

# Connecting fruit production to seedling establishment in two co-occurring *Miconia* species: consequences of seed dispersal by birds in upper Amazonia

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**Abstract** This study investigated links between seed production by two species of *Miconia* (Melastomataceae), whose seeds are dispersed by birds, and later stages of recruitment in lowland forests of eastern Ecuador. Seed dispersal and survival in later stages are crucial for understanding and predicting patterns of plant population dynamics as well as for understanding patterns of diversity in tropical forests. A major goal was to determine if the spatial template of seed deposition established by birds predicted probability of recruitment. We used observational and experimental approaches to compare patterns of recruitment in *Miconia fosteri* and *M. serrulata*. We calculated probabilities of transition between successive stages of recruitment for each species in three habitats. The

number of plants with fruit, number of fruits removed, and, to a lesser extent, patterns of seed deposition varied between species and among habitats, whereas seed survival, germination, and establishment showed little variation among habitats. The location of seed deposition directly influenced the cumulative probabilities of survival. Among-habitat differences in the probabilities of recruitment set by seed deposition were not modified by later stages, although probability of recruitment was 2.5 times higher for *M. serrulata* than for *M. fosteri* after 1 year. The more critical stages for recruitment were seed removal and deposition. Our results from multiple life-cycle stages suggest that habitat associations among plants that reach reproductive maturity become established at early life stages and were mostly a consequence of seed dispersal by birds. These results differ from those obtained in temperate zones and suggest fundamental differences in the importance of recruitment processes. Dispersers, such as manakins, play significant roles in recruitment and population dynamics of *M. fosteri*, *M. serrulata* and numerous other understory plants of Neotropical forests. Their role in plant recruitment could be much greater than previously considered in megadiverse tropical forests. Thus, loss of dispersers could have long-term and far-reaching implications for maintenance of diversity.

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## Introduction

Seed dispersal by animals plays a major role in plant population dynamics, connecting reproduction of adult plants to recruitment processes (Wang and Smith 2002).

Starting with the publications of Howe and collaborators (Howe et al. 1985; Howe 1986, 1990) and, especially, that of Herrera et al. (1994), a series of ecological studies of seed dispersal by animals have attempted to establish the actual link between seed dispersal itself (i.e., the movement of seeds by animals) and the following stages of plant recruitment. Establishing this link requires simultaneous consideration of the principal processes that occur between the production of fruits and the establishment of saplings (i.e., fruit removal, seed deposition, seed predation, seed germination and seedling recruitment), ideally entailing the following of one cohort (Herrera et al. 1994; Rey and Alcántara 2000; Wenny 2000; García 2001). However, given the complexity of such processes involved in even relatively simple ecosystems, an alternative approach entails the simultaneous study of the different stages of recruitment, combining observations and experiments to infer the potential demographic consequences of seed dispersal (Calviño-Cancela 2002; Passos and Oliveira 2002; Traveset et al. 2003; Gulias et al. 2004).

Processes that act during recruitment can have critical consequences for individual fitness and plant population dynamics. In temperate climates, seedlings represent the critical recruitment stage for the majority of species that have been studied (Herrera et al. 1994; Rey and Alcántara 2000; García 2001; Traveset et al. 2003; Gulias et al. 2004). There, climatic conditions (e.g., drought) strongly affect germination efficiency and seedling survival, prompting substantial differences in recruitment among sites with and without tree cover, and causing the main bottleneck during recruitment (but see Calviño-Cancela 2002 for a pioneer species). In the tropics, many factors could impose limits to the initial recruitment, among which quality of dispersal, density-dependent mortality of seeds and seedlings, availability of light, and asymmetric competition with adults can be particularly important (Brokaw 1985; Howe 1990; Curran and Webb 2000; Harms et al. 2000; Russo and Augspurger 2004; Moles and Westoby 2004).

To determine which mechanism(s) might impose limits on recruitment (Clark et al. 1999; Müller-Landau et al. 2002), and to determine potential critical stages, requires joint evaluation of several processes. Unfortunately, the majority of studies that have linked successive stages of recruitment in tropical species have not explicitly considered fruit production or removal (Schupp 1990; Laman 1995; Loiselle and Blake 1999; Dalling et al. 2002; Holl 2002; Passos and Oliveira 2002; Pizo 2003). Although more than 80% of the plants of tropical forests depend on vertebrate frugivores for seed dispersal, only for three species [*Virola surinamensis* (Howe and Vande-Kerckhove 1981; Howe et al. 1985; Howe 1990), *Ocotea endresiana* (Wenny 2000) and *Monodora myristica* (Balcomb and

Chapman 2003)] has there been a thorough evaluation of the relationships among distinct processes and factors that affect dispersal and recruitment and their consequences for plant establishment. In those species, seed survival was critical for recruitment because of post-dispersal predation; quality of dispersal as well as predation on and mortality of seedlings also exerted a strong influence on the success of recruitment.

The link between fruit removal and seed deposition by vertebrate frugivores is a key aspect of dispersal and recruitment of plant populations and in the maintenance of diversity in tropical forests. It has been hypothesized that there is a high spatial specificity in where seeds dispersed by animals are likely to establish because of the interrelationships of independent processes that act during successive recruitment stages (Jordano and Herrera 1995). Critical events in the life cycle may vary spatially (spatial discordance), and patterns produced by one specific process could be obscured by variation in later stages (i.e., decoupling among stages) (Jordano and Herrera 1995; Schupp 2007). As a consequence, the outcome of dispersal and recruitment could depend on a critical process operating during one stage, or on the interactions among independent processes that act during different stages of recruitment. In temperate and subtropical environments, the demographic consequences of seed dispersal appear to be highly dependent on the microsite of deposition (Herrera et al. 1994; Rey and Alcántara 2000; Traveset et al. 2003; Calviño-Cancela 2002). In tropical forests, available evidence (e.g., Howe et al. 1985; Murray 1988; Laman 1995; Wenny 2000; Dalling et al. 2002) suggests more species-specific responses with respect to the relative importance of deposition site on probability of recruitment.

