 0.048 (0.037, 0.063) |
| <i>Protium tenuifolium</i> | Bird, mam | 2.4 | 13.3 | 407 | 112 | 86 | 397 | 3.51 (2.73, 4.04) | -4.22 (-5.03, -3.36) | 1.35 (0.86, 2.27) | 0.072 (0.057, 0.091) |
| <i>Pterocarpus rohrii</i> | Wind | 1 | 20 | 1 | 75 | 12 | 41 | 5.19 (3.88, 5.92) | -5.17 (-6.51, -4.23) | 1.23 (0.51, 2.69) | 0.118 (0.057, 0.245) |
| <i>Quararibea asterolepis</i> | Mam, bat | 1.7 | 20 | 9 825 | 9473 | 176 | 594 | 4.24 (4.02, 4.48) | -3.06 (-3.65, -2.47) | 1.19 (0.87, 1.78) | 0.165 (0.152, 0.179) |
| <i>Randia armata</i> | Bird, mam | 38.6 | 3.3 | 3 311 | 46 | 151 | 786 | 4.68 (4.3, 5.1) | -1.63 (-2.02, -1.21) | 0.68 (0.35, 1.08) | 0.04 (0.035, 0.045) |
| <i>Simarouba amara</i> | Mam, bird | 4 | 20 | 390 | 138 | 84 | 210 | 6.02 (5.59, 6.44) | -5.18 (-5.99, -4.42) | 1.53 (1, 2.42) | 0.082 (0.064, 0.103) |
| <i>Tabebuia guayacan</i> | Wind | 1 | 20 | 3 093 | 7 | 79 | 25 | 4.65 (4.06, 5.13) | -4.3 (-5.75, -2.94) | 2.71 (1.83, 4.33) | 0.103 (0.086, 0.124) |
| <i>Tabebuia guayacan*</i> | Wind | 1 | 20 | 3 093 | (7) | 79 | 25 | 4.61 (4.07, 5.05) | -4.39 (-5.76, -3.09) | 2.58 (1.74, 4.14) | 0.132 (0.108, 0.161) |
| <i>Tabebuia rosea</i> | Wind | 1 | 20 | 3 122 | 2 | 158 | 45 | 6.13 (5.94, 6.3) | -1.67 (-1.88, -1.44) | 0.38 (0.27, 0.59) | 0.389 (0.347, 0.437) |
| <i>Tabebuia rosea*</i> | Wind | 1 | 20 | 3 122 | (2) | 158 | 45 | 6.3 (6.11, 6.48) | -1.79 (-2.01, -1.56) | 0.41 (0.28, 0.6) | 0.411 (0.364, 0.466) |
| <i>Terminalia amazonia</i> | Wind | 1 | 20 | 64 | 10 936 | 188 | 23 | 8.24 (8.1, 8.4) | -1.07 (-1.78, -0.42) | 1.43 (1.03, 2.1) | 0.909 (0.844, 0.98) |
| <i>Tetragastris panamensis</i> | Bird, mam | 4.7 | 20 | 2 163 | 231 | 120 | 240 | 4.6 (4.23, 4.95) | -4.46 (-5.2, -3.74) | 1.44 (1.04, 2.21) | 0.1 (0.086, 0.117) |
| <i>Trattinnickia aspera</i> | Bird, mam | 1 | 20 | 330 | 19 | 95 | 39 | 8.75 (8.12, 9.63) | -4.29 (-4.83, -3.81) | 0.84 (0.51, 1.42) | 0.09 (0.07, 0.115) |
| <i>Trichilia tuberculata</i> | Mam, bird | 1.8 | 20 | 28 347 | 5 619 | 188 | 1253 | 3.93 (3.78, 4.08) | -2.24 (-2.75, -1.74) | 1.07 (0.76, 1.54) | 0.291 (0.274, 0.307) |
| <i>Triplaris cumingiana</i> | Wind | 1 | 13.3 | 0 | 1 608 | 44 | 139 | 3.86 (3.39, 4.24) | -3.81 (-4.96, -2.75) | 2.18 (1.45, 3.4) | 0.253 (0.199, 0.324) |
| <i>Unonopsis pittieri</i> | Bird, mam | 1 | 5.3 | 71 | 309 | 31 | 401 | 2.65 (1.65, 3.37) | -4.15 (-5.03, -3.23) | 1.39 (0.82, 2.31) | 0.071 (0.045, 0.11) |
| <i>Virola sebifera</i> | Mam, bird | 1 | 13.3 | 798 | 718 | 124 | 367 | 6.09 (5.74, 6.43) | -3.83 (-4.17, -3.5) | 0.61 (0.36, 0.95) | 0.072 (0.061, 0.083) |
| <i>Zanthoxylum ekmanii</i> | Bird, mam | 1.5 | 20 | 522 | 53 | 106 | 167 | 8.4 (7.61, 9.56) | -5.71 (-6.6, -4.86) | 1.63 (1.05, 2.66) | 0.073 (0.059, 0.091) |

Dispersers gives the major classes of dispersal agents: wind, explosive dispersal (exp), birds and/or mammals (mam), with the predominant class listed first. SF ratio is the seed-to-fruit ratio, the average number of seeds per fruit. Rdbh is the minimum diameter (in cm) at which trees were considered potentially reproductive. Fruits and seeds are the total fruits and simple seeds captured in the 188 traps > 20 m from the plot edge in the 19 complete phenological years between January 1987 and January 2007. Traps are the number of those 188 traps that captured seeds and/or fruits during that period. Adults are the total number of trees that qualified as reproductive during any part of the census period. α , μ , σ and κ are the fitted parameters, with their 95% credible intervals. *Fits to seed data only; these do not include seed equivalents falling as fruits.

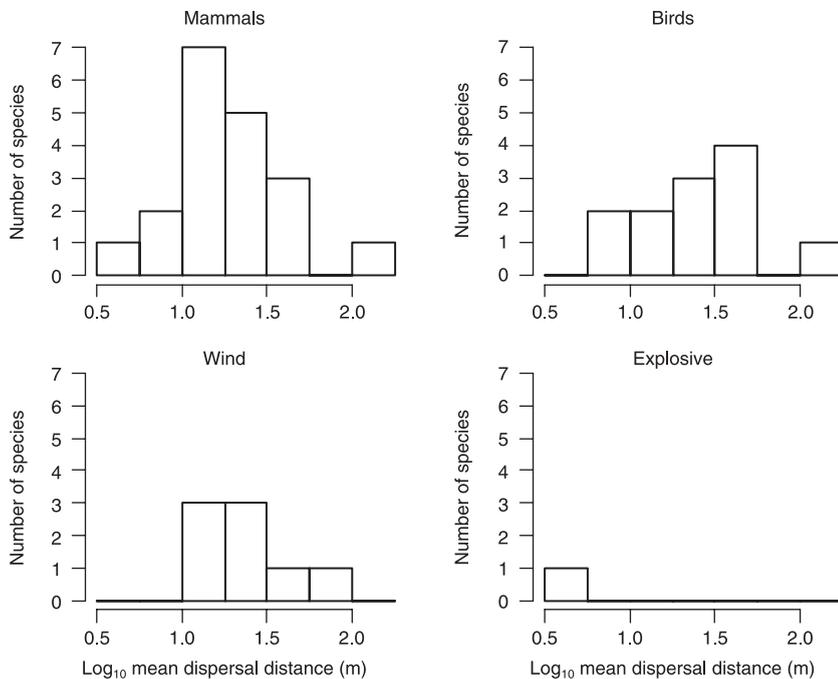


Fig. 2. Mean dispersal distances vary widely among tree species within dispersal syndromes.

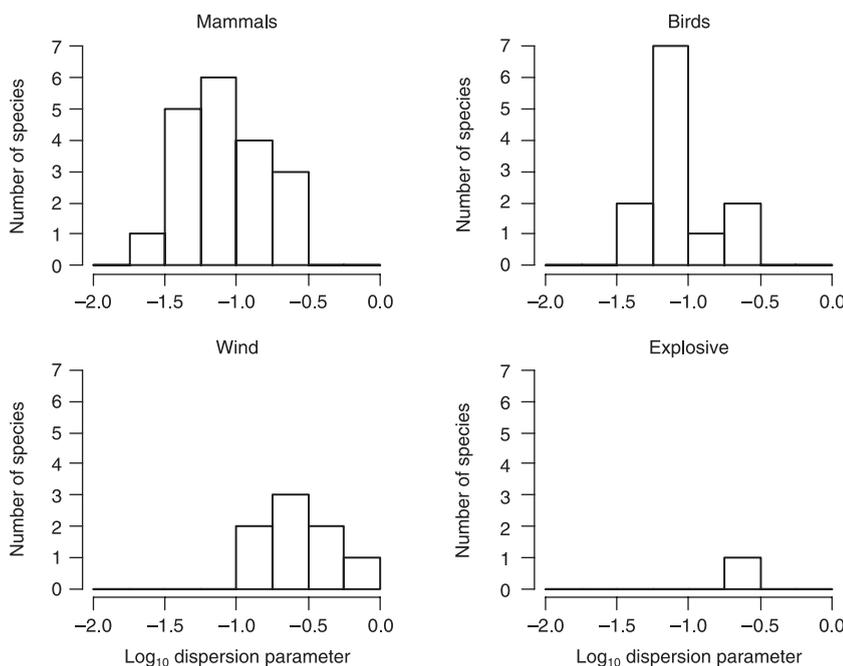


Fig. 3. The negative binomial dispersion parameter was significantly larger (reflecting less clumping) for wind-dispersed species than for animal-dispersed species.

case, the abiotically dispersed or wind-dispersed species showed significantly higher values of the dispersion parameter while there was no significant variation among the other groups (ANOVA on abiotic vs. biotic dispersal: $F_{1,38} = 21.31$, $P < 0.0001$).

Among the nine wind-dispersed species, variation in mean diaspore dispersal distance was correlated with our integrated estimate of predicted dispersal distance ($r = 0.63$, $P = 0.035$, one-tailed test). None of the individual factors alone explained significant variation in dispersal distance,

although trends were in the expected direction (Fig. 4). Dispersal distances were longer for species having lower diaspore mass ($r = -0.56$, $P = 0.11$, Fig. 4a), lower diaspore terminal velocity ($r = -0.39$, $P = 0.30$, Fig. 4b), and larger adult tree height ($r = 0.38$, $P = 0.31$, Fig. 4c). There was no trace of a relationship with wind speed in the peak fruiting month on its own ($r = 0$, $P = 0.98$, Fig. 4d). The large outlier on the left in Fig. 4e is *Pterocarpus rohrii*, which is unusual in dispersing its seeds in the rainiest part of the year when average wind speeds are lowest, thus depressing the dispersal distance expected

