

The relevance of ants as seed rescuers of a primarily bird-dispersed tree in the Neotropical cerrado savanna

Alexander V. Christianini · Paulo S. Oliveira

Received: 22 November 2007 / Accepted: 31 March 2009 / Published online: 28 April 2009
© Springer-Verlag 2009

Abstract The scale at which seed dispersal operates has many implications for the spatial patterns of plant recruitment and diversity. We investigated the effect of short- (ants) and long-distance (birds) seed dispersal of the fleshy-fruited melastome, *Miconia rubiginosa*, in the Brazilian savanna. We estimated the contribution of dispersal vectors to the removal of the fruit crop from the canopy (birds), and once seeds have reached the cerrado floor (ants) over two fruiting seasons. Birds (13 species) removed up to 23.7% of the fruit crop from the crown, but dropped a substantial proportion of fruits beneath the parent plant. Birds removed a greater proportion of fruits from trees producing large fruit crops, as predicted by the fruit crop size hypothesis. However, up to 18.9% of the fruit crop fell beneath the parent plant as ripe fruit. Most fallen fruits were removed by ants (seven genera), which are

likely to play a relatively important role in terms of the quantity of seeds dispersed, especially for plants producing small fruit crops (a conceptual model is presented). Birds and ants did not influence seed germination, but they differ in terms of the spatial scale of dispersal and deposition patterns. Ants probably play an important role in the local population dynamics of *Miconia*, whereas birds are responsible for long-distance dispersal associated with the colonization of new patches and metapopulation dynamics. By removing seeds from bird droppings, ants may also reshape at a finer scale the seed rain generated by primary dispersers. Indeed, seedlings and saplings of *Miconia* are more frequently found around leaf-cutter ant nests than in control areas away from ant nests or around large *Miconia* trees. The quantitative component of dispersal effectiveness by ants acting as “rescuers” of seeds that fail to be dispersed, or fall under parent trees, is probably more important than currently recognized in other systems.

Communicated by Diethart Matthies.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-009-1349-2) contains supplementary material, which is available to authorized users.

A. V. Christianini
Programa de Pós-Graduação em Ecologia,
Departamento de Zoologia, Universidade Estadual de Campinas,
C.P. 6109, Campinas, SP 13083-970, Brazil

P. S. Oliveira (✉)
Departamento de Zoologia, Universidade Estadual de Campinas,
C.P. 6109, Campinas, SP 13083-970, Brazil
e-mail: pso@unicamp.br

Present Address:
A. V. Christianini
Universidade Federal de São Carlos, Campus Sorocaba, Rod. João
Leme dos Santos km 110, Sorocaba, SP 18052-780, Brazil

Keywords Diplochory · Dispersal distance ·
Disperser effectiveness · Fruit crop size · Seed dispersal

Introduction

Plants producing large fruit crops are likely to attract a great number and variety of frugivores and attain higher seed dispersal success compared to plants producing fewer fruits, as predicted by the fruit crop size hypothesis (e.g. Snow 1971; McKey 1975; Howe and Estabrook 1977). Large fruit crops, however, are frequently associated with a loss of great amounts of the seed output to frugivores that behave as poor dispersers, or that are satiated by an excess of food supply (Sallabanks 1993; Jordano and Schupp 2000; García et al. 2001), or even due to a mismatch

between frugivores and their fruiting plants (Ortíz-Pulido and Rico-Gray 2000). As a consequence of a large crop in the canopy, many fruits fall naturally (i.e. unmanipulated by frugivores) under the parent plant, or are dropped by animals feeding on the fruit pulp but providing no dispersal away from the parent plant. Such waste of seeds is usually viewed as an inherent cost of attracting good dispersal agents (Howe 1980; Sallabanks 1993; Jordano and Schupp 2000), since seeds that fail to be dispersed and are dropped under the parent plant face a low probability of recruitment due to density-dependent mortality of seeds and seedlings (e.g. Harms et al. 2000).

Certain events, however, may dramatically change the probability of recruitment for seeds that fall under parents. Seeds may be secondarily scattered by insects, rodents or water between fruit fall and germination. Indeed, due to increased mortality near parent plants, even very local dispersal can be advantageous (e.g. Schupp 1988). Although local versus long-distance dispersal in plant regeneration has many implications for the spatial patterns of recruitment and plant diversity (Howe 1989; Hubbell et al. 1999; Nathan and Muller-Landau 2000), it has received little empirical investigation (Horvitz and Le Corff 1993; Fragoso et al. 2003; Jordano et al. 2007; Spiegel and Nathan 2007). Similarly, recent studies have shown that seed dispersal systems are frequently more complex than previously thought, and may include a series of subsequent dispersal vectors (i.e. diplochory) whose effects on plant regeneration are still poorly understood (see Vander Wall and Longland 2004). Despite recent progress at revealing such multi-phased dispersal systems (e.g. Böhning-Gaese et al. 1999; Passos and Oliveira 2002), we still need a conceptual framework for the factors driving diplochory and the spatial scales of seed dispersal. An approach that may help to sort out the components affecting such complex interactions includes the effectiveness of each vector of dispersal. The concept of disperser effectiveness (Schupp 1993) highlights two main factors contributing to dispersal: the quantity of seeds dispersed, and the quality of seed dispersal (fate of dispersed seeds and their probability of reaching maturity). Investigation comparing the effectiveness of plant–frugivore interactions in the crown and on the cerrado floor (either as dispersed seed, or as a waste beneath the canopy) may thus change the current view on the role of wasted fruit under parent plants.

The prominence of the interactions between ground-dwelling ants and fleshy fruits has been highlighted in recent studies in tropical forests (Rico-Gray and Oliveira 2007). Ants can transport fruits that have fallen spontaneously with the pulp intact, or have been dropped by birds with bits of pulp attached (Böhning-Gaese et al. 1999; Pizo and Oliveira 2000; Passos and Oliveira 2003), and can also collect seeds from frugivore faeces (Kaspari 1993; Pizo and

Oliveira 1999). These interactions can modify the fate of seeds and markedly affect seedling growth and survival (Levey and Byrne 1993; Passos and Oliveira 2002). In the cerrado savanna of central Brazil, ants remove small fruits or seeds that fall to the ground, even those of plant species that present no visible adaptation for ant dispersal (Leal and Oliveira 1998; Christianini et al. 2007). For instance, although the huge fruit crops of the fleshy-fruited *Miconia rubiginosa* in the cerrado attract many vertebrate frugivores that remove seeds from the crown, many fruits fall under the parent plant and are frequently harvested by leaf-cutter ants (Attini), as also reported in rainforests (Wirth et al. 2003). Until recently leaf-cutters were recognized only as seed predators, but field and laboratory studies indicate that attine ants can positively affect plant recruitment by increasing seed germination and seedling establishment (Oliveira et al. 1995; Farji-Brener and Silva 1996; Leal and Oliveira 1998; Farji-Brener and Ghermandi 2004). In this study we investigated the effectiveness of seed dispersal vectors acting in the crown (birds) and on the cerrado floor (ants) for the regeneration of *M. rubiginosa* in the cerrado. Specific questions were:

1. Do ants “rescue” seeds that fail to be dispersed and fall beneath the crown?
2. What are the relative roles of birds and ants in the quantitative and qualitative components of seed dispersal?
3. What is the spatial scale of seed delivery provided by birds and ants?

We show that ants give a second chance of dispersal to the fallen seeds of *M. rubiginosa* in the cerrado. We used these data to build a conceptual model to account for the relative contribution of seed removal by different vectors—birds (canopy) versus ants (once seeds have reached the cerrado floor)—to the quantitative component of dispersal effectiveness under variable crop sizes of *M. rubiginosa*.

Materials and methods

Study site

Field observations and experiments were carried out from December 2003 to August 2005 in the reserve of the Estação Experimental de Itirapina (22°12'S, 47°51'W), a 200-ha fragment of cerrado in southeast Brazil. Average annual rainfall is 1,190 mm, concentrated in the warm and wet season (December–March). A dry and cold season occurs from April to November. Mean annual temperature is 19.7°C. The vegetation at the study site is the cerrado sensu stricto, the typical fire-prone savanna that grows on sandy, nutrient-poor soils of the cerrado domain, characterized

by 50–80% of ground cover by small palms, shrubs and trees (Oliveira-Filho and Ratter 2002). Leaf litter and herbaceous vegetation cover 30% of the soil. Trees can reach 4–6 m, with emergent *Dalbergia miscolobium* Benth. (Fabaceae) reaching up to 8 m. Details about the flora of the study site can be found in Giannotti (1988).

The plant

Miconia rubiginosa (Bonpl.) DC. (Melastomataceae) (hereafter referred to only by the genus name) is a fleshy-fruited tree (crown radius 1.9 ± 0.9 m; mean \pm SD) widespread in the cerrado. It produces large fruit crops annually from February to June. Fruits are purple berries with a mean fresh mass of 0.12 g, each bearing a mean of 11 ± 2 (SD) tiny, 1.2-mg seeds. The fruit pulp is rich in carbohydrates (87.3% dry mass), and contains a small amount of protein (8.3%), lipids (2.8%), and ash (1.6%) (A. V. Christianini and P. S. Oliveira, unpublished data). Like other melastomes (Loiselle and Blake 1999), *Miconia* is primarily dispersed by birds and presents no morphological trait that may suggest secondary dispersal by ants or other animals. *Miconia* species usually have persistent seed banks (Dalling et al. 1998). In the study site, adult plants are aggregated in a large patch of dense cerrado woodland (ca. 100 ha), but isolated individuals are also found scattered in more open savanna (A. V. Christianini and P. S. Oliveira, personal observation). This study was carried out within a plot of 30 ha of dense cerrado woodland where *Miconia* was one of the most abundant tree species.

Fruit production and seed fate

In order to examine fruit production by representative plant individuals, we arbitrarily selected ten trees of *Miconia* (five in 2004, and five in 2005) distributed within the savanna reserve. Each tree was isolated from the nearest reproductive conspecific by a distance of 5–30 m. Direct counts of fruits on the tree crown were unreliable because of the huge fruit crop of trees. To obtain an estimate of fruit production, we multiplied the mean number of fruits obtained by direct counts of three to four bunches of fruits collected randomly at each focal *Miconia* by the number of bunches visually estimated at the same tree at the beginning of the fruiting season.

Fruit traps were used to evaluate seed dispersal rates by primary dispersers, and seed fall to the ground. Traps consisted of 0.14-m² plastic trays lined with 0.2-mm nylon mesh placed at random below the crown of focal trees. Traps were kept 20 cm above ground by four stakes, each coated by a sticky resin (Tanglefoot) to prevent ants from reaching fallen fruits or seeds. We placed two to ten traps under each tree to catch fallen fruits, as well as seeds

embedded in bird faeces. We removed fruit debris in the traps every 2–4 weeks throughout the entire fruiting season. Fruits or seeds were then counted and classified as: (1) ripe (dark purple, mature fruit with viable seed, falling spontaneously or dropped by birds after handling failures); (2) unripe (green, mostly aborted undeveloped fruits); (3) damaged (partially damaged fruit with seeds exposed, showing signs of pre-dispersal seed predation); or (4) seeds dropped by primary dispersers (seeds embedded in faeces or regurgitated/dropped by birds). This latter category may include an unknown number of seeds detached from damaged fruit, seeds from ripe fruits of the same tree, as well as seeds brought by dispersers from other conspecific trees. We did not consider fruits that were dropped by birds after handling failures as a separate category because they were functionally equivalent to ripe fruits falling under the parent crown. An indirect estimation of the relative importance of ripe fruits dropped by birds under parents was obtained from observations of frugivorous birds in the canopy (see below). By the end of the fruiting season, all unremoved fruits inevitably fall to the ground. Fruit traps allowed us to estimate how much of the crop was removed by birds, as well as the number of fruits/seeds that reached the cerrado floor. Calculations were made as follows. We determined the number of non-dispersed seeds for each tree by dividing the sum of ripe, unripe, and damaged fruit in the sampled material in traps by the fraction of canopy area sampled (Jordano 1995). To estimate the number of seeds dispersed by birds, we subtracted the number of non-dispersed seeds (within the three categories specified above) from the total crop size estimated by the visual counts. Since an unknown fraction of seeds dropped by birds under the canopy (category 4 above) could come from other conspecific trees, we ignored this category in the calculation of the number of non-dispersed seeds. Thus our estimate of the proportion of the fruit crop falling under the parent crown is probably conservative. An estimate of relative seed dispersal failure was obtained by the relation between crop size and the proportion of fruit crop falling under the parent plant using linear regression. Additional observations on a set of fruit traps placed >3 m away from the edge of the crown of each sampling *Miconia* was used to evaluate the decrease in seed shadow with distance from fruiting plants.

Plant-frugivore interactions in the crown: observation of frugivorous birds

To obtain information about frugivorous visitors we monitored 28 fruiting trees of *Miconia* in the study plot. Observations were conducted throughout the day, between 0550 and 1830 hours. Altogether there were 86.4 h of simultaneous observations on 1.7 ± 1.1 (mean \pm SD) trees, totalling 131.1 tree observation hours in the 2004, and 21.7 h in

the 2005 fruiting season, respectively. For each visitor we recorded the duration of the visit, seed handling behaviour, and counted the number of fruits either dropped under the plant, or removed from the crown. Seeds swallowed by birds that left the tree afterwards were considered dispersed away. We also recorded post-feeding flight distances of birds departing from the focal tree until the first landing perch as an estimate of minimum dispersal distance (Jordano and Schupp 2000). We used the following distance intervals: 0–1.9, 2–4.9, 5–9.9, 10–19.9, 20–39.9, and >40 m. Casual observations of birds interacting with fruits of *Miconia* in the crown were also recorded to increase sample sizes.

