Birds and ants provide complementary seed dispersal in a neotropical savanna

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Summary

1. A substantial portion of the crop of fruiting trees falls beneath parent plants as a result of dispersal failure. Such diaspores are considered as waste because the likelihood of plant recruitment is usually very small close to parent trees. However, many animals may rescue fallen diaspores and provide them with another chance of dispersal and establishment.

2. We investigated the effectiveness of two broad types of seed dispersal vectors for the regeneration of *Xylopia aromatica* in the Brazilian cerrado savanna: birds that remove diaspores from plant canopies and ants that harvest diaspores on the ground under the parent plant (as rescuers) or from bird feces (as secondary dispersers).

3. Birds removed a mean of 32% of the crop from plant canopies, but removal was independent of crop size. A large part of the crop (mean of 25%) landed beneath parent plants or was dropped after manipulation by vertebrate frugivores as viable diaspores. Ants from at least five genera removed most fallen diaspores (up to 83%) within 24 h. Ants influenced the fate of a large amount of the crop, and for some trees ants removed as many diaspores as birds.

4. Large ants rescued some diaspores to distances beyond the parent plant crown, but birds may remove diaspores 40-fold farther. However, seedlings of *X. aromatica* were only found close to nests of large ants, probably due to diaspore rescuing and/or directed secondary dispersal by certain ant groups following primary dispersal by birds. Although an unknown percentage of seeds was lost to granivorous ants, diaspore removal by ants potentially enhances the likelihood of plant recruitment due to distance-related benefits and directed dispersal to ant nests, while birds play a premier role in long-distance seed dispersal and metapopulation dynamics.

5. *Synthesis.* Birds and ants provide complementary seed dispersal at different spatial scales to *X. aromatica*. Since ants remove most fallen diaspores beneath parent plants, the use of diaspore removal rates from plant canopy as a surrogate of plant fitness may be misleading. By acting as secondary dispersers, ants may also provide a fine-tuned dispersal following long-distance dispersal by birds (i.e. diplochory).

Key-words: cerrado, diplochory, directed dispersal, dispersal distance, dispersal syndrome, disperser effectiveness, fruit crop size, secondary seed dispersal, seed predation

Introduction

Seed dispersal has been advocated as one of the main processes driving plant population ecology because most plants are dependent on seeds for regeneration, