



Composition and clumping of seeds deposited by frugivorous birds varies between forest microsites

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More frequent deposition of seeds by frugivores beneath plants in fruit could impose spatial limits to the distribution of plants dispersed by animals and contribute to species coexistence. Also, differences in diet and use of microhabitats by seed dispersers could promote spatial variation in the combination of seed species deposited. We investigated patterns of seed deposition of *Miconia fosteri* and *Miconia serrulata* (Melastomataceae) by birds in the Amazon. The goal was to determine how distribution and abundance of fruiting plants, both con- and hetero-specifics, affect the spatial variability in clumping and composition of multi-specific seed deposition. We established two 9-ha plots in undisturbed terra-firme understorey in the Ecuadorian Amazon. Seed rain was sampled with seed traps located in four microsites: below plants of the focal species, below *Anthurium eminens* (Araceae), and in randomly selected microsites. We examined seed deposition in these microsites in relation to habitat, fruiting neighborhood (fruit abundance, and distance to and density of plants of the target species), and crop size of *M. fosteri* or *M. serrulata* to determine if microsites differed in abundance and species composition of seeds. Seed traps below plants in fruit received more seeds than did randomly located traps. Seeds of the target species were, moreover, more commonly deposited below con- rather than hetero-specific plants. Seed aggregation below fruiting plants increased in forest neighborhoods where the abundance of fruits and the combination of fruiting plant species contributed to the arrival of seeds. Microsites differed notably in the combination of seeds deposited by frugivores, and differences were less pronounced among microsites that received seeds of *M. fosteri* and *M. serrulata* than among all microsites where at least some seed species were deposited by birds. We demonstrate that two closely related, ecologically similar species possess many similarities in their patterns of seed deposition and in the factors that affect those patterns. The combination of seed species deposited below foci of dispersal depended on the fruiting plant species, and the spatial patterns of seed deposition varied with the location of the microsite and the combination of co-dispersed species in the neighborhood. Similar species that share the same dispersers were confronted with different combinations of seeds depending on the microsite where they arrived, which could promote forest heterogeneity in the combination of plant species.

Patterns of seed deposition by animals are a central aspect of plant population dynamics because they establish the spatial template from which post-dispersal processes determine recruitment of new reproductive individuals (Nathan and Müller-Landau 2000, Wang and Smith 2002). Knowledge of spatial patterns of deposition, and the mechanisms that promote them, is fundamental for understanding how the mother plant and its surroundings influence abundance and distribution of plants in the population, and for understanding how frugivores affect the distribution of the plants (Willson and Traveset 2000, Levine and Murrell 2003). Patterns of seed rain in a population are a combined result of the contribution of all plants whose seeds were dispersed. Further, the spatial distribution of dispersed seeds often reflects both the structure of the habitat and the habitat preferences of the dispersers (Kollmann 2000, Calviño-Cancela 2002).

In plants dispersed by birds, patterns of seed deposition are complex, molded by attributes of the landscape that influence movements of the dispersers, by the production of fruits, and by the distance to the mother plants (Alcántara et al. 2000, Jordano et al. 2007, Levey et al. 2008). Concentration of seeds below sites where frugivores spend more time (sites for display, rest and eating) causes spatially contagious patterns of deposition (Wenny and Levey 1998, Schupp et al. 2002, Clark et al. 2005), with consequences for patterns of recruitment. Because the diets of frugivorous birds include multiple fruit species which they encounter while foraging, bird droppings typically include more than one seed species. Thus, several seed species co-occur in deposition sites (Kwitt et al. 2004, García et al. 2007). This could generate different combinations of seeds in deposition sites, where the probability of individual survival depends on the context of coexisting seeds (Loiselle 1990, Schupp et al. 2002, Kwitt et al. 2004).

The scale of habitat seems to be appropriate for studying the most significant processes that control seed rain (Kollmann 2000). For example, in landscapes with discontinuous tree cover, open sites receive fewer seeds dispersed by birds from the forest (Jordano and Schupp 2000, García et al. 2010). Within the forest, deposition of seeds is conditioned by the heterogeneous structure of the canopy and by the fruiting neighborhood. Many seeds fall or are deposited beneath the mother plant, contributing in large measure to the spatial aggregation of seeds (Godoy and Jordano 2001). The spatial structure of seed rain mediated by avian frugivores also could be strongly influenced by the neighborhood of con- and hetero-specific plants with synchronous fruiting, as these may act as dispersal foci (Herrera et al. 1994, Clark et al. 2004, Kwitt et al. 2004). Birds that visit new sites for feeding move the seeds from the parent plants, and in this manner, the plants of the neighborhood that share dispersers contribute strongly to the deposition of seeds beneath their crowns. At a smaller scale, plants with larger fruit crops, where the activity of frugivores should be more intense (Howe and Estabrook 1977, Ortiz-Pulido et al. 2007, Blendinger et al. 2008), contribute to the spatial variation in seed rain by receiving more seeds beneath their crowns than do plants with smaller crops (Takahashi and Kamitani 2004, Christianini and Oliveira 2009). The more frequent deposition of seeds beneath plants in fruit could be a key mechanism that imposes spatial limits to the distribution of plants dispersed by animal vectors and, thus, contributes to the coexistence of species. Such a pattern would seem to contradict one of the advantages of seed dispersal, to avoid the high density-dependent mortality of seeds and seedlings beneath the mother plant (Kwitt et al. 2004). Similarly, it could limit the arrival of seeds to sites adequate for establishment, with consequences that could scale from the population dynamics of one species (Herrera et al. 1994, Russo and Augspurger 2004) to maintenance of plant diversity in the whole community (Nathan and Müller-Landau 2000).