Plant–frugivore interactions on the ground: ant attendance to fallen fruits

To determine which ants interact with fallen fruits of *Miconia* we recorded all ant–fruit/seed interactions observed throughout the entire fruiting seasons of 2004 and 2005 (a subset of these data was reported in Christianini et al. 2007). Systematic sampling was also carried out by placing marked fruits at 30 ground stations 10 m apart, 1–2 m from two parallel transects that crossed the study site. Two fruits per sampling station were placed on white filter paper (4 × 4 cm) to facilitate visualization on the leaf litter. The filter paper had no detectable effect on ant behaviour (see Passos and Oliveira 2002). Fruits were set at 0800 and 1800 hours and checked at regular intervals over a 2-h period during the fruiting season of *Miconia*. During observations we recorded the ant species attracted, and their behaviour toward the fruits. Ant behaviour was classified as follows: (1) remove (>5 cm) whole fruit to nest; (2) clean fruit pulp at the spot, no removal; (3) inspect or manipulate fruit, but without removal (<5 cm). We followed ants carrying fruits until they entered their nests or disappeared in the leaf litter. The distance of fruit displacement was then measured. Voucher specimens of the ants are deposited in the collection of the Universidade Federal Rural do Rio de Janeiro (CECL).

Since leaf-cutter ants (*Atta* spp.) were commonly found in interaction with fallen fruits of *Miconia* (see below), we recorded the foraging activity of three colonies of *Atta sexdens* throughout a 24-h cycle in the peak *Miconia* fruiting period in 2004. Activity measurements were made at 2-h intervals, with surveys beginning at 0400 hours and ending at 0200 hours the following day (11–12 April). For each sampling period, we counted the number of returning ants laden with *Miconia* fruits or other plant material for 15 min along an active foraging trail. During previous observations we noted that some harvested fruits were rejected by the ant colony and deposited on the refuse pile around the nest entrance. To estimate the proportion of fruit harvested that was discarded, we also counted the number of ants laden

with *Miconia* fruits leaving the nest and depositing the fruit in the refuse pile. We estimated the total daily input of harvested items through extrapolation.

To evaluate the fate of fruits fallen under *Miconia* trees, we measured fruit removal rates below the crown of focal trees over two fruiting seasons (2004 and 2005). The relative contribution of ants and vertebrates was assessed by performing an enclosure experiment during the fruiting period of *Miconia*. Vertebrates were excluded from fruits with the aid of a wire cage (17 × 17 × 8 cm), covered on the top and sides with mesh (1.5 cm) and staked to the ground (see Roberts and Heithaus 1986). Ten fruits of *Miconia* were set out at about 0800 hours at each paired treatment placed at random beneath fruiting trees ($n = 33$ in 2004, and $n = 30$ in 2005). Fruits were marked with a small dot of enamel paint (Testors, Rockford, USA) to distinguish them from naturally fallen ones. Each paired treatment consisted of ten fruits placed directly on the ground under a wire cage, and ten other exposed fruits. After 24 h we recorded the ant species interacting with fruits, and the number of fruits missing in each group. A fruit was considered removed if not found within a 30-cm radius from its original location. We kept a minimum distance of 20 m between replicates to increase the probability of independent discoveries by different ant colonies (see Levey and Byrne 1993). Due to the tiny size of *Miconia* seeds (ca. 1 mm), the experiments were restricted to fruit removal only. Data on fruit removal were analysed using generalized linear models for the number of fruits removed (quasi-binomial distribution, Logit link; Crawley 2002). The enclosure treatment (caged vs. uncaged) was a fixed effect. Fruit removal experiments were performed under warmer weather in 2004 than in 2005, which may have influenced removal rates by ants (mean monthly temperature for the period of February–April 2004 was $23.0 \pm 1.1^\circ\text{C}$ versus $18.2 \pm 0.1^\circ\text{C}$ for the same period in 2005). To evaluate differences in fruit removal rates between the two sampled years, we also treated year as a fixed effect. Thus, our conclusions about temporal variation on fruit removal are confined to those levels of the effect actually studied. Statistical analyses were implemented in the R program (<http://www.r-project.org>).

To evaluate the potential of ants to reshape the seed shadow provided by primary dispersal, we recorded the removal of seeds from bird droppings. We collected fresh bird faeces containing seeds of *Miconia* in the early morning in the study site. We prepared small faecal portions containing ten seeds each, which resembled a defecation from a small frugivorous bird. Faecal portions ($n = 17$) were placed in the same morning on small pieces of filter paper (4 × 4 cm) on the leaf litter and protected by wire cages. We recorded the number of seeds remaining after 24 h.

Seed germination

To compare the effects of bird and ant dispersal on germination of *Miconia*, we obtained seed samples from five nest refuse piles produced by each of two ant species (*A. sexdens*, and *Odontomachus chelifer*) that frequently interact with these fruits in the field (Christianini et al. 2007; see below). Other samples were obtained from seeds embedded in fresh bird faeces ($n = 15$), as well as from control seeds removed from mature fruits of ten plants. Seeds were rinsed using a 0.5% sodium hypochlorite solution to surface sterilize seeds. Seed samples were placed in plastic trays, on regularly moistened filter paper kept in a germination chamber at 20°C and constant light, and checked weekly for germination. Groups were compared by *G*-tests.

Plant dispersion pattern

To describe the density of *M. rubiginosa* trees we counted all adults in five 10-m × 250-m plots set randomly throughout the study plot. To evaluate the influence of ant nests and the proximity of adult plants on the establishment of *Miconia* we compared the abundance of plants in the following patch categories: (1) around nest mounds of leaf-cutter ants (*Atta* spp.), (2) around a *Miconia* tree larger than 40 cm circumference at breast height sampled at 20–60 m in a random direction away from the *Atta* nest mound sampled in category (1), (3) around randomly selected trees of any other tree species (control) at least 20 m from the nearest adult *Miconia* tree or *Atta* nest mound. All *Miconia* found within a circular plot of 10-m radius centred at a patch category were classified either as immature (usually seedlings or saplings up to 1.5 m in height), or adult trees [usually larger than 5 cm diameter at breast height (DBH)]. These data were recorded from May to July 2008 (end of fruiting season). We used a Kruskal–Wallis test to compare the abundance of immature *Miconia* among the three patch types.

Results

Fruit production and seed fate

Overall, fruit crop was related to plant size (DBH, in cm) [number of fruits/tree (log) = $4.01 + 0.49 \text{ DBH}$, $F_{1,8} = 15.7$, $r^2 = 0.62$, $P = 0.004$], and fruit production did not differ between fruiting seasons (analysis of covariance: comparison of slopes, $F_{1,6} = 0.062$, $P = 0.81$; comparison of intercepts, $F_{1,7} = 0.0096$, $P = 0.93$). The number of seeds produced per fruit did not differ between plants in different fruiting seasons (Mann–Whitney *U*-test: $U = 6.0$, $P = 0.79$; median 10.9, range 8.9–13.7 seeds per fruit/plant, data

pooled for both seasons). Thus, we pooled data for fruit production in both years to increase power in the statistical comparisons of seed fate.

