Directed seed dispersal by bellbirds in a tropical cloud forest

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ABSTRACT   A fundamental goal of plant population ecology is to understand the consequences for plant fitness of seed dispersal by animals. Theories of seed dispersal and tropical forest regeneration suggest that the advantages of seed dispersal for most plants are escape from seed predation near the parent tree and colonization of vacant sites, the locations of which are unpredictable in space and time. Some plants may gain in fitness as a fortuitous consequence of disperser behavior if certain species of dispersers nonrandomly place seeds in sites predictably favorable for seedling establishment. Such patterns of directed dispersal by vertebrates long have been suggested but never demonstrated for tropical forest trees. Here we report the pattern of seed distribution and 1-year seedling survival generated by five species of birds for a neotropical, shade-tolerant tree. Four of the species dispersed seeds to sites near the parent trees with microhabitat characteristics similar to those at random locations, whereas the fifth species, a bellbird, predictably dispersed seeds under song perches in canopy gaps. The pattern of seedling recruitment was bimodal, with a peak near parent trees and a second peak, corresponding to bellbird song perches, far (>40 m) from parent trees. Seedling survival was higher for seeds dispersed by bellbirds than by the other species, because of a reduction in seedling mortality by fungal pathogens in gaps. Thus, bellbirds play a significant role in seed dispersal by providing directed dispersal to favorable sites and therefore may influence plant recruitment patterns and species diversity in Neotropical forests.

Seed dispersal determines the spatial arrangement and physical environment of seeds and thus is an important step in the reproductive cycle of most plants (1–5). In Neotropical forests, birds are particularly important seed dispersers, because up to 75% of tree species produce fruits eaten by birds (3, 6). Considering the energetic costs to the plant of producing a dispersal structure that includes a fleshy pericarp as a reward for dispersers, it is reasonable to expect an advantage of seed dispersal (7, 8). Three nonexclusive advantages have been proposed (3, 9): (*i*) escape from high seed or seedling mortality under and near the parent tree (Escape Hypothesis); (*ii*) colonization of unpredictable, ephemeral, or newly created sites (Colonization Hypothesis); and (*iii*) directed dispersal to particular favorable microhabitats (Directed Dispersal Hypothesis).

The escape hypothesis (10, 11) is expected to be an advantage for most plants and is supported by numerous studies showing density- or distance-dependent mortality near parent trees (2, 3, 12–15). However, colonization or directed dispersal also could be important for the seeds that do escape such mortality. The colonization hypothesis is most relevant when suitable sites for establishment are unpredictable or randomly distributed, as is the case for new treefall gaps in tropical

forests (3, 16, 17). In tropical rain forests, virtually all canopy tree species (regardless of the degree of shade tolerance) require at least small canopy gaps to reach reproductive maturity (18–21). The expected dispersal strategy of these trees is colonization via blanketing the understory with propagules capable of dormancy or suppressed growth until a gap forms and increased light levels allow germination, more rapid growth, and/or higher survival (3, 22, 23). Alternatively, directed dispersal can result if the plant attracts dispersers that deposit seeds nonrandomly in suitable locations, thereby increasing plant fitness (e.g., mistletoes; refs. 24 and 25). Although directed dispersal has been postulated for vertebrate-dispersed tropical trees (3, 26–28), it has never been demonstrated by showing nonrandom dispersal to especially favorable sites for seedling growth and survival.