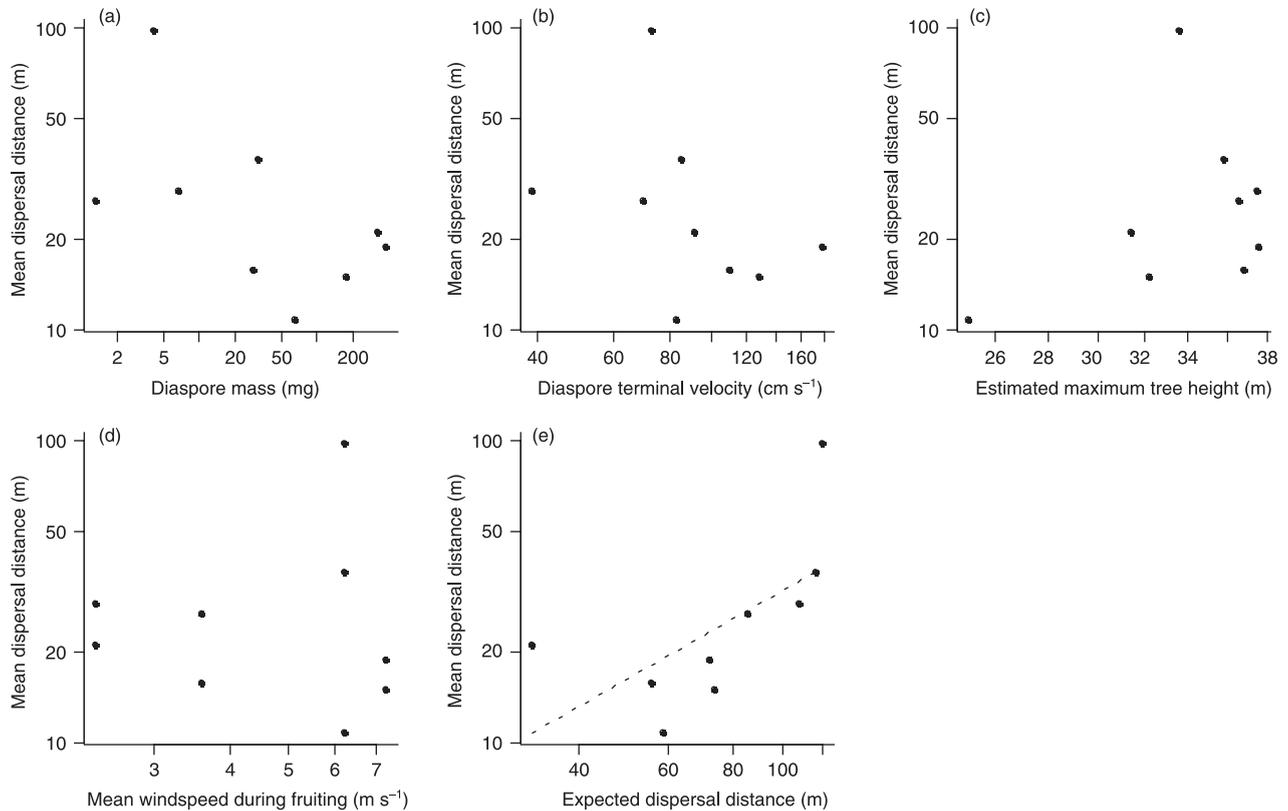


Fig. 4. Relationships with mean dispersal distance for wind-dispersed tree species. Mean dispersal distance vs. (a) diaspore mass, (b) diaspore terminal velocity, (c) estimated tree height, (d) mean wind speed in the month of peak fruiting, and (e) estimated dispersal distance taking calculated from terminal velocity, wind speed, and tree height combined. Only the last relationship is marginally significant; the line shows the fitted linear regression on log-transformed data.

based on its terminal velocity, tree height and wind speed in its fruiting season.

Among the animal-dispersed species, the factors we examined explained less of the variation among species with dispersal distances (adjusted $r^2 = 0.20$), but the higher sample sizes allowed for greater statistical confidence in the relationships – or lack thereof (Fig. 5). Mean dispersal distance increased with decreasing seed mass ($r = -0.35$, $P = 0.05$, Fig. 5a), and also tended to increase with decreasing fruit mass ($r = -0.27$, $P = 0.17$, Fig. 5b) and increasing tree height ($r = 0.30$, $P = 0.10$, Fig. 5c), but was unrelated to the number of species fruiting at the same time ($r = 0.10$, $P = 0.57$, Fig. 5d). When seed mass and tree height were included together in a multiple regression, both terms were significant ($F_{2,28} = 4.69$, $P = 0.02$). Adding fruit mass and/or the number of co-fruiting species to the regression did not improve explanatory power.

Across all species combined, dispersal distance was negatively correlated with seed mass ($r = -0.32$, $P = 0.04$) and positively correlated with tree height ($r = 0.37$, $P = 0.02$). Seed mass, tree height, and dispersal syndrome (wind, explosive, animal) together explained 28% (adjusted r^2) of the variation in dispersal distance, with the dispersal syndrome term marginally significant ($P = 0.055$) (ANCOVA $F_{4,35} = 4.712$, $P = 0.004$).

Seed production was strongly inversely related to seed mass (Fig. 6). The relationship was well-fit by a power-law (log-log

regression: $r = -0.66$, $P < 0.0001$). In the type 1 regression, the fitted exponent was -0.60 (SE 0.11) and the coefficient was 122; in the type 2 regression, the exponent was -0.89 .

Discussion

THE PREDICTABILITY AND UNPREDICTABILITY OF SEED RAIN

Tropical tree species employ a wide variety of strategies to disperse their seeds (Muller-Landau & Hardesty 2005). Thus, it is not surprising that there are major quantitative and qualitative differences in seed dispersion patterns among species. This study and others show that relatively little of this variation can be explained by dispersal syndrome alone. We found that dispersal syndrome explained significant variation in clumping of seed deposition, but not of seed dispersal distances. Similarly, Clark *et al.* (2005) found only small differences in mean dispersal distances between bird-, monkey- and wind-dispersed species in an African forest based on three species per syndrome, with much larger variation within syndromes (their Table 2). Seidler & Plotkin (2006) found significant differences in individual tree spatial patterns – which reflect both dispersal distances and clumping of seed deposition – between dispersal syndromes in an Asian forest, with

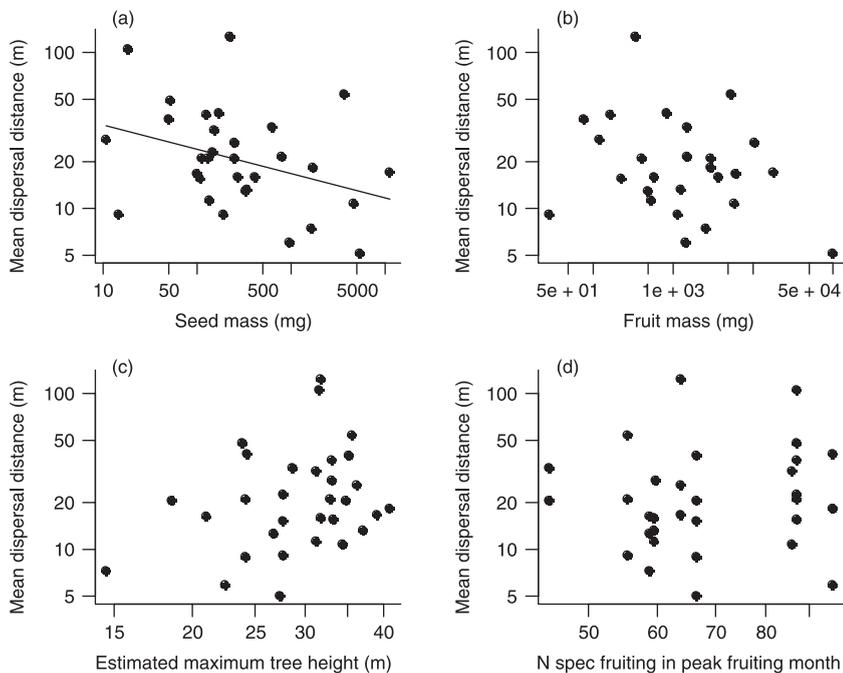


Fig. 5. Relationships with mean dispersal distance for animal-dispersed species. Mean dispersal distance vs. (a) seed mass, (b) fruit mass, (c) tree height, and (d) number of species fruiting in the peak fruiting month. The relationship with seed mass is significant; the line shows the linear regression on log-transformed data.

