CASE REPORT

High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications

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Abstract

Dispersal limitation may promote high tree-species diversity in rain forest by slowing local competitive exclusion, but evidence is scarce. By comparing the species lists of tree plots with those of nested seedling plots in rain forest at Gunung Palung, we found that the proportion of local seedlings arising from active dispersal events (via wind or animals, but not simply dropped from parent trees) was high: 68% of species and 46% of the individual seedlings. Local seedling species richness was not limited by the local richness of adults. Using these data, a spatially explicit simulation model indicated that dispersal limitation may not contribute substantially to the maintenance of tree diversity in this forest. We predict that the loss of animal seed dispersers would reduce local species richness of seedlings by 60%. While this reduction could possibly increase the influence of dispersal limitation, it would interfere with other mechanisms maintaining diversity.

INTRODUCTION

Information on rates and spatial patterns of seed dispersal is increasingly recognized as important for understanding the maintenance of species diversity in plant communities (e.g. Tilman 1994; Hurtt & Pacala 1995; Clark *et al*. 1999; Hubbell *et al*. 1999; Harms *et al*. 2000). By moving seeds away from parent-associated pathogens and insect herbivores, and by decreasing conspecific seed and seedling density, dispersal can benefit individual plants and promote species diversity (Janzen 1970; Connell 1971). The action of dispersal in mixing juveniles of many species and forming diverse local assemblages of seedlings may also increase seedling survival, via diversity dependent effects (Wills *et al*. 1997; but see Wright 1999). However, an alternative, contrary hypothesis is that high tree species diversity is promoted when seed dispersal is limited. Limited dispersal can slow the rise of dominance of superior competitors, who simply fail to arrive in many locations, so that inferior competitors "win by default" (Tilman 1994; Hurtt & Pacala 1995; Hubbell *et al*. 1999; Tilman 1999). Note that we refer in this paper to "dispersal limitation" on a local scale (10–100 m); Hubbell (1997, 2001) describes the consequences of dispersal limitation among communities, on the larger scale of the metacommunity.

Determining empirically the interaction of seed dispersal with distance, density and diversity dependence will depend in part upon quantifying overall rates of dispersal. Unfortunately, dispersal events, especially those involving animal vectors, are usually difficult to observe directly. Progress has been made in modelling dispersal-distance distribution curves (Ribbens *et al*. 1994; Clark *et al*. 1999), but large numbers of seedlings are required for each species, so assessing dispersal of rare species (the majority of species in species-rich communities) is difficult.

Here, we take an alternative, simpler approach to estimating community-wide seed dispersal rates. By comparing comprehensive species lists of tree communities surrounding seedling sample plots in rain forest, we determine the proportion of species of seedlings in local areas that must have arrived via active dispersal (by wind or animals) vs. those that could have originated from seeds dropping directly from the crowns of parent trees. We then model community dynamics to assess whether the observed dispersal rate is consistent with dispersal limitation being important for the maintenance of species diversity in this community.

STUDY AREA AND METHODS

If we (i) estimate the radius, r, beyond which seeds are very unlikely to fall, nondispersed, from a tree crown (ii) inventory all seedlings in a sample area, and (iii) inventory all possible adult (reproductive) trees within distance r of the

sample area, then seedlings of species that are not represented in the list of adults must have been "actively" dispersed in from outside. This estimate of dispersal (percentage of total seedlings from seeds that were actively dispersed), though not directly based on counts of dispersed seeds, does measure the incidence of active dispersal from parent to established seedling. The individual plant that is successful in reaching the canopy after the death of a tree generally arises from the pool of locally available seedlings (Uhl *et al.* 1988; Connell 1989; Hubbell *et al.* 1999). Hence, for the purpose of evaluating the implications of seed dispersal for eventual tree recruitment, this estimate may be more appropriate than one derived from seed rain data. It may also be more accurate than an estimate from seed rain data, because (i) intra- and interannual variation in seed fall will be "smoothed" over time in the formation of the seedling community, and (ii) strong distance and/or density dependent mortality of seeds or very young seedlings (Augspurger 1992; Blundell & Peart 1998) may alter the spatial distribution of establishing seedlings after seed fall.