METHODS

We studied seed dispersal of a common shade-tolerant neotropical montane tree, *Ocotea endresiana* (Lauraceae). Our study was conducted from May 1993 to June 1996 in undisturbed lower montane rain forest at 1,600 m elevation in the Monteverde Cloud Forest Preserve, Costa Rica. Only data from the 1993 and 1995 fruiting seasons (late May to late July) are included here because the trees produced few fruits in 1994 and bellbirds left the 5-ha study area in early June. The seeds (0.76 ± 0.15 g; mean ± SD, $n = 184$) are dispersed predominantly by five species of birds: black guan (*Chamaepetes unicolor*), resplendent quetzal (*Pharomachrus mocinno*), emerald toucanet (*Aulacorhynchus prasinus*), three-wattled bellbird (*Procnias tricarunculata*), and mountain robin (*Turdus plebejus*) (29). By following birds until they regurgitated or defecated *O. endresiana* seeds, we were able to determine the actual sites where seeds were dispersed. Seed dispersers were observed foraging in fruiting *O. endresiana* trees ($n = 21$) and were followed until they regurgitated or defecated seeds. Because of the difficulty in following the birds, these methods are biased against detecting long-distance dispersal. Note, however, that with 21 fruiting trees in a 5-ha area, the farther a bird gets from one tree, the closer it gets to another. Indeed, on several occasions, we followed birds from one fruiting *O. endresiana* tree to another. Because we could not always be certain of the source tree of dispersed seeds, we considered the closest fruiting conspecific to be the parent. Thus, some of the dispersal distances are likely underestimates of the actual dispersal distances. In addition, the most important result (see below) is differential dispersal to gaps, which is not susceptible to the distance bias.

Each dispersed *O. endresiana* seed was protected from postdispersal seed predation by rodents with a $4 \times 4 \times 2$-cm cage made of 3-mm galvanized wire mesh held in place by two 25-cm metal stakes. Each site was checked weekly and as each seed germinated and the shoot began to grow (typically 4–6 weeks after dispersal), the cage was removed to allow normal seedling growth, as well as exposure to mammalian herbivores and seed predators. Weekly seed monitoring continued for 4

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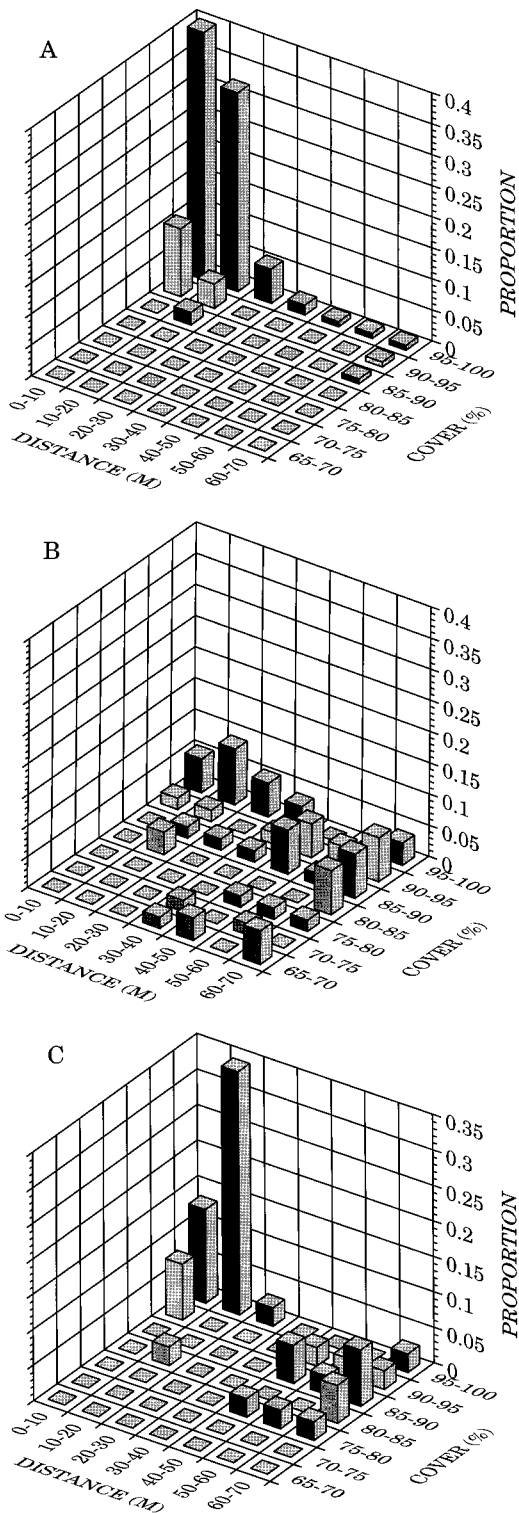
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FIG. 1. The frequency of dispersed seeds (*A* and *B*) and seedlings surviving 1 year (*C*) as functions of distance from the closest fruiting *O. endresiana* tree and canopy cover for guans, quetzals, toucanets, and robins combined ($n = 128$) (*A*) and bellbirds ($n = 56$) (*B*). Each bar represents the proportion of seeds dispersed by particular dispersers (*A* and *B*) or surviving seedlings (*C*) in each distance/canopy cover category. In this study site, all bellbird perches were >40 m from the closest fruiting *O. endresiana* tree. Values <90% for canopy cover represent gaps (28). Note the bimodal pattern of seedling recruitment (*C*) reflects that of seed dispersal, with one peak close to the parent trees (*A*) and a second peak corresponding to the bellbird perches (*B*). The increase in seed input at greater distances is not a result of the increase in annulus area with distance but rather is due to the

months or until the seed or seedling died. Additionally, all sites were checked 12 months after dispersal (June 1994 and 1996). In a separate experiment, seed predation by mammals was the predominant source of mortality before germination and did not differ between seeds in gaps (including bellbird gaps) and seeds in the forest understory ($n = 689$, $X^2 = 0.55$, df = 1, $P = 0.46$). No evidence of secondary dispersal by seed-caching rodents was found (D.W., unpublished data). Thus, even though our seeds likely experienced unusually high initial survival, the cages did not influence the relative survival of seedlings from seeds dispersed by bellbirds and by other species. Also, because the cages were removed after germination, the seedlings were exposed to all the normal biotic and abiotic conditions faced by seedlings in this habitat. Use of the cages to minimize early mortality allowed a larger sample size to detect differences in mortality at later stages.

Habitat variables were measured at all locations of naturally dispersed seeds as well as at 70 randomly located sites. Habitat variables included canopy cover (measured with a spherical densiometer), amount of leaf litter (the number of leaves pierced by a knife thrust into the soil), number of stems within a 50-cm radius, and distances to the nearest herbaceous stem, woody stem, tree >10 cm dbh, fruiting conspecific tree, and fallen log. Data were analyzed with the SAS statistical package by using procedures described below (30).

RESULTS AND DISCUSSION

Four of the five bird species usually remain in or nearby the fruiting tree (31) and, in our study, dispersed most seeds within 20 m of the parent tree in closed canopy forest (Fig. 1*A*). In contrast, male bellbirds typically spend as much as 80% of the day at exposed song perches, where they advertise to females with loud vocalizations (32). Such perches in our study site were located in standing dead trees on the edges of canopy gaps. Thus, most seeds (59%) dispersed by bellbirds landed in sites >40 m from conspecific trees and most (52%) also landed in gaps (Fig. 1*B*). The overall pattern of dispersal therefore was bimodal, with peaks near parent trees and under bellbird song perches. Overlap between the peaks generated by bellbirds and by the other species was relatively small (compare Fig. 1*A* with *B*) and usually was caused by female bellbirds, which spent little time at song perches and regurgitated seeds under or near parent trees.

Microhabitat characteristics of dispersal sites generated by bellbirds, but not the other four species, were significantly different from those at random locations (Fig. 2). Thus, bellbirds predictably placed seeds in nonrandom microhabitats, in contrast with other dispersers, which predictably failed to do so. This difference was important to seedling recruitment. Although 1-year seedling survival was numerically highest near the parent trees, where seed deposition was numerically highest, disproportionately more seedlings survived elsewhere (Fig. 1*C*). In particular, seedlings from bellbird-dispersed seeds were significantly more likely to survive to 1 year, and the resulting seedlings were significantly taller than seedlings from seeds dispersed by the other four species (Fig. 3). A contributing mechanism for higher survival of seedlings at bellbird sites was significantly lower mortality by fungal pathogens (e.g., damping off; refs. 33 and 34) than for seedlings from seeds dispersed by the other species (Fig. 3). Additionally, because canopy gaps expand as trees on the gap edges fall

concentration of seeds in the vicinity of bellbird perches. In particular, the number of seeds dispersed to gaps by bellbirds was greater than expected by chance ($X^2 = 36.45$, df = 1, $P < 0.001$) based on the area of the study site (5 ha) in gaps (5.3%) and forest (94.7%). No seedlings survived in the two lowest canopy cover categories, suggesting a limit to the benefits of higher light levels.
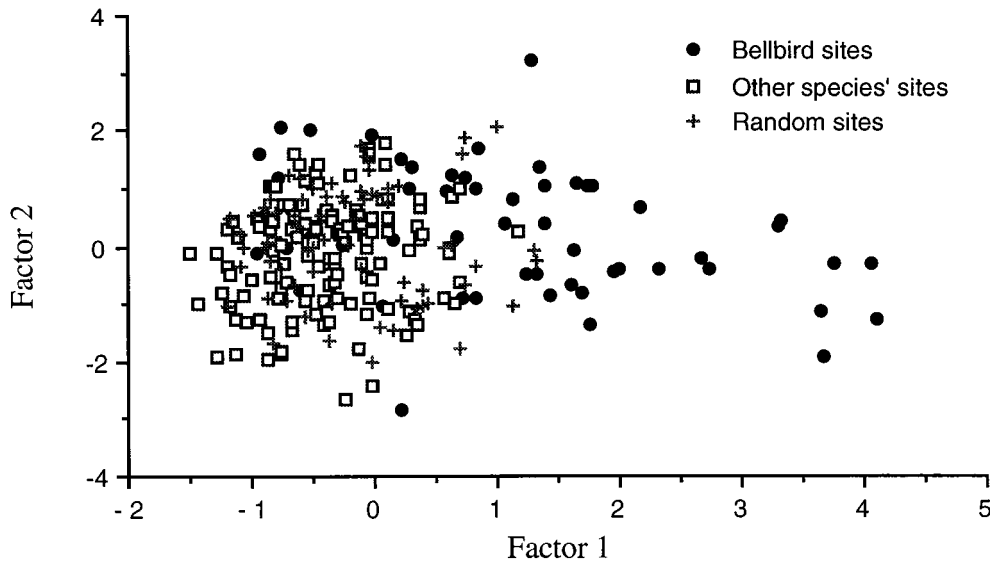
FIG. 2.   Plot of all seed locations as functions of the first two axes of a principal component analysis of the correlation matrix (SAS PROC FACTOR; ref. 30) of habitat variables. The first two factors explained 48% of total variance. The first factor is characterized most by high loadings of canopy cover (-0.86), number of stems (0.72), distance to nearest woody stem (0.65), and distance to parent (0.64). The second factor was characterized most by leaf litter (0.67). Note that seeds dispersed by bellbirds extend into regions farther from the parent trees and with more open canopy (i.e., higher loadings on factor 1) than seeds dispersed by the other four species. The loadings for factor 1 are significantly different among the random sites, bellbird sites, and other species' sites (ANOVA: F = 71.6, df = 2, 252; $P < 0.0001$). The bellbird sites differ from random sites and from other species' sites (post-hoc Fisher's Protected LSD tests P values < 0.0001), but the random sites do not differ from the other species' sites ($P = 0.12$).

(17, 35, 36), seeds in gaps or on gap edges are more likely to encounter favorable growth conditions in the future than seeds under shaded conditions, where the chance of formation of a new gap is low and essentially random (3, 16, 17). Gap expansion, or at least perpetuation, certainly occurs in bellbird gaps as the dead tree used for the song perch sheds large branches over the course of several years before falling entirely. Thus, *O. endresiana* seeds dispersed by bellbirds have a greater chance of experiencing favorable growth conditions and reaching reproductive maturity than seeds dispersed by the other disperser species.