clumping increasing from animal to wind to gravity and ballistically dispersed species, yet the distributions of species within each syndrome showed much wider variation (their Fig. 2; note that the plotted bars are SEs of the mean). They repeated their analysis for BCI, and found qualitatively consistent patterns, albeit a statistically weaker one due at least in part to the smaller sample size or number of species (Seidler & Plotkin 2006).

Though dispersal distance alone is relatively uninformative, we found that seed mass, tree height and dispersal syndrome together explain substantial variation in dispersal distances among species. The negative effect of seed mass is easily explained for wind-dispersed species, as heavier diaspores travel shorter distances, all else equal. This result is more surprising for animal-dispersed species, especially in a forest with as diverse a community of frugivores as found here. It suggests that there are general underlying patterns relating seed mass to the likelihood of seed dispersal by different animal species moving different distances. The positive effect of tree height is again logical for wind-dispersed species. For animal-dispersed species it may reflect systematic variation in the animal species that forage at different heights in the canopy. For both wind- and animal-dispersed species, the longer mean estimated dispersal distances here no doubt also reflect at least in part the fact that taller trees tend to have broader crowns, and that our estimator measures dispersal distance as distance from the trunk of the tree (thus non-dispersed seeds would have larger 'dispersal' distances in species with broader crowns).

For wind-dispersed species, the results presented here, as well as those of other studies, demonstrate the potential predictability of their seed dispersal. Physics dictates that the distance of seed dispersal by wind is determined fundamen-

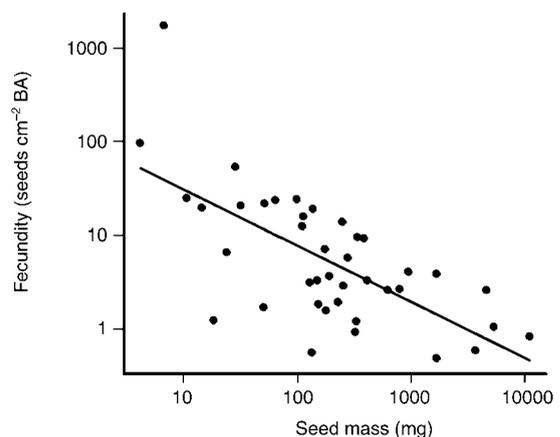


Fig. 6. Seed mass is strongly inversely related to estimated mean seed production per unit basal area among tropical tree species.

tally by the wind speed at the time of seed release, the location of the release point, and the aerodynamic characteristics of the diaspore (Greene & Johnson 1989; Okubo & Levin 1989; Nathan *et al.* 2002a). While determination of these factors is hardly trivial, given atmospheric turbulence that can lift seeds above the canopy (Nathan *et al.* 2002b) and plant characteristics that bias seed release towards higher wind speeds (Greene 2005), even simple approximations can predict the relative magnitude of ordinary dispersal (Augsburger 1986), as seen here. The development of ever-better mechanistic models of seed dispersal by wind will continue to improve our understanding of dispersal patterns in wind-dispersed plant species (Nathan *et al.* 2001; Tackenberg 2003; Soons *et al.* 2004; Bohrer *et al.* 2008; Pouden *et al.* 2008). Unfortunately, wind-dispersed species account for only a minority – typically well under 20%

– of tropical tree species (Gentry 1983; Muller-Landau & Hardesty 2005).

The tremendous variation in seed dispersal patterns among animal-dispersed species in tropical forests is ultimately related to the great diversity of animal dispersal vectors and their behaviours. We were able to explain a smaller fraction of interspecific variation in dispersal distance among animal-dispersed species, and our fitted models had lower values of the negative binomial parameter (indicating that less of the variation in seed deposition is explained by the best fit model and that there is greater variation around the expected). However, seed mass and tree height did explain substantial variation among animal-dispersed species alone, again suggesting that despite the complexity of species interactions and behaviours involved, there are underlying generalities. This complexity should not be understated – at our study site, known animal seed dispersers include 24 species of nonvolant mammals (Leigh 1999), 20 species of bats (Kalko *et al.* 1996), and 86 species of birds (Willis 1990). Within each group, species differ in their body sizes, their diets, their home ranges and many other factors. They respond differently to different fruit traits of focal species as well as to the availability of alternate food sources, and interact differently with other species as competitors, predators, and/or prey.

Finally, our results clearly show that interspecific variation in seed production is more predictable than variation in seed dispersal – as we would expect. Fundamentally, trees have limited resources to allocate towards reproduction, and those producing larger seeds must produce fewer of them. Like previous studies, we found that seed production was a power function of seed mass (Greene & Johnson 1994; Henery & Westoby 2001). Our model 2 regression slope was not significantly different from the value of -1 that would be expected under constant total biomass allocation; this accords with results for 47 Australian woody perennial species (Henery & Westoby 2001).

INTERPRETING INVERSE MODEL FITS TO SEED TRAP DATA

The information about dispersal patterns that can be provided by inverse modelling of seed densities within mapped stands depends on the spatial scales of variation in seed rain relative to the scales of the data, and on the appropriateness of model assumptions. Contrary to many statements in the literature, inverse models do *not* assume that the nearest tree is the source, and they are *not* inherently biased to shorter (or longer) dispersal distances. Inverse models are unbiased estimators of dispersal kernels even when there is extensive overlap in seed shadows, provided that the model being fit is a reasonably good representation of the underlying seed shadow (Jones & Muller-Landau 2008). In contrast, genetic estimates of dispersal distances of particular seeds do not in and of themselves provide a better estimate of the dispersal distance distribution; indeed, seed sampling strategies for genetic data can easily produce biases towards under- or over-estimation of dispersal distances, and the best estimates

of dispersal distances are achieved by combining genetic data and inverse modelling techniques (Jones & Muller-Landau 2008). That said, inverse modelling techniques cannot glean meaningful information about dispersal from every seemingly appropriate data set. In particular, the information on seed production as a function of tree size and seed arrival as a function of distance from source tree that can be gleaned from a seed trap data set is limited by the amount of independent variation among traps in the numbers of source trees of a given size and distance away. Further, even given a potentially informative data set, the insight provided by inverse modelling depends, as in any statistical analysis, on the appropriateness of model assumptions. As with many complex models, spotting violations or problems with the assumptions can be challenging; examination of residuals with respect to distance to and size of the nearest tree, and comparisons with patterns expected under simulated data sets, can help in this respect.

