

Crop size, plant aggregation, and microhabitat type affect fruit removal by birds from individual melastome plants in the Upper Amazon

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Abstract We studied the efficiency (proportion of the crop removed) and quantitative effectiveness (number of fruits removed) of dispersal of *Miconia fosteri* and *M. serrulata* (Melastomataceae) seeds by birds in lowland tropical wet forest of Ecuador. Specifically, we examined variation in fruit removal in order to reveal the spatial scale at which crop size influences seed dispersal outcome of individual plants, and to evaluate how the effect of crop size on plant dispersal success may be affected by conspecific fruit abundance and by the spatial distribution of frugivore abundance. We established two 9-ha plots in undisturbed terra-firme understory, where six manakin species (Pipridae) disperse most seeds of these two plant species. Mean levels of fruit removal were low for both species, with high variability among plants. In general, plants with larger crop sizes experienced greater efficiency and effectiveness of fruit removal than plants with smaller crops. Fruit removal, however, was also influenced by microhabitat, such as local topography and local neighborhood. Fruit-rich and disperser-rich patches overlapped spatially for *M. fosteri* but not *M. serrulata*, nonetheless fruit removal of *M. serrulata* was still much greater in fruit-rich patches. Fruit removal from individual plants did not decrease in patches with many fruiting conspecifics and, in fact, removal effectiveness was enhanced for *M. fosteri* with small crop sizes

when such plants were in patches with more conspecifics. These results suggest that benefits of attracting dispersers to a patch balanced or outweighed the costs of competition for dispersers. Spatial pattern of fruit removal, a measure of plant fitness, depended on a complex interaction among plant traits, spatial patterns of plant distribution, and disperser behavior.

Keywords Fruit-eating bird · Manakin · *Miconia fosteri* · *Miconia serrulata* · Seed dispersal

Introduction

Fruit consumption by vertebrates can influence the dynamics of plant populations as frugivores differentially disperse seeds away from the parent plant where intraspecific competition and predation risk often are intense and survival of seeds and seedlings low (Janzen 1970; Howe and Smallwood 1982; Augspurger 1983; Howe et al. 1985; Hammond and Brown 1998). Demographic consequences for plants of this mutualistic interaction with seed dispersers depend on the spatial patterns of fruit removal and seed deposition (Loiselle et al. 1995; Jordano and Godoy 2002; Russo and Augspurger 2004). Fruit consumption can influence plant demography directly through the actual removal of seeds and indirectly based on the condition and location in which seeds are deposited (cf. Schupp 1993).

All stages in the seed dispersal process vary across spatial scales and environmental gradients, and often are context-dependent (Schupp 2007). For example, high intraspecific variation in fruit removal can occur both between (e.g., Herrera et al 1994; Alcántara et al. 1997; García et al. 2001) and within sites (Gryj and Domínguez 1996; Jordano and Schupp 2000; Ortiz-Pulido and Rico-Gray

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2000; Carlo 2005), as a function of plant and plant-neighborhood attributes, as well as the activity and habitat use patterns of the dispersers. Patchy distributions of plants and heterogeneous forest environments contribute to spatial and temporal variation in fruit resources (Levey 1988; Loiselle and Blake 1993; García and Ortiz-Pulido 2004). In some systems, the activity and distribution of frugivores may track this variation (Loiselle and Blake 1993; Rey 1995; Blake and Loiselle 2002; Saracco et al. 2004) with consequences for patterns of seed dispersal. At the plant level, number of fruits removed, a reflection of frugivore activity, can be positively correlated with fruit crop size, a very local measure of fruit abundance (e.g., Jordano and Schupp 2000; Ortiz-Pulido and Rico-Gray 2000). Yet, in other systems, dispersers showed little (van Ommeren and Whitham 2002; Parciak 2002; Saracco et al. 2005) or no tendency (Restrepo et al. 1999) to be more abundant in fruit-rich patches or to track fruit resources. In such cases, percentage of fruits removed may not be correlated with fruit crop size (Laska and Stiles 1994; Russo 2003).

The diversity of responses of fruit consumers to the spatial scale and distribution of fruit abundance may have species-specific consequences to plant fitness. Given that plants and frugivores are distributed heterogeneously in tropical lowland forests (Loiselle and Blake 1999; Blake and Loiselle 2002; Tuomisto et al. 2003), one can envision the forest environment as supporting patches that differ in fruit abundance and seed disperser availability. The degree to which these fruit-rich and disperser-rich patches overlap is expected to affect seed dispersal. If the number of seeds removed is a proxy of the reproductive success of an individual plant, then plants that grow in sites characterized by different environmental conditions or disperser assemblages likely will also differ in their reproductive outcomes and may influence the genetic structure of plant populations. Although recruitment processes following seed deposition may transform this initial stage set by fruit consumers, such changes are unlikely to negate entirely the importance of seed dispersal to plant recruitment (Herrera et al. 1994; Russo and Augspurger 2004).

In this study, we use two understory plants (*Miconia fosteri* and *M. serrulata*, Melastomataceae) in Amazonian lowland forests as our model system to investigate the efficiency (proportion of the crop removed) and quantitative effectiveness (number of fruits removed) of seed dispersal by birds. Ecological and morphological attributes are shared by these closely related plant species; fruits are similar in morphology, display, and patterns of ripening, and are consumed by the same suite of seed dispersers. Despite the fact that frugivory has been a central issue in ecology over the last 30 years (Levey and Benkman 1999; Wang and Smith 2002), surprisingly few studies have been undertaken to examine simultaneously the relative weight of ecological factors that affect fruit removal in

