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DISPERSAL OF MELASTOME SEEDS BY FRUIT-EATING BIRDS OF TROPICAL FOREST UNDERSTORY

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Abstract. Birds directly affect seed dispersal through (1) the number of seeds they remove and (2) where and in what condition those seeds are deposited. Dispersal effectiveness is a composite of these quality and quantity components of seed dispersal. In this study, number of seeds removed and patterns of seed deposition by six bird species were determined for four shrubs in the Melastomataceae.

Bird species differed in both quantity and quality components of seed dispersal. Bird species that contributed most to the quantity component of seed dispersal were not always the same as those that contributed most to the quality component. Thus, to evaluate the ecological roles of frugivores and their effectiveness as seed dispersers requires integration across various processes involved in seed dispersal (removal, deposition, etc.). In contrast to canopy trees, shrubs apparently have a relatively small set of seed dispersers, which makes them more vulnerable to the extinction of a seed disperser.

Key words: birds, impact on plants; diets of understory frugivores; frugivory; habitat selection; La Selva, Costa Rica; Melastomataceae; seed dispersal by birds; tropical wet forest.

INTRODUCTION

Animals disperse the seeds of most plant species in Neotropical wet forests, especially in the understory where about 98% of treelet and shrub species have fleshy fruits (e.g., Gentry 1982). The ubiquity of animal seed dispersal indicates that such dispersal benefits plants, yet fruits are eaten by many kinds of frugivores, some of which provide little or no dispersal benefit to the plants (e.g., Howe 1980). A key to evaluating the influence of seed dispersers on plant recruitment is to know how many seeds are removed from parents and where and in what condition those seeds are deposited (Herrera and Jordano 1981, Jordano 1992, Schupp 1993). Thus, dispersal "effectiveness" depends on both quantity (number of visits and number of seeds removed) and quality (condition of seeds following seed handling; probability of seeds surviving to later plant stages) components of seed dispersal (Schupp 1993). Three processes—fruit selection, seed handling, and habitat selection—directly influence the number of seeds removed and where viable seeds are deposited in the environment.

Understanding the roles of individual disperser species in plant recruitment dynamics necessitates dissecting these components of dispersal effectiveness and determining which, if any, component is more important in plant establishment (Schupp 1993, Herrera et al. 1994, Schupp and Fuentes 1995). These components of dispersal effectiveness are not necessarily coupled, as frugivores that remove the greatest number of seeds may not necessarily deposit those seeds in sites where survival is favored (Howe 1980, Howe and Vande Kerckhove 1981, Murray 1988, Reid 1989, Jordano and Herrera 1995). Here, we evaluate components of dispersal effectiveness of six bird species that feed on fruits of four shrubs. In particular, we examine how fruit and habitat selection by these birds affect patterns of seed removal and seed deposition. Specifically, we ask the following questions: (1) Do birds contribute equally to the number of seeds removed from these plant species?; (2) Do birds deposit seeds in similar habitats?; and, (3) Do seed deposition patterns reflect distribution of adult plants? Finally, we speculate on which bird species is the most effective disperser and which component, quality or quantity, is likely more important for each of these four plant species. Although we do not have the data to evaluate post-dispersal events in plant recruitment, the questions we address are, nonetheless, extremely relevant to seed dispersal and plant population studies because they concern the potential importance of different frugivores in shaping the abundance and distribution of adult plants. This study thus represents a first step to unraveling the eco-

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logical roles and importance of frugivores to plant populations in a tropical lowland wet forest.

Study Area and Methods

This study was conducted in mature forest at Estación Biológica La Selva, Costa Rica (10°25′ N, 84°01′ W). Two-thirds of La Selva's 1536 ha is in mature tropical wet forest (McDade and Hartshorn 1994). Approximately 4000 mm of rain falls annually, with the main dry season occurring from January to April.