So how good are our assumptions? Clearly our fitted seed shadow model is a simplified caricature of real seed dispersal in many respects. The probability of seed arrival in the model depends only on distance from the source tree, not on direction as it clearly does for wind-dispersed species in reality (Tufto *et al.* 1997; Nathan *et al.* 2002a), or on the characteristics of the habitat along the path from the source (Schurr *et al.* 2008). The shape of the dispersal kernel is fixed at one particular form – a one-parameter version of the student's *T* distribution – for the purposes of making comparisons of the scale of dispersal among species, even though species undoubtedly differ in the shapes of their dispersal kernels (Clark *et al.* 2005). Though taller trees are likely to disperse seed farther by wind, trees with larger fruit crops may attract more or different animal seed dispersers (Howe & Manasse 1983), and seed dispersal kernels may vary among years (Nathan & Muller-Landau 2000), we fitted a single dispersal kernel to all trees of a species in all years. The large-scale clumping caused by many animal seed dispersers due to their repeated use of particular sites for sleeping or travelling, the tendency in some species for multiple individual seeds to move together, and discrete defecation and regurgitation events can be captured in our model only by the negative binomial dispersion parameter (Morales & Ellner 2002; Westcott *et al.* 2005; Russo *et al.* 2006). Variation in fecundity among trees is represented only in terms of proportionality with basal area, and seed production per basal area is assumed to vary in parallel among all trees.

Given all these problematic assumptions, what can our analyses really tell us about seed dispersal in tropical forests? Despite their shortcomings, our fitted models explain an average of 20% of the variation among traps in seed rain (and 22% of the variation among trap-years) within each species. Like a first set of linear fits to a more complex relationship between variables, our models capture a substantial first outline of the seed dispersal pattern of these species, offer a small window into interspecific variation in seed dispersal, and provide an initial basis for predicting spatial variation in seed rain in this site (Dalling *et al.* 2002). Additional data and analyses will in time provide a fuller picture, and thereby no doubt reveal additional similarities and differences among

species in dispersal patterns. However, we believe that the initial general view, however fuzzy, provided by our results will be reinforced by later studies.

One way in which our fits represent advances over many past inverse models of seed dispersal is their accounting for seed rain from outside the plot. Though the mapped area of potential reproductive adult trees employed for this study is very large (1×0.5 km), we know that some seeds and fruits are arriving from trees outside the mapped area (Wehncke *et al.* 2003; Jones *et al.* 2005; Hardesty *et al.* 2006). We account for such arrival in our estimation by numerically integrating potential seed rain from off the plot, assuming the average density of source trees off the plot is equal to that on the plot. This constrains the total size of the tails of the fitted seed dispersal kernels, because any large exports of seeds from the plot through long-distance dispersal would be balanced by comparable imports – and the latter contribute to expected seed rain into our traps. If data that include seeds arriving from off plot are fitted with models that do not consider seed arrival from off plot, the resulting best-fit models are biased towards higher fecundity and fat tails – that is, lots of phantom seeds produced on the plot and disappearing off the plot where there were no seed traps to constrain their abundances (Jones & Muller-Landau 2008). Similarly biased estimates are also observed if trees on the edge of the plot are excluded as potential sources, with higher biases in species that disperse seeds longer distances (Clark *et al.* 1998). As a result, we highly recommend accounting for off plot seed rain whenever there is good reason to believe seeds are arriving onto the plot from outside it, and seeds from off the plot cannot be clearly identified as such (e.g. via genetic methods).

As with any study restricted to data on seed rain into above-ground seed traps, the results here provide information on primary seed dispersal but shed no light on secondary dispersal after seeds reach the ground. Secondary dispersal by scatter-hoarding rodents, especially agoutis, is known to be important for large-seeded neotropical tree species (Forget 1992; Jansen *et al.* 2004). Ants and dung beetles may also secondarily disperse small seeds (Byrne & Levey 1993; Andresen 2001). This secondary dispersal can be critical in reducing local seed densities and carrying seeds to safe sites for survival and germination. In the case of secondary dispersal by rodents, it may also substantially increase seed dispersal distances – agoutis have been recorded caching seeds as far as 160 m from their original source (Jansen *et al.* 2004). One of our species, *Prioria copaifera*, appears to experience virtually no primary dispersal at all in our site, but is known to be secondarily dispersed by agoutis on BCI as well as by water in seasonally flooded forests elsewhere in Panama (Lopez & Kursar 2003). We expect that total dispersal distances are substantially larger than our estimated primary dispersal distances in this species as well as in *D. oleifera*, *Attalea butyracea*, and several other large-seed species that did not meet criteria for analysis here. This suggests that the relationship of seed mass with total dispersal distance among animal-dispersed species is likely to be less negative than the relationship with primary dispersal distance.

Based on the results of extensive field trials, we are confident that any seed removal from traps is too small to affect our results. These trials were motivated by our own concerns as well as isolated observations of seeds or fruits being removed from seed traps by squirrels (J. Giacalone, personal communication) or coatis (K. Milton, personal communication). We added marked fruits or seeds of a given species to 40 traps at a time, and monitored their removal, focusing especially on large-seeded species known to be attractive to squirrels. We found that removal rates from the traps used in this study are zero in 36 of 38 species tested; in the remaining two species, *Attalea butyracea* and *D. panamensis*, removal was < 25%. Interestingly, removal rates were much higher from smaller sized seed traps (0.25 m^2) being employed for another study at the same site (DeSteven & Wright 2002), which may account for the occasional observations of animals in traps. Removal rates from 0.5 m^2 traps were also much larger at a parallel study in tropical forest in Pasoh, Malaysia, suggesting that such trials should always be conducted at every study site where seed traps are used to assess seed production and primary seed dispersal.

CONCLUSIONS AND FUTURE DIRECTIONS

Our results on seed dispersal distances for 41 tropical tree species demonstrate that a substantial proportion of interspecific variation in seed dispersal patterns in tropical forests can be explained by plant functional traits. Overall, seed mass, dispersal syndrome, and other relatively easily measured traits predict 20–40% of the tremendous interspecific variation in estimated mean seed dispersal distances and clumping. This suggests that even in diverse ecosystems and even where there are complex webs of species interactions involved (as for seed dispersal), plant traits can provide the basis for useful generalizations. This is an important result, especially given the many attempts to model the dynamics of these forests (Chave 1999), and empirical evidence for strong seed limitation that suggests that such models cannot ignore the limited nature of seed dispersal (Hubbell *et al.* 1999; Wright *et al.* 2005b).

There is considerable room for improvement in phenomenological models of seed dispersal fitted through inverse modelling to data sets such as ours, and improved models as well as the collection of auxiliary data will make it possible to extract more information about individual species' dispersal patterns. One of the most obvious failings of current models is their treatment of trees as point sources of seeds, when in fact the entire crown area is generally the source and is often of significant size relative to the scale of seed dispersal. Some of the decrease in seed arrival probability with distance from tree in existing models is thus simply the decrease in the probability of being directly under the crown – a factor that likely also explains some of the increase in dispersal distance for taller (and larger-crowned) species. Future models should explicitly treat trees as area sources, and ideally incorporate data on crown areas and locations. Existing models also vary expected seed rain based only on distance to and size of

source trees, when we know that the local vegetation also affects the probability of seed deposition through its influences on atmospheric turbulence and animal movement. This is observed in data sets such as ours where particular traps have, for example, positive residuals for wind-dispersed species in general. Fitting models with trap-specific deposition probabilities to data sets for multiple species at once could begin to capture these influences, as could the incorporation of additional data on trap site conditions.

Mechanistic models of seed dispersal are an alternative approach with considerable promise. Such models have already had considerable success in explaining patterns of seed dispersal by wind (Nathan *et al.* 2001; Nathan *et al.* 2002b; Tackenberg 2003; Soons *et al.* 2004). Though they are often very complex, in the best case scenario such models require no fitting to the data, but instead are based on independently measured parameters such as diaspore terminal velocities and wind fields (Nathan *et al.* 2002a). The application of such models to tropical forests will increase our understanding of dispersal patterns in the substantial minority of tropical tree and liana species that are wind-dispersed.

Can we ever hope to have similarly successful mechanistic models for seed dispersal by animals? Simple models based on animal movement distances and gut passage times have provided some insight (Murray 1988; Sun *et al.* 1997; Wenny & Levey 1998). Technical advances make it ever easier to document spatial and temporal patterns of animal movement (Nathan 2006). Increased computing power has enabled the development and application of ever more sophisticated models of animal behaviour and movement (Moorcroft *et al.* 1999; Morales *et al.* 2005). These are likely to be increasingly able to predict seed dispersal patterns of particular plant species by particular animal species from the spatial patterns of fruiting trees (Morales & Carlo 2006; Russo *et al.* 2006). However, the total seed shadow of a plant species is the sum of the deposition patterns of all animals that disperse its fruits. Thus, to capture this seed shadow, we need to also be able to predict the proportions of seed crops taken by each of potentially scores of consumer species, each with potentially distinct food preferences, behaviours, etc. Mechanistic models of seed dispersal by wind can relatively easily substitute the characteristics of one plant species for another in the same models of complex wind fields, so increased plant diversity brings no increase in model complexity, merely a linear increase in computation time. In contrast, models of seed dispersal by animals must deal with interactions among species and thus model complexity increases with the square of the number of interacting species – not only of dispersers, but of alternative food sources, etc. Thus, such models may be more feasible to construct where the number of interacting species that must be considered remains small.

Alternatively, research on seed dispersal by animals in diverse communities may move forward by identifying key seed disperser species for particular plant species – dispersers that are responsible for all or virtually all of the dispersal events that result in successful recruitment events. Many consumers of fruit may serve not as mutualists but as ‘fruit

thieves’, gaining food yet depositing seeds in locations that provide little or no hope for successful seedling establishment (Howe & Westley 1988). For the purposes of modelling the contributions of dispersal patterns to plant population dynamics, these dispersal events and the dispersers that are responsible for them can be ignored. Unfortunately, collecting the necessary information on seed fate to make such determinations is hardly a trivial task either. One way or another, the development of a better understanding of seed dispersal patterns in tropical forests will continue to occupy many tropical ecologists and modellers for many years into the future.

Acknowledgements

We gratefully acknowledge financial support from HSBC's Climate Partnership, a Packard Fellowship in Science and Engineering (to H.C.M.), the Smithsonian Tropical Research Institute, the National Science Foundation (DEB 043665, 0453445, and 0614055), the University of Minnesota, the National Center for Ecological Analysis and Synthesis, and Princeton University. The Minnesota Supercomputing Institute provided computing resources and support. We thank the many colleagues who provided constructive comments including Simon Levin, Steve Pacala, Henry Horn, Ran Nathan, Jérôme Chave, Bert Leigh, Ben Bolker, Jonathan Dushoff, Joshua Plotkin, and Jim Clark, and the many technicians, botanists, and data base managers of the BCI Forest Dynamics Plot who collected the tree census data that made this study possible.