In both years, most seeds were wasted and reached the ground beneath rather than away from the parent plant. Fruit traps indicated that a mean of 22.8–23.7% of the fruit crop was removed by primary dispersal agents, while 76.3–77.2% was “wasted” in both fruiting seasons, falling under the parent plant (Table 1). Fruits fell beneath the tree spontaneously, or were dropped by birds (Fig. 1). Relative dispersal failure (measured by the proportion of seed crop falling under the parent plant) decreased with increasing crop size [proportion of seeds wasted (arcsin transformed) = $2.19 - 0.23 \text{ crop size (log)}$, $F_{1,8} = 5.88$, $r^2 = 0.35$, $P = 0.042$]. Thus plants producing larger fruit crops had a greater proportion of their seeds dispersed away from the crown by birds, as predicted by the fruit crop size hypothesis. Plants producing smaller fruit crops wasted a comparatively larger number of seeds that failed to be dispersed and fell beneath the parent plant. On average, 11.3–18.9% of these fallen fruits were ripe. The remaining fruit crop was wasted as unripe fruit or damaged fruit under the crown (Table 1). We observed that plants producing larger fruit crops attained higher dispersal success (measured by the number of fruits removed by birds from the canopy), as also predicted by the fruit crop size hypothesis [number of fruits removed (log) = $-2.22 + 1.32 \text{ crop size (log)}$, $F_{1,8} = 91.8$, $r^2 = 0.91$, $P < 0.001$]. However, large crop size also increased the number of fruits that fell under parent plants, increasing the absolute dispersal failure (the number of fruits falling under the parent plant) [number of fallen fruits (log) = $0.55 + 0.86 \text{ crop size (log)}$, $F_{1,8} = 199.6$, $r^2 = 0.96$, $P < 0.001$]. Thus, larger crop sizes also increase the number of fruits available for secondary dispersal under parent plants.

Seed shadows were quite patchy. Estimates reached a mean of 10,428 seeds per 0.14 m² under the parent plant.

Table 1 Production and fate of *Miconia rubiginosa* fruit during the 2004 and 2005 fruiting seasons in a cerrado savanna in southeast Brazil

Fruit fate category	2004	2005
Removed from crown	23.7%	22.8%
Dropped under crown		
Ripe fruit	11.3%	18.9%
Unripe fruit	64.2%	56.7%
Damaged fruit	0.8%	1.6%
Total fruit production per tree (mean ± SD)	168,696 ± 115,977	97,896 ± 129,415
Range	32,462–318,368	11,930–325,864

Values express the mean relative importance of each fate category relative to total fruit production of five different plants in each year

Fruit traps set >3 m way from the canopy edge of fruiting *Miconia* received a mean of 22.9 ± 38.7 seeds per 0.14 m^2 (range 0–151, $n = 20$, data for 2005). Forty percent (eight in 20) of the fruit traps received no seeds.

Plant–frugivore interactions in the crown: observation of frugivorous birds

We observed a total of 57 visits of 13 species of small- to medium-sized birds feeding on fruits of *Miconia* (including casual observations, both fruiting seasons pooled; Fig. 1). Focal observations indicated a visitation rate of 0.26 visits/h per tree. Several birds acted as legitimate dispersers by ingesting the whole fruit, and afterwards defecating the seeds (e.g. *Cyanocorax cristatellus*, *Elaenia flavogaster*). Birds interacted with a mean of 3.1 ± 2.6 fruits per visit ($n = 31$). Fresh bird faeces collected on the ground contained 21.2 ± 23.7 seeds of *Miconia* (mean \pm SD, range 1–92, $n = 19$). Many fruits were also dropped under the canopy by birds that act as pulp consumers and provide no dispersal away from the parent plant (e.g. *Tangara cayana*). Some of these birds, however, may disperse the seeds when they remove the fruit and fly to feed on it on another tree, acting both as pulp consumers and seed dispersers (Fig. 1). Four out of five of the most common bird visitors dropped most of the fruits they interacted with in the canopy, and ultimately half of the fruits manipulated by birds were dropped under the parent tree (Fig. 1). Estimated distance of seed dispersal by birds based on mean flight distances from fruiting trees was 19.8 ± 8.7 m (mean \pm SD)

(Fig. 2). Although flight distances were certainly biased (short flights are easier to observe than long ones, and seeds may take a long time to pass through the bird gut), the scale of estimated dispersal by birds was clearly larger than that by ants (Fig. 2). Because bird visits to *Miconia* were short in duration (162 ± 133 s, range 1–480, $n = 41$), it is unlikely that ingested seeds could pass the gut while the bird was perched on a given fruiting tree. It is possible, however, that some seeds were dispersed beneath another conspecific tree. In fact, because birds frequently flew among fruiting trees, the first landing perch by a bird after departing from a *Miconia* in fruit was often another individual of *Miconia* (six out of 18 observations, or 33%).

Plant–frugivore interactions on the ground: ant attendance to fallen fruits

Twelve ant species (seven genera) were attracted to fallen fruits, but four species that consistently transported the fruits to their nests accounted for 83% of the interactions (Fig. 1). Some seeds were destroyed by granivorous ants. A close inspection of 50 seeds recovered from three nests of *Pheidole* spp. revealed only hollowed, damaged seeds. Attini ants (mainly *Atta laevigata* and *A. sexdens*) were responsible for 66% of the interactions recorded ($n = 55$), including many records of removal of seeds embedded in bird faeces. Although *Atta* workers were occasionally observed climbing *Miconia* trees to remove fruits, the bulk of fruits harvested by these ants were collected on the floor. Ants displaced fallen fruits to 6.54 ± 4.08 m (Fig. 2). Ant

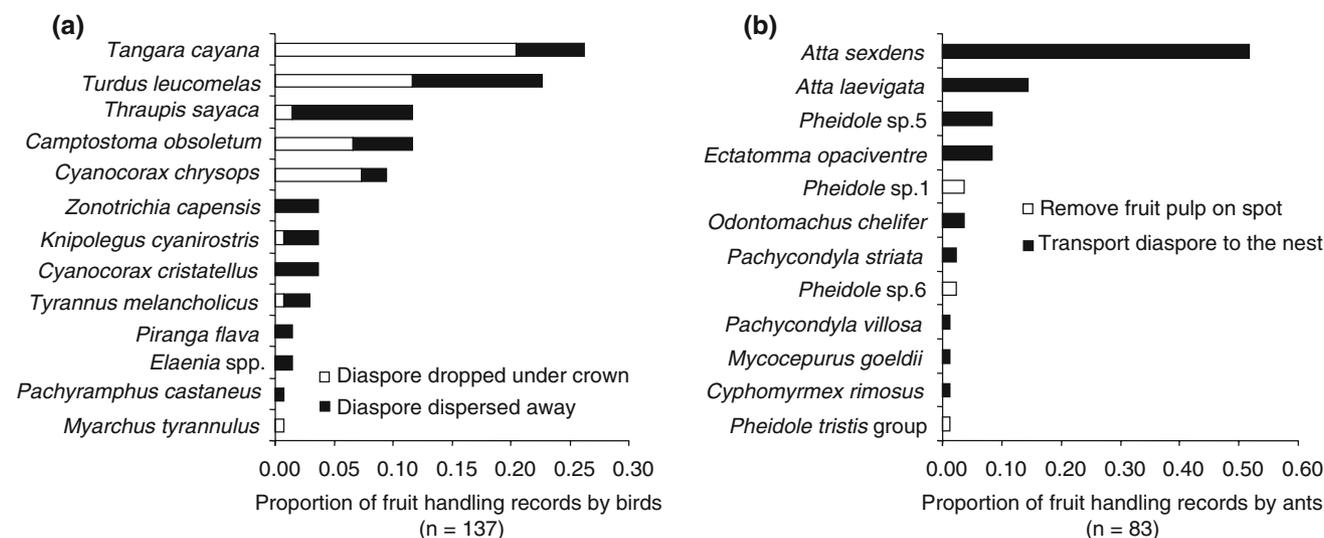


Fig. 1a, b Interactions of frugivorous bird and ant assemblages with fruits of *Miconia rubiginosa* in the crown and on the floor of the Brazilian cerrado savanna, respectively. **a** Relative importance of different species of birds interacting with fruits in the canopy. Birds may take fruits and drop seeds beneath the canopy, or swallow the fruit and

defecate seeds further away; **b** relative importance of ant species interacting with fallen fruits. Ants may remove fruit pulp on the spot, or carry the whole fruit to the nest. See Fig. 2 for distances of seed displacement achieved in each phase of dispersal