Our studies of habitat use and diets of fruit-eating birds began at La Selva in January 1985 when we established a study plot in old-growth forest. We set mist nets to capture birds and transects to document fruit abundance. Sixty nets were distributed at 40-m intervals throughout a 10-ha area in a 10 × 6 grid; two transects, each 2 × 12.5 m, were established alongside each mist-net lane to sample fruit abundance. Disturbance to surrounding vegetation was kept minimal and nets were placed without bias (i.e., uniformly without regard to what we considered "good" or "bad" locations for capturing birds).

Information on fruit consumption was based on identification of seeds found in fecal samples of birds captured on the 10-ha plot (e.g., Loiselle and Blake 1990, Blake and Loiselle 1991). We placed captured birds in a closed container for 5–10 min to collect fecal samples. Fecal and regurgitated material were preserved in alcohol and seeds were later identified using a reference collection (Loiselle and Blake 1990, 1993). Diet data included in this study are from 1985 through 1993 (December-April) for six species of understory frugivorous birds: *Mionectes oleagineus* (Ochre-bellied Flycatcher, Tyrannidae), *Pipra mentalis* (Red-capped Manakin) and *Corapipo leucorrhoa* (White-ruffed Manakin, Pipridae), *Hylocichla mustelina* (Wood Thursh, Muscicapidae: Turdinae), and *Chlorothraupis carmioli* (Olive Tanager) and *Euphonia gouldi* (Olive-backed Euphonia, Emberizidae: Thraupinae) (hereafter referred to by genus). These six species accounted for 85% of 1094 fecal records that contained seeds. Two of these species undergo latitudinal (*Hylocichla*) or altitudinal (*Corapipo*) migrations and are present at La Selva only seasonally (Loiselle and Blake 1991). We used diet records collected after December 1988 to calculate the proportion of seeds removed from adult plants because we did not count seeds before this. All four plant species had seeds <1.5 mm in length, embedded within fruit pulp. *Chlorothraupis* and *Euphonia* mandibulate fruits in their bill before ingestion; we therefore may have underestimated fruit consumption by these two frugivores as some seeds are dropped while handling fruits. Yet, if seed survival is relatively low under or near parents where dropped seeds are likely to land, then their absence from our data is not critical.

Mist-net locations were classified by habitat: (1) upland flat and ridge sites; (2) upper, middle, and lower slopes; and (3) bottomland or swale sites (hereafter referred to as ridge, slope, and lowland habitats, respectively). Habitat use by birds was quantified by combining captures of birds at net sites grouped by habitat. When captures of all six bird species were combined, the distribution of bird captures among habitats did not differ from expected (goodness-of-fit $\chi^2 = 3.5$, df = 2, $P \geq 0.10$). Similarly, deposition of seeds into habitat categories was quantified by summing the number of seeds found in fecal samples at each net site and combining net sites according to habitat. These measures of habitat use and seed deposition assume that capture at a net truly reflects activity of birds and seed-deposition patterns (see Levey 1988). We feel these assumptions are valid because nets located between two "high-activity" areas (i.e., areas with significantly more bird captures) do not capture more birds than nets not so located (B. A. Loiselle and J. G. Blake, *unpublished data*). If birds were flying directly from one high-activity area to another, then nets situated between these sites might be expected to capture more birds due to their location. Moreover, our observations of flight distances of these six bird species suggest that short flights are much more common than long flights; thus, capture at a net site likely represents foraging activity near that net site (Remsen and Good 1996). Furthermore, independent censuses and casual observations largely confirm patterns of habitat use revealed by mist-net captures (J. G. Blake and B. A. Loiselle, *unpublished data*).

The four plant species included in this study occur regularly in the diets of birds and have similar-sized fruits, but differ from one another in habitat association. These plants, all in the Melastomataceae, are *Clidemia densiflora, Miconia simplex, Ossaea macrophylla,* and *Henriettea tuberculosa* (hereafter referred to by genus). Plants varied in abundance on our plot from an estimated 53 (*Ossaea*) to 220 (*Clidemia*) reproductive individuals per hectare (based on 50-m^2 samples per net site, or 3000 m^2 total). Together, seeds of these species occurred in 60% of all bird feces containing plant seeds during this study period, and of bird species captured in mist nets, the six focal species accounted for 95–99% of all seeds recovered in fecal samples from these four plant species.