References

- Andresen, E. (2001) Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. *Journal of Tropical Ecology*, **17**, 61–78.
- Augsburger, C.K. (1986) Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany*, **73**, 353–363.
- Bell, T., Freckleton, R.P. & Lewis, O.T. (2006) Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters*, **9**, 569–574.
- Bohman, S.A. & O'Brien, S.T. (2006) Allometry, adult stature and regeneration requirements of 65 tree species on Barro Colorado Island, Panama. *Journal of Tropical Ecology*, **22**, 123–136.
- Bohrer, G., Katul, G.G., Nathan, R., Walko, R.L. & Avissar, R. (2008) Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. *Journal of Ecology*, **96**, 569–580.
- Bullock, J.M., Shea, K. & Skarpaas, O. (2006) Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology*, **186**, 217–234.
- Byrne, M.M. & Levey, D.J. (1993) Removal of seeds from frugivore defecations by ants in a Costa Rican rain forest. *Vegetatio*, **107/108**, 363–374.
- Chave, J. (1999) Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecological Modelling*, **124**, 233–254.
- Clark, J.S. (2007) *Models for Ecological Data: An Introduction*. Princeton University Press, Princeton.
- 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. & HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.
- Clark, J.S., LaDeau, S. & Ibanez, I. (2004) Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs*, **74**, 415–442.
- Clark, C.J., Poulsen, J.R., Bolker, B.M., Connor, E.F. & Parker, V.T. (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, **86**, 2684–2694.
- Condit, R. (1998) *Tropical Forest Census Plots*. Springer-Verlag, Berlin, and R. G. Landes Company, Georgetown, TX, USA.
- Croat, T.B. (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford, CA.
- Dalling, J.W., Swaine, M.D. & Garwood, N.C. (1998) Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology*, **79**, 564–578.

- Dalling, J.W., Muller-Landau, H.C., Wright, S.J. & Hubbell, S.P. (2002) Role of dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology*, **90**, 714–727.
- Daws, M.I., Garwood, N.C. & Pritchard, H.W. (2005) Traits of recalcitrant seeds in a semi-deciduous tropical forest in Panamá: some ecological implications. *Functional Ecology*, **19**, 874–885.
- DeSteven, D. & Wright, S.J. (2002) Consequences of variable reproduction for seedling recruitment in three neotropical tree species. *Ecology*, **83**, 2315–2327.
- Forget, P.-M. (1992) Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica*, **24**, 408–414.
- Garwood, N.C. (1983) Seed germination in a seasonal tropical forest in Panamá: a community study. *Ecological Monographs*, **53**, 159–181.
- Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (2006) *Bayesian Data Analysis*. Chapman and Hall, London.
- Gentry, A.H. (1983) Dispersal ecology and diversity in neotropical forest communities. *Dispersal and Distribution: An International Symposium* (ed. K. Kubitzki), Paul Parey, Hamburg.
- Greene, D.F. (2005) The role of abscission in long-distance seed dispersal by the wind. *Ecology*, **86**, 3105–3110.
- Greene, D.F. & Johnson, E.A. (1989) A model of wind dispersal of winged or plumed seeds. *Ecology*, **70**, 339–347.
- Greene, D.F. & Johnson, E.A. (1994) Estimating the mean annual seed production of trees. *Ecology*, **75**, 642–647.
- 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.
- Grubb, P.J. (1998) Seeds and fruits of tropical rainforest plants: interpretation of the range in seed size, degree of defence and flesh/seed quotients. *Dynamics of Tropical Communities* (eds D.M. Newbery, H.H.T. Prins & N.D. Brown), pp. 1–24. Blackwell Scientific, Oxford.
- Handley, J., Charles O., Wilson, D.E. & Gardner, A.L. eds (1991) *Demography and Natural History of the Common Fruit Bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panamá*. Smithsonian Institution, Washington D.C.
- Hardesty, B.D., Hubbell, S.P. & Bermingham, E. (2006) Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecology Letters*, **9**, 516–525.
- Harms, K.E., Wright, S.J., Calderón, O., Hernández, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, **404**, 493–495.
- Henery, M.L. & Westoby, M. (2001) Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos*, **92**, 479–490.
- Hilborn, R. & Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, NJ.
- Howe, H.F. (1989) Scatter and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia*, **79**, 417–426.
- Howe, H.F. (1993) Aspects of variation in a neotropical seed dispersal system. *Vegetatio*, **107/108**, 149–162.
- Howe, H.F. & Manasse, R.S. (1983) Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia*, **59**, 185–190.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.
- Howe, H.F. & Westley, L.C. (1988) *Ecological Relationships of Plants and Animals*. Oxford University Press, New York.
- Hubbell, S.P. & Foster, R.B. (1983) Diversity of canopy trees in a neotropical forest and implications for conservation. *Tropical Rain Forest: Ecology and Management* (eds S.L. Sutton, T.C. Whitmore, & A.C. Chadwick), pp. 25–41. Blackwell Scientific Publications, Oxford.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & Loo de Lao, S. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **283**, 554–557.
- Jansen, P.A., Bongers, F. & Hemerik, L. (2004) Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs*, **74**, 569–589.
- Janson, C.H. (1983) Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science*, **219**, 187–189.
- Jones, F.A. & Muller-Landau, H.C. (2008) Measuring long distance seed dispersal in complex natural environments: evaluation and integration of the contributions of classical and genetic methods. *Journal of Ecology*, in press.
- Jones, F.A., Chen, J., Weng, G.-J. & Hubbell, S.P. (2005) A genetic evaluation of seed dispersal in the Neotropical tree *Jacaranda copaia* (Bignoniaceae). *American Naturalist*, **166**, 543–555.
- Kalko, E.K.V., Handley, Jr., C.O. & Handley, D. (1996) Organization, diversity, and long-term dynamics of a neotropical bat community. *Long-Term Studies of Vertebrate Communities* (eds M.L. Cody & J.A. Smallwood), pp. 503–553. Academic Press, San Diego.
- Kitajima, K. (1992) *The importance of cotyledon functional morphology and patterns of seed reserve utilization for the physiological ecology of neotropical tree seedlings*. PhD. University of Illinois at Urbana-Champaign.
- Leigh, E.G. Jr. (1999) *Tropical Forest Ecology: A View from Barro Colorado Island*. Oxford University Press, Oxford.
- Leigh, J., Egbert, G., Rand, S. & Windsor, D.M. eds (1996) *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes*, 2nd edn. Smithsonian Institution Press, Washington, DC.
- Levey, D.J., Moermond, T.C. & Denslow, J.S. (1994) Frugivory: an overview. *La Selva: Ecology and Natural History of a Tropical Rain Forest* (eds L.A. McDade, K.S. Bawa, H.A. Hespenheide & G.S. Hartshorn), pp. 282–294. University of Chicago Press, Chicago.
- Lopez, O.R. & Kursar, T.A. (2003) Does flood tolerance explain tree distribution in seasonally flooded forests? *Oecologia*, **132**, 193–204.
- Moorcroft, P.R., Lewis, M.A. & Crabtree, R.L. (1999) Home range analysis using a mechanistic home range model. *Ecology*, **80**, 1656–1665.
- Morales, J.M. & Carlo, T.S. (2006) The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology*, **87**, 1489–1496.
- Morales, J.M. & Ellner, S.P. (2002) Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology*, **83**, 2240–2247.
- Morales, J.M., Fortin, D., Frair, J.L. & Merrill, E.H. (2005) Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecology*, **20**, 301–316.
- Muller-Landau, H.C. & Hardesty, B.D. (2005) Seed dispersal of woody plants in tropical forests: concepts, examples, and future directions. *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity* (eds D. Burslem, M. Pinard & S. Hartley), pp. 267–309. Cambridge University Press, Cambridge.
- Murray, K.G. (1988) Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs*, **58**, 271–298.
- Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.
- 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.
- Nathan, R., Safriel, U.N., Noy-Meir, I. & Schiller, G. (1999) Seed release without fire in *Pinus halepensis*, a Mediterranean serotinous wind-dispersed tree. *Journal of Ecology*, **87**, 659–669.
- Nathan, R., Safriel, U.N. & Noy-Meir, I. (2001) Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. *Ecology*, **82**, 374–388.
- Nathan, R., Horn, H.S., Chave, J. & Levin, S.A. (2002a) Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 69–82. CABI International, Oxfordshire, UK.
- Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., Pacala, S.W. & Levin, S.A. (2002b) Mechanisms of long-distance dispersal of seeds by wind. *Nature*, **418**, 409–413.
- O'Brien, S.T., Hubbell, S.P., Spiro, P., Condit, R. & Foster, R.B. (1995) Diameter, height, crown, and age relationships in eight Neotropical tree species. *Ecology*, **76**, 1926–1939.
- Okubo, A. & Levin, S.A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology*, **70**, 329–338.
- Paton, S. (2007) (2006) Meteorological and Hydrological Summary for Barro Colorado Island. Smithsonian Tropical Research Institute.
- Piperno, D.R., Bush, M.B. & Colinvaux, P.A. (1990) Paleoenvironments and Human Occupation in Late-Glacial Panama. *Quarterly Research*, **33**, 108–116.
- Pounden, E., Greene, D.F., Quesada, M. & Contreras Sánchez, J.M. (2008) The effect of collisions with vegetation elements on the dispersal of winged and plumed seeds. *Journal of Ecology*, **96**, 591–598.
- Ribbens, E., Silander, Jr., J.A. & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.
- Russo, S.E. (2005) Linking seed fate to natural dispersal patterns: factors affecting predation and scatter-hoarding of *Viola calophylla* seeds in Peru. *Journal of Tropical Ecology*, **21**, 243–253.
- Russo, S.E., Portnoy, S. & Augspurger, C.K. (2006) Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology*, **87**, 3160–3174.
- van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, **24**, 353–377.
- Schurr, F.M., Steinitz, O. & Nathan, R. (2008) Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology*, **96**, 628–641.