We used species composition data from 28 tree plots (40 m × 40 m) and nested seedling plots (6 m × 8 m) in mixed dipterocarp rain forest at the Gunung Palung National Park (Indonesian Borneo), arranged in a stratified random pattern, and distributed over an area of 150 ha (Webb & Peart 1999, 2000). All trees (≥ 10 cm diameter at breast height (d.b.h.)) and seedlings (5–50 cm tall) in their respective plots were identified and the trees were measured for diameter. The location of a tree was noted as being either in the central 20 m × 20 m square or in the outer part of the 40 m × 40 m plot (Fig. 1). Note that with *c.* 1 cm/year growth rates (C. O. Webb, unpub. data), 50 cm seedlings could be 50 years old.
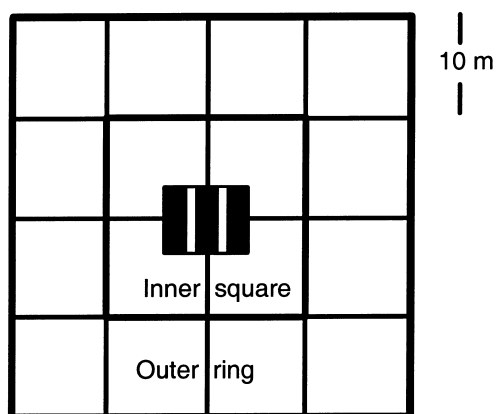

Figure 1 A 6 m × 8 m seedling plot (solid black) nested within a 40 m × 40 m tree plot, with inner, 20 m × 20 m square. Within the seedling plot, two "walkways" of 6 m × 1 m were included, which were not sampled for seedlings; seedling plot area was therefore 36 m².

We refer to "active dispersal" as the movement of a seed away from a parent by a vector, either wind or animal, or by an intrinsic explosive mechanism. A proportion of a tree's seed crop generally fails to be actively dispersed, but simply falls to the ground, referred to here as "dropped" (Chapman & Chapman 1996). However, not all the trees in the tree plot could have been "passive parents" (from which nondispersed seeds dropped and germinated) to seedlings in the central plot: some trees were too short and too far away for falling fruits to reach the seedling plot, and/or were too young to be reproductive. We eliminated these trees using estimates of seed shadows for dropped seeds, and reproductive phenology data.

We assessed the maximum "dropping" distance by examining the spatial distribution on the ground of fruits and seeds that are almost fully developed, but unripe. In most species, the mechanisms of active dispersal (e.g. attractive flesh or dry wings) only become functional in the fully mature state of the fruit. In a separate study of 33 fruiting trees (of 25 species, and a range of diameters and dispersal syndromes), we observed that no unripe (and therefore nondispersed) fruit from trees of ≤ 20 cm diameter fell farther than 6 m from the tree bole (C. O. Webb, unpublished data). We were therefore able to eliminate trees of ≤ 20 cm d.b.h. in the outer "ring" (Fig. 1) as potential parents of seedlings via passive seed dispersal, because the minimum distance from a tree in the outer ring to a seedling in the seedling plot was 6 m. From the relationship between maximum distance from bole to "dropped" fruits and tree diameter (derived using a linear fit to the outside of the envelope of 33 points), we estimated that trees outside the 40 m × 40 m tree plot could have dropped fruit into the seedling plot only if they were larger than 80 cm d.b.h. However, because of the low density (mean: 11.1 trees ha⁻¹; range: 6.2–31.3) of trees ≥ 80 cm d.b.h., there would on average be only 1.8 stems (between 80 cm and the maximum recorded size of 152 cm d.b.h.) outside the plot large enough and close enough to drop fruit into the seedling plot. Hence, a maximum of 1.8 species of seedling that we classed as dispersed could actually have been dropped.

From 2- to 3-monthly phenological surveys of every tree in the tree plots, conducted over 19 months (Webb 1997), we observed the minimum diameter of reproductive trees for 223 of the 325 species. The median value of the ratio of the minimum fertile diameter to the largest recorded diameter for that species was 63%; we used this median relative size at first (observed) reproduction to estimate the minimum reproductive diameter for those species that did not reproduce during the study. From the observed and inferred minimum reproductive diameters, we estimated that 2147 trees out of a total of 2807 identified trees (in 4.48 ha of plots) could possibly have been reproductive.

Then, combining these estimates of maximum distance travelled by dropped seeds and minimum reproductive diameters, we calculated that 1305 trees out of 2807 trees in the tree plots could possibly have been parents of seedlings via passive seed dropping. This list of trees was compared with the list of seedlings (5–50 cm) in each plot to determine the proportions of species and individuals in seedling plots that must have arrived via active dispersal.

There are two reasons why this measure of effective dispersal rate was probably an underestimate. First, where seeds had actually been actively dispersed from outside the plot, but were of the same species as a possible parent tree inside it (e.g. Gibson & Wheelwright 1995), their seedlings were necessarily excluded from the "actively dispersed" class. Second, we were unable to exclude male trees of dioecious species from the possible parent pool. On the other hand, we may have overestimated the dispersal rate, if (i) many of the "actively dispersed" seedlings were actually dropped from parents that had since died, or (ii) more of the "dropped" seedlings have died since germination than "actively dispersed" seedlings. However, we found that the estimate of dispersal rate was almost unaffected when only seedlings ≤ 25 cm tall were included (see Results); such seedlings are generally younger and less likely to have been dropped from a now-dead tree. Similarly, we found that there was no significant difference in 16-month mortality rate between "dropped" and "dispersed" seedlings ($\chi^2 = 0.323$, d.f. $= 1$, P $=$ n. s.). Hence, overall, it is most probable that our measures of the proportions of seedlings arising from active dispersal underestimate the true values.

We next evaluated dispersal syndromes to compare patterns between species dispersed by animals vs. other dispersal mechanisms. Where possible, published accounts of the dispersal mode were used (Table 1), but where no information was available, species were allocated to syndromes on the basis of fruit morphology: fleshy fruits were classed as animal-dispersed, dry fruits with wings or wing-like morphology were classed as wind-dispersed, and dry, explosively dehiscing fruits were classed as explosive (Ridley 1930; van der Pijl 1982; Janson 1983).

To assess the role of dispersal limitation in reducing competitive dominance and competitive exclusion, we modelled the process of canopy tree replacement with a computer. We sought the simplest possible model

Table 1 Dispersal syndromes of the 26 genera with the most species present in tree plots at Gunung Palung

Genus	Family	N spp.	Disp. mode	Reference
Syzygium	Myrtaceae	15	A (ba/m)	Ridley (1930)
Shorea	Dipterocarpaceae	13	W	Ashton (1982)
Baccaurea	Euphorbiaceae	12	A (m/bi)	Ridley (1930)
Calophyllum	Clusiaceae	9	A (ba/bi)	Stevens (1980)
Diospyros	Ebenaceae	9	A (m/bi)	Ridley (1930)
Aglaia	Meliaceae	9	A (bi/m)	Mabberley et al. (1995)
Eugenia	Myrtaceae	9	A (ba/m)	Ridley (1930)
Garcinia	Clusiaceae	8	A (m)	Ridley (1930)
Dacryodes	Burseraceae	7	A (bi/ba)	Leenhouts (1956)
Memecylon	Melastomataceae	7	A (bi/ba)	D/PO*
Canarium	Burseraceae	6	A (bi/ba)	Leenhouts (1956)
Aporusa	Euphorbiaceae	6	A (bi)	D/PO
Beilschmeidia	Lauraceae	6	A (bi)	Ridley (1930); D/PO
Palaquium	Sapotaceae	6	A (bi/m)	Ridley (1930); D/PO
Santiria	Burseraceae	5	A (bi/ba)	Leenhouts (1956)
Lithocarpus	Fagaceae	5	A (m)	Soepadmo et al. (2000)
Horsfieldia	Myristicaceae	5	A (bi)	de Wilde (2000)
Gluta	Anacardiaceae	4	W/N	Ding Hou (1978); D/PO
Mangifera	Anacardiaceae	4	A (ba)	Ding Hou (1978)
Elaeocarpus	Elaeocarpaceae	4	A (m/bi/ba)	Ridley (1930)
Mallotus	Euphorbiaceae	4	E	D/PO
Dialium	Fabaceae	4	A (bi/m)	Ridley (1930)
Knema	Myristicaceae	4	A (bi)	de Wilde (2000)
Myristica	Myristicaceae	4	A (bi)	de Wilde (2000)
Xanthophyllum	Polygalaceae	4	A (m)	D/PO

Key to syndromes: A, animal (ba, bat; bi, bird; m, nonbat mammals); W, wind; E, explosive; N, no apparent adaptation for dispersal.
*D/PO: Deduction from fruit morphology (Ridley 1930; van der Pijl 1982), and personal field observations/personal communication.

incorporating space, adult mortality, spatially explicit recruitment, and recruit competition. Models similar to the one we used have been well-explored by other researchers (e.g. Chesson & Warner 1981; Shmida & Ellner 1984; Comins & Noble 1987; Hurtt & Pacala 1995). Following the death of an individual canopy tree, a grid cell position was filled by one of the seedlings recruited into the cell. We varied the proportion of recruited seedlings originating in a local neighbourhood (corresponding to "dropped" seedlings) vs. those that arose from seeds dispersed from outside that neighbourhood ("actively dispersed"). We also varied the size of the neighbourhood itself, and the total number of recruited seedlings in the emptied cell. We focused on the rate of increase in dominance by the best 10 competitor species, over a range of parameter space that included the levels of dispersal-rate and neighbourhood size observed in the field.

In detail, our model comprised the following: each tree occupied a single cell on a grid of 100×100 squares (wrapping back onto itself in both x and y directions). Initially, 300 species were randomly allocated (with replacement) to fill the squares (giving an even abundance for each species of c. 33 trees). At each time step, each tree had a probability of death of 0.01 (c. 1% annual tree mortality, ≥ 10 cm d.b.h., has been observed in this forest; Webb 1997). Gaps in several adjacent cells might occur by chance, but replacement processes in each cell in a multicell gap were modelled independently. The seedling pool (of 400 individuals) in each gap was filled in the same time-step as the death of an adult, the seedlings competed, and the gap was filled. The seedling pool was created by adding a single seedling from randomly chosen (with replacement) parent trees inside and outside the local (square) neighbourhood, in proportions that we varied to reflect a range of active dispersal from low to high (dispersal method 1). We also modelled dispersal from outside the local neighbourhood more realistically (dispersal method 2), with a decreasing probability of dispersal with increasing distance: the first 50% of the "actively dispersed" seedlings came from trees with a distance of less than one neighbourhood radius from the local neighbourhood, the next 25% from the next one-neighbourhood-radius (square) annulus, and the remaining 25% randomly from the remainder of the grid.

Competition was also modelled in two ways. In both cases, species of seedlings were assigned a competitive ability that varied linearly from the "strongest" species to the "weakest". In competition method 1, the extreme deterministic case, the top-ranked ("strongest") species in any pool won the empty grid cell (irrespective of its abundance). Method 2 was a more realistic method where the probability of a species winning a cell was based on the product of the abundance of its seedlings in the pool and its competitive ability score. If the competitive ability parameter was, for instance, 5, then the probability of one seedling of the best

competitor species winning was equal to that of five seedlings of the poorest competitor. The program code (in C) is available from the authors.

This model was designed primarily to explore the effect of dispersal limitation on species dominance and competitive exclusion: the eventual outcome of the model will always be mono-dominance by the best competitor. However, the model could easily be modified to investigate the conditions needed for long-term coexistence, e.g. by adding a trade-off between competitive ability and dispersal ability, but this is beyond the empirical scope of this study. Real data on such trade-offs would also be formidable to gather in a rain forest.

RESULTS

From the field data, we found that 67.9% (S.E. = 1.4%) of seedling species and 45.6% (S.E. = 2.7%) of individual seedlings in the 36 m^2 plots must have arisen from actively dispersed seeds (there was an average of 436.4 seedlings per 36 m^2 plot, S. E. = 52.7). These values probably underestimate the real contribution of dispersal to local seedling pools (see Methods). Nevertheless, the proportion of dispersed species was so high (ranging from 56.3% to 80.8% per seedling plot), that total seedling species richness in a plot was strongly determined by the richness of these dispersed species (Fig. 2A), and not by the species diversity of the surrounding tree plot (Fig. 2B). As expected, the most abundant dispersed species were generally represented by fewer individual seedlings than the most abundant dropped species (Fig. 3). However, past the first c. 10 most abundant species, the dispersed species were actually more abundant, indicating that conclusions based on dispersed species (vs. dispersed individuals) should not be biased by the presence of many species with single individuals. The result was also nearly independent of the size of seedlings used: for 5–25 cm tall seedlings, dispersed seedling species were 66.1% (S.E. = 1.6%) of the total and dispersed individuals were 47.1% (S.E. = 3.0%).

We tested the sensitivity of our main result to variation in our assumptions. When the only tree that we observed of a species was fertile, the minimum size at first observed reproduction was equal to the maximum size observed, which could cause a systematic overestimate of the mean relative size at first reproduction (mean RSFR). To assess this effect, we used the 5% quantile of RSFR; the results were very similar to those using the median: dispersed seedling species, 67.8% (S.E. = 1.4%), mean dispersed individuals, 45.5% (S.E. = 2.7%). Conversely, when only juveniles were found of rare species, maximum tree size for these species was underestimated, and the projected size at first reproduction would also be underestimated. To assess bias in this direction, we used the 95% quantile of RSFR; the
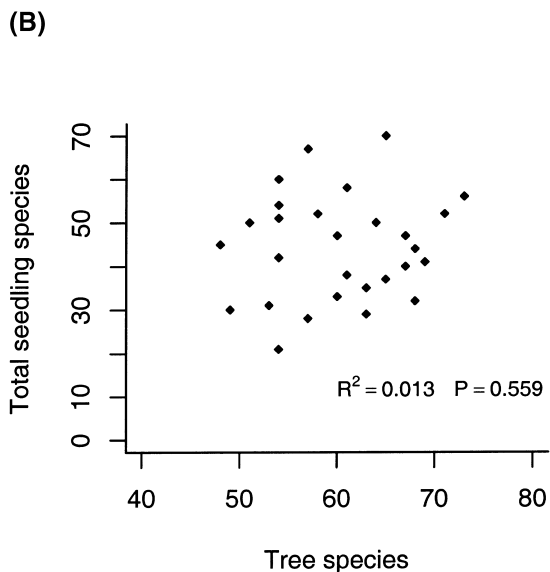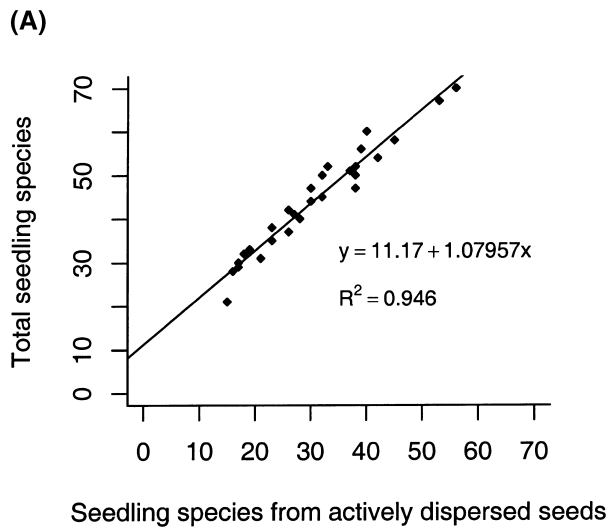
(A)

y = 11.17 + 1.07957x

$R^2 = 0.946$

Seedling species from actively dispersed seeds

(B)

$R^2 = 0.013$ P = 0.559

Tree species

Figure 2 The relationship between total seedling species richness in 36 m^2 plots at Gunung Palung and (A) seedling species in the plot that had to have been actively dispersed, and (B) species richness of trees ($\geq$ 10 cm d.b.h.) in the square, 0.16 ha plot in which the seedling plots were centrally nested.

results were again very similar to those using the median: dispersed seedling species, 68.1% (S.E. = 1.4%), mean dispersed individuals, 45.7% (S.E. = 2.7%). When we did not permit the projected SFR to be less than 20 cm diameter for species we did not see fertile, the results were very similar: dispersed seedling species, 68.0% (S.E. = 1.4%), mean dispersed individuals, 45.6% (S.E. = 2.7%). Altering the assumption that trees less than 20 cm d.b.h. in the outer ring could not have dropped seeds into the seedling plot had
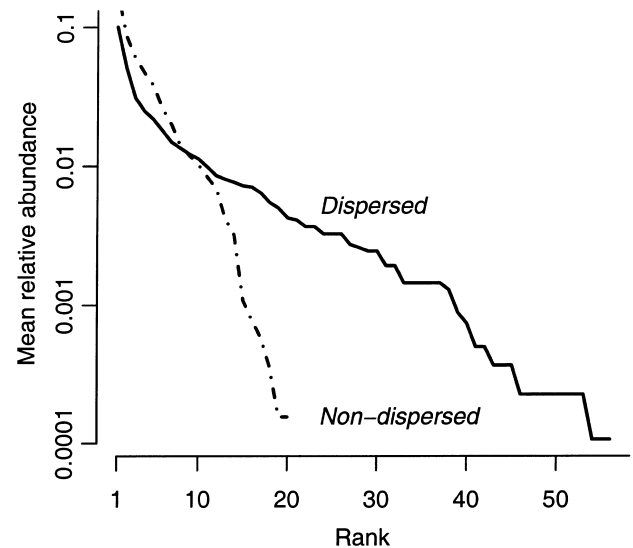

Figure 3 Rank-abundance curves for seedlings classified as either actively dispersed ("Dispersed") or dropped ("Nondispersed"). Each ranked position represents the average relative abundance for all the species that have that rank in 28 plots; i.e. no single species is associated with a given rank. Abundances are expressed relative to all the seedlings in a plot, not just those in the same class.

more effect on the results: when all (possibly reproductive) trees in the 40 m × 40 m plot were considered as able to drop seeds into the seedling plot, the mean dispersed species fell to 60.3% (S.E. = 1.4%), and the mean dispersed individuals to 38.4% (S.E. = 2.5%). Using a 40-cm d.b.h. cut-off for dropping from the outer ring raised the mean dispersed species to 76.4% (S.E. = 1.0%), and the mean dispersed individuals to 54.8% (S.E. = 2.9%). Overall, however, varying our assumptions did not greatly alter the basic result, because of the great difference in the species lists between the seedling plots and the surrounding trees of any size or reproductive status.

Of the 325 species recorded as trees, 84.6% were adapted for dispersal by vertebrates, 10.7% by wind, and 4.3% by explosive self-dispersal (see Table 1 for dispersal syndromes of speciose genera). On average, 26.9 of the 30.7 seedling species per seedling plot that were classified as actively dispersed had adaptations for dispersal by vertebrates, and 2.6 for wind-dispersal. The ratio of dispersal syndromes was different in the "dropped" species (animal, 8.9, and wind, 4.3, out of 13.6 species). This difference suggests that ripe wind-dispersed seeds travel shorter distances than ripe vertebrate-dispersed seeds, and their seedlings are more likely to be misclassed here as "dropped" (see Methods). Overall, in the seedling plots, an average of at least 60% of all seedling species in a plot must have been actively dispersed by animals.

In the simulation, dispersal limitation became most effective at slowing competitive dominance only when most

of the seedling recruits came from a small local neighbourhood (Fig. 4A and 4B). When model parameters were used that best match field estimates (*c.* 400 seedlings per cell, and *c.* 50% of individuals originating from outside the "dropped-seed" neighbourhood, and a diameter of that neighbour-
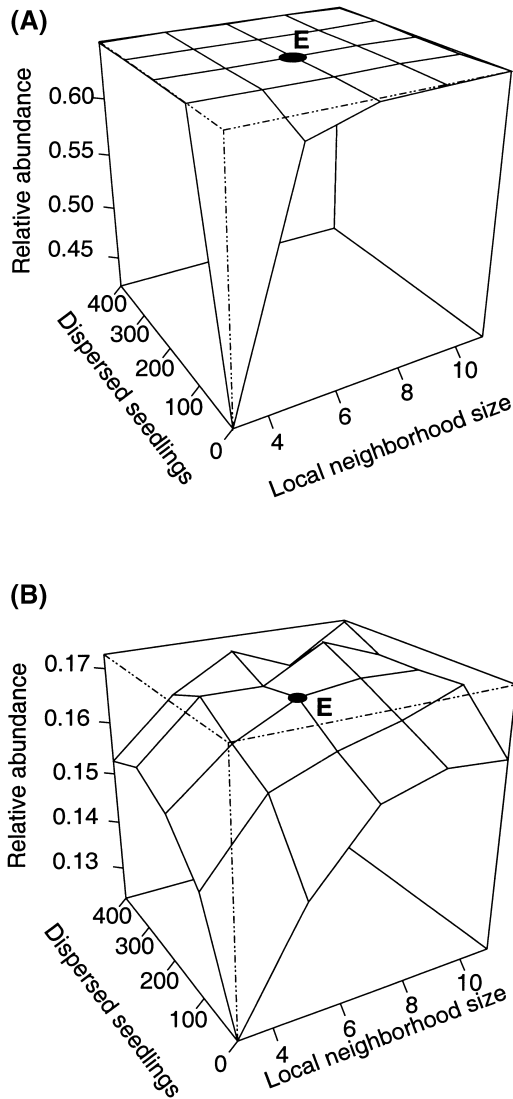
hood of seven cells, i.e. seven tree-crown-diameters or *c.* 40 m), dispersal limitation did not substantially slow the increase in competitive dominance (point E in Fig. 4A and 4B). This result (i.e. shape of response curve) was similar for both methods of dispersal and competition, although using stochastic competition (method 2; competitive ability parameter = 5), the sharpness of the threshold was not as marked (Fig. 4B), and the rate of takeover by the best competitors was *c.* 20 times slower.

As remarked above, the eventual outcome of all runs was mono-dominance by species 1. However, the rate of exclusion of species was influenced by the parameter values chosen: small neighbourhoods with little active dispersal retained species in the model longer than large neighbourhoods and much active dispersal (Fig. 5). Middle values of the parameters gave more intermediate values of species persistence, producing less of a threshold than that seen with relative abundance of top competitors (Fig. 4A and 4B).

Increasing the competitive ability parameter in competition method 2 increased the rate of attainment of dominance by top competitors, and increased the rate of exclusion of species from the grid. With dispersal method 1, and competition method 2, competitive ability parameters of 2, 5, and 10 gave top-10 dominance of 0.10, 0.17, 0.19, respectively, and species extinct (out of 300) at 500 time-steps of 8, 46, and 57 (for the case of no dropped seedlings and a neighbourhood diameter of 3 cells).
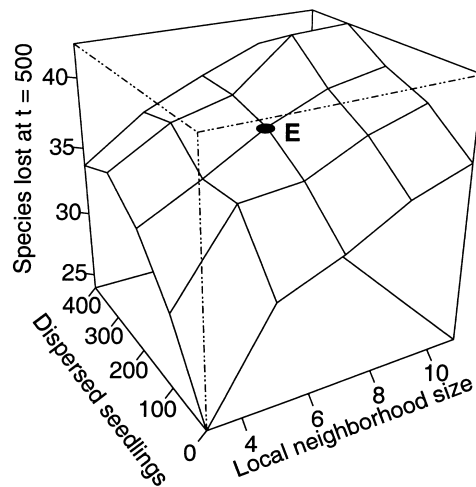