Data analysis

To partially address our first question of whether bird species contributed equally to seed removal for the study plant species, we compared the distribution of fecal records of each plant in the diet of birds using chi-square contingency tests (six bird × four plant species). As data were based only on presence of seeds

TABLE 1. Fecal-sample contents relative to four shrub species for each of six frugivorous birds in lowland wet forest (La Selva, Costa Rica).

Bird species	*Clidemia densiflora*	*Henriettea tuberculosa*	*Miconia simplex*	*Ossaea macrophylla*	Total no. of fecal samples†	Total no. of plant species in diet
Mionectes oleagineus	4	20	1	4	163	38
Corapipo leucorrhoa	30	66	9	30	154	43
Pipra mentalis	69	97	42	47	438	74
Hylocichla mustelina	23	15	11	4	92	31
Euphonia gouldi	2	9	1	5	26	24
Chlorothraupis carmioli	36	19	4	9	56	20

† The total number of fecal samples generally reflects the relative number of capures of each bird species on the plot.

within the feces, fecal samples from all years (1985–1993) were included in this analysis. These data reflect whether the different bird species are equally reliable visitors, but only partially address the quantity component of dispersal effectiveness. We compared the actual number of seeds removed from each plant species by each bird species by summing the number of seeds found in fecal samples. Average number of seeds per fecal sample was compared using Kruskal-Wallis tests (distribution of seed numbers was not normal) for each plant species separately.

We used Kendall's coefficient of concordance to determine whether bird species deposited seeds of a given plant species into habitats in the same rank order; for each bird species, ranks were assigned to each habitat category based on the number of seeds dispersed there by that bird. This coefficient (W) varies from 0 to 1, with "perfect" concordance ($W = 1$) occurring when the ranks are equivalent among all species. These tests address whether birds were similar in one aspect of the quality component of effectiveness: where seeds are deposited. Yet, it does not say which frugivore was a more effective disperser with respect to quality, only that the birds likely differ in quality assuming unequal probability of seed and seedling survival among habitats. We evaluated the degree to which these dispersers differentially remove seeds from the habitat of adults by comparing distribution of seeds (from fecal samples) of that plant species to distribution of adult plants using concordance tests; a separate test was run for each bird and plant species. Distribution of adults was based on the number of reproductive adults found in transects, according to the three habitat categories. Significant concordance means, in this case, that a given bird species distributed seeds among habitats in the *same* rank order as the distribution of adult plants among those habitats. Concordance tests only compare the rank order between the two distributions, and although perfect association can occur, there may still be marked deviations in values of the proportions between the two distributions. Consequently, we further compared the difference in proportions of seeds and adult plants graphically to examine the "match" in the distribution of seeds and adults in each habitat.

RESULTS

Quantity components of seed dispersal

All six bird species consumed fruit of all four shrubs, but relative consumption of these plants differed ($\chi^2 = 59.1$, df = 15, $P \leq 0.001$) (Table 1). In terms of fecal records containing plant seeds, *Pipra* clearly was the most abundant frugivore overall, accounting for 47% (438/929) of fruit records. Seeds of all plants were recorded most often in fecal samples of *Pipra*, which likely simply reflects the abundance of this bird species in our samples (Table 1).

Mean number of seeds per fecal sample for a given plant species was highly variable among samples and was not related to average body size of the bird species (Table 2); there were no significant differences among bird species in mean number of seeds found in feces. In terms of absolute seed numbers, *Pipra* removed the most seeds for three of the four shrub species (Table 2). *Corapipo* removed the second-most number of seeds for three of four plant species, whereas *Chlorothraupis* removed the greatest number of *Clidemia* seeds. *Mionectes* and *Hylocichla* were the least important in terms of quantity of seeds removed overall, which reflects the fact that Melastome fruits are not important components of their diet relative to other fruit species.