plant species sharing the same suite of seed dispersers. The similarities between *M. fosteri* and *M. serrulata* allow us to assess how intraspecific variation in fruit removal is affected by crop size and context-dependent environmental conditions, and to examine more generally the relative importance of ecological factors on the strength of the interaction between fleshy-fruited plants and fruit consumers through a hierarchy of structural heterogeneity levels that differ in spatial extent (García 2008). Specifically, we examine variation in fruit removal in order to reveal the spatial scale at which crop size influences seed dispersal outcome of individual plants, and to evaluate how the effect of crop size on seed dispersal is affected by conspecific fruit abundance and the spatial distribution of frugivores. We expect that plants with larger crop sizes experience greater fruit removal than plants with smaller crops, as the crop-size hypothesis predicts (Howe and Estabrook 1977). Furthermore, the presence of neighboring fruiting conspecifics is expected to increase the conspicuousness and attractiveness of the fruiting patch, as well as the predictability of rewards that a patch offers to fruit consumers. Nevertheless, benefits to individual plants in a fruiting patch may be restricted by intraspecific competition due to disperser limitation. Thus, aggregation of conspecific plants may result in either positive or negative effects on fruit removal from individual plants (Sargent 1990; Saracco et al. 2005; Carlo and Morales 2008). We predict that plants with small crop sizes might receive greater benefits, through increased seed-disperser activity, if they are located in patches with more fruit. We expect these relationships to be mediated, however, by spatial patterns of disperser activity.

As a group, manakin species (Pipridae) are the most numerous fruit-eating birds in the understories of neotropical wet forests. Spatial variation in the habitat use by manakins (e.g., Tello 2001; Blake and Loiselle 2002; Loiselle et al. 2007a) likely results in differential visitation to fruiting plants and a heterogeneous deposition of seeds into the forest environment (Loiselle and Blake 1993). Our specific research questions are: (1) Is fruit removal a function of plant crop size? (2) Is fruit removal influenced by fruit availability at larger scales (local neighborhood, microhabitat type, and plot levels)? (3) Does spatial pattern of conspecific fruit availability and frugivore abundance influence fruit removal in a context-dependent manner? (4) Is there spatial concordance in the variation of plant-disperser interactions between ecologically and taxonomically similar plant species?

Materials and methods

Study site and study species

We conducted our research in lowland tropical wet forest at the Tiputini Biodiversity Station (0°38'31''S, 76°8'92''W),

Orellana Province, Ecuador. The station is situated north of the Tiputini River, a tributary of the Napo River in the Upper Amazon basin. The station covers 650 ha of undisturbed wet lowland forest and is bordered by the 1.5 million-ha Yasuní Biosphere Reserve. The landscape is slightly hilly, with an intricate net of small streams. Elevation ranges from 190 to 270 m, with the station dominated by terra-firme forest with small areas of flooded forest. The mean annual precipitation is about 2,800 mm (1998–2002, <http://www.usfq.edu.ec/1TIPUTINI/research.html>). There is a rainy season from April to early August when more than 65% of the annual rain falls; 15% occurs in the dry season from November to February.

Melastome shrubs and treelets are conspicuous constituents of terra-firme forest understories; *Miconia* is the most speciose melastome genus in the region (Tuomisto et al. 2002). The two species we studied, *M. fosteri* and *M. serrulata*, reach up to 6 m in the understory of undisturbed terra-firme forest. Fruit maturation occurs during the rainy season. Most fruits ripen from May to July in *M. fosteri* and from June to August in *M. serrulata*. Unripe fruits are yellow in *M. fosteri* and green in *M. serrulata*. Fruits of both species are small subspherical berries, dark purple when ripe, and are presented in terminal infructescences. *M. fosteri* fruits (mean fruit diameter \pm SD, 6.2 ± 0.8 mm, $n = 40$) are arranged in short infructescences close to the foliage; infructescences usually have less than 10 fruits. *M. serrulata* infructescences, on the other hand, bear 70–100 fruits (fruit diameter, 8.4 ± 0.9 mm, $n = 40$).

Fruit-eating birds found in the forest understory disperse the seeds of these melastomes. Analysis of faecal samples obtained from captured birds showed that only seven species of birds consume *M. fosteri* and *M. serrulata* fruits at Tiputini (P.G.B., unpublished data). These species are 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 (Turdidae, *Turdus albicollis*). Manakins are primarily frugivorous and their activity patterns and habitat preferences may have a strong effect on the distribution of fleshy-fruited plants (Loiselle and Blake 1999; Loiselle et al. 2007b). They have lek-mating systems, in which males congregate in display areas with high site fidelity over time, and which females visit solely for the purpose of mating. Males spend a considerable amount of time at lek sites through an extended breeding period, while females are distributed more homogeneously and hold larger home ranges. Such difference likely promotes variation in fruit removal and seed deposition between the sexes. As a group, manakin leks are distributed regularly in Tiputini, although there are heterospecific differences in local

topography of lek locations (Loiselle et al. 2007a). This study focused solely on manakins, as the relative importance of *T. albicollis* as a seed disperser of understory *Miconia* trees likely is small in our study area because this thrush species is uncommon in the plots, its diet includes a large quantity of invertebrates, and it forages from the ground level to the forest canopy. The exclusion of *T. albicollis* is unlikely to affect our results, as only 1 of 120 frugivore feces that contained seeds of *M. serrulata* or *M. fosteri* was from this species.

Quantification of fruit abundance and fruit removal

We established two 9-ha plots in February 2003; plots were 400 m apart. On each, we established a 6×6 grid with points located 50 m apart, for a total of 36 points per plot. Each point was the centre of a sampling station, where we counted the number of adult plants and estimated fruit production and fruit removal of the two target species during the 2003 reproductive season. To quantify abundance of fruiting plants, we counted all plants within a 20-m radius circle centered at every sampling station. All fruit-bearing plants were at least 2 m high; thus, we also counted all plants that were taller than 2 m, whether or not they had fruit, to estimate adult-plant density. We measured fruit crop size by directly counting fruits on each study plant within the 20-m radius circles at the beginning of the dispersal period. In the case of two *M. serrulata* plants with more than 3,000 fruits, however, we only estimated crop size to the nearest 100. We used these fruit abundance measures to examine impact of fruit abundance on fruit removal at the individual plant, microhabitat, and plot levels.

To quantify fruit removal by frugivores, we selected several focal plants per station (79 of a total of 122 fruiting plants in *M. fosteri*; 39 of 43 in *M. serrulata*; all except one station with fruiting plants were represented), including, when possible, plants with small and large fruit crops, as well as isolated and aggregated plants of each species. Up to seven infructescences per plant were randomly selected to estimate daily fruit removal during the peak of fruit ripening, i.e., June for *M. fosteri* and July for *M. serrulata*. All ripe and ripening fruits were counted on a daily basis during 2 weeks, recording the number of removed and new ripe fruits. If not removed, ripe fruits rot and can remain on the plant for several days before they fall to the ground; these fruits were not included in the removed category to avoid overestimation of fruit consumption.

We used two measures of fruit removal per sampling station, the mean proportion of the fruit crop removed per focal plant and the estimated total number of fruits removed per focal plant, to explore variation in seed dispersal. Proportion of fruits removed, a measure of removal efficiency (e.g., Alcántara et al. 1997; Izhaki 2002), reflects

the success of the reproductive investment of the plant. In contrast, the number of fruits removed is a measure of the quantity component of seed-dispersal effectiveness (Schupp 1993; Jordano and Schupp 2000) and is more directly related to plant fitness. As the quantity of fruits removed was not measured directly, we estimated number of removed fruits per focal plant by multiplying known crop size by the proportion of fruits removed from the plant. Consequently, our estimation of number of fruits removed is essentially equivalent to fruit removal success of each individual plant (Alcántara et al. 1997), which is hypothesized to be a reliable measure of relative fitness of individuals (Ortiz-Pulido et al. 2007). To evaluate if patterns of conspecific plant abundance influenced the proportion of fruits removed, we took the average distance of the two nearest conspecific fruiting plants to each focal plant where we directly measured fruit removal, as a measure of plant aggregation.

We classified sampling stations into three microhabitat categories considered relevant to bird dispersers 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); and (3) slopes, intermediate between streams and ridges (slope). To measure environmental heterogeneity in the study plots and among sample stations, we estimated slope and elevation. The elevation surface was created based on a set of over 600 point measures of elevation (measured with altimeter to the nearest meter) and a map of streams within a larger 100-ha study area. Slope was then interpolated using a digital elevation model. All interpolations were done using Geographic Information Systems (GIS) technology (ARC/INFO Ver. 8.1); raster surfaces were UTM projections with 1×1 m cell size. We used the maximum and minimum elevations per sampling station to assign every station to one of three microhabitats (i.e., ridge, slope, and bottom).

Estimation of seed disperser abundance

We used observational data on spatial distribution of manakin display areas (a detailed description of sampling design can be found in Loiselle et al. 2007a), as well as mist-net data from each station (see next paragraph) to estimate the local abundance of seed dispersers at each station. Observational and mist-netting data have their strengths and weaknesses to estimate bird activity patterns. With the first method, we assumed that lek locations also reflect high-activity areas of females and non-territorial males; mist-net data, in contrast, provide a more direct indication of activity levels of understory frugivores (Blake and Loiselle 2002). All manakin leks in a 100-ha study area were mapped from January to March of 2003 and 2004 and incorporated into

GIS databases. The number of displaying males at every lek was determined by direct observation, facilitated by a population of individually color-banded birds. Our two 9-ha plots are embedded in this larger 100-ha plot, so we used GIS to measure the shortest distance from a lek border to the centre of every station. Additionally, we estimated the mean maximum recapture distances of male manakins as a measure of the regular departure distances of male manakins from lek sites. To do this, we used all the recapture data of banded males obtained during an extensive mist-netting study in Tiputini (Loiselle et al. 2007a; ca. 106 manakin recaptures in more than 4,422 mist-net h between February 2001 and March 2004 on 100-ha study plot). For each manakin species, we recorded the net location where each bird was captured and then calculated the maximum distance among recaptures for each individual. We then calculated the mean maximum recapture distance among individuals for each species of manakin. The estimated abundance of birds at a single sampling station was the combination of all individual manakins that potentially overlapped with the centre of the station based on the mean maximum displacement distance from the border of a lek.

To explore the match between frugivore abundance and fruit supply, we used the estimation of manakin abundance derived from lek locations described above, as well as additional data of birds mist-netted at each station, as a surrogate measure of frugivore activity within the study plots. Mist nets were oriented and placed systematically at the centre of each sampling station; a mist net (36-mm mesh, 12×2.4 m) was operated during 7 days distributed throughout the full 2003 fruiting season of both *Miconia* species. Mist nets were opened before sunrise and kept open for approximately 6 h per day, for an average of 42 mist-net h per sampling station.

Data analysis

All analyses were applied to both *M. fosteri* and *M. serrulata* unless indicated. We used the general-linear-models (GLM) module available in STATISTICA 7.0 (StatSoft 2004), to investigate the effects of fruit abundance and plant aggregation on fruit removal. Specifically, to examine the combined effects of crop size, plant aggregation, microhabitat type, plot, and their interactions on fruit removal, we used ANCOVA with microhabitat and plot as fixed effects, and fruit crop size and mean distance to conspecific neighbors as continuous predictors.

In ANCOVA models, the assumption of slope homogeneity was tested with homogeneity-of-slope models. The slope-homogeneity criterion was not met for number of *M. serrulata* fruits removed and, consequently, a separate-slope model of covariance analysis was performed, omitting the main effects for continuous predictors. Assumptions

of normality (Kolmogorov–Smirnov test) and homogeneity of variances (Cochran C test) were checked prior to conducting parametric tests. We used transformations to normalize data when needed. As the number of focal fruiting plants varied among microhabitat types, we used Type III sums-of-squares test to assess whether there was a microhabitat effect. The Unequal-N HSD post hoc test was used to identify differences among microhabitat means. An α -level of 0.05 was used for all statistical tests unless otherwise specified.

To determine if frugivore activity matched the spatial patterns of fruit abundance, we used a bivariate generalization of the Crámer–von Mises nonparametric test (Syrjala 1996) with 1,000 permutations. Abundance data of each population (fruit, frugivores) were normalized by dividing the number of individual plants or birds at a station by the total number of plants and birds to obtain a test independent of population sizes. This allows a test of differences in the way two populations are distributed across the study area, unaffected by abundance differences between populations. To explore the effect of manakin activity on the proportion and number of fruits removed per sampling station, we used a general-factorial ANCOVA with microhabitat and plot as fixed effects and the estimated abundance of manakins, based on captures (see later in “Results”), as a covariate.

Results

Approximately one-half of *Miconia fosteri* ($n = 122$, 53%) and *Miconia serrulata* ($n = 43$, 53%) adult plants produced fruit in 2003. *M. fosteri* plants with fruit were present at 46 of 72 sampling stations; *M. serrulata* was present at 29 (Fig. 1). Density of *M. fosteri* with fruit (mean \pm SE, 1.7 ± 0.3 plants per sampling station) was higher than for *M. serrulata* (0.6 ± 0.1 , $t = 3.65$, $df = 142$, $P < 0.001$), but the mean number of fruits per plant was lower in *M. fosteri* (170 ± 27) than in *M. serrulata* (548 ± 155 , $t = 3.42$, $df = 215$, $P < 0.0001$). As a result, fruit abundance was similar for the two species (*M. fosteri*: 303 ± 81 fruits per sampling station; *M. serrulata*: 463 ± 182 ; $t = 0.80$, $df = 142$, $P = 0.42$). For *M. fosteri*, number of adult plants was larger than expected on ridges and less than expected in bottomlands ($\chi^2 = 51.6$, $df = 2$, $P < 0.0001$). Similarly, average crop size tended to be larger on ridges and slopes than in bottomlands, although this difference was not significant (Kruskal–Wallis test, $H_{2,79} = 4.15$, $P = 0.12$). *M. serrulata* was more abundant on slopes and less abundant than expected in bottomlands ($\chi^2 = 7.65$, $df = 2$, $P < 0.05$). Also, plants on slopes had higher average crop sizes than plants in other microhabitat types ($H_{2,39} = 10.85$, $P < 0.01$), resulting in a larger total fruit abundance on slopes.

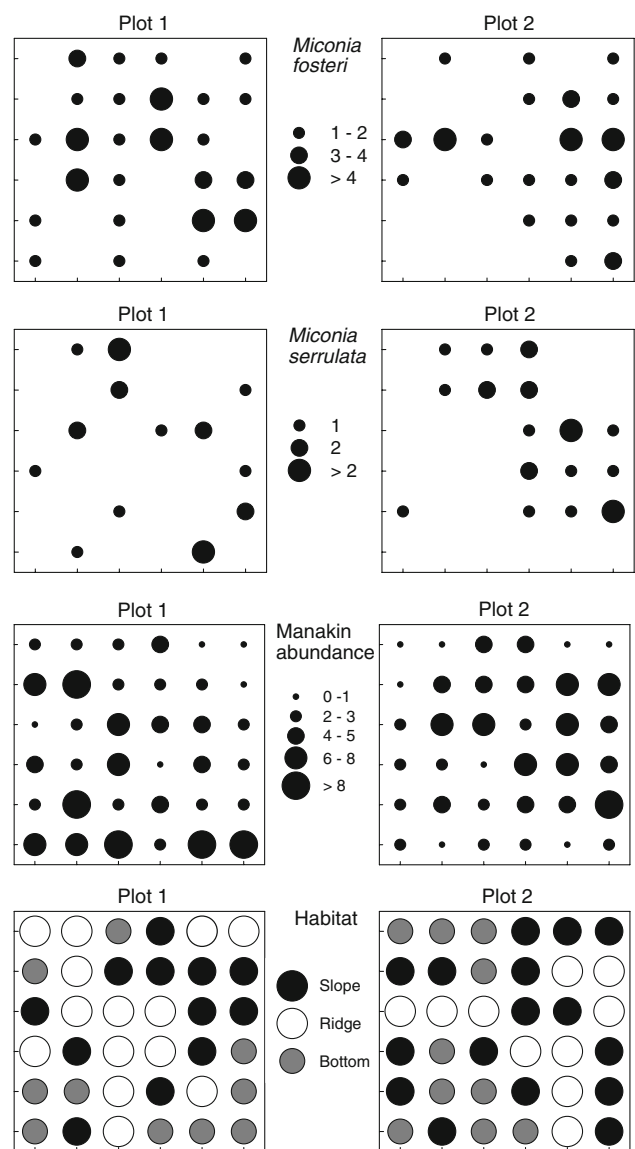


Fig. 1 Spatial distribution of *Miconia fosteri* and *M. serrulata* fruiting plants (number of plants within 20-m radius circles) and manakin abundance (number of captures in 42 mist-net h) in 72 sampling stations located in two 9-ha plots of undisturbed lowland tropical forest at Tiputini Biodiversity Station, Ecuador, in the Upper Amazon basin. Sampling stations were classified into three microhabitats (slope, ridge, and bottom) that reflect differences in slope and elevation

Effect of fruit crop size, plant aggregation, microhabitat and plot on fruit removal in *Miconia fosteri*

We examined the direct and combined effects of crop size, plant aggregation, microhabitat type, plot, and microhabitat by plot interaction, on removal of fruits from individual plants. Proportion of fruits of an individual plant removed by frugivores was correlated with total number of fruits removed for *M. fosteri* (Pearson product-moment correlation: $r = 0.52$, $n = 79$, $P < 0.0001$) and was positively