The main objective of this study was to evaluate comparatively the outcome of processes that act during successive demographic stages of two related and ecologically similar species, crucial to understand limiting mechanisms during the recruitment. We investigated processes that act from the production of fruits until seedling establishment in *Miconia fosteri* and *M. serrulata*, whose seeds are primarily dispersed by birds and which co-occur locally in the understory of the upper Amazon basin. We estimated probabilities of transition among successive stages in three types of habitat characterized by subtle differences in topography. With this information, we estimated the expected magnitude of seedling recruitment in each habitat based on the spatial patterns of seed deposition. We used observational and experimental approaches to evaluate six specific questions. (1) How important is variation in the probability and magnitude of individual recruitment stages among types of habitat, from production of fruits until establishment of seedlings? (2) Do the consequences of factors and processes (i.e., fruit removal, seed deposition,

seed predation, germination, seedling survival) that act during recruitment differ among types of habitat? (3) Is the importance of these recruitment processes comparable between *M. fosteri* and *M. serrulata*? (4) What is the spatial overlap among expected patterns of abundance of recruits among stages of the plant's life cycle? (5) Can patterns of recruitment be determined by activity of seed dispersers? (6) Do ecologically equivalent species experience similar critical stages during the initial recruitment? To our knowledge, this is the first study to compare, between co-occurring plant species, the consequences of the link between the quantitative and qualitative components of the effectiveness of bird-mediated seed dispersal and their consequences on subsequent establishment processes.

## Materials and methods

### Study area

We conducted our research in lowland tropical rain forest at the Tiputini Biodiversity Station (0°38'S, 76°08'W, 190–270 m elevation), Orellana Province, Ecuador. The station encompasses 650 ha of undisturbed wet lowland forest in the Ecuadorian Amazon on the northern bank of the Tiputini River. It is bordered by the ~1.7 million ha Yasuní Biosphere Reserve. The reserve is dominated by terra firme forests, which are dissected by many streams. The mean annual precipitation was approximately 2,800 mm (1998–2002, <http://www.usfq.edu.ec/1TIPUTINI/research.html>). More than 65% of the annual rain falls during the rainy season (April–August), with an average monthly rainfall of 390 mm.

We established two 9-ha plots (300 × 300 m each) in terra firme forest; minimum distance between plots was 400 m. Plots were gridded on a 50 × 50 m scale, producing 36 cells per plot. Although plots ranged only from 200 to 230 m in elevation, the intricate network of streams and ravines produced substantial heterogeneity in the forest. Additionally, our previous studies in the area indicated that the distribution of the principal dispersers of seeds in the understory (manakins, Pipridae) and their interactions with the plants they disperse (removal and deposition of seeds), were influenced by the topographic heterogeneity of the forest (Loiselle et al. 2007a, b; Blendinger et al. 2008). Thus, we classified grid cells into three habitat 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); and (3) slopes, intermediate between streams and ridges (slope). We used the maximum and minimum elevations per cell to assign every cell to one of three habitats

(Blendinger et al. 2008), which resembled closely the bottom to ridge gradient. We studied the recruitment of *M. fosteri* and *M. serrulata* on the two plots between April 2002 and August 2003. Within each grid cell, we measured fruit production and fruit removal by birds, seed deposition by frugivorous birds, seed survival, seed germination, seedling establishment and density of saplings and reproductive plants.

### The plant species

*Miconia* is the most speciose melastome genus of terra firme forest in the region (Tuomisto et al. 2002). Broadly distributed in Neotropical rainforests, the genus is primarily dispersed by frugivorous birds (Snow 1965; Stiles and Rosselli 1993; Loiselle and Blake 1999; Luck and Daily 2003; Gridi-Papp et al. 2004). Approximately 30 species of *Miconia* occur at Tiputini Biodiversity Station and differ in reproductive phenology, crop size, density, and specificity for habitats and microhabitats. During the rainy season, *M. fosteri* and *M. serrulata* were the two species with greatest production of fruits in both plots; fruit maturation occurred from May to July in *M. fosteri* and from June to August in *M. serrulata*. Other less abundant species with fruit maturation periods that partially or totally overlapped the sample period were *M. abbreviata*, *M. centrodesma*, *M. lugonis*, *M. phaeochaeta*, *M. nervosa* and *M. schunkei*. *M. fosteri* and *M. serrulata* are small trees that reach up to 6 m in the understory of undisturbed terra firme forest; most plants have a mean height of 4 m. Fruits of both species are small subspherical berries, dark purple when ripe, and similar in size (*M. fosteri* mean fruit diameter ± 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).

### The seed dispersers

We used mist-nets to determine the consumption of *M. fosteri* and *M. serrulata* fruits by birds inhabiting the forest understory. Mist-nets are an effective technique to study the diet of bird species that forage in the understory of tropical forests. Within each cell, a mist-net (36 mm mesh, 12 × 2.4 m) was operated during 7 days distributed throughout the 2002 and 2003 fruiting seasons of both *Miconia* species, for an average of 42 mist-net hours per cell. Fruit-eating birds were kept in plastic boxes for approximately 10 min to obtain regurgitated seeds and fecal samples. We carefully examined the soil beneath captured birds and collected any fecal samples and regurgitated seeds that we could assign to the captured bird with certainty. We identified seeds to species or morphospecies

and counted the total number of seeds in each sample. We found eight species of *Miconia* in the fecal samples, most of which could be assigned with confidence to the species level based on the seed size and shape, seed appendages, and the structure of the testa. Seeds of *M. fosteri* and *M. serrulata* could be readily identified; together, they represented 21% of 131,872 seeds we recorded in the feces of understory frugivores, including feces collected from mist-netted birds or in seed traps used to quantify seed deposition (see below). The mean abundance of dispersers varied significantly among habitats, with more birds in slopes or ridges than in bottoms (Blendinger et al. 2008).

#### Recruitment stages: observational methods

Methods used to measure production of fruit, the consumption of fruits by dispersers, and the deposition of seeds were explained in detail in Blendinger et al. (2008, 2011), here we present a summary of those methods. All fruit-bearing plants were  $\geq 2$  m high; thus, to estimate adult-plant density, we counted all plants taller than 2 m within a 20-m-radius circle centered on every cell. 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. To quantify fruit removal by frugivores, we selected several focal plants per station (79 of a total of 122 fruiting *M. fosteri*; 39 of 43 *M. serrulata*). Up to seven infructescences per plant were selected to estimate daily fruit removal during the peak of fruit ripening. Ripe fruits were counted daily during 2 weeks, recording the number of removed and new ripe fruits. If they are 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 over-estimation of fruit consumption. To estimate the quantity of fruit removed per 20-m-radius circle, we multiplied the mean proportion of removed fruits per focal plant by the total number of fruits in the circle.

We used seed traps to quantify mean seed deposition per cell on each plot. Seed traps consisted of sheets of plastic suspended horizontally 0.5 m above the soil by means of four poles. We placed seed traps in four types of microsites: in randomly selected locations and beneath each of the three plant species that were considered foci of seed dispersal and that could, therefore, impose spatial limits to plant distribution (Blendinger et al. 2011). A single seed trap was placed at random in each cell; randomly seed traps were composed of two  $1.5 \times 1$  m plastic sheets placed 5 m apart. In addition, we placed one seed trap (a single  $1.0 \times 0.5$  m plastic sheet) per cell beneath each of three species of plants (*M. fosteri*, *M. serrulata* and *Anthurium eminens*) whose fruits are often consumed by avian frugivores. Sample sizes differed among microsites because all

three species did not occur in every cell; all 72 cells had traps located at random, 67 had seed traps below fruiting *A. eminens*, 22 had seed traps below *M. fosteri*, and 20 cells had traps below plants of *M. serrulata*. Each day we selected approximately 12 cells for sampling. We cleaned the seed traps at dawn and collected defecations in the afternoon or before the first rain of the day (6.7 h/day, on average). We sampled the randomly-distributed seed traps throughout the entire dispersal phase until we reached or exceeded a sample effort of 50 h/trap; in contrast, we sampled traps placed beneath target plants while there were mature fruits on the plant, or until a sample effort of 50 h was reached.

To compare seed deposition among cells, we first converted the data for each microsite to number of seeds deposited per  $0.5 \text{ m}^2$  in 50 h and then averaged the values of the microsites present in each cell. We obtained 98 fecal samples from avian frugivores with 6,222 seeds of *M. fosteri*, and 167 samples with 9,017 seeds of *M. serrulata*. Our data on seed deposition per cell reflect the primary dispersal of seeds by birds; we did not consider non-dispersed fruits that fell below the parent plant nor possible secondary dispersal movements by ants. Nonetheless, we do not believe that secondary dispersal affected our interpretation of the data, given that the scale of our samples ( $50 \times 50$  m) is much greater than the distances seeds are displaced by the majority of ants in tropical forests (Pizo et al. 2005).

#### Recruitment stages: experimental methods

We took an experimental approach to assess the importance of seed predation, seed germination, and seedling survival to plant recruitment. To perform seed survival and germination tests in the field, we collected seeds from different parent plants from the site. Fleshy pulp surrounding seeds can decrease and slow germination of many species, including *Miconia* species (Traveset 1998; Christianini et al. 2007), so fruit pulp was carefully removed from seeds prior to germination tests. Although this procedure does not consider other possible effects of seed passage through the frugivore's gut upon the germination performance of seeds (Traveset 1998), potential biases should be similar in all germination tests. For both target species, we placed three plastic Petri dishes, 11 cm in diameter and 1 cm in depth, in each cell; dishes were placed close to randomly selected seed traps. We used two Petri dishes to quantify germination and one to measure survival of seeds in the soil. The bottom part of each Petri dish was perforated to allow water to drain out, and covered successively with a cloth mesh to prevent loss of seeds through the perforations, a disk of filter paper to conserve moisture, and a covering of 3 mm of soil collected at the



same site. In each test, we deposited 20 seeds directly on the soil. In the germination trials, to prevent removal of seeds by invertebrates (primarily ants), we glued each Petri dish to the top of a 7-cm PVC tube that was covered with Tanglefoot®. Seed survival trials were similar in all respects except the Petri dishes were not protected from granivores. Given the small size of the seeds ( $0.6\text{--}0.8 \times 0.3\text{--}0.5$  mm), we had to protect the trials from the strong rains and the water dripping from leaves in the canopy to be able to evaluate removal and germination (i.e., to prevent loss of seeds to rain). Thus, we arranged Petri dishes beneath a  $1\text{-m}^2$  sheet of transparent plastic, suspended 70 cm above the ground. To prevent desiccation of the seeds, we watered the dishes weekly.

Germination tests under shadehouse conditions were conducted in 2002, before doing field experiments, and allowed us to check for dormancy. In both species, germination started after 1 month, with a peak before the end of 2 months. Therefore, to evaluate germination in the forest, we counted the number of seedlings that emerged in 2 months' time. We considered that a seed had germinated when the radicle had emerged. To evaluate survival of seeds from removal by granivores, we brought the Petri dishes back to the laboratory after 2 months and, using a stereoscope, counted the number of remaining seeds and germinated seeds. Removal of seeds does not necessarily reflect seed depredation, as ants can secondarily disperse species of *Miconia* (Kaspari 1993; Levey and Byrne 1993; Christianini and Oliveira 2009). Although this could influence the fate of seeds removed in the experimental trials, most seeds removed by ants in tropical forests are consumed (Levey and Byrne 1993), probability of secondary dispersal is reduced at lower seed densities (Kaspari 1993), and secondary dispersal seems to be more frequent when seeds are included in the feces (Pizo and Oliveira 1999; Passos and Oliveira 2002). Therefore, we considered our experimental design appropriate to answer comparative questions about the fate of seeds dispersed in different types of habitat.

Given the low density of seedlings in the plot, we evaluated seedling survival experimentally. We sowed and grew seedlings of both species under nursery conditions, using soil from the site and watering regularly. Six months after germination, we transplanted 10 seedlings of each species to each sample station, arranged in two groups of five seedlings in quadrats of  $20 \times 20$  cm placed close to randomly located seed traps. We selected seedlings that were of similar size at the moment of transplantation (six to eight leaves, approximately 2 cm tall in *M. fosteri* and 4 cm tall in *M. serrulata*). During the first 2 weeks, we inspected seedlings regularly and replaced those that had been negatively affected by the transplantation process. To estimate establishment success, we counted the number of seedlings that survived after 6 months.

## Transition probabilities

We combined observational and experimental results to calculate six transition probabilities (TPs) between successive stages for each species of *Miconia* in each habitat (Rey and Alcántara 2000; Traveset et al. 2003). TPs (mean, SD and 95% CI) associated with production of fruits and deposition of seeds by dispersers were calculated as the proportion registered in each habitat with respect to the total in all habitats. The remaining TPs for each habitat were calculated as the ratio between the number of individuals finishing each stage and the number of individuals that entered that stage. Specifically, we estimated the TP that a fruit was removed as the mean proportion of fruits removed per cell in each habitat. The TP that a deposited seed could be available to germinate was estimated as the mean number of seeds not removed from the soil by granivores with respect to the total number of seeds arranged in each cell; in a similar way, we estimated in each habitat the TP of seedling emergences with respect to the total number of seeds arranged, and the TP of seedling establishment with respect to the total number of seedlings planted. The cumulative probability of recruitment per habitat, from the production of mature fruit until the establishment of seedlings, was calculated as the product of the five TPs, with the TP of seed deposition weighted by the TP of fruit removal as the measure of seed dispersal. The probability of recruitment in the population of each species was estimated from the combined data of both plots. As a rough estimation of uncertainty of the cumulative probabilities of recruitment by habitat and at the population level of each species, an envelope of probabilities was calculated by multiplying successive upper and lower 95% CI of every stage-specific TP (i.e., for every stage, we multiplied the 95% CI of one stage by the 95% CI of the previous one).

Estimations of TPs have various limitations that have to be taken into account in their interpretation. In the seed deposition samples, microsites represented by plants in fruit were over-estimated with respect to their availability and we do not know the effect of other microsites potentially important for the deposition of seeds (e.g., below display sites of lekking male manakins; Krijger et al. 1997). Further, when we calculated TPs based on experimental methods, where the initial density of individuals was maintained constant, our approach ignored density-dependent effects and competitive interactions with other species that could affect the transition between stages. For example, deposition of seeds of *M. fosteri* and *M. serrulata* shows a strongly aggregated spatial pattern, with peaks of deposition beneath plants with fleshy fruits (Blendinger et al. 2011), and probability of survival of seeds and seedlings likely diminishes with density (Janzen 1970;

Kaspari 1993; Hammond and Brown 1998). Therefore, our results must be interpreted as the probability that one individual reaches a certain stage of recruitment when found in low densities, as could be the fate of a seed deposited in an isolated fecal clump.

### Statistical analyses

Analyses were applied separately to *M. fosteri* and *M. serrulata*. We used transformations to normalize the data and reduce the influence of outliers; count and frequency data were log-transformed and proportions were arc-sine transformed. To examine the effects of habitat type (bottom, slope and ridge) on every recruitment stage, we used general linear models ANOVA when the data met the assumptions of parametric tests. Count data whose distributions were strongly biased were analyzed with generalized linear models with the dependent variable following a Poisson distribution and using the log-link function. We evaluated goodness-of-fit of generalized linear models with deviance and Pearson Chi-square statistics; in cases when the adjustment was not sufficient, we used Kruskal–Wallis non-parametric tests. Between species differences in TPs were compared with Mann–Whitney *U* tests.

Stages of early recruitment varied spatially within and between 50 × 50 m grid cells (Blendinger et al. 2008, 2011). We evaluated the degree of spatial association between stages at the scale of cell, based on fruit production, mean values of seeds deposited in seed traps, and seedling survival in experimental trials. We used Spatial Analysis by Distance Indices (SADIE) methodology, developed for the spatial analysis of ecological data in the form of spatially referenced counts (Perry and Dixon 2002). SADIE is appropriate for situations where data are distributed patchily into discrete aggregations rather than as smoothly-varying surfaces, and it is specially designed to measure and test spatial patterns (Winder et al. 2001). SADIE assesses local spatial association using an index *X* based on the similarity between cluster indices of the two datasets and intrinsically allows for the spatial pattern in each component population. In a first step, cluster indices are calculated for each population of data, where large positive values indicate significant patchiness and large negative values indicate the presence of a gap (Perry and Dixon 2002). Then, the spatial association index *X*, which represents the correlation coefficient between the cluster indices of the two populations, is calculated. A positive value of *X* indicates that the two datasets are associated, with patches coinciding spatially, and a negative value indicates dissociation between locations of patches (Winder et al. 2001); thus, we assume that a greater positive value of *X* indicates greater coupling between stages.

The significance of *X* was tested with a randomization test that included Dutilleul adjustment for spatial autocorrelation. In the tests of association, we compared the quantity of units of recruitment by cell in the following manner: the observed number of fruits produced (i.e., the summation of crop sizes per cell), the mean number of seeds deposited by birds in seed traps in every cell, and the estimated number of established seedlings of 1 year (calculated as the product of the observed mean number of seeds deposited by the probability of transition from deposition of seeds until establishment, estimated in every cell). Values with decimals of seed deposition and seedling establishment were transformed to whole numbers. The magnitude of seedling establishment depended in part on seed deposition; nevertheless, the comparison permits us to evaluate whether processes that act between both stages do or do not modify the spatial template of recruitment initiated by dispersal by avian frugivores.

## Results

### Avian seed-dispersers

We captured 1,321 individuals, representing 95 species of birds, in mist-nets but only 7 species of understory frugivores dispersed seeds of *M. fosteri* or *M. serrulata*. These species were six manakins (Pipridae: striped manakin *Machaeropterus regulus*, blue-crowned manakin *Lepidothrix coronata*, blue-backed manakin *Chiroxiphia pareola*, white-crowned manakin *Pipra pipra*, wire-tailed manakin *Pipra filicauda*, and golden-headed manakin *Pipra erythrocephala*) and the white-necked thrush (Turdidae: *Turdus albicollis*). All these species are primarily frugivorous and swallow fruits whole, moving the seeds away from the parent plant. The two most abundant species of manakins, *L. coronata* and *P. pipra*, comprised 82% of the birds that consumed *M. fosteri* and *M. serrulata* fruits; the two species dispersed the majority of *Miconia* seeds (Table 1).

### Between-habitat comparison of individual recruitment stages

#### *Miconia fosteri*

The mean number of plants with fruit was greater in ridge and slope habitats than in bottoms (Generalized Linear Model, Wald  $\chi^2_2 = 15.93$ ,  $P < 0.001$ ). The number of fruits per cell was very variable; although the number was less in bottoms than in slopes or ridges, the differences were not significant (Kruskal–Wallis test,  $H_{2,72} = 1.90$ ,  $P = 0.39$ ). The mean estimated number of fruits of *M. fosteri* removed by frugivores varied among types of habitat (General

**Table 1** Avian dispersers of seeds of *Miconia fosteri* and *M. serrulata* in undisturbed terra firme forest recorded through captures in mist nets

Bird species	Fecal samples ( $n = 283$ )	<i>M. fosteri</i>		<i>M. serrulata</i>	
		Feces with seeds	Seeds	Feces with seeds	Seeds
<i>Machaeropterus regulus</i>	8	2	163	1	241
<i>Lepidothrix coronata</i>	125	23	1,277	25	1,545
<i>Chiroxiphia pareola</i>	11	2	27	2	108
<i>Pipra pipra</i>	88	18	2,765	31	1,999
<i>P. filicauda</i>	4	0	–	2	209
<i>P. erythrocephala</i>	31	5	160	6	456
<i>Turdus albicollis</i>	16	0	–	1	901

For each bird species, number of fecal samples obtained, quantity of fecal samples with seeds of each plant species, and total number of seeds recorded are indicated

Linear Model,  $F_{2,38} = 4.64$ ,  $P = 0.016$ ), being greater in ridges than in bottoms (Unequal-N HSD post hoc test), whereas slopes had intermediate values of removal and did not differ significantly from the other habitats. Mean deposition of seeds was greater in slopes and less in bottoms, with intermediate values in ridges (Wald  $\chi^2 = 15.07$ ,  $P < 0.001$ ). Inspection of residuals of Pearson and results of the goodness-of-fit test (deviance–df ratio = 2.3) showed a poor model fit, so we explored the data with a nonparametric test. The results obtained were similar although the differences were less marked ( $H_{2,72} = 6.88$ ,  $P = 0.03$ ); the greatest differences were between slopes and bottoms (Multiple Comparisons of  $P$  values,  $P = 0.057$ ).

Although seed survival was somewhat less in ridges than in slopes or bottoms, there was no effect of habitat type on the mean proportion of seeds not removed from the experimental deposition sites ( $F_{2,69} = 2.17$ ,  $P = 0.12$ ). Similarly, the mean proportion of seeds that germinated was greater in bottoms than in the other habitats, but the differences were not significant ( $F_{2,69} = 2.28$ ,  $P = 0.11$ ). The mean proportion of established seedlings after 1 year was similar in the three types of habitat ( $F_{2,69} = 0.50$ ,  $P = 0.61$ ). Online Resource 1 presents a synthesis of the mean values by species and habitat for each of the comparisons conducted.

#### *Miconia serrulata*

The mean number of plants with fruit was greater in slopes than in bottoms or ridges (Wald  $\chi^2 = 8.45$ ,  $P = 0.014$ ). The mean number of fruits per cell tended to be greater in slopes than in the other types of habitat ( $H_{2,72} = 5.20$ ,  $P = 0.07$ ). There was a strong effect of habitat on estimated mean number of fruits removed ( $F_{2,26} = 5.66$ ,  $P = 0.009$ ), with more fruits removed from slopes than bottoms or ridges (Unequal-N HSD post hoc test). Mean deposition of seeds was similar in the three types of habitat

(Wald  $\chi^2 = 3.62$ ,  $P = 0.16$ ); however, the variability was much greater in slopes, where a few cells received a disproportionately higher number of seeds.

We did not find an effect of habitat on stages of recruitment in any of the experimental trials. The mean proportion of surviving seeds did not differ among habitats ( $F_{2,69} = 0.27$ ,  $P = 0.76$ ). We did not find differences either in the mean proportion of seeds that germinated ( $F_{2,69} = 0.81$ ,  $P = 0.45$ ), or in the mean proportion of plants established after 1 year in the three types of habitat ( $F_{2,69} = 0.90$ ,  $P = 0.41$ ).

#### Probabilities of transition between recruitment stages

In the majority of comparisons, the probability of survival in a specific stage was similar among habitats (i.e., with few discordances in TPs among types of habitats) (Table 2) and with limited evidence of uncoupling between successive stages (Table 3). In *M. fosteri*, removal of fruits and survival of seedlings were the most critical stages, in agreement with the low TP values. Production of fruits and, especially, the dispersal of seeds (both in terms of removal of fruits and deposition of seeds) were much less in bottoms than in other types of habitat (Table 2). In *M. serrulata*, no stage was clearly more limiting for recruitment than others; only the probability of germination was somewhat less than other TPs. Spatial concordance among types of habitat was similar for most stages of recruitment, with the notable exception that the TP in seed deposition was much greater in slopes (Table 2) because of pronounced peaks of seed deposition in a few cells.

The starting point in the estimations of cumulative probabilities of survival was set at the total number of mature fruits produced, of which 25% (*M. fosteri*) and 47% (*M. serrulata*) were removed by frugivores; the fate of the remainder (not quantified) was distributed between fruits that fell without being dispersed and fruits that rotted on

**Table 2** Synthesis of stage-specific transition probabilities of *M. fosteri* and *M. serrulata* estimated by habitat type and at the population level

	Bottom	Slope	Ridge	Population
<i>Miconia fosteri</i>				
Fruit maturation	0.062	0.349	0.589	
Seed dispersal				
Fruit removal	0.172 ± 0.103	0.238 ± 0.059	0.319 ± 0.107	0.250 ± 0.104
Seed deposition <sup>a</sup>	0.025 (0.006)	0.438 (0.109)	0.537 (0.134)	
Seed survival	0.634 ± 0.321	0.610 ± 0.326	0.435 ± 0.361	0.558 ± 0.344
Seedling emergence	0.557 ± 0.222	0.384 ± 0.230	0.405 ± 0.262	0.436 ± 0.247
Seedling survival	0.321 ± 0.232	0.245 ± 0.261	0.308 ± 0.222	0.286 ± 0.240
<i>Miconia serrulata</i>				
Fruit maturation	0.087	0.824	0.089	
Seed dispersal				
Fruit removal	0.420 ± 0.211	0.544 ± 0.144	0.408 ± 0.173	0.472 ± 0.176
Seed deposition <sup>a</sup>	0.132 (0.062)	0.707 (0.334)	0.161 (0.076)	
Seed survival	0.539 ± 0.267	0.548 ± 0.319	0.485 ± 0.279	0.525 ± 0.290
Seedling emergence	0.414 ± 0.256	0.335 ± 0.243	0.411 ± 0.244	0.382 ± 0.246
Seedling survival	0.447 ± 0.193	0.438 ± 0.247	0.525 ± 0.269	0.469 ± 0.242

Mean ± SD of probabilities measured by grid cells are given, except for ripe fruits and seed deposition which were estimated as the proportion of fruits or seeds recorded in each habitat with respect to the total in all habitats

<sup>a</sup> Values in parentheses represent the transition probabilities weighted by the proportion of fruit removed in the population

**Table 3** Synthesis of stage-wise cumulative recruitment probabilities of *M. fosteri* and *M. serrulata* in three habitats

	<i>Miconia fosteri</i>			<i>Miconia serrulata</i>		
	Bottom	Slope	Ridge	Bottom	Slope	Ridge
Seed deposition	0.0061	0.1094	0.1342	0.0621	0.3335	0.0759
Seed survival	0.0039	0.0668	0.0584	0.0335	0.1829	0.0369
Seedling emergence	0.0022	0.0256	0.0237	0.0139	0.0613	0.0152
Seedling survival	0.0007	0.0063	0.0073	0.0062	0.0269	0.0080