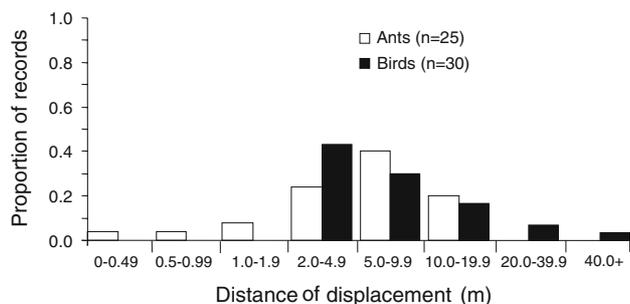


Fig. 2 Comparative distances of seed displacement by birds (departing from feeding trees) and ants (on the ground) during phases 1 and 2 of seed dispersal of *M. rubiginosa* in the Brazilian cerrado. The graph does not include data of seeds that were not dispersed (i.e. seeds cleaned on the spot by ants with no displacement, or dropped under the crown by birds). See text and Fig. 1 for further details. *n* Number of independent records of seed displacement by ants, or number of flights observed for birds

dispersal microsites and *Atta* nest mounds were located under trees other than *Miconia*, or under open canopy in almost 70% of observations (31 out of 45).

One colony of *A. sexdens* can collect fallen fruits from one to five *Miconia* trees during the fruiting season (A. V. Christianini, personal observation). Fruits of *Miconia* comprised 31.9–96.6% of all items taken by *A. sexdens* to their nests (Table 2). Estimated daily inputs of *Miconia* reached more than a 1,000 fruits per ant colony. This is probably a conservative estimate since an ant colony could have several active foraging trails at a time (Wirth et al. 2003). An average of 47% of the ripe fruits harvested were rejected and deposited intact in refuse piles around the nests, but there was considerable variation among ant colonies (18–96% of the ripe fruits harvested by three *Atta* colonies monitored in this study were discarded in refuse piles).

Removal of fallen fruits over 24 h did not differ between caged and open treatments ($F_{1,124} = 1.28, P = 0.26$), but removal decreased considerably from the 2004 to 2005 fruiting season ($F_{1,123} = 8.16, P = 0.005$), with a consistent effect for both caged and open treatments ($F_{1,122} = 0.18, P = 0.67$; see Fig. 3). Ants removed 11.8% (data pooled for both fruiting seasons) of the seeds embedded in bird faeces after 24 h of exposure on the cerrado floor. Fruit removal by ants was related to plant crop size to investigate if short-term removal by ants was dependent on the local density of fallen fruits. Since plant size was significantly related to total fruit production (see above), we used tree basal area as a surrogate of crop size against the number of fruits removed by ants under the same trees in Spearman rank correlations. There was no correlation between fruit removal by ants and plant size in 2004 ($t = 1.06, r = 0.20, P = 0.30$) or 2005 ($t = 1.16, r = 0.22, P = 0.26$). Therefore, ant removal of fallen fruits was independent of crop size.

Table 2 Daily pattern of fruit harvesting by three *Atta sexdens* colonies at the peak of the *M. rubiginosa* fruiting season in cerrado vegetation

Ant colony	Daily input of <i>Miconia</i> fruits ^a (% unripe)	Daily input of all items ^a	<i>Miconia</i> (%)
1	1,136 (1.4)	1,176	96.6
2	1,360 (12.4)	1,424	95.5
3	1,040 (0.8)	3,264	31.9
Mean ± SD	1,179 ± 164 (4.8 ± 6.5)		74.7 ± 37.1

Values indicate the number of fruits brought to the nest during a 24-h cycle, the number of all items collected by ants, and the percentage of the total harvest composed of *Miconia* fruits

^a Daily inputs were obtained through extrapolations of 15-min observation sessions at 2-h intervals for 24 h

Seed germination

The germination experiments indicated that seeds taken from ant nest refuse piles or bird faeces had similar germination performances compared to those taken from ripe fruits collected directly on plants (Table 3). Thus neither bird nor ant dispersers had an effect on seed viability.

Plant dispersion pattern

Adult *Miconia* reached a mean density of 78.4 trees per 2,500 m² (SD = 31.5; 74, 66, 101, 116, and 35 trees per plot) within the study plot at the study site. There was an average of 9.3 ± 5.1 (SD) adult trees per 314 m² within 10 m from an *Atta* nest mound ($n = 15$), and 9.5 ± 6.6 around *Miconia* trees ($n = 15$), a non-significant difference (paired *t*-test: $t = 0.10, P = 0.92$). The abundance of seedlings and saplings differed among patches surrounding *Atta* nest mounds (median 3; range 0–6), *Miconia* trees (1; 0–4),

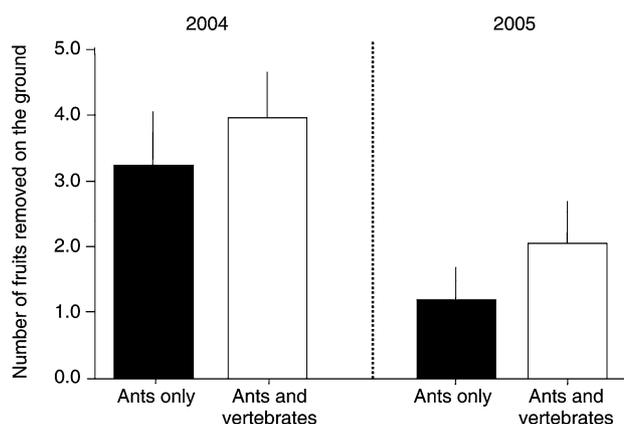


Fig. 3 Mean (±SE) removal rates over 24 h of fallen fruits under the canopy of fruiting *M. rubiginosa* in cerrado, in caged treatments (accessed by ants only) and in paired open controls (accessed by ants and vertebrates) over the 2004 and 2005 fruiting seasons

Table 3 Results from seed germination experiments performed with *M. rubiginosa* under constant light and temperature (20°C)

Source of seeds ^a	Nests or faeces		Controls		G-value ^b
	Sowed	Germinated (%)	Sowed	Germinated (%)	
<i>Atta</i> refuse piles	207	39 (18.8)	113	20 (17.7)	0.064
<i>Odontomachus</i> refuse piles	220	81 (36.8)	112	38 (33.9)	0.271
Bird faeces	197	40 (20.3)	225	58 (25.8)	1.774

^a Seeds used in the experiments were obtained from refuse piles of ants (*Atta sexdens*, *Odontomachus chelifer*), fresh bird faeces, or taken directly from plants (controls)

^b Comparisons of germination frequencies were performed with G-tests (all non-significant)

and around control non-*Miconia* trees (0; 0–3) (Kruskal–Wallis test, $H = 9.58$, $P = 0.008$). Seedlings and saplings were more abundant around *Atta* nest mounds than *Miconia* trees (Student–Newman–Keuls post-hoc test, $P = 0.035$), but they did not differ between patches around *Miconia* and non-*Miconia* trees ($P = 0.38$). Therefore, the area surrounding an *Atta* nest mound was a hotspot of *Miconia* recruitment.