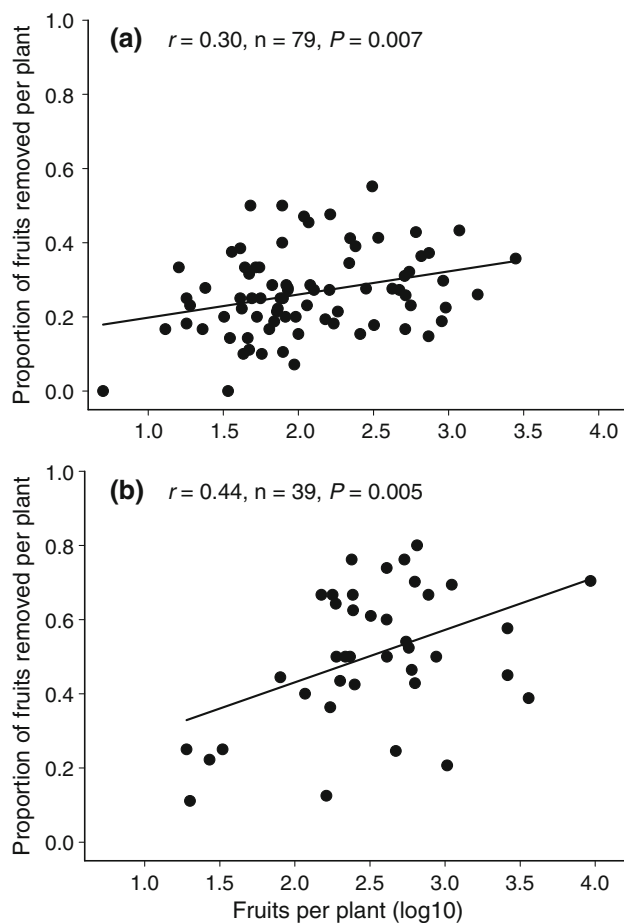


Fig. 2 Ordinary least square regression of the proportion of fruits removed by birds in relation to plant crop size in **a** *Miconia fosteri* and **b** *M. serrulata* plants in two 9-ha plots located at Tiputini Biodiversity Station, Ecuador

affected by crop size (factorial ANCOVA: $F_{1,71} = 4.50$, $P < 0.05$). The proportion of fruits removed also differed between plots ($F_{1,71} = 4.53$, $P < 0.05$) and among microhabitats ($F_{2,71} = 4.01$, $P < 0.05$). A larger proportion of fruits was removed from plants located on ridges (mean \pm SE, 0.31 ± 0.02) than from plants on slopes (0.25 ± 0.02) or bottomlands (0.19 ± 0.03) (Fig. 3a). The proportion of fruits removed did not vary with mean distance to conspecifics ($F_{1,71} = 0.12$, $P = 0.73$), a measure of fruiting plant aggregation. There were no significant interactions between microhabitat and plot (factorial ANCOVA; $F_{2,71} = 0.52$, $P = 0.60$), nor between crop size and microhabitat or crop size and plot (homogeneity of slopes test, respectively, $F_{2,67} = 1.87$, $P = 0.16$ and $F_{1,67} = 1.12$, $P = 0.29$).

There was a strong effect of crop size ($F_{1,71} = 17.9$, $P < 0.0001$) and mean distance between fruiting conspecifics ($F_{1,71} = 43.4$, $P < 0.0001$) on the number of *M. fosteri* fruits removed per focal plant. The mean number of fruits removed was lowest for isolated plants with small crop

sizes (Fig. 4a). Microhabitat type affected removal of total number of fruits per plant (factorial ANCOVA: $F_{2,71} = 3.63$, $P < 0.05$; Fig. 3c); more fruits were removed from the ridge (mean \pm SE, 326 ± 130) than from slope (102 ± 27) and bottomland (32 ± 14) microhabitats. In contrast to the proportion of fruits removed, plot did not affect the number of fruits removed ($F_{1,71} = 2.01$, $P = 0.17$). The slopes of the relationships between number of fruits removed and crop size or mean distance to conspecifics plants were similar among the three microhabitats and between the two plots (homogeneity of slopes tests, $P \geq 0.35$).

Effect of fruit crop size, plant aggregation, microhabitat and plot on fruit removal in *Miconia serrulata*