The starting density corresponded to the total number of ripe fruits produced, arbitrarily considered with a probability equal to 1. Transition probabilities of seed deposition was weighted by mean proportion of fruit removed per habitat

the plant. In both species, the habitats with the greatest production of mature fruits were, in turn, those with greatest probability of seed deposition (Table 2). In all cases, the high probability of recruitment provided by the deposition of seeds in one particular habitat was not modified for the following stages (Fig. 1), as was observed in the successive products of the TPs (Table 3). Thus, the quality of dispersal directly influenced the cumulative probabilities of survival, which were greater in habitats that had greater probabilities of arrival of seeds; i.e., slope and ridge in *M. fosteri* (Fig. 1b, c) and slope in *M. serrulata* (Fig. 1e). The two species had low cumulative probabilities of recruitment in the bottom of ravines and high on slopes. However, the visual comparison of the cumulative stage-

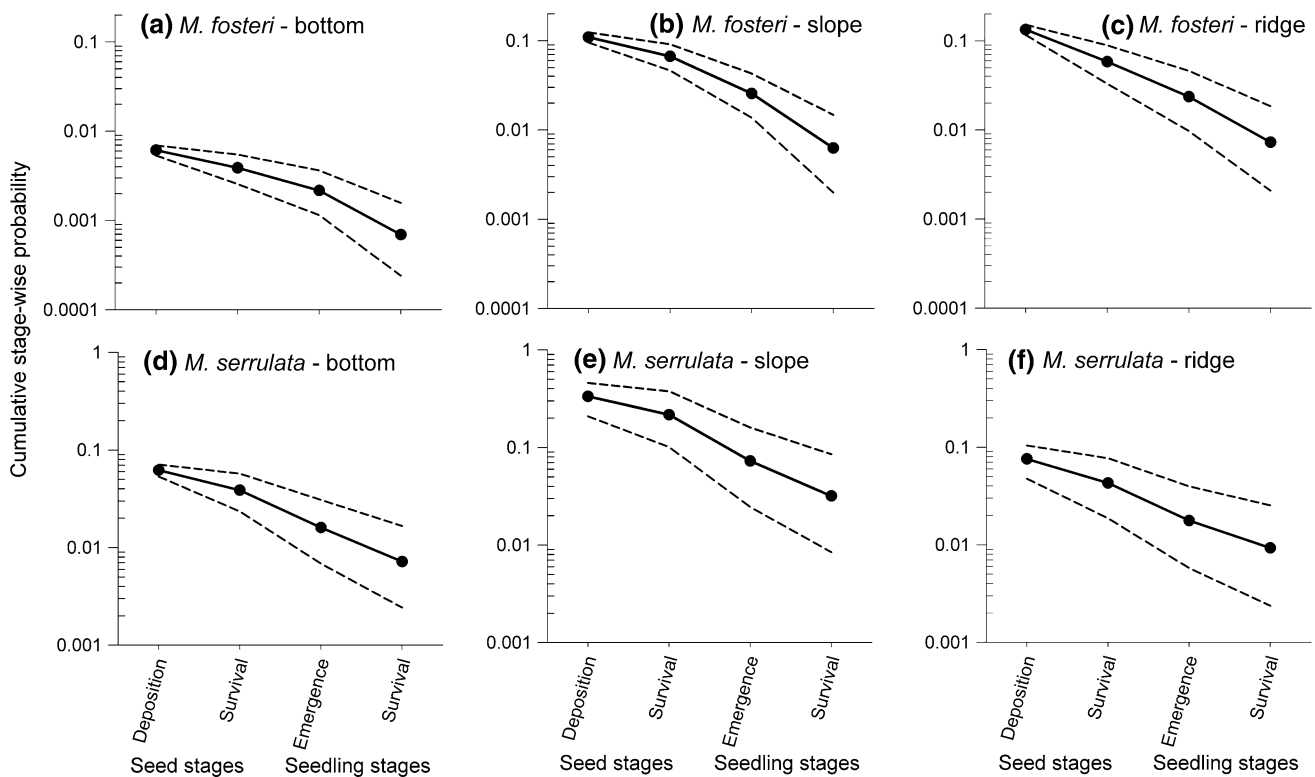
wise probabilities and their 95% confidence limits (Fig. 1) demonstrated that within bottom or slope, the recruitment probability was always one to two orders of magnitude greater in *M. serrulata* than in *M. fosteri*.

The probability of recruitment into the population, estimated as the probability of producing a 1-year-old sapling from one seed in a mature fruit, was more than double for *M. serrulata* (4.43%; 95% CI: 2.47–7.39%) than for *M. fosteri* (1.74%; 0.09–3.06%). The cumulative curve of probabilities of recruitment differed between the two species (Fig. 2). The mean probability of transition in the removal of fruits was greater in *M. serrulata* than in *M. fosteri* (Mann–Whitney *U* test,  $z = 3.55$ ,  $N_1 = 33$ ,  $N_2 = 41$ ,  $P < 0.001$ ). Mean TPs related to survival of seeds in the soil and seed germination did not differ between species ( $P > 0.20$  in all three comparisons). The TP in the seedling establishment recorded in the experimental trials was significantly greater in *M. serrulata* than in *M. fosteri* ( $z = 4.35$ ,  $N_1 = 72$ ,  $N_2 = 72$ ,  $P < 0.0001$ ).

#### Spatial association between stages of recruitment

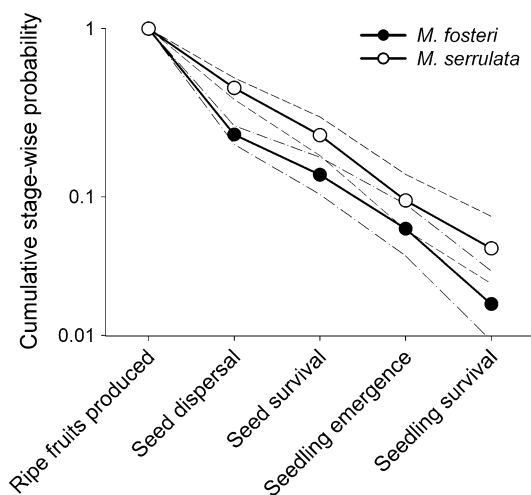
The degree of spatial association between stages of recruitment varied slightly between *M. fosteri* and *M. serrulata*. However, the strength of spatial association between stages of recruitment differed more between the two study plots than between species (Table 4), suggesting differences within and between species in the strength of