Here, we investigated the patterns of seed deposition of *Miconia fosteri* and *Miconia serrulata* (Melastomataceae) by birds in the upper basin of the Amazon, taking into account both the microsite where seeds were deposited and production of ornithochorous fruits in the neighborhood of deposition microsites. The first objective of this study was to examine how, through its influence on the activity of frugivores, the presence and attributes of plants in fruit determine the distribution of seeds in the forest soil. For plants dispersed by animal vectors, the presence of plants in fruit could be more important than the distance to the source as an influence on aggregation of seeds (Willson and Traveset 2000). The second objective was to examine if the identity of the fruiting plant determines the deposition of specific combinations of seeds below its crown. In addition to the quantity of seeds, the combination of species of seeds that are deposited together also could vary among foci of dispersal (Loiselle 1990, García et al. 2007). To examine the nature of the patterns of seed deposition of *M. fosteri* and *M. serrulata*, we evaluated the following specific questions. (1) What are the patterns of seed deposition below conspecifics and other species with synchronous fruiting phenology whose fruits are frequently consumed by dispersers? (2) How is deposition of seeds affected by spatial variation (distance and aggregation)

in the production of fruits? (3) How variable is the combination of species of seeds that arrive below different foci of deposition? To answer these questions, we evaluated deposition of seeds by birds below plants of three species of fruits (*Anthurium eminens*, *M. serrulata* and *M. fosteri*) that were consumed with great frequency by the dispersers of the two target *Miconia* species.

Methods

Study site

The investigation was carried out in the Tiputini Biodiversity Station, Orellana Province, Ecuador (0°38'S, 76°08'W, 190–270 m elevation). Its 650 ha of undisturbed lowland rainforest are within the ~1.7 million ha of the Yasuní Biosphere Reserve. Located on the north bank of the Tiputini River, it hosts a variety of habitats dominated by terra firme forests dissected by numerous ravines. The mean annual precipitation is approximately 2800 mm (1998–2002, <www.usfq.edu.ec/1TIPUTINI/research.html>). More than 65% of the annual rain falls during the rainy season (April to August), with an average monthly rainfall of 390 mm. Two 9-ha plots (300 × 300 m each) were established in terra firme forest and were gridded (50 × 50 m grid lines, 36 cells per plot). Plots ranged from 200 to 230 m in elevation; streams and ravines contributed substantially to forest heterogeneity. We classified grid cells into three categories according to topographic relief: (1) bottom of ravines, including the lowest part of the slopes, usually with a narrow and shallow stream (hereafter called bottom); (2) high sites, including ridges and the upper part of the slopes (ridge); (3) slopes, intermediate between streams and ridges. We used the maximum and minimum elevations per cell to assign every cell to one of three habitats (Blendinger et al. 2008).

Between May and August 2003, the seed rain of *Miconia fosteri* and *M. serrulata* was studied on the two plots using seed traps. Although seed rain was studied during a single fruiting season, we found that interannual variation in fruit production of *M. fosteri* and *M. serrulata* was very low between 2002 and 2003. Melastomes are conspicuous constituents of terra firme forest understories; *Miconia* is the most speciose melastome genus in the region (Tuomisto et al. 2002).

Study species

Miconia fosteri and *M. serrulata* reach up to 6 m tall in the understory of undisturbed terra firme forest. *Miconia fosteri* adult plants were more abundant on ridges and less abundant in bottomlands, whereas *M. serrulata* was more abundant on slopes and less abundant in bottomlands (Blendinger et al. 2008). Fruit maturation occurred during the rainy season. Most fruits ripened from May to July in *M. fosteri* and from June to August in *M. serrulata*. Total fruit production was very similar for both species, although *M. serrulata* plants were less abundant and had larger mean crop size than *M. fosteri* (Blendinger et al. 2008). Fruits of both species are small subspherical berries, dark purple when ripe, similar in size (*M. fosteri* mean fruit diameter ± standard deviation (SD)

6.2 ± 0.8 mm, *M. serrulata* 8.4 ± 0.9 mm). Each fruit has numerous tiny seeds (*M. fosteri* mean seed number per fruit 198.4 ± 31.2, n = 40; *M. serrulata* 267.0 ± 60.0, n = 40), ranging in size between 0.6–0.8 × 0.3–0.5 mm.

We mapped the location of all fruiting plants of both study species in the plots prior to fruit ripening. We measured fruit crop size by counting all fruits on each plant at the beginning of the dispersal period, except for two *M. serrulata* plants with more than 3000 fruits whose crop size was estimated to the nearest 100. We used these fruit abundance measures to examine impact of fruit abundance on seed deposition at the microsite and habitat levels. In an interspecific comparison of the effectiveness of bird-mediated seed dispersal and their consequences for subsequent establishment processes (Blendinger et al. unpubl.), analysis of 299 fecal samples obtained from fruit-eating birds captured during extensive mist netting in the plots showed that *M. fosteri* and *M. serrulata* seeds were dispersed by only seven species of birds inhabiting the understory. These species were six manakins (Pipridae, golden-headed manakin *Pipra erythrocephala*, wire-tailed manakin *P. filicauda*, white-crowned manakin *P. pipra*, blue-crowned manakin *Lepidothrix coronata*, blue-backed manakin *Chiroxiphia pareola* and striped manakin *Machaeropterus regulus*) and the white-necked thrush *Turdus albicollis*, Turdidae.

Seed rain

Seed deposition was sampled with seed traps in four types of microsites: below three species of plants (i.e. *M. fosteri*, *M. serrulata* and *A. eminens*) frequently consumed by frugivores and in randomly selected microsites. Seed traps consisted of a plastic sheet suspended horizontally by four poles 0.5 m above the ground. In every grid cell, we arranged at random a seed trap composed of two 1.5 × 1 m plastic sheets 5 m apart, whereas we used traps of 1 × 0.5 m for sampling beneath plants with fruit. We used different size seed traps for the random locations and the focal plants because the smaller traps could be placed completely beneath the foliage of the target plant, whereas in random sites we used larger traps to increase the probability of obtaining fecal samples. Beneath plants with fruit, we arranged one seed trap below plants of *M. fosteri* and *M. serrulata*, but no more than one plant per species per cell and only under plants with a fruit crop of ≥ 70 fruits. Fruits of the hemi-epiphytic genus *Anthurium* (Araceae) are common in the diet of understory frugivores at the study site and in other tropical forests of the Neotropics (Loiselle and Blake 1990, Loiselle et al. 2007). *Anthurium eminens* was the most abundant species of the genus in fruit during the study period. In each cell where *A. eminens* was present, we arranged one seed trap below a plant with ripe fruits. Sample size differed between microsites because all three species did not occur in every cell; all 72 cells of the two plots combined had traps located at random, 67 had plants of *A. eminens* in fruit below which we placed seed traps, 22 had seed traps below *M. fosteri*, and 20 cells had traps below plants of *M. serrulata*. Four of 72 seed traps disposed randomly had some understory cover with fruit. The locations of all seed traps were mapped within the grids.

The study was conducted during two months from the end of May to the end of July 2003. To minimize potential

disturbance to frugivores, seed traps were installed before the start of the study and kept in place until the end of the sampling period. The combination of frequent precipitation and the minuscule size of the *Miconia* seeds imposed a challenge to sampling seed rain with seed traps. To accomplish this, we operated seed traps in a selected, separate group of cells each day of the study. The procedure consisted of cleaning the seed traps at dawn and collecting defecations in the traps in the evening or before the first rain of the day (6.7 h day⁻¹ on average). This method avoids errors due to loss of seeds by rainfall, allows differentiating seeds in feces from seeds in fallen fruit, and minimizes potential errors by post-dispersal predation of seeds. We sampled diurnal seed rain because it is known that birds are the main consumers of *Miconia* fruits in the Neotropics (Snow 1981, Stiles and Rosselli 1993, Michelangeli et al. 2008). In the randomly located seed traps, samples were distributed homogeneously throughout the dispersal phase of the two *Miconia* species, until a sample effort of at least 50 h was reached. Traps located below plants with fruit were operated only while there were mature fruits on the plant, up to 50 h of sample per trap, if possible. To reduce biases in the comparison of microsites with small differences in sample effort or in the area effectively sampled, we converted all the data to seeds deposited during 50 h in 0.5 m². Data obtained with this method reflect seed rain that results from the dispersal of seeds by distinct species of frugivores that remove and swallow the fruits.

All fecal samples were numbered and preserved in 95% alcohol. In the laboratory, we examined the samples under a stereo microscope to identify and count all the seeds. Identification of seeds was accomplished by comparison with reference material (i.e. herbarium plants, seed collection) that had been collected on the study plots and identified based on literature, comparison with material in the Herbario Nacional del Ecuador (QCNE), and by consulting specialists. Seeds of *Anthurium* were classified to the level of genus, given our inability to differentiate seeds at the level of species because of the similarity between species combined with the seed variability within species. We collected a total of 463 fecal samples from avian frugivores, of which 57% had seeds of *M. fosteri* (98 fecal samples with 6222 seeds) or of *M. serrulata* (167 fecal samples with 9017 seeds).

Each seed trap was classified according to type of microsite and habitat. Additionally, we calculated the abundance of fruits and density of fruiting plants of *M. fosteri* or *M. serrulata* in a radius of 20 m around each trap and the distance from the trap to the nearest fruiting plant of *M. fosteri* or *M. serrulata*. Previously, we demonstrated a positive association between the activity of frugivorous birds and crop size of *M. fosteri* and *M. serrulata* (Blendinger et al. 2008), so we also measured the distance to the nearest plant with a large fruit crop (defined as a crop size within the upper third of all observed crops, > 100 fruits in *M. fosteri* and > 409 fruits in *M. serrulata*). To calculate the distances between seed traps and plants in fruit, we generated a symmetric matrix of Euclidean distances based on the coordinates in the grids of the study plots. Abundance of fruits of *M. fosteri* and *M. serrulata* was calculated in a 20-m radius circle centered on the seed traps for the analysis at microsite level, or in the center of the cells of the 9-ha study plot grid for the analysis at the spatial level of cell.

Data analyses

For each species of *Miconia*, we analyzed the number of seeds deposited in seed traps by microsite (i.e. traps situated at random and below plants of *A. eminens*, *M. fosteri* and *M. serrulata*). In each microsite, we simultaneously analysed the direct effects of type of habitat (bottom, slope, ridge), fruiting neighborhood of the microsite (the abundance of fruits, distance to other plants and density of plants of the focal species), and crop size on quantity of seeds deposited. Patterns of seed deposition by microsite were analyzed by generalized linear models, with the dependent variable following a Poisson distribution and using log-link function to perform nonlinear transformation of the predicted values. To test if the presence of plants in fruit, considered as foci of dispersal, affected seed deposition of *M. fosteri* or *M. serrulata* at the level of cells, we used generalized linear models ANOVA where for each species we modeled the number of seeds deposited as a function of the presence of *A. eminens* and the abundance of fruits of *M. fosteri* and *M. serrulata*. In these analyses, we excluded cells with missing data (i.e. cells with fruiting plants of *M. fosteri* or *M. serrulata* but in which we did not measure seed rain in corresponding microsites). We estimated mean seed rain by cell as the number of seeds deposited per 0.5 m² trap, averaging the microsites in each cell. Deviance and Pearson χ^2 statistics were used to evaluate the goodness-of-fit of the generalized linear models. Seed counts showed right-skewed distributions and were square-root transformed to reduce the influence of outliers.

We used nonparametric analysis of similarity (ANOSIM module run on PRIMER, ver. 5; Clarke and Gorley 2002) to (1) determine if the four microsites received different combinations (i.e. composition and abundance) of seeds dispersed by birds and (2) determine if the microsites that received seeds of *M. fosteri* (or *M. serrulata*) differed in the combination of seeds deposited in the fecal samples. In the first case, we included all the seed traps where we obtained samples of dispersed seeds and in the second case the unit of sample was each trap that received seeds of *M. fosteri* or *M. serrulata*. The analyses of similarity permitted us to determine if all the combinations of seeds observed in traps below each microsite were more similar among each other than with respect to sites selected at random from among all the microsites. ANOSIM calculates the level of global difference among all the groups as well as the level of difference among all the pairs of microsites analyzed. Significance of ANOSIM test statistics were determined by comparison with values obtained by Monte Carlo randomization procedures with 9999 permutations. In all the analyses, we used Bray-Curtis similarity index without data transformation, standardising the original matrix by dividing each value by the total of the seed species and multiplying by 100. To explore differences among microsites in composition and abundance of seeds dispersed by birds, we conducted separate analyses on matrices of presence/absence and on matrices of seed abundance.

Results

Mean number of seeds deposited by birds differed significantly among microsites (*M. fosteri*, Wald $\chi^2_{(3)} = 107.25$,

$p < 0.001$; *M. serrulata*, Wald $\chi^2_{(3)} = 284.81$, $p < 0.001$), and was much greater below plants with fruit than in microsites distributed randomly below the canopy (Fig. 1A–B). Below plants with fruits, the mean number of seeds that arrived below conspecific plants was 1.5 times greater in *M. fosteri* and 3.0 times greater in *M. serrulata* than below plants of other species in fruit, although differences were significant only for *M. serrulata*.

Seed deposition by microsite

Miconia fosteri

Deposition of seeds below plants with fruits, but not at randomly selected microsites, was positively affected by the abundance of fruits at the three spatial levels analyzed: plant, neighborhood and habitat (Table 1). Crop size is a very local measure of fruit abundance that directly affected the deposition of seeds below the canopy of *M. fosteri* and *M. serrulata* plants. Crop size of the *M. fosteri* plant where we measured the seed rain was positively correlated with abundance of fruits of *M. fosteri* in the neighborhood ($R^2 = 0.46$, $n = 22$, $p < 0.001$), but not with the abundance of *M. serrulata* fruit ($p = 0.77$). Similarly, crop size of *M. serrulata* plants was positively correlated with *M. serrulata* fruit abundance in the neighborhood ($R^2 = 0.66$, $n = 18$, $p < 0.001$), but only marginally associated with the fruit abundance of *M. fosteri* ($R^2 = 0.21$, $p = 0.05$).

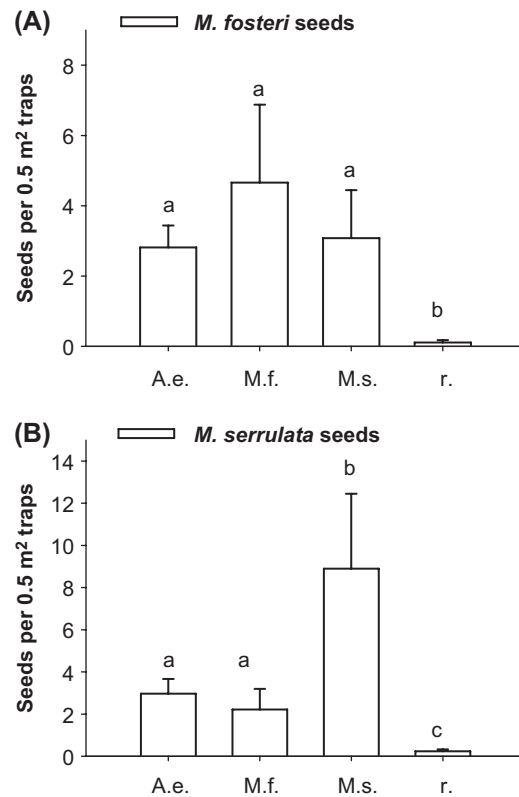


Figure 1. Seed deposition variation among microsites (A.e.: *Anthurium eminens*, M.f.: *Miconia fosteri*, M.s.: *Miconia serrulata*, r.: randomly disposed) by frugivorous birds in (A) *Miconia fosteri* (Wald $\chi^2_{(3)} = 107.25$, $p < 0.001$) and (B) *Miconia serrulata* (Wald $\chi^2_{(3)} = 284.81$, $p < 0.001$). Means and standard error bars are shown; means with different letters were significantly different.

Table 1. Effect tests for fruit-related determinants at three spatial levels (habitat, neighborhood and plant) on *Miconia fosteri* seed deposition in four microsites. Significant effects ($p < 0.05$) are highlighted in bold. Number of cells with seed traps for each microsite analyzed is in parentheses.

	<i>M. fosteri</i> (n = 22)			<i>M. serrulata</i> (n = 18)			<i>A. eminens</i> (n = 63)			Randomly located (n = 72)		
	Wald χ^2	DF	p-value	Wald χ^2	DF	p-value	Wald χ^2	DF	p-value	Wald χ^2	DF	p-value
Habitat [†]	4.54	2	0.10	4.24	1	0.04	35.49	2	<0.001	4.70	2	0.10
<i>M. fosteri</i> plant density (0.126 ha)	12.93	1	<0.001	3.72	1	0.05	0.73	1	0.39	1.29	1	0.26
Distance to nearest <i>M. fosteri</i> with large crop size	0.00	1	0.99	14.18	1	<0.001	0.04	1	0.84	2.93	1	0.09
<i>M. fosteri</i> fruit abundance (0.126 ha)	2.54 [§]	1	0.11	6.32	1	0.02	14.69	1	<0.001	1.53	1	0.22
<i>M. serrulata</i> fruit abundance (0.126 ha)	14.15	1	<0.001	10.84[§]	1	<0.001	6.62	1	0.01	0.52	1	0.47
Crop size	25.27	1	<0.001	12.93	1	<0.001						

[†]Three categories according to topographic relief: bottom of ravines, slopes and ridges.

[§]Does not include the plant crop size above the seed trap in *M. fosteri* and *M. serrulata* microsites.

Seed deposition below fruiting plants was positively affected by the abundance of fruits of *M. fosteri* or *M. serrulata* in the neighborhood, whereas the density of fruiting *M. fosteri* plants strongly affected the arrival of seeds below *M. fosteri* and was marginally significant below *M. serrulata* (Table 1). Shorter distance to a plant of *M. fosteri* with a large fruit crop only influenced arrival of seeds below *M. serrulata*, while there was no pattern in the deposition of seeds in randomly selected microsites (Table 1). Type of habitat significantly affected the deposition of *M. fosteri* seeds below plants of *M. serrulata* and of *A. eminens*.

Miconia serrulata

Deposition of *M. serrulata* seeds depended on *M. fosteri* and *M. serrulata* crop size above the microsite, on the spatial context of the microsite in the neighborhood and on the type of habitat, although the effect of each factor varied among seed deposition microsites (Table 2). Crop size of *M. serrulata* was positively correlated with the abundance of fruits of *M. serrulata* in the neighborhood ($R^2 = 0.55$, $n = 20$, $p < 0.001$) and weakly correlated with *M. fosteri* fruits ($R^2 = 0.20$, $p < 0.05$).

Similarly, crop size of *M. fosteri* plants where seed rain was measured was positively correlated with the fruit abundance of *M. fosteri* in the neighborhood ($R^2 = 0.55$, $n = 22$, $p < 0.001$), but not with *M. serrulata* fruit abundance ($p = 0.95$).

Abundance of fruits of *M. serrulata* or *M. fosteri* in the neighborhood positively affected the deposition of seeds in selected microsites below plants with fruits (Table 2). Distance to plants with large crops was negatively related to number of seeds deposited below *M. serrulata* and *M. fosteri*, whereas the density of fruiting plants only weakly affected deposition of seeds below *M. serrulata*. The type of habitat had little or no effect on deposition of seeds below fruiting plants. No neighborhood or habitat variables affected the deposition of seeds in microsites distributed randomly in the forest (Table 2), due in large part to the very low seed deposition by birds in microsites away from plants in fruit.

Seed deposition by site (0.25 ha cell)

The quantity of seeds deposited in one cell of the grid depended positively on the fruiting plants in the cell.

Table 2. Effect tests for fruit-related determinants at three spatial levels (habitat, neighborhood and plant) on *Miconia serrulata* seed deposition in four microsites. Significant effects ($p < 0.05$) are highlighted in bold. Number of cells with seed traps for each microsite analyzed is in parentheses.

	<i>M. serrulata</i> (n = 20)			<i>M. fosteri</i> (n = 22)			<i>A. eminens</i> (n = 63)			Randomly located (n = 72)		
	Wald χ^2	DF	p-value	Wald χ^2	DF	p-value	Wald χ^2	DF	p-value	Wald χ^2	DF	p-value
Habitat [†]	0.83	2	0.66	7.30	2	0.03	2.65	2	0.26	2.69	2	0.26
<i>M. serrulata</i> plant density (0.126 ha)	3.65	1	0.06	1.94	1	0.16	3.33	1	0.06	0.40	1	0.53
Distance to nearest <i>M. serrulata</i> with large crop size	5.35	1	0.02	12.92	1	<0.001	1.26	1	0.26	1.06	1	0.30
<i>M. serrulata</i> fruit abundance (0.126 ha)	2.24 [§]	1	0.13	2.15	1	0.14	3.71	1	0.04	0.34	1	0.56
<i>M. fosteri</i> fruit abundance (0.126 ha)	0.66	1	0.42	5.79[§]	1	0.02	3.37	1	0.05	1.99	1	0.16
Crop size	23.64	1	<0.001	10.81	1	0.001						

[†]three categories according to topographic relief: bottom of ravines, slopes and ridges.