Figure 4 Summed relative abundance of 10 best competitor species (A) after 100 time steps in a cell-based simulation model with extreme competition (competition method 1; see text) and random dispersal outside neighbourhood (dispersal method 1), and (B) after 500 time steps, with less extreme competition (competition method 2; competitive parameter of species 1 is 5) and distance dependent dispersal outside local neighbourhood (dispersal method 2), as a function of (*x*) neighbourhood diameter (in cell-widths) and (*y*) number of seedlings from outside local neighbourhood ("actively dispersed" vs. from inside, "dropped"), out of a total of 400. Point E indicates results using parameters most consistent with field data.

Figure 5 Number of species lost from the grid after 500 time steps, with competition method 2 (competitive parameter of species 1 is 5) and distance dependent dispersal outside local neighbourhood (dispersal method 2), as a function of (*x*) neighbourhood diameter (in cell-widths) and (*y*) number of seedlings from outside local neighbourhood ("actively dispersed" vs. from inside, "dropped"), out of a total of 400. Mono-dominance by species 1 was achieved between *c.* 600 and *c.* 900 time-steps, depending on parameter values. Point E indicates results using parameters most consistent with empirical data.

While the distance dependent model of dispersal (dispersal method 2) is clearly more realistic than random dispersal (method 1), under competition method 1 it gave results that varied little (on average by < 1%) from random dispersal. However, the difference between dispersal methods was more marked with the stochastic competition method 2, e.g. random dispersal gave a top-10 dominance of 0.17, with 46 species lost from the grid, while distance dependent dispersal gave 0.15 and 34 species, respectively (with no dropped seeds and a neighbourhood diameter of 3 cells, after 500 time-steps).

The form of the response surface was identical when the seedling pool was 10 times smaller or larger (with competition model 1 and dispersal model 1), and the rate of takeover varied hardly at all: e.g. 40 dispersed seedlings gave a top-10 dominance of 0.64, 400 gave 0.65, and 4000 gave 0.65 (with a neighbourhood diameter of 3 cells, with no dropped seedlings, after 100 time steps).

DISCUSSION

As far as we are aware, this is the first community-wide estimate of active seed-dispersal rate in a tropical forest. A number of studies have measured multispecies seed-fall into seed traps, but have not compared the species composition of the seed-fall to the local tree composition around the seed traps (Hubbell *et al.* 1999; B. D. Hardesty & V. T. Parker, unpublished work). In the most directly comparable study, Martinez-Ramos & Soto-Castro (1993) found that *c.* 50% of seeds arriving at seed traps belonged to species from outside their 25 m × 25 m study plots. Although the methods of Martinez-Ramos & Soto-Castro (1993) differed substantially from ours, and the authors did not attempt to exclude tree species outside their plots that may have passively dropped seeds into the seed traps, their results also suggest that a large proportion of local seedlings arise from active dispersal.

Our simulations confirm that the rate of dispersal in this forest is high, and almost beyond the level at which dispersal limitation curtails the rate of attainment of competitive dominance (Fig. 4A and 4B), and competitive exclusion (Fig. 5). The structure and assumptions of a model obviously determined the results obtained, but we argue that we have captured the essential components of the system, with minimal additional complexity. Models showing that dispersal limitation is of more generalized importance are also dependent on their assumptions. Most notably, our results would initially appear to differ from those of Hurtt & Pacala (1995), who found that recruitment limitation was sufficiently strong to permit the coexistence of many species with large competitive differences. However, their goal, to explore the potential for long-term coexistence, was different to ours, which was to isolate the

effect of dispersal limitation on community dominance and competitive exclusion. Long-term coexistence in their model was primarily a consequence of habitat heterogeneity at the scale of the individual tree, with every species having a spatial location where it was the dominant competitor. While large-scale habitat heterogeneity has been shown to be important at Gunung Palung (Webb & Peart 2000), it is still unclear whether every species has its own "niche", and whether the spatial scale of such niches is equal to the size of individual plants. In addition, recruitment limitation has two primary components: limited seed dispersal in space ("dispersal limitation"; seeds *cannot* reach everywhere), and limited parent fecundity ("seed limitation" or "fecundity limitation"; not enough seeds are produced to cover all the space, even if dispersal were not limited). Our simulation focused primarily on the first component, while that of Hurtt & Pacala focused primarily on the second. However, because of the only slight difference in top-competitor takeover rate between cases when 40, 400 and 4000 seedlings were sampled, the "fecundity limitation" component also appears to be unimportant in slowing the rate of attainment of competitive dominance in our model.