In summary, these results indicate that the study bird species differed overall in patterns of fruit selection and in the absolute number of seeds removed, and thus do not appear to be equally reliable consumers for these four plant species.

Quality components of seed dispersal

Patterns of habitat use following fruit consumption generally differed among bird species, as indicated by comparison of the absolute proportion and rank order of seeds brought to the three major habitats (Fig. 1). Birds that fed on *Henriettea*, however, distributed seeds

TABLE 2. Number of seeds deposited in fecal samples by six frugivorous birds for four shrub species in lowland wet forest.

Plant species	MOLE (13 g)	COLE (12.5 g)	PIME (16 g)	HYMU (48 g)	EUGO (12 g)	CHCA (38 g)
Miconia simplex†						
Total no. of seeds	...	205	395	75	2	2
Mean no. of seeds	...	51.2	21.9	75.0	2.0	2.0
1 SE	...	32.05	5.90	...	...	...
No. of fecal samples	0	4	18	1	1	1
Ossaea macrophylla‡						
Total no. of seeds	135	3051	4936	58	722	113
Mean no. of seeds	135.0	179.5	182.8	58.0	144.4	28.2
1 SE	...	43.83	49.71	...	64.48	26.25
No. of fecal samples	1	17	27	1	5	4
Henriettea tuberculosa§						
Total no. of seeds	1429	5527	9736	65	4728	2794
Mean no. of seeds	178.6	167.5	180.3	21.7	675.4	465.7
1 SE	50.69	40.50	40.46	3.84	360.25	285.98
No. of fecal samples	8	33	54	3	7	6
Clidemia densiflora‖						
Total no. of seeds	18	1844	2488	585	13	3744
Mean no. of seeds	9.0	141.8	65.5	97.5	6.5	198.6
1 SE	1.00	48.72	14.51	47.86	5.50	66.02
No. of fecal samples	2	13	38	6	2	19

Notes: Comparison of mean number of seeds is based on Kruskal-Wallis analysis of variance and includes only those birds with a minimum of three fecal samples. Bird mass is provided parenthetically below bird species codes. Bird codes are: MOLE = *Mionectes oleagineus*, COLE = *Corapipo leucorrhoa*, PIME = *Pipra mentalis*, HYMU = *Hylocichla mustelina*, EUGO = *Euphonia gouldi*, and CHCA = *Chlorothraupis carmioli*.

† Kruskal-Wallis $\chi^2 = 1.64$, df = 1, $P > 0.20$.
‡ Kruskal-Wallis $\chi^2 = 5.08$, df = 3, $P > 0.15$.
§ Kruskal-Wallis $\chi^2 = 8.14$, df = 5, $P > 0.14$.
‖ Kruskal-Wallis $\chi^2 = 7.12$, df = 3, $P > 0.05$.

in a similar way among habitats, with the greatest number of seeds deposited in slope followed by ridge and then lowland habitats in all cases ($W = 1$; $\chi^2 = 12.0$, df = 2, $P \leq 0.001$, which rejects the null hypothesis of no association among bird species). We failed, however, to reject the null hypothesis for the other three shrub species, indicating that birds likely dispersed the seeds among habitats in different ways; *Miconia*: $W = 0.75$, $\chi^2 = 3.0$, df = 2, $P \geq 0.05$, test using *Corapipo* and *Pipra* only; *Ossaea*: $W = 0.33$, $\chi^2 = 2.00$, df = 2, $P \geq 0.10$, *Corapipo, Pipra,* and *Euphonia*; and *Clidemia*: $W = 0.44$, $\chi^2 = 3.50$, df = 2, $P \geq 0.05$, *Corapipo, Pipra, Hylocichla,* and *Chlorothraupis* (Fig. 1).