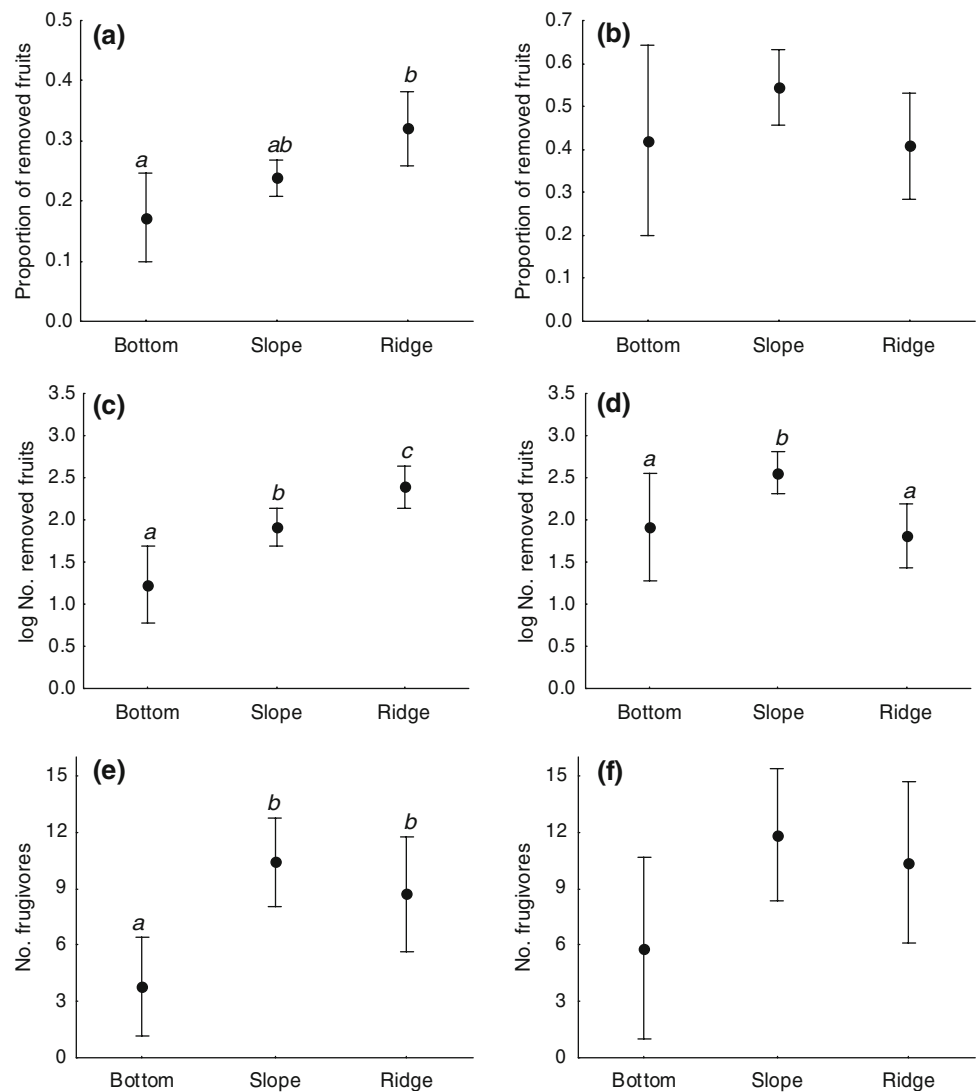
Proportion of fruits removed at individual *M. serrulata* plants was correlated with total number of fruits removed per plant (Pearson product-moment correlation, $r = 0.65$, $n = 39$, $P < 0.0001$). Spatial variation in the proportion and number of *M. serrulata* fruits removed per plant was analyzed with one-way ANCOVA because the unbalanced distribution of fruiting plants per microhabitat prevented inclusion of both plot and microhabitat in the same model. We found a positive effect of crop size ($F_{1,35} = 5.54$, $P < 0.05$) on the proportion of fruits removed per plant but no effect of microhabitat ($F_{1,34} = 0.04$, $P = 0.96$) (Fig. 3b), plot ($F_{1,35} = 1.88$, $P = 0.18$) or mean distance to fruiting plants ($F_{1,35} = 3.00$, $P = 0.09$). Slope of the regression of the proportion of fruits removed from individual plants on crop size was steeper for *M. serrulata* (Fig. 2) than *M. fosteri*, suggesting a stronger effect of crop size on fruit consumption for this species.

We examined the effect of plot and crop size on the number of fruits removed from *M. serrulata* individual plants. Quantity of fruit removed increased strongly with crop size (one-way ANCOVA: $F_{1,35} = 445.7$, $P < 0.0001$); we found no effect of mean distance between plants ($F_{1,35} = 0.18$, $P = 0.19$; Fig. 4b) or plot ($F_{1,35} = 0.17$, $P = 0.29$). Number of fruits removed per plant was affected by microhabitat type (separate-slope model of covariance; $F_{2,30} = 4.08$, $P < 0.05$; Fig. 3d) and was strongly affected by the interaction between crop size and microhabitat ($F_{3,30} = 153.2$, $P < 0.0001$); however, it was not affected by mean distance between fruiting plants ($F_{3,30} = 2.41$, $P = 0.09$). Mean number of fruits removed was greater on slopes (mean \pm SE, 522 ± 153 fruits removed per focal plant) than on ridges (151 ± 61) or bottomlands (282 ± 131).

Spatial overlap in fruit abundance and frugivore activity

We obtained similar results when analyses were based on manakin abundance estimated from lek locations as when

Fig. 3 *Miconia fosteri* (a, c) and *M. serrulata* (b, d) weighted means and 0.95 confidence intervals, adjusted by local fruit abundance of the same species with ANCOVA models in three microhabitats of a wet lowland tropical forest, for a, b proportion of fruits removed and c, d number of fruits removed per plant. Estimated mean number and 0.95 confidence intervals of adult male manakins per sampling station with fruiting plants (e *M. fosteri*, f *M. serrulata*) was calculated by adding the abundance of the six species (*Pipra erythrocephala*, *P. filicauda*, *P. pipra*, *Lepidothrix coronata*, *Chiroxiphia pareola* and *Mach-aeropterus regulus*) that consume *M. fosteri* and *M. serrulata* fruits at Tiputini Biodiversity Station, Ecuador. Different letters above bars (a, b, c) indicate significant differences between microhabitat means (Unequal-N HSD post hoc test)



estimates were obtained from mist-net captures; thus, we present results based on the mist-net approach only (Fig. 1). Spatial distribution of manakins, the primary consumers of fruit for both study species, did not differ from the spatial distribution of fruit abundance of *M. fosteri* (bivariate generalization of the Cramér-von Mises test, $\psi = 0.51$, $P = 0.63$), indicating a general match between *M. fosteri* fruit availability and manakin activity. In contrast, spatial distributions of manakins and *M. serrulata* fruit abundance were not similar ($\psi = 2.30$, $P < 0.01$), indicating that the spatial pattern of fruit supply of *M. serrulata* did not match the spatial distribution of its primary seed dispersers.