[§]does not include the plant crop size above the seed trap in *M. fosteri* and *M. serrulata* microsites.

For *M. fosteri*, abundance of conspecific fruits exerted the greatest effect (Wald $\chi^2_{(1)} = 35.21$, $p < 0.001$), and there was a significant effect of the production of fruits of *M. serrulata* (Wald $\chi^2_{(1)} = 10.27$, $p = 0.001$) and of the presence of fruiting plants of *A. eminens* (Wald $\chi^2_{(1)} = 6.19$, $p = 0.01$). A similar pattern was found for *M. serrulata*, with a strong effect of conspecific fruit abundance (Wald $\chi^2_{(1)} = 68.02$, $p < 0.001$) and dependence on the abundance of fruits of *M. fosteri* (Wald $\chi^2_{(1)} = 6.64$, $p = 0.01$) and of the presence of *A. eminens* fruiting plants (Wald $\chi^2_{(1)} = 4.63$, $p = 0.03$).

Comparison of seed composition and abundance among deposition sites

We identified a total of 42 morphospecies of seeds in the fecal samples collected in the seed traps. The combinations of seeds dispersed by birds varied significantly among microsites. The global difference among microsites was similar whether based on the abundance of seeds deposited (ANOSIM Global $R = 0.17$, $p < 0.001$) or composition of seeds (Global $R = 0.21$, $p < 0.001$). Each microsite below a fruiting plant species was characterized by distinct seed combinations, including several species found only in a given microsite (Fig. 2). The *Anthurium* microsite received more exclusive seed species (e.g. melastome species such as *Blakea bracteata*, *Clidemia heterophylla*, *Miconia bubalina*, *Miconia triplinervis*) than other microsites (Fig. 2), probably because of the larger number of feces (53%) found there. Results of the paired comparisons among microsites differed between approaches. Using abundance of the species of seeds deposited below plants, sites below *M. serrulata* were significantly different from all other microsites (Table 3). In contrast, there was no difference between *M. fosteri* and either *A. eminens* or randomly disposed microsites (Table 3). Paired comparisons based on the identity of dispersed species demonstrated strong differences between *A. eminens* with *M. serrulata* or randomly selected microsites, but there were no significant differences in other paired comparisons (Table 3).

Considering only the combination of seeds in microsites where seeds of *M. fosteri* or *M. serrulata* arrived, we found few differences among microsites (abundance: Global $R = 0.07$, $p = 0.09$, composition: Global $R = 0.13$, $p = 0.01$). Paired tests demonstrated a similar tendency with both approaches, with differences in the deposition of seeds between randomly sites with *M. fosteri* and *A. eminens*, and between *M. serrulata* with *A. eminens* (Table 3).

Discussion

Spatial patterns of seed deposition

Fruiting plants in the understory act as foci for dispersal of seeds of *M. fosteri* and *M. serrulata*, receiving much greater quantities of seeds than do microsites representing conditions randomly available below the canopy. Among these foci of dispersal, avian frugivores dispersed more seeds below conspecific plants than below fruiting plants of other species whose fruits they consumed. In this way, the spatial distribution of adult plants had a strong influence on the deposition of conspecific seeds, spatially conditioning the probabilities

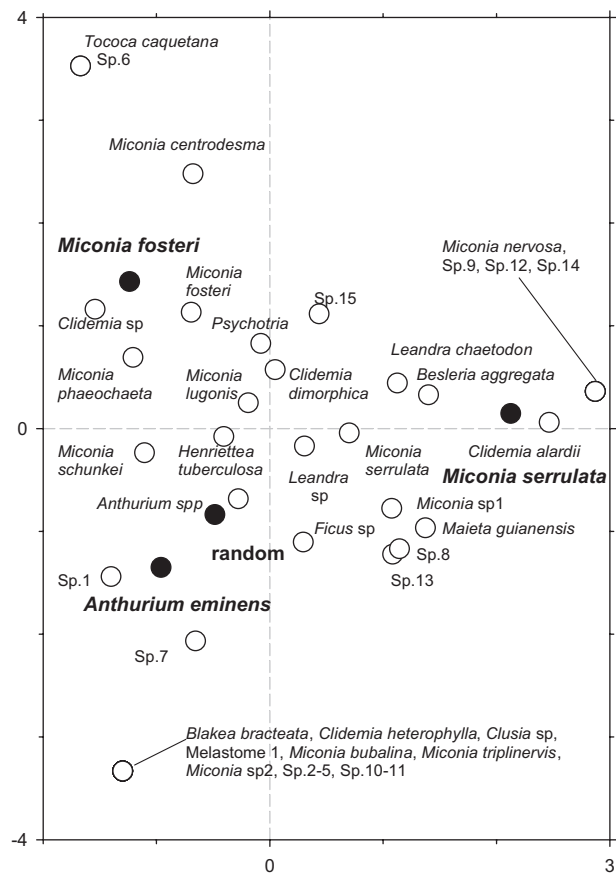


Figure 2. Correspondence analysis (CA) of the abundance of 42 seed species (*Psychotria* and *Anthurium* are morphospecies, including several species each) deposited by understory birds in four microsites (below fruiting plants of *Anthurium eminens*, *Miconia fosteri*, *Miconia serrulata*, and randomly disposed seed traps). First and second axes account for 49.1% and 26.9% of the total variance.