Distribution patterns of seeds deposited by a given bird species often differed from distribution patterns of adult plants (i.e., divergence of values from 0 in Fig. 1). When dispersal by all frugivores combined was examined, the distribution of seeds among habitats matched that of adult plants except in the case of *Ossaea* (Fig. 1). Moreover, the deviations between the two distributions (i.e., height of bars in "Total" frugivore category, Fig. 1) were usually smaller than those between individual frugivores and respective fruiting plants (i.e., height of bars for individual bird species), thus indicating complementarity among birds in where seeds were deposited. In some cases, deposition of seeds by individual bird species matched the distribution of adult plants quite well, which suggests that seeds may remain in the vicinity of adults and that dispersal may be quite local (e.g., see patterns for *Miconia* dispersed by *Pipra,* Fig. 1). Even when perfect concordance between the two distributions occurred (as indicated by the plus sign in Fig. 1), deviations might still be high (e.g., *Chlorothraupis* and *Henriettea,* Fig. 1), indicating that birds brought proportionately more seeds into the habitat where the greatest proportion of adults occurred. Yet birds also deposited seeds outside of the major habitat of adults. For example, *Corapipo* delivered relatively more seeds of *Clidemia* outside of dominant habitats of fruiting adults. Similarly, *Pipra* and *Euphonia* deposited proportionally more *Ossaea* seeds in ridge and slope habitats compared to the distribution of fruiting adults (Fig. 1).

In summary, differences likely exist among bird species with respect to the quality component of dispersal effectiveness for plant species, although these differences were least pronounced for *Henriettea.* Seed-deposition patterns were generally not consistent across plant species for any single frugivore species; the hab-