We did not find a significant effect of manakin abundance (as measured by numbers of captures in mist nests per sampling station) on removal of *M. fosteri* fruits (proportion of fruits removed: $F_{1,34} = 1.49$, $P = 0.23$; number of fruit removed: $F_{1,34} = 2.14$, $P = 0.15$). Similarly, removal of *M. serrulata* fruits at individual plants was not related to manakin abundance (proportion of fruits removed:

$F_{1,22} = 0.02$, $P = 0.36$; number of fruits removed: $F_{1,22} = 0.78$, $P = 0.39$). Mean number of captures of manakins per sampling station varied significantly among microhabitats (one-way ANOVA: $F_{2,69} = 9.06$, $P < 0.001$), with captures being lower in bottomland (mean \pm SE, 4.0 ± 0.8) than on slopes (10.1 ± 0.9) or ridges (9.0 ± 1.2). A similar pattern was found when the analysis was restricted to the 41 sampling stations with *M. fosteri* fruiting plants ($F_{2,38} = 6.51$, $P < 0.01$; bottomland: 3.8 ± 1.2 , slope: 10.4 ± 1.1 , ridge: 8.7 ± 1.4 ; Fig. 3e), but not when we analyzed only the 29 stations where *M. serrulata* was fruiting ($F_{2,26} = 2.31$, $P = 0.12$; bottomland: 5.8 ± 1.9 , slope: 11.8 ± 1.6 , ridge: 10.4 ± 1.9 ; Fig. 3f).

Discussion

Efficiency and quantity of fruit removal from *Miconia fosteri* and *M. serrulata* increased with crop size, supporting

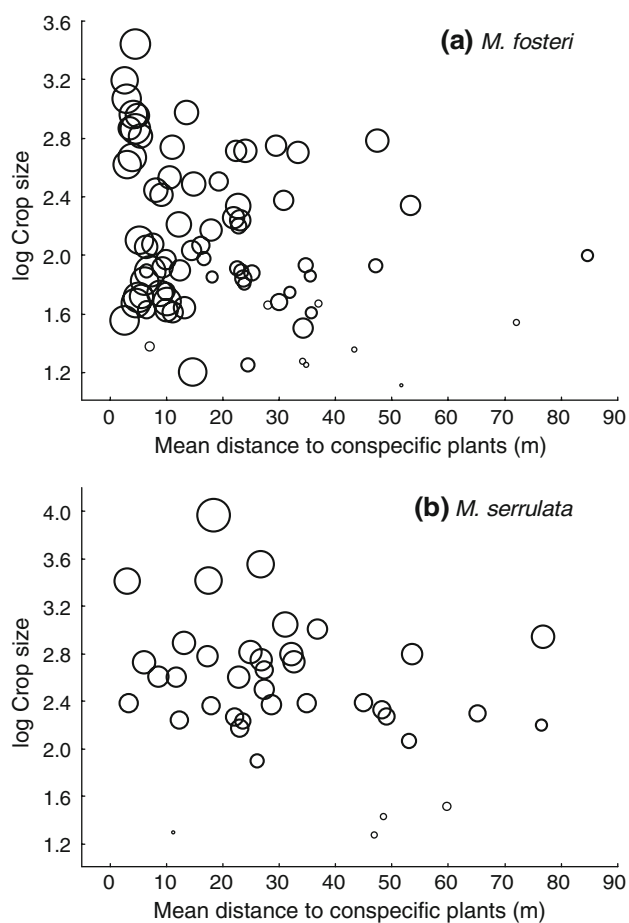


Fig. 4 Relationships among crop size, plant aggregation, and number of fruit removed per plant in **a** *Miconia fosteri* and **b** *M. serrulata*. Bubble size shows the magnitude of fruit removal effectiveness at each individual plant

the prediction that plants with more fruit experience greater potential reproductive success, as measured by fruit removal. At small spatial scales, however, fruit removal from individual plants was not influenced by richer conspecific fruit neighborhoods, except for the number of fruits removed from *M. fosteri*. Also, fruit removal in *M. fosteri* appeared to respond more to microhabitat and plot differences when compared to *M. serrulata*. These differences in spatial patterns of fruit removal between these two ecologically and taxonomically similar plant species that share a similar suite of seed dispersers, suggest that factors other than fruit availability are important cues for frugivores when making foraging decisions.

Efficiency of fruit removal

Efficiency of fruit removal is a reflection of the success of a plant's reproductive investment (Alcántara et al. 1997; Izhaki 2002). Individual plants should benefit from factors that enhance the efficiency of fruit removal, such as crop

size, energy and nutrient content, fruit size or other heritable traits that could be subject to selection pressures, as well as environmental cues, such as microhabitat type or neighborhood fruit abundance. Additionally, differences within and between *Miconia* species in fruit removal efficiency might be explained by plant and manakin spatial distributions. An increase in efficiency of fruit removal at individual plants may occur through three mechanisms that are not mutually exclusive: parent plants located where fruit consumers are more abundant or more active, and display attributes that attract more fruit consumers. Overall, spatial match among plants and fruit consumer abundance would seem to favor greater efficiency of removal from *M. fosteri* because spatial distribution of manakin captures matched the abundance of *M. fosteri* but not *M. serrulata* fruiting plants, and because microhabitat and plot effects significantly affected the efficiency of fruit removal in *M. fosteri* but not *M. serrulata*. There was, however, a positive effect of crop size for fruit removal in both species, supporting an expected effect of frugivore activity or plant traits on the efficiency of fruit removal. Lack of an effect of conspecific plant aggregation on removal efficiency does not conflict with the mechanisms proposed, because influence of plant aggregation on proportion of fruit removed may depend on whether frugivore availability was limited or not (Saracco et al. 2005; Carlo and Morales 2008).