**Fig. 1** Cumulative stage-wise probabilities (mean  $\pm$  95% confidence limits) of recruitment expected for **a–c** *Miconia fosteri* and **d–f** *M. serrulata* in three different habitats of terra firme forests. The graphs summarize the probabilities that a seed contained in a mature fruit reaches successive stages in the cycle of recruitment. The

starting density (not included in the figure) corresponded to the number of ripe fruits produced at the population level, arbitrarily considered with a probability equal to 1. Note differences in the scale of cumulative probabilities between *M. fosteri* and *M. serrulata*



**Fig. 2** Cumulative stage-wise probabilities (mean  $\pm$  95% confidence limits) of recruitment expected for *Miconia fosteri* and *M. serrulata* in an undisturbed terra firme forest. The graph summarizes the probabilities that a seed contained in a mature fruit reaches successive stages in the cycle of recruitment

processes that act between recruitment stages. The spatial match between patchiness and gaps in the abundance of recruits in successive stages was pronounced for *M. fosteri*

and *M. serrulata* in the same plot (plot 1); however, it was weak or absent for both species in the other plot. Specifically, the distribution of fruit abundance and seed deposition of *M. fosteri* was positively associated to the distribution of the number of seedlings established after 1 year in only one plot (Table 4). In *M. serrulata*, the quantity of fruits produced was not spatially associated with successive stages of recruitment in one plot, but the spatial template of recruitment set by the activity of avian frugivores was correlated with seedling establishment in the two plots (Table 4).

In both species, there was a clear tendency for local spatial association between stages; in the 12 comparisons conducted, between 72 and 92% of the 36 cells had positive values of association. Nevertheless, in each comparison, only a few cells had significant values of local association, indicating that the spatial association in the plots was influenced by a few cells with strong, positive local association and the absence of clustering of local association. Similarly, the absence of spatial association between stages recorded for *M. fosteri* and *M. serrulata* in several comparisons in plot 2 (Table 4), was due to the presence of a few cells with significant values of local dissociation.

**Table 4** Indices of spatial association ( $X$ ) comparing the distribution of abundance of three stages of recruitment in two 9-ha plots divided into a  $6 \times 6$  grid of cells

	<i>M. fosteri</i>		<i>M. serrulata</i>	
	$X$	$P$	$X$	$P$
<b>Plot 1</b>				
Fruit production–seed deposition	0.80	<0.01	0.93	<0.05
Seed deposition–seedling establishment	0.74	<0.001	0.99	<0.05
Fruit production–seedling establishment	0.67	<0.001	0.95	<0.05
<b>Plot 2</b>				
Fruit production–seed deposition	0.49	<0.05	0.27	ns
Seed deposition–seedling establishment	0.17	ns	0.72	<0.001
Fruit production–seedling establishment	0.22	ns	−0.01	ns

ns Not significant

## Discussion

In the Ecuadorian Amazon, two understory plant species that differ in patterns of habitat use but that share a small group of bird species as primary dispersers, possess strong similarities in the initial phases of recruitment that lead to establishment of saplings. Notably, in both species, the spatial template of seed deposition was a good predictor of the differences among habitats in the probability and magnitude of recruitment. These results differ from similar studies in temperate zones, where seedling survival can be the principal process that determines the initial pattern of recruitment, modifying the spatial patterns of seed dispersal (Herrera et al. 1994; Rey and Alcántara 2000; García 2001; Traveset et al. 2003; Gulias et al. 2004). The spatial discordance generated by dispersal did not become decoupled in later stages, and was the main determinant of which sectors of the forest and types of habitat had more recruitment of saplings (in terms of cumulative probability and potential number of individuals that could reach this stage).

Processes that intervene during recruitment can act with distinct intensities depending on the spatial scale (Kollmann 2000; Blendinger and Villegas 2011). We focused at the habitat scale to measure these processes. It is to be expected that processes such as fruit removal and seed deposition by frugivorous understory birds act with highest intensity over ranges of hundreds to thousands of square meters (Loiselle and Blake 1999; Saracco et al. 2004; Carlo and Morales 2008), coinciding with the size of our sample units. On the other hand, the habitat scale includes the combined effects of those factors and their variability acting with greater force at a finer scale (e.g., availability of

microsites and light for germination and establishment; Clark et al. 1999; Kollmann 2000). We found that the spatial patterns of association among successive stages of recruitment at a smaller scale than habitat type was strongly affected by the location of a few local patches, suggesting that more fine-tuned spatial approaches should be used to fully understand the specific requirements of recruitment of these species. For example, deposition of seeds of *M. fosteri* and *M. serrulata* was strongly aggregated beneath plants with fruits that were preferred by frugivores (Blendinger et al. 2011). This contagious deposition in specific microsites could lead to subsequent density-dependent mechanisms (not evaluated with our design) acting at the same scale, such as depredation and secondary dispersal of seeds by ants, as is known to occur in other species of *Miconia* (Levey and Byrne 1993; Christianini and Oliveira 2009). In general, density-dependence in tropical forests operates over fine spatial scales in localized microsites (De Steven and Wright 2002).

Abundances of adult plants of both species of *Miconia* were related to small differences in relief of terra firme forest. The association of tropical plant species with local topographic gradients is a frequent phenomenon (Harms et al. 2001; Valencia et al. 2004; John et al. 2007). Differences in distribution of adult plants along local gradients of topography could reflect habitat preferences of juvenile stages, or could be a consequence of limited dispersal to sites close to the source even when seedlings do not have habitat preferences (Webb and Peart 2000; Comita et al. 2007). Analysis of multiple life-cycle stages of the plants permits exploration of whether associations between plant species and topographic habitat types become established at early life stages, as our results suggest. During the dispersal and recruitment of *M. fosteri* and *M. serrulata*, the major variation among habitats occurred in the fruit removal and seed deposition stages. In *M. fosteri*, density of reproductive plants, abundance of fruits, fruit removal and seed deposition were consistently less in bottomland habitat. Similarly, in *M. serrulata*, there was consistency in the spatial pattern of reproductive plants and early stages of recruitment. Neither of the two study species demonstrated consistent habitat preferences for germination or establishment, suggesting that habitat differences among adults were mostly a consequence of seed dispersal by birds.