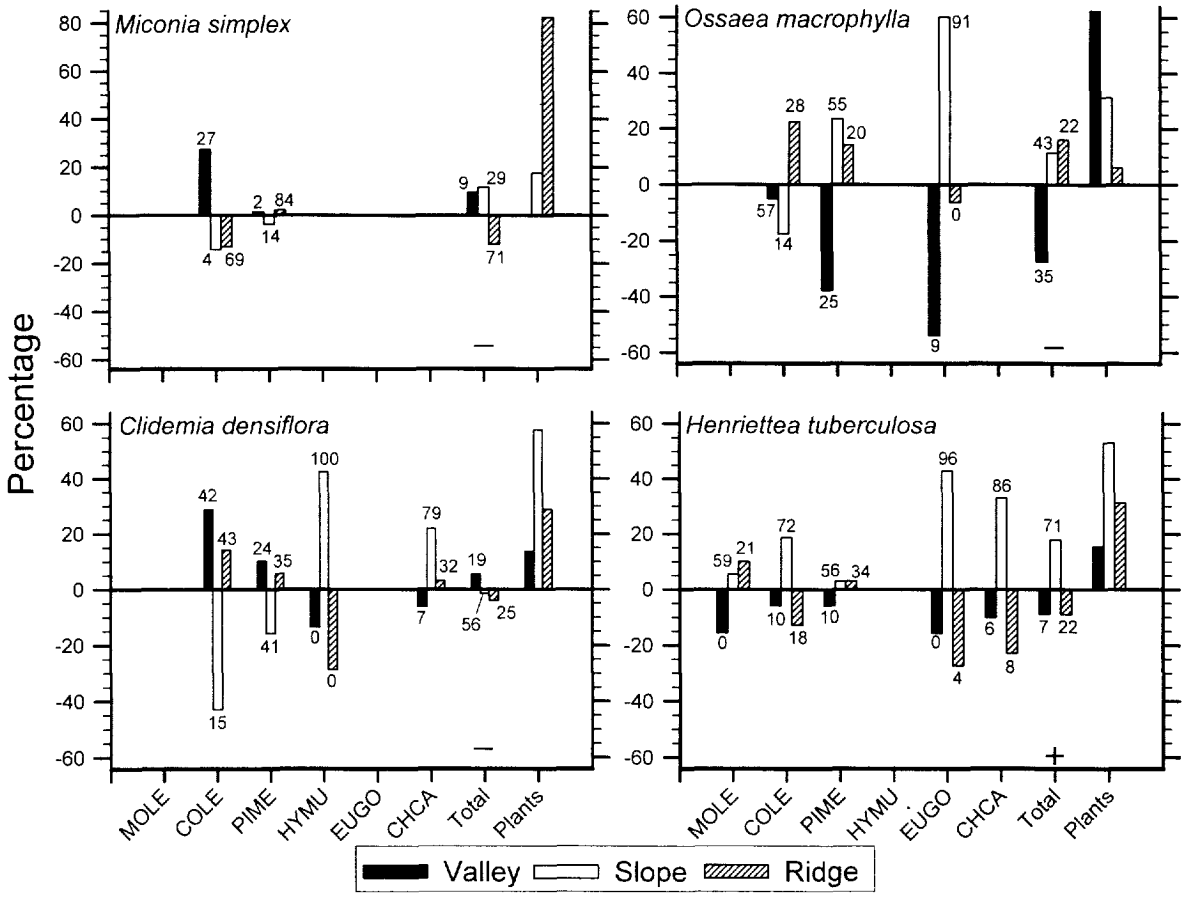

FIG. 1. Difference between the proportion of seeds dispersed by birds and the proportion of adult fruiting plants in three habitats for four shrub species in the Melastomataceae in lowland wet forest. (Note that the scale for *Miconia simplex* differs from the scale drawn for the other three plant species.) Positive percentages indicate that proportionately more seeds were deposited in that habitat, whereas negative percentages indicate that proportionately fewer seeds were deposited in that habitat when compared to the proportion of adult plants. Deviations are shown only for those bird species that contributed >5% of the estimated seeds removed. (Although *Hylocichla* removed >5% of seeds from *Miconia*, it was not included because seed totals were based on a single fecal sample [Table 2].) The percentage of seeds deposited in each habitat is indicated above or below the bar. For example, 27% of *Miconia simplex* seeds dispersed by COLE were dispersed into lowland sites; this represents a deviation of 27% relative to the distribution of adult plants because no adults were found in lowland sites. In contrast, 69% of the seeds were dispersed into ridge sites, representing a difference of −13% because 82% of *Miconia* adults were found in ridge sites. For definition of bird code names, see Table 2 caption. Total = sum of all six bird species.

Results of Kendall's coefficient of concordance tests are indicated by "+" when deposition patterns are significantly concordant ($W = 1$, $\chi^2 = 4.0$, df = 2, $P < 0.05$), and "−" when patterns are not significantly concordant ($W \leq 0.75$, $\chi^2 \leq 3.5$, df = 2, $P > 0.05$).

The distribution of adult plants among habitats is shown at the far right for comparison. Plants = fruiting adult plants.

itat that received the most or fewest seeds differed depending on which plant species was consumed.

DISCUSSION

Dispersal effectiveness

Results of this study demonstrate that birds are not equivalent in their ecological roles as seed dispersers for these four Melastome shrubs; bird species differ in both the quantity and quality components of seed dispersal. In terms of the number of seeds removed (quantity component), the most frequently captured frugivore was the most effective disperser for three of the four plant species. Yet, abundance alone was not a valid predictor of effectiveness, as the second most frequently captured frugivore, *Mionectes*, was relatively unimportant as a disperser for these Melastomes. Clearly, differences in fruit selection among bird species influence the quantity component of dispersal effectiveness,

with some birds consuming fewer or more seeds than would be expected based on the seeds' relative abundance.