These results suggest that male bellbirds provide directed dispersal to existing canopy gaps, whereas the other four bird species provide dispersal conducive to random colonization of future gaps. The combination of these different dispersers results in a wide range of conditions faced by seeds and seedlings. This pattern is consistent with recent studies that suggest species considered shade-tolerant actually recruit under a wide range of conditions (37–39). Although some studies show disproportionate seed or seedling mortality in gaps (40, 41), others show no difference between gaps and understory (34, 42, 43). Thus, the notion that early mortality is disproportionately high in gaps (22) needs to be examined in more detail.

Bellbirds eat many different species of fruits (29) and are active at song perches for about 4 months during the breeding
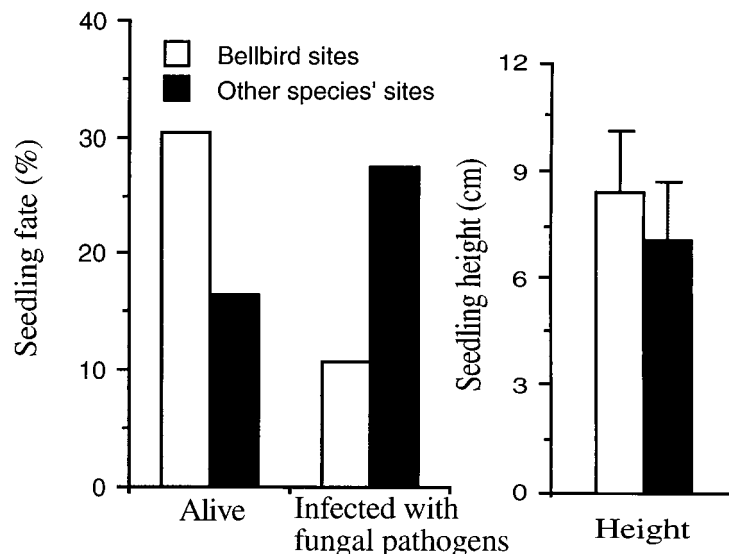

FIG. 3.   One-year seedling survival, proportion of mortality caused by fungal pathogens, and seedling height (mean + 1 SD) for seeds dispersed by bellbirds (open bars) and four other species (shaded). Seeds dispersed by bellbirds were more likely to survive to 1 year (X^2 = 4.6, df = 1, P = 0.03), and the resulting seedlings (n = 17) were taller (t test = 2.37, df = 36, P = 0.02) than were seedlings from seeds dispersed by the other four species (n = 21). Bellbird sites had a lower incidence of mortality by fungal pathogens than did the seedlings from seeds dispersed by the other four species (X^2 = 4.28, df = 1, P = 0.03).

season (32). Thus, the pattern shown here for one common tree species is likely for other bellbird-dispersed plants in Monteverde, as well as in Neotropical forests where other bellbird species occur. Other species that use habitual perches or defecation sites, such as cocks-of-the-rock (44), manakins (45), howler monkeys (46), gorillas (47), and tapirs (48), may also have a disproportionate influence on local plant species recruitment.

The dispersal of *Ocotea endresiana* seeds by bellbirds is the clearest link between a disperser and the reproductive success of a tropical forest tree yet documented. The lack of other examples likely stems from the difficulty of tracking individual dispersers through the canopy until they deposit seeds. As argued above, we suspect the pattern we found also to occur in other sites and for other species. This pattern is noteworthy because large fruit-eating birds, such as bellbirds and other species of Cotingidae, appear especially vulnerable to forest fragmentation (49). Because gaps are necessary for regeneration of many tree species and bellbirds appear to provide directed dispersal to gaps, the loss of these birds may lead to a marked decrease in fitness for many tree species and subsequent changes in tropical forest community structure.

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