Quantitative and qualitative aspects of dispersal (Schupp 1993; Loiselle and Blake 1999) could be key factors that contribute to plant reproductive success (Schupp et al. 2010). Efficiency of dispersal, a reflection of the success of the reproductive investment by a plant (Alcántara et al. 1997), was relatively low in all types of habitat (Blendinger et al. 2008) and, in *M. fosteri*, only 25% of mature fruits, on average, were removed from the plant. On the other hand,

the spatial deposition of seeds seems to have marked consequences for the habitat associations of plants that reach reproductive maturity. For canopy trees of tropical forests, there is abundant evidence that survival and growth of juvenile stages is critical if plants are to obtain and occupy a space as reproductive individuals of the canopy, but may not be a critical stage for many plants that develop their life cycle in the shade of the understory (e.g., Schupp 1990; De Steven and Wright 2002). Although we did not examine the ultimate consequences of the cycle of dispersal and recruitment (i.e., the survival of saplings until reaching reproductive maturity), the number of saplings up to 0.5 m tall was very low in all types of habitat ( $<0.015$  plants  $\text{m}^{-2}$ ). In this case, a higher mortality after establishment could significantly filter the number of seedlings that advance to maturity, although it did not seem to modify spatial patterns generated by dispersers, which endured at least until the seedlings were 1 year old.

Cumulative recruitment probabilities were greater in ridge and slope habitats for *M. fosteri* and in slope for *M. serrulata*. This was a consequence of the combined effects of, on the one hand, the interaction of spatial discordances among types of habitat in successive stages that unite production with dispersal and, on the other hand, the fact that post-dispersal processes up to establishment were similar among different types of habitat. Unlike our results, previous studies of multiple sequential stages in a whole population, or in particular habitats occupied by a species, have demonstrated that decoupling among successive stages is much more frequent than its absence (Herrera et al. 1994; Laman 1995; García 2001; Balcomb and Chapman 2003; Traveset et al. 2003). As a consequence, in species dispersed by vertebrates, the result of processes that act over one stage is usually contravened or obscured by processes that act in later stages (Jordano and Herrera 1995).

In the few studies of tropical plants dispersed by frugivorous vertebrates where the relationships among multiple successive stages of recruitment have been evaluated, quality of dispersal, mortality of seedlings, and, in particular, survival of seeds were critical stages for initial recruitment of *V. surinamensis*, *O. endresiana* and *M. myristica* (Howe and Vande-Kerckhove 1981; Howe et al. 1985; Wenny 2000; Balcomb and Chapman 2003). Using very short-term field data (i.e., 24 h exposure to predators), Moles et al. (2003) did not find a significant relationship between seed mass and seed mortality by post-dispersal predation in tropical humid forests. However, it is suggestive that post-dispersal seed survival was not critical for the recruitment of the two very small-seeded species ( $<0.001$  g) we studied, whereas it was a critical stage for the three large-seeded species (0.8–2.0 g) mentioned above. In the upper Amazon, the most critical stage for

*M. fosteri* at early life stages was the removal of seeds and, in both species, the template of seed deposition was not modified in later stages. This result also differs from that reported for canopy tree species in tropical forests (Comita et al. 2007) where, in general, associations of species with specific habitats are not formed during the first stages of life (i.e., they exhibit different habitat preferences through their life cycle). Our results should, however, be interpreted with caution. On one hand, we do not know if density-dependent mortality of seeds and seedlings could modify our estimations of the TPs among stages of recruitment. On the other hand, to fully understand the demographic consequences of recruitment requires longer-term studies that examine interannual variability in the different stages and processes involved. Although production of fruits of *M. fosteri* and *M. serrulata* was similar during 2002 and 2003, temporal variation in other stages and processes of recruitment are well known for many tropical species that are dispersed by avian frugivores (Schupp 1990; Ortiz-Pulido and Rico-Gray 2000; De Steven and Wright 2002).

Dispersal by manakin species seems to be a key component of the recruitment of *M. fosteri* and *M. serrulata*, and numerous understory species of Neotropical rainforest could depend in a similar manner on few species of birds for maintenance and regeneration. It has been suggested that species such as *Miconia* produce generalized fruits that depend on diverse dispersal agents (Snow 1981). Nevertheless, few species of avian frugivores are common in the understory of Amazonian terra firme forests [Loiselle et al. (2007) and Loiselle and Blake (1999) reported the same pattern from tropical forests in Costa Rica]. At Tiputini Biodiversity Station, the four most common manakins accounted for about 58% of understory frugivorous birds (Blake and Loiselle 2009) and dispersed more than 80 plant species of the understory between January and August (Loiselle et al. 2007b); a randomization test with these data gives an upper estimate of 150 plant species dispersed (PGB, unpublished data). Thus, the role of manakins with respect to recruitment of understory plants of terra firme forest in the upper Amazon could be much greater than normally considered in megadiverse tropical forests.

## Conclusions

In summary, physical and biological factors that act from the production of seeds until establishment (Wang and Smith 2002) reduce, across sequential stages, the magnitude of recruitment of *M. fosteri* and *M. serrulata*. The possible resultant spatial patterns that are maintained during the demographic filter of sapling recruitment suggests that the deposition of seeds could be a critical factor to explain the habitat associations of both species. The

abundance of *M. fosteri* and *M. serrulata* plants that reach reproductive maturity was related to small differences in topography of terra firme forest; locally, *M. serrulata* seems to reach its optimum on slopes, and both species are scarce along ravines in streams. However, decoupling between successive stages at a smaller spatial scale that habitat type in one of the two study plots, and considerable uncertainty in the estimation of the cumulative recruitment probability per habitat in *M. serrulata*, indicated that important variability also occurs that is not associated with types of habitat, emphasizing the importance of studies that consider spatial–temporal scales of variability (Herrera et al. 1994; Balcomb and Chapman 2003; García et al. 2005) to make robust conclusions over the causes of population dynamics. Our findings suggest that, in both species of *Miconia*, the profound asymmetry in seed deposition at fine scales (Blendinger et al. 2011) means that only some of the sites available in a habitat receive seeds, and those habitats with low availability of fruits received less seeds. Thus, seed limitation may be a more important limitation mechanism than limitations of availability of sites appropriate for establishment. The relative importance of seed limitation and the limitation of appropriate sites for establishment are not only important for understanding the demography of a species but also have profound consequences for the abundance and coexistence mechanisms of species in communities (Clark et al. 1999; Müller-Landau et al. 2002). Future studies of the multiple stages that lead to recruitment should evaluate coexisting species with contrasting ecological requirements (e.g., gap dependent vs. shade tolerant), which could provide significant information about the relative importance of the limitations to establishment that confront species of the understory that depend on the same set of bird species for their dispersal.

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