The quality component of dispersal effectiveness is determined both by the treatment of seeds within the gut and by where seeds are deposited (Schupp 1993). Seed treatment was not evaluated in this study but it is likely to be equivalent among bird species given the small seed size and rapid gut passage times (e.g., see Ellison et al. 1993). Seed-deposition patterns differed among the bird species for three of four plant species, suggesting that birds differed in this component of dispersal effectiveness due to patterns of habitat selection following fruit consumption. However, to best evaluate differential effectiveness of these birds in terms of dispersal quality, we would need information on the probability of a seed surviving to become a reproductive adult in a given habitat. We do not yet have this information, so interpretation of relative dispersal quality provided by these six bird species is speculative.

If seeds survive equally well in all habitats and are treated similarly in digestive systems of birds, then *Pipra* is the most effective disperser for all plant species except *Clidemia,* and *Chlorothraupis* is the most effective disperser for *Clidemia* based on the quantity component of dispersal effectiveness. Moreover, one might speculate that *Pipra* has, in large part, "shaped" the current distribution of adult *Miconia* and *Henriettea* as the deviations between the distribution patterns of seeds left by this bird and that of adults are relatively minor (Fig. 1; see Herrera 1985).

However, if probability of plant survival is highest in habitats in which the greatest proportion of adults occur, then the most effective disperser for *Ossaea* is likely *Corapipo* (see Schupp [1995] and Schupp and Fuentes [1995] for a discussion of concordance among plant life-history stages). In this case, the quality component of dispersal becomes important, as *Corapipo* deposits most seeds (58%) in lowland habitats where adults are most common and seed and seedling survival are presumed to be highest. In contrast, *Pipra,* which removes the most seeds, leaves only 25% of those seeds in lowland habitats (Fig. 1). Under this scenario of seed and seedling survival being greatest in sites where adults are most common, the quality component of dispersal also becomes important for *Miconia* and *Clidemia.* For these two plants, the bird species that provides the greatest quantity of dispersal also provides the best quality. Finally, for *Henriettea* under this scenario, dispersal effectiveness likely is more equivalent among bird species because birds (e.g., *Euphonia, Chlorothraupis*) that remove fewer seeds (i.e., contribute less to the quantity component of dispersal effectiveness) bring proportionately more of them to habitats where adult plants are commonly found. Thus, this increased quality of seed dispersal may compensate for lower quantity of seed dispersal (Fig. 1).

Thus, it would appear that frugivorous bird species may at times have high quantity components of dispersal effectiveness, at other times high quality components, and on occasion, have both high quality and quantity components.

Implications for plant populations

Knowledge of events at early plant life-history stages is necessary to interpret the abundance and habitat associations of later stages, and to interpret quality components of dispersal effectiveness (De Steven 1991, Jordano 1992, Herrera et al. 1994, Schupp 1995, Schupp and Fuentes 1995). Spatial patterns of seed deposition by the different dispersal agents may cascade through the entire recruitment phase or may be partially or largely masked by events acting on seed and seedling survival (De Steven 1991, Jordano and Herrera 1995). For plants with a dispersal agent that consistently provides both high quantity and quality seed dispersal, the deviations between seed, seedling, and adult distributions are expected to be low (Schupp 1993).

There have been few studies that have dissected the ecological roles of the assemblage of seed dispersers that visit a plant (but see Howe 1980, Herrera and Jordano 1981, Howe and VandeKerckhove 1981, Hoppes 1987, Murray 1988, Horvitz and Schemske 1994). The assemblage of species that consume fruits of tropical plants can be quite large (e.g., Kantak 1979). However, the set of effective dispersers may often be quite small, as appears to be the case for the four shrub species in this study. Although we have captured 27 frugivore species at this lowland forest site, 95–99% of seeds recovered in feces were from 6 bird species. For some shrubs, the set of effective dispersers was essentially two or three species (Fig. 1). Consequently, interactions between avian seed dispersers and fruiting plants may be much more specific in forest understory at La Selva when compared to other systems, especially the species-rich tropical canopy. This higher degree of specificity does not, however, imply that such mutualisms are more co-evolved (Wheelwright and Orians 1982, Herrera 1986). Yet, it may mean that the local disappearance of a single seed disperser may have a significantly larger impact on the abundance and distribution of the plants whose seeds they disperse (Howe 1984). The ecology of seed dispersal is indeed complex, and our ability to understand the relative importance of contributing processes and players will require in-depth studies that integrate among plant stages and environmental scales (Herrera et al. 1994, Alvarez-Buylla et al. 1996; cf. Jordano 1992).