Discussion

Previous experiments with other *Miconia* species in the cerrado have shown that plant recruitment is seed limited and may increase with some disturbance (Hoffmann 1996). In this study, birds removed on average up to 23.7% of the total fruit crop from the crown of *Miconia rubiginosa*. However, the view that fruits falling under the tree canopy would be a waste of plant resources is not true for *Miconia* in the cerrado. Many ripe fruits which drop under the parent tree are promptly harvested by ants, especially by leaf-cutters, which give a second chance of dispersal for the seeds. The quantitative contribution of ants to seed removal seems to be lower than that for birds, at least on a short-term basis. A mean of up to 32% of the fallen fruits are removed by ants over 24 h, but this removal rate must be balanced against the proportion of the fruit crop that falls as ripe fruit to the ground. Although fruit removal by ants was also subjected to variation between the fruiting seasons investigated, at least five factors suggest that ants do provide a relevant contribution to seed fate: the short duration of our fruit removal experiments on the floor relative to the fruiting phenology of an individual plant, the removal of faeces with embedded seeds, the possible viability of seeds in unripe fruits, the negative correlation between crop size and failure of dispersal from the canopy, and the higher abundance of young stages of *Miconia* around leaf-cutter ant nests.

Fruit trap data indicate that an individual *Miconia* is likely to fruit over 2 months, and our field observations indicate that fallen fruits remain attractive to ants for a few

days (A. V. Christianini, personal observation). Our approach likely captured the contribution of birds to fruit removal from the canopy, but ideally our fruit-removal experiments on the cerrado floor should run for the whole fruiting season of a given plant. However, observations on the plant material brought to the nests by leaf-cutter ants suggest that their contribution to the removal of fallen fruits may be higher than indicated by the removal experiments. For instance, a single colony of *Atta colombica* harvested 136,200 fruits of *Miconia argentea* over 49 days in Barro Colorado Island, Panama (Dalling and Wirth 1998). This is well above the total fruit crop of some individuals of *M. rubiginosa* in our study site. In the cerrado, ants also remove bird droppings with seeds, as well as unripe fruits of *Miconia*. This complicates the interpretation of the quantitative role of ants in the seed dispersal of *M. rubiginosa*, because they rearrange a proportion of the seeds originally deposited by frugivorous birds, and because unripe fruits removed by ants may contain viable seeds. Dalling et al. (1998) found no differences in seedling emergence between *M. argentea* seeds removed from mature and immature fruits buried in experimental seed banks for up to 6 months. Removal of fallen fruits by ants under the canopy, together with seed loss to pathogenic fungi, may also account for part of the spatial uncoupling between seed rain input and seed bank density below the crown found by Dalling et al. (1998). Finally, the increase in the proportion of seeds dispersed from the crown with increasing crop size supports the fruit crop size hypothesis. This suggests that birds tend to shift with ants in the quantitative component of dispersal effectiveness between *Miconia* trees producing large or comparatively smaller fruit crops in cerrado (Fig. 4). Although the amount of fruit removal is frequently variable in space and time (Ortiz-Pulido and Rico-Gray 2000), and can be affected by local neighbourhood and frugivore abundance (García et al. 2001; see Blendinger et al. 2008 for examples with other *Miconia* species), fruit crop size usually accounts for a large proportion of among-plant variation in fruit removal by primary dispersal agents (Howe 1980; Davidar and Morton 1986; Jordano and Schupp 2000; Blendinger et al.

2008). Thus birds could be comparatively more important for seed dispersal in plants producing large fruit crops (e.g. larger or older plants). On the other hand, by rescuing seeds from beneath the crown and providing them with a second chance of dispersal, ants may be more important for the relative dispersal success of plants with less attractive fruit displays to birds (e.g. smaller or younger plants), or that attract poor seed dispersers (Fig. 4). The absence of a density-dependent response of ants to fallen fruits of *Miconia* suggests that ants may remain important in removal of fruits from plants of variable crop sizes. Fruit removal by leaf-cutter ants should be more dependent on features other than fruit crop size, including quality of harvesting, distance to the foraging trail, or ant nest (see Pizo and Oliveira 2001; Wirth et al. 2003).

Birds and leaf-cutter ants do not affect seed germination levels and viability of dispersed seeds. Previous germination experiments indicated that removal of the fleshy coat covering seeds enhances germination of *Miconia* by more than 70% (Christianini et al. 2007). Birds seem more effective in removing fleshy matter from around seeds. While several cleaned seeds were frequently observed in the periphery of bird faeces, most seeds discarded by ants in refuse piles were still within fruits. Ants (mostly *Atta*)

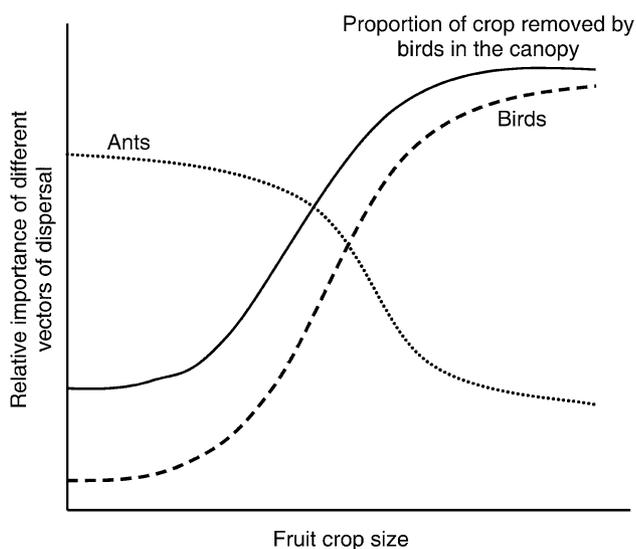


Fig. 4 A conceptual model for the relative importance of different dispersal vectors to the quantitative component of dispersal effectiveness under variable crop sizes of *M. rubiginosa* in the cerrado. The continuous line indicates the proportion of seed crop removed by birds from the canopy. Birds (dashed line) probably play a relatively greater role in seed fate in plants producing large fruit crops, such as larger or older trees. Ants (dotted line) would be far more important for plants producing comparatively smaller fruit crops that waste a greater proportion of the crop under the parent crown, such as smaller or younger trees. The quantitative contribution of ants to seed fate would not drop so sharply with increasing crop size, however, because large plants still waste many fruits under the canopy, and ants also remove bird faeces with embedded seeds

possibly play a greater role in seed bank dynamics than in prompt germination of *Miconia* in the cerrado. Because *Miconia* species have persistent seed banks, the uneven spatial distribution of seeds in the horizontal and vertical soil profile provided by ants (Dalling et al. 1998) may be a mechanism of dispersal in space and time for species in this genus (Farji-Brener and Medina 2000). Costs of the interaction with ants possibly include some seed predation by *Pheidole* spp. (but see Levey and Byrne 1993), deposition at deep soil levels inappropriate for germination (Christian and Stanton 2004), or death due to fungal infection (Wirth et al. 2003). This reinforces the dual role of *Atta* spp. as predators and dispersers of seeds (Retana et al. 2004).