The introduction of a distance dependent dispersal kernel for the actively dispersed seeds (dispersal method 2) had only a surprisingly small effect on the rate of attainment of community dominance. This indicates that with a relatively large number of seedlings sampled (400 per tree replacement cell), the representation of community composition in the resulting seedling pool was similar whether seedlings were predominantly from nearby, or from far away. It is possible that a larger grid, with more spatial heterogeneity in community composition, may increase the difference between random and distance dependent dispersal. Our model started with no patchiness in the spatial distribution of species, and an even relative abundance structure, neither of which are characteristic of tropical forests (Condit *et al.* 2000; Hubbell 2001). However, uneven relative abundances were rapidly established, because of the competitive differences among species, and spatial distributions also rapidly became patchy (detected by visual examination of maps of abundant species), because locally dominant species tended to win nearby cells with high frequency. Hence, because this unevenness in community structure developed intrinsically, we do not believe that our not imposing this unevenness at the start led to misleading results.

While further theoretical and model development is needed to fully understand the role of recruitment limitation in real systems, at the least we have demonstrated with our simulation that strong dispersal limitation is not always a necessary outcome in spatially explicit, community dynamics models, but is dependent on parameters chosen. However, we further suggest that in forests with active seed dispersal, recruitment limitation (and therefore competition-dispersal

trade-offs) may be less important for the maintenance of species diversity than other mechanisms, such as density dependence and habitat partitioning (which both appear to be operating in this forest; Webb & Peart 1999, 2000).

At the time of this study, the vertebrate fauna at Gunung Palung occurred at densities probably influenced little by human activities (Laman 1995, 1996; Curran *et al.* 1999; Curran & Webb 1999), there being little or no hunting (Salafsky 1993). Gunung Palung is one of the few places left in Indonesia and Malaysia with natural populations of orang-utans at high densities (Knott 1998, 1999). However, if these and other animals responsible for seed dispersal were to become locally extinct, as is happening throughout the tropics (Chapman & Onderdonk 1998; Wright *et al.* 2000), and sadly beginning now at Gunung Palung, we would expect to see a reduction in local seedling diversity of up to 60% (because 60% of total seedling species were classed as actively dispersed and adapted for animal dispersal). Even after heavy hunting, some small rodents would remain and might provide some short-distance dispersal (e.g. Brewer & Rejmanek 1999), although in this forest rodents appear to operate primarily as seed predators (Blate *et al.* 1998).

Theory and recent empirical results indicate what the consequences of this collapse in local seedling diversity for the species composition and relative abundance of trees may be. On the one hand, while our results indicate that dispersal limitation and recruitment limitation may be currently ineffective in slowing competitive exclusion in this system, this could change if dispersal rates were severely reduced. Our simulation indicates that if all active dispersal were to fail, and seeds fell no more than a crown diameter, even extreme forms of competitive exclusion could be significantly slowed.

On the other hand, if being in a diverse local seedling community reduces the probability of mortality for individual seedlings ("herd immunity"), as found for rain forest in Panama (Wills *et al.* 1997), and for this forest (C. O. Webb, unpublished data), then the expected 60% reduction in seedling diversity may significantly affect seedling mortality rates. Whether the predicted increase in diversity dependent mortality would fall evenly on all species is not known, but increases in intraspecific density and distance dependent mortality ("Janzen-Connell" effects; Janzen 1970; Connell 1971) should affect all animal-dispersed species, common or rare. The dominant species in this forest are wind-dispersed trees in the family Dipterocarpaceae. As they would be unaffected by a loss of animal dispersers, they may increase still further in dominance, at the expense of vertebrate-dispersed species (which are less abundant, but more diverse). Additionally, if diversity is indeed partly maintained by trade-offs between dispersal ability and competitive ability (Tilman 1994), the collapse of vertebrate dispersal could lead to a rapid competitive exclusion of the "dispersal

specialists". However, the extent to which increased dispersal limitation may offset the detrimental effects of loss of seed dispersal on other mechanisms promoting coexistence is not known. Research on dispersal and seedling recruitment in forests that have lost most or all vertebrate dispersers, but are otherwise intact, will help greatly in understanding the role of dispersal in sustaining tropical forest diversity. Such forests are not hard to find in the tropics today.

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BIOSKETCH

Cam Webb's research records local and island-wide patterns of Bornean tree diversity and aims to explain these patterns in evolutionary, biogeographic and contemporary ecological terms. His theoretical interests include the use of phylogenetic analysis in community ecology. He is committed to helping conserve and manage these magnificent forests.