- Seidler, T.G. & Plotkin, J.B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, **4**, e344.
- Soons, M.B., Heil, G.W., Nathan, R. & Katul, G.G. (2004) Determinants of long-distance seed dispersal by wind in grasslands. *Ecology*, **85**, 3056–3068.
- Sun, C., Ives, A.R., Krauter, H.J. & Moermond, T.C. (1997) Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia*, **112**, 94–103.
- Svenning, J.C. (2001) On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). *Botanical Review*, **67**, 1–53.
- Tackenberg, O. (2003) Modeling long-distance dispersal of plant diaspores by wind. *Ecological Monographs*, **73**, 173–189.
- Tewksbury, J.J. & Nabhan, G.P. (2001) Seed dispersal – Directed deterrence by capsaicin in chillies. *Nature*, **412**, 403–404.
- Tufto, J., Engen, S. & Hindar, K. (1997) Stochastic dispersal processes in plant populations. *Theoretical Population Biology*, **52**, 16–26.
- Turchin, P. (1998) *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer, Sunderland, Massachusetts.
- Vander Wall, S.B. (1994) Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. *Ecology*, **75**, 1911–1926.
- Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology and Evolution*, **17**, 379–385.
- Wehncke, E.V., Hubbell, S.P., Foster, R.B. & Dalling, J.W. (2003) Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species. *Journal of Ecology*, **91**, 677–685.
- Wenny, D.G. (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs*, **70**, 331–351.
- Wenny, D.G. & Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of USA*, **95**, 6204–6207.
- Westcott, D.A., Bentrupperbaumer, J., Bradford, M.G. & McKeown, A. (2005) Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**, 57–67.
- Willis, E.O. (1990) Ecological roles of migratory and resident birds on Barro Colorado Island, Panama. *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (eds A. Keast & E.S. Morton), pp. 205–225. Smithsonian Institution Press, Washington, DC.
- Willson, M.F. (1993) Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*, **107/108**, 261–280.
- Wright, S.J. & Calderón, O. (1995) Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology*, **83**, 937–948.
- Wright, S.J., Gompper, M.E. & Deleon, B. (1994) Are large predators keystone species in Neotropical forests – the evidence from Barro-Colorado Island. *Oikos*, **71**, 279–294.
- Wright, S.J., Carrasco, C., Calderón, O. & Paton, S. (1999) The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest. *Ecology*, **80**, 1632–1647.
- Wright, S.J., Zeballos, H., Dominguez, I., Gallardo, M.M., Moreno, M.C. & Ibanez, R. (2000) Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology*, **14**, 227–239.
- Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S.P. & Foster, R.B. (2005a) Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology*, **21**, 307–315.
- Wright, S.J., Muller-Landau, H.C., Calderón, O. & Hernández, A. (2005b) Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest. *Ecology*, **86**, 848–860.
- Yavitt, J.B. (2000) Nutrient dynamics of soil derived from different parent materials on Barro Colorado Island, Panama. *Biotropica*, **32**, 198–207.
- Zimmerman, J.K., Wright, S.J., Calderón, O., Aponte Pagan, M. & Paton, S. (2007) Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of irradiance. *Journal of Tropical Ecology*, **23**, 231–251.

Received 3 August 2007; accepted 14 April 2008

Handling Editor: James Bullock