Demographic data are needed to indicate the exact effectiveness of each vector of dispersal for the recruitment of *Miconia* (Godínez-Alvarez et al. 2002). Nevertheless, birds and ants differ markedly in the scale over which they transport *Miconia* seeds in the cerrado. Our estimated dispersal distances indicate that ants disperse most seeds at a comparatively smaller spatial scale (up to 20 m) than do birds, although longer distances of seed transport by *Atta* (up to a 100 m) are reported in the literature (Dalling and Wirth 1998; Leal and Oliveira 1998; Wirth et al. 2003; Christianini et al. 2007). *Atta* workers should thus produce a more clumped seed distribution pattern than birds (Dalling and Wirth 1998; Dalling et al. 1998), which may negatively affect *Miconia* by increasing density-dependent mortality and sibling competition among seedlings (Dalling et al. 1998; Retana et al. 2004). However, several fruits are often dropped and not recovered during transport to the ant nest (Dalling and Wirth 1998; Leal and Oliveira 1998), which may decrease the clumped pattern by spreading out seeds at variable distances from the parent tree. Indeed, young stages of *Miconia* are more frequently found growing in the surroundings of *Atta* nest mounds than in control spots in the cerrado. Thus ants should play an important role in shaping the local population dynamics of *Miconia*. Birds on the other hand may scatter some seeds locally, but have the unique role of dispersing seeds of *Miconia* at distances of 40 m and beyond. A similar mechanism of plant regeneration operating at variable spatial scales was demonstrated by Fragoso (1997) and Fragoso et al. (2003) in the Amazon rain forest, where tapirs are responsible for long-distance seed movement of the palm *Maximiliana maripa* (up to 2 km away from the nearest palm clump), while smaller mammals (mainly rodents) disperse seeds at much shorter distances. Heavy mortality of seeds and seedlings constrain plant recruitment in the surroundings of palm clumps, but tapirs are responsible for the creation of new palm patches at mesoscales (hundreds to thousands of metres; Fragoso et al. 2003). In the cerrado, birds should play a crucial role in the colonization of new habitats and metapopulation dynamics of *Miconia*. Nevertheless, even short-distance

dispersal by ants may change the spatial structure from adult plants to recruits. García et al. (2009) found that the short-distance movements of a frugivorous marsupial were enough to expand the spatial structure of a mistletoe population in southern Argentina. This stratified seed dispersal system suggests that birds and ants switch roles as a function of spatial scale, and provide complementary seed dispersal to *Miconia* trees in the cerrado, in a case of distance-dependent disperser effectiveness (Fragoso 1997; Jordano et al. 2007; Spiegel and Nathan 2007).

Although both birds and ants carry seeds away from the parent plant, *Miconia* probably also takes advantage of a diplochorous seed dispersal system in the patchy environment of the cerrado. Several seeds would first benefit from long-distance dispersal (e.g. >100 m) by birds. Once on the ground, ants may then reshape part of the seed shadow by moving bird faeces with embedded seeds to specific nutrient-rich sites (i.e. the ant nests; Kaspari 1993; Passos and Oliveira 2002). Each of these phases of dispersal may provide specific benefits to the plant (Vander Wall and Longland 2004). Extending the tail of the seed shadow may be important for seeds that need to land in particular microsites for regeneration, increasing the probability of a seed hitting a safe site (Green 1983; Murray 1988). This may be particularly important for *Miconia* species in cerrado, which take advantage of uncovered microhabitats for germination and establishment (Hoffmann 1996). Leaf-cutter ants often prune the vegetation above the mound and around the nest entrances, creating “bottom-up gaps” in the vegetation (Farji-Brener and Illes 2000). Such effects may partially account for the higher recruitment of *Miconia* around *Atta* nest mounds. Tropical plants are usually strongly establishment limited as well as seed limited (Hubbell et al. 1999; see Hoffmann 1996 for examples in the cerrado). Although the high fecundity of *Miconia* may suggest that this species is less likely to be seed limited, small-seeded species have much lower seed to seedling transition probabilities than do large-seeded species (Harms et al. 2000).

Complementary seed dispersal by ants and birds may lead to differences in the spatial patterns of plant recruitment and dispersal (Horvitz and Le Corff 1993; Fragoso 1997), and in the genetic structure of populations of *Miconia* (Kalisz et al. 1999; Jordano et al. 2007). Although the effect of ants as rescuers of seeds in the quantitative component of dispersal effectiveness of vertebrate-dispersed species is mostly unappreciated, data from several studies suggest that they could be more important than currently recognized (Roberts and Heithaus 1986; Levey and Byrne 1993; Farji-Brener and Silva 1996; Passos and Oliveira 2002, 2004). Additionally, in a conservation context, ants can be of relevance for the rescue of seeds that cannot achieve high rates of dispersal due to an impoverishment of vertebrate dispersal assemblages in fragmented or

heavily hunted habitats (Chapman and Chapman 1995; Wright et al. 2000).

Acknowledgments This study was supported by FAPESP (proc. 02/12895-8), and the Wisconsin Society of Science Teachers, and is part of the Ph.D. dissertation of A. V. C. at the Programa de Pós-Graduação em Ecologia da Universidade Estadual de Campinas. We benefited from criticisms by A. G. Farji-Brener and C. M. Herrera (who called our attention to the role of ants as seed rescuers). We thank A. J. Mayhé-Nunes for ant identification, J. Y. Tamashiro for plant identification, C. Haddad for permission to use the germination chamber of the Departamento de Fisiologia Vegetal, H. C. Menezes for the chemical analyses of the fruits, and L. E. Lopes for help with the statistical analyses. We thank the Instituto Florestal de São Paulo for allowing us to work in its cerrado reserve. C. Cestari, M. M. Martins, and P. Rubim helped during fieldwork. P. S. O. was supported by research grants from the CNPq (proc. 304521/2006-0), and FAPESP (proc. 08/54058-1). The experiments presented in this study comply with the current laws of Brazil.