of recruitment of new individuals into the population. However, the overall abundance of fruits in their surrounding neighborhoods had a deciding role over the aggregation of seeds below fruiting plants, which could be explained by the capability of birds to track the abundance of fruits over small spatial scales (Moegenburg and Levey 2003, Saracco et al. 2004, Hampe 2008). Thus, the process of seed aggregation below the foci of dispersal increased in areas of forest where the surrounding abundance of fruits and the combination of species of fruiting plants contributed significantly to the arrival of seeds of both species.

In systems where deposition of seeds is strongly biased in favor of a restricted set of available microsites, recruitment of new individuals could be spatially limited by dispersal. Spatial variation among microsites where avian frugivores deposited seeds was due to the marked contrast between sites below fruiting plants and randomly located microsites that primarily represent areas of the understory without fleshy-fruited plants. We observed the same pattern for seven other small-seeded morphospecies (*Clidemia dimorphica*, *Henriettea tuberculosa*, *Leandra chaetodon*, *Miconia schunkei* Melastomataceae, *Besleria aggregata* Gesneriaceae, *Ficus* Moraceae and *Anthurium*) for which we had sufficient records ($n = 21\text{--}231$ fecal samples with seeds); seeds of these species also

Table 3. ANOSIM pairwise-test R values and p values for comparisons among microsites of seed deposition based on matrices of abundance (above the diagonal) and of presence/absence (below the diagonal) of all seed species found in fecal samples of birds that were recovered in seed traps. Significant effects ($p < 0.05$) are highlighted in bold.

Microsite	All seed traps receiving seeds				Seed traps receiving <i>M. fosteri</i> or <i>M. serrulata</i> seeds			
	<i>A. eminens</i>	<i>M. fosteri</i>	<i>M. serrulata</i>	Randomly located	<i>A. eminens</i>	<i>M. fosteri</i>	<i>M. serrulata</i>	Randomly located
<i>A. eminens</i>	—	R = 0.03 p = 0.32	R = 0.12 p = 0.03	R = 0.32 p < 0.001	—	R = 0.01 p = 0.42	R = 0.09 p = 0.06	R = 0.08 p = 0.17
<i>M. fosteri</i>	R = 0.01 p = 0.45	—	R = 0.14 p = 0.04	R = -0.05 p = 73.3	R = -0.08 p = 0.77	—	R = 0.16 p = 0.05	R = 0.23 p = 0.03
<i>M. serrulata</i>	R = 0.23 p = 0.002	R = 0.03 p = 0.29	—	R = 0.07 p = 0.03	R = 0.22 p = 0.001	R = -0.02 p = 0.54	—	R = -0.01 p = 0.47
Randomly located	R = 0.39 p < 0.001	R = -0.06 p = 0.82	R = 0.04 p = 0.10	—	R = 0.26 p = 0.005	R = 0.23 p = 0.03	R = -0.01 p = 0.48	—

arrived more frequently below fruiting plants than in randomly located microsites (χ^2 -test, all $p < 0.001$). These differences at a very small spatial scale determined a strongly grouped pattern of seed distribution in the soil of the forest. Although it is possible that ants secondarily redistribute the seeds deposited by birds, it would be difficult to modify the general pattern of variation in abundance produced by the primary dispersal, given that seeds manipulated by ants usually are not moved more than a few meters (Levey and Byrne 1993, Pizo et al. 2005, Gove et al. 2007). We did not follow seed fate after dispersal; however, one of the predicted consequences of contagious seed dispersal is elevated mortality of seeds. Sites with high concentrations of seeds could be associated with density-dependent mechanisms of regulation acting over the initial stages of recruitment (seed depredation, herbivory of seedlings, attacks on seeds and seedlings by pathogens, competition with adult plants where seeds were deposited, and competition with seedlings and saplings). The recruitment that results from these processes appears to be context dependent, and may or may not modify the spatial template established by dispersal (Herrera et al. 1994, Wenny 2000, Balcomb and Chapman 2003, Russo and Augspurger 2004), nevertheless, in most cases the probability that one seed is established and grows to adult size is lower below the foci of dispersal.

The reason why the quantity of seeds below plants of the same species was greater than below other species in fruit is not obvious. Seed rain was estimated from fecal samples and did not include seeds from fallen fruits. Thus, the greater frequency of deposition below conspecifics probably reflects the spatial knowledge that birds have about the availability of scattered and patchy resources within their territories, which could influence their foraging decisions during subsequent foraging bouts, allowing them to return to plants where probability of food reward is high (Hampe 2003, Temeles et al. 2006). Most seeds of *M. fosteri* and *M. serrulata* were dispersed by six species of manakins (Pipridae) (Blendinger et al. 2008), with *Pipra pipra* and *Lepidothrix coronata* accounting for more than 75% of the seeds dispersed. Manakins swallow the fruits whole and are likely to move seeds away from the parent plant, given that they stay a short time (<2–3 min) in each plant but need > 10 min after fruit ingestion for fruit processing and passing seeds of small-seeded fruits like *Miconia* (Levey 1986, Worthington 1989).