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LITERATURE CITED

Alvarez-Buylla, E. R., A. Chaos, D. Piñero, and A. A. Garay. 1996. Demographic genetics of a pioneer tropical tree species: patch dynamics, seed dispersal, and seed banks. Evolution **50**:1155–1166.

Blake, J. G., and B. A. Loiselle. 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. Auk **108**:114–127.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology **72**:1076–1088.

Ellison, A. M., J. S. Denslow, B. A. Loiselle, and D. Brenés M. 1993. Seed and seedling ecology of Neotropical Melastomataceae. Ecology **74**:1733–1749.

Gentry, A. H. 1982. Patterns of neotropical plant species diversity. Evolutionary Biology **15**:1–84.

Herrera, C. M. 1985. Habitat–consumer interactions in frugivorous birds. Pages 341–365 *in* M. L. Cody, editor. Habitat selection in birds. Academic Press, Orlando, Florida, USA.

———. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. Pages 5–20 *in* A. Estrada and T. H. Fleming, editors. Frugivores and seed dispersal. Dr. W. Junk, Dordrecht, The Netherlands.

Herrera, C. M., and P. Jordano. 1981. *Prunus mahaleb* and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. Ecological Monographs **51**:203–221.

Herrera, C. M., P. Jordano, L. López Soria, and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs **64**:315–344.

Hoppes, W. G. 1987. Pre- and post-foraging movements of frugivorous birds in an eastern deciduous forest woodland, USA. Oikos **49**:281–290.

Horvitz, C. C., and D. W. Schemske. 1994. Dormancy and seedling emergence of an ant-dispersed tropical herb, *Calathea ovandensis*. Ecology **75**:1949–1958.

Howe, H. F. 1980. Monkey dispersal and waste of a neotropical fruit. Ecology **61**:944–959.

———. 1984. Implications of seed dispersal by animals for tropical reserve management. Biological Conservation **30**: 261–281.

Howe, H. F., and G. A. VandeKerckhove. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology **62**:1093–1106.

Jordano, P. 1992. Fruits and frugivory. Pages 105–156 *in* M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. Commonwealth Agricultural Bureau International, Wallingford, UK.

Jordano, P., and C. M. Herrera. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. EcoScience **2**:230–237.

Kantak, G. E. 1979. Observations on some fruit-eating birds in Mexico. Auk **96**:183–186.

Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology **69**:1076–1089.

Loiselle, B. A., and J. G. Blake. 1990. Diets of understory fruit-eating birds in Costa Rica. Studies in Avian Biology **13**:91–103.

Loiselle, B. A., and J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology **72**:180–193.

Loiselle, B. A., and J. G. Blake. 1993. Spatial dynamics of understory avian frugivores and fruiting plants in lowland wet tropical forest. Vegetatio **107/108**:177–189.

McDade, L. A., and G. S. Hartshorn. 1994. La Selva Biological Station. Pages 6–14 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. La Selva: ecology and natural history of a Neotropical rain forest. University of Chicago Press, Chicago, Illinois, USA

Murray, K. G. 1988. Avian seed dispersal of three Neotropical gap-dependent plants. Ecological Monographs **58**:271–298.

Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. Ecology **70**:137–145.

Remsen, J. V., Jr., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk **113**:381–398.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio **107/108**:15–29.

———. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany **82**:399–409.

Schupp, E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. EcoScience **2**:267–275.

Wheelwright, N. T., and G. H. Orians. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist **119**:402–413.