References

- Blendinger PG, Loiselle BA, Blake JG (2008) Crop size, plant aggregation, and microhabitat type affect fruit removal by birds from individual melastome plants in the Upper Amazon. *Oecologia* 158:273–283
- Böhning-Gaese K, Gaese BH, Rabemanantsoa SB (1999) Importance of primary and secondary seed dispersal in the Malagasy tree *Commiphora guillaumini*. *Ecology* 80:821–832
- Chapman CA, Chapman LJ (1995) Survival without dispersers: seedling recruitment under parents. *Conserv Biol* 9:675–678
- Christian CE, Stanton ML (2004) Cryptic consequences of a dispersal mutualism: seed burial, elaiosome removal, and seed-bank dynamics. *Ecology* 85:1101–1110
- Christianini AV, Mayhé-Nunes AJ, Oliveira PS (2007) The role of ants in the removal of non-myrmecochorous diaspores and seed germination in a Neotropical savanna. *J Trop Ecol* 23:343–351
- Crawley MT (2002) Statistical computing. An introduction to data analysis using S-plus. Wiley, Chichester
- Dalling JW, Wirth R (1998) Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*. *J Trop Ecol* 14:705–710
- Dalling JW, Swaine MD, Garwood NC (1998) Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* 79:564–578
- Davidar P, Morton ES (1986) The relationship between fruit crop sizes and fruit removal rates by birds. *Ecology* 67:262–265
- Farji-Brener AG, Ghermandi L (2004) Seedling recruitment in a semi-arid Patagonian steppe: facilitative effects of refuse dumps of leaf-cutting ants. *J Veg Sci* 15:823–830
- Farji-Brener AG, Illes AE (2000) Do leaf-cutting ant nests make “bottom-up” gaps in neotropical rain forests? A critical review of the evidence. *Ecol Lett* 3:219–227
- Farji-Brener AG, Medina CA (2000) The importance of where to dump the refuse: seed bank and fine roots in nests of the leaf-cutting ants *Atta cephalotes* and *Atta colombica*. *Biotropica* 32:120–126
- Farji-Brener AG, Silva JF (1996) Leaf cutter ants (*Atta laevigata*) aid to establishment success of *Tapirira velutinifolia* (Anacardiaceae) seedlings in a parkland savanna. *J Trop Ecol* 12:163–168
- Fragoso JMV (1997) Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *J Ecol* 85:519–529
- Fragoso JMV, Silvius KM, Correa JA (2003) Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology* 84:1998–2006

- García D, Zamora R, Gómez JM, Hódar JA (2001) Frugivory at *Juniperus communis* depends more on population characteristics than on individual attributes. *J Ecol* 89:639–647
- García D, Rodríguez-Cabal MA, Amico GC (2009) Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. *J Ecol* 97:217–229
- Giannotti E (1988) Composição florística e estrutura fitossociológica da vegetação de cerrado e da transição entre cerrado e mata ciliar da Estação Experimental de Iitirapina (SP). Master's thesis, Universidade Estadual de Campinas, Campinas
- Godínez-Alvarez H, Valiente-Banuet A, Rojas-Martínez A (2002) The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*. *Ecology* 83:2617–2629
- Green DS (1983) The efficacy of dispersal in relation to safe site density. *Oecologia* 56:356–358
- Harms KE, Wright SJ, Calderón O, Hernández A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495
- Hoffmann WA (1996) The effects of fire and cover on seedling establishment in a Neotropical savanna. *J Ecol* 84:383–393
- Horvitz CC, Le Corff J (1993) Spatial scale and dispersion pattern of ant- and bird-dispersed herbs in two tropical lowland rain forests. *Vegetatio* 107(108):351–362
- Howe HF (1980) Monkey dispersal and waste of a Neotropical fruit. *Ecology* 61:944–959
- Howe HF (1989) Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79:417–426
- Howe HF, Estabrook GF (1977) On intraspecific competition for avian dispersers in tropical trees. *Am Nat* 111:817–832
- Hubbell SP, Foster RB, Harms KE, O'Brien ST, Condit R, Wechsler B, Wright SJ, Loo de Lao S (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* 283:554–557
- Jordano P (1995) Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology* 76:2627–2639
- Jordano P, Schupp EW (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecol Monogr* 70:591–615
- Jordano P, García C, Godoy JA, García-Castaño JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proc Natl Acad Sci USA* 104:3278–3282
- Kalish S, Hanzawa FM, Tonsor SJ, Thiede DA, Voigt S (1999) Ant-mediated seed dispersal alters pattern of relatedness in a population of *Trillium grandiflorum*. *Ecology* 80:2620–2634
- Kaspari M (1993) Removal of seeds from Neotropical frugivore feces: ant responses to seed number. *Oecologia* 95:81–88
- Leal IR, Oliveira PS (1998) Interactions between fungus-growing ants (Attini), fruits and seeds in cerrado vegetation in southeast Brazil. *Biotropica* 30:170–178
- Levey DJ, Byrne MM (1993) Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology* 74:1802–1812
- Loiselle BA, Blake JG (1999) Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *Ecology* 80:330–336
- Mckey D (1975) The ecology of coevolving seed dispersal systems. In: Gilbert LE, Raven P (eds) *Coevolution of animals and plants*. University of Texas Press, Austin, pp 159–191
- Murray KG (1988) Avian seed dispersal of three Neotropical gap-dependent plants. *Ecol Monogr* 58:271–298
- Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol Evol* 15:278–285
- Oliveira PS, Galetti M, Pedroni F, Morellato LPC (1995) Seed cleaning by *Mycocepurus goeldii* ants (Attini) facilitates germination in *Hymenaea courbaril* (Caesalpinaceae). *Biotropica* 27:518–522
- Oliveira-Filho AT, Ratter JA (2002) Vegetation physiognomies and woody flora of the cerrado biome. In: Oliveira PS, Marquis RJ (eds) *The cerrados of Brazil: ecology and natural history of a Neotropical savanna*. Columbia University Press, New York, pp 91–120
- Ortiz-Pulido R, Rico-Gray V (2000) The effect of spatio-temporal variation in understanding the fruit crop size hypothesis. *Oikos* 91:523–527
- Passos L, Oliveira PS (2002) Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree. *J Ecol* 90:517–528
- Passos L, Oliveira PS (2003) Interactions between ants, fruits and seeds in a restinga forest in south-eastern Brazil. *J Trop Ecol* 19:261–270
- Passos L, Oliveira PS (2004) Interaction between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian sandy plain rainforest: ant effects on seeds and seedlings. *Oecologia* 139:376–382
- Pizo MA, Oliveira PS (1999) Removal of seeds from vertebrate faeces by ants: effects of seed species and deposition site. *Can J Zool* 77:1595–1602
- Pizo MA, Oliveira PS (2000) The use of fruits and seeds by ants in the Atlantic forest of southeast Brazil. *Biotropica* 32:851–861
- Pizo MA, Oliveira PS (2001) Size and lipid content of nonmyrmecochorous diaspores: effects on the interaction with litter-foraging ants in the Atlantic rain forest of Brazil. *Plant Ecol* 157:37–52
- Retana J, Picó FX, Rodrigo A (2004) Dual role of harvesting ants as seed predators and dispersers of a non-myrmecochorous Mediterranean perennial herb. *Oikos* 105:377–385
- Rico-Gray V, Oliveira PS (2007) *The ecology and evolution of ant-plant interactions*. The University of Chicago Press, Chicago
- Roberts JT, Heithaus R (1986) Ants rearrange the vertebrate-generated seed shadow of a Neotropical fig tree. *Ecology* 67:1046–1051
- Sallabanks R (1993) Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74:1326–1336
- Schupp EW (1988) Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76:525–530
- Schupp EW (1993) Quantity, quality, and effectiveness of seed dispersal by animals. *Vegetatio* 107(108):15–29
- Snow DW (1971) Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194–202
- Spiegel O, Nathan R (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecol Lett* 10:718–728
- Vander Wall SB, Longland WS (2004) Diplochory: are two seed dispersers better than one? *Trends Ecol Evol* 19:297–314
- Wirth R, Herz H, Ryel RJ, Beyschlag W, Hölldobler B (2003) Herbivory of leaf-cutting ants: a case study of *Atta colombica* in the tropical rainforest of Panama. Springer, Berlin
- Wright SJ, Zeballos H, Dominguez I, Gallardo MM, Moreno MC, Ibanez R (2000) Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conserv Biol* 14:227–239