Many ecological factors could influence the behavior of birds and affect deposition of seeds below a plant with fruit. From the perspective of a frugivore, abundance and diversity of fruits (Moegenburg and Levey 2003, Saracco et al. 2004) and the presence of species of preferred fruits (Carlo et al. 2007) could be perceived by birds while they look for food, affecting their patterns of activity and contributing to the spatial distribution pattern of seed deposition. We found that the principal factor that determines arrival of seeds below a plant with fruit differed between microsites: crop size was very important for plants of the same species, whereas neighborhood or habitat characteristics were more influential for seed deposition below plants of other species. At a larger spatial scale, the arrival of seeds of *M. fosteri* and *M. serrulata* to sites in the forest depends strongly on the abundance and presence of plants with fruit in the neighborhood. Sites with a greater diversity of available fruits could experience a positive feedback if arrival of seeds is also greater; such a process could produce strong spatial structure in plant distribution patterns (Lázaro et al. 2005). For example, Ryder et al. (2006), in a study conducted at the same site, demonstrated that fruit was more abundant in areas of the forest where manakins were more active (i.e. leks). Such a pattern could have developed if the multispecific spatial template of seed deposition was maintained during the recruitment of adult plants; alternatively, manakins could establish their leks in areas where fruits were already more abundant.

In our study, crop size of one species of *Miconia* had a positive effect on the deposition of seeds of the other species, suggesting that, for foraging birds, similarities among these *Miconia* species (e.g. habitat overlap, nutrient and energy reward) may be more important than their differences (e.g. microhabitat mismatch, mean crop size, infructescence display). Previously, we demonstrated that in *M. fosteri* and *M. serrulata*, crop size and, in certain situations, aggregation of plants, positively influenced the quantity of fruits removed by birds (Blendinger et al. 2008). Fruit removal is a reflection of bird activity, which explains the strong effect of fruit abundance (in the plant and its neighborhood) on seed deposition. The effect of habitat type on seed deposition of *M. fosteri* matched the distribution of adult plants and the production of fruits reported for the study site (Blendinger et al. 2008). In *M. serrulata*, where the number of plants with fruit was greater on slopes, we found a weak effect of habitat type on

arrival of seeds. Our results suggest a spatial coupling (sensu Jordano and Herrera 1995) between habitats of production and seed deposition for both species.

Dispersed seed combination at microsites

In megadiverse tropical forests, the web of plant-seed disperser interactions is dominated by generalist frugivores that consume and disperse a wide variety of plant species. In the study area, all species of manakins together disperse more than 150 species of seeds (Ryder et al. 2006, Loiselle et al. 2007), generating a complex pattern of multi-specific seed rain. Although it is known that dispersal by frugivores can lead to strongly clumped patterns of seed deposition (Schupp et al. 2002, Levine and Murrell 2003), mechanisms of spatial variability in clumping and composition of multi-specific seed rain are not well understood. Here, we provide an empirical demonstration that distribution and composition of fruiting plants determine the combination of seeds dispersed by animals. We report notable differences among microsites in the combination of seeds that arrive in the feces. These differences principally occurred between randomly located microsites and below plants of *A. eminens*, but the combination of seeds also varied among pairs of microsites located below distinct foci of dispersal. Variation in the combination of seeds was due both to variation in relative abundance of each species of seed and to differences in the composition. The relative importance of the abundance of different species of seeds or of the composition of seed species as the main source of variation in seed combinations among microsites was variable and specific to every comparison.

We demonstrated that the combination of seeds among microsites that received seeds of *M. fosteri* and *M. serrulata* differed less than among all microsites where seeds dispersed by avian frugivores arrived. This indicates an important aspect that merits more consideration in future studies for their potential consequences over dynamics of recruitment: for an individual species, the possible combination of species with which a seedling must compete represents only a fraction of the spectrum of seed combinations that are dispersed to available microsites. This leads to a questions for further research on dispersal of fleshy-fruited species. Do distinctive patterns of seed combinations determined by deposition microsites lead to different outcomes for recruitment of individual species, whose survival depends on the species with which it is deposited?

Conclusions

Our comparison of two closely related, ecologically similar species, *M. fosteri* and *M. serrulata*, that synchronously share the same dispersers, demonstrated that they possess many similarities in their patterns of seed deposition and in the factors that affect those patterns. A disproportionately large number of dispersed seeds were deposited below focal plants, to which seed dispersers were attracted because of the abundance of fruits both on the plant and in the neighborhood. In spite of the fact that certain conditions that favor recruitment might be more favorable below foci of dispersal (e.g. avoidance of predators of less preferred species, García et al.

2007), the bulk of evidence strongly suggests that in tropical rain forest, microsites with high seed deposition suffer a higher seed and seedling mortality (Janzen 1970, Wills et al. 1997, Harms et al. 2000). In such cases, seed dispersal quality in terms of recruitment probability should be very low, because it does not enable seeds and seedlings to escape high density-dependent mortality.

The influence of the spatial distribution of fruiting trees on the composition of seeds deposited in different microsites is poorly understood (Schupp et al. 2002, García et al. 2007). We have provided new information about the mechanisms that determine non-random patterns of seed combinations deposited by frugivorous animals. We demonstrated that the combination of species of seeds deposited by birds below foci of dispersal depends on the species of plant with fruit, where spatial patterns of seed deposition vary with the position and location of the microsite and on the combination of co-dispersed species in the neighborhood.

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