Yet, despite factors that would seem to favor removal of fruits from *M. fosteri*, birds removed fruit more efficiently from *M. serrulata*, probably because a bird's foraging decisions do not depend only on fruit availability but may also be influenced by fruit attributes that determine the reward obtained by the disperser (Sallabanks 1993; Alcántara et al. 1997; Schaefer et al. 2003). In this system, *M. serrulata* fruits are larger than those of *M. fosteri*, occur in larger infructescences, and plants have larger crop size. Thus, rewards for feeding on *M. serrulata* likely exceed those from *M. fosteri*, and this may explain the tighter correlation between crop size and fruit removal for *M. serrulata*. Manakins, as other frugivores, might be expected to make more visits and be willing to travel greater distances to reach plants that offer a larger reward.

Effectiveness of fruit removal

The number of fruits removed from a plant (effectiveness) has direct consequences on fitness because it determines the number of seeds the plant succeeds in having disseminated into the environment, an important component of the seed-dispersal cycle (Schupp 1993; Jordano and Schupp 2000; Wang and Smith 2002). In our study system, number of fruits removed was a good surrogate for number of seeds dispersed, as all frugivores that consumed fruit swallow the fruits whole and move the seeds away from the parent

plant. Although we did not assess the amount of time manakins spent foraging in *Miconia* patches, it is likely they disperse seeds out of the patch. Manakins pass seeds of small seeded fruits like *Miconia* > 10 min after fruit ingestion (Levey 1986) but only stay a short time (i.e., <2–3 min) in each patch.

In our system, the number of fruits removed was at least partially a reflection of manakin activity, and the scale at which birds respond to fruit abundance provides insight into foraging decisions made by manakins. We found that the number of fruits removed was strongly and positively related with crop size and also varied among microhabitat types. In both *Miconia* species, more fruits per plant were removed in the microhabitats where plant abundance and fruit production were greater; these were the same microhabitats in which manakins were more frequently captured and where leks of most disperser species (*Pipra erythrocephala*, *Macheropterus regulus*, *Pipra pipra*) were situated (Loiselle et al. 2007a). Number of fruits removed from 20-m radius areas, which included up to 4 fruiting plants of *M. serrulata* or up to 11 *M. fosteri* plants, was not, however, correlated with manakin abundance. On the other hand, plant aggregation did influence number of fruits removed, at least for *M. fosteri* where conspecific plants were generally closer together than was the case for *M. serrulata*. These apparently contradictory results are likely explained by the spatial scale at which manakins respond to fruit abundance; that is, manakins may respond to fruit patches at a smaller scale than a 20-m radius area. Activity within these fruit-rich patches is greater and, thus, more fruits are removed. For example, *M. fosteri* plants with small crop sizes situated in fruit-rich patches experienced increased fruit removal effectiveness. Manakins also likely learn the locations of individual trees with large fruit crops and, thus, such plants are visited more frequently and have more fruit removed (but are not necessarily at sites with greater manakin abundance).

Other studies also have shown that plant aggregation could increase probabilities of fruit removal from individual plants by attracting more dispersers (Sargent 1990). On the other hand, a superabundance of fruit may also increase chances for intraspecific competition via frugivore satiation if seed-disperser availability was limited (Gryj and Domínguez 1996; Saracco et al. 2005). Low levels of fruit removal and high variability in removal among plants, as we recorded for *M. fosteri* and *M. serrulata*, could result in strongly skewed individual contribution of seeds to the populations. Such skew is indicative of intraspecific competition for seed dispersers (Alcántara et al. 1997). Nevertheless, individual fruit removal did not decrease in patches with closely aggregated plants. Moreover, removal effectiveness in plants of *M. fosteri* with small crop sizes was enhanced when plants were clumped, suggesting that bene-

fits of attracting dispersers to a patch in this system balance or overcome costs of competing for dispersers. Thus, any increase in attractiveness to frugivores that results from occurrence in larger patches of conspecifics may have positive consequences on plant fitness.

Conclusion

In summary, this study demonstrates that spatial pattern of fruit removal, a measure of plant fitness, may depend on a complex interaction among plant traits, spatial patterns of plant distribution, and disperser behavior. Understanding spatial patterns of fruit removal is important for understanding plant demography and spatial patterns of recruitment because seed dispersers set the initial template of seeds in the environment. Interspecific comparisons of spatial patterns of fruit removal in plants that share the same suite of seed dispersers are necessary to explain the role of seed dispersal in species sorting. Here, intraspecific variation in the efficiency and effectiveness of fruit removal in two *Miconia* species was similarly affected by crop size. However, the strength of the interaction between these two species of *Miconia* and their seed dispersers differed along a hierarchy of levels of structural heterogeneity in a context-dependent mode. Birds responded to fruit abundance in a manner specific to each plant species, such that covariation in fruit abundance and fruit removal differed between species with the scale of spatial heterogeneity (plant, conspecific neighborhood, microhabitat). The finding of positive, and null, effects of local plant aggregation on fruit removal in both *Miconia* species are in accord with predictions of specialized plant-frugivore systems where fruit abundance would be a key factor guiding foraging movements (Carlo and Morales 2008).

Factors not directly related with fruit abundance likely influence manakin distribution and movement and, thus, make general relationships between fruit abundance and manakin activity difficult to establish. For example, spatial activity and habitat use by manakins likely are constrained by location of leks, nesting sites, or availability of non-fruit resources (Levey 1988; Blake and Loiselle 2002; Saracco et al. 2005). Consequently, the perceived costs and benefits of fruit foraging are constrained by other activities of seed dispersers and are influenced by species-specific traits of plants (e.g., fruit crop size, nutritional reward) and spatial patterns of occurrence, including patchiness. In the case of *M. serrulata*, increased crop size appeared to compensate for relative isolation from sites of greater seed disperser activity, resulting in increased efficiency and effectiveness of fruit removal. In *M. fosteri*, individual plants with smaller fruit crops could still have relatively high fruit removal if these plants were either located in fruit-rich patches or if they occurred in habitats where seed dispersers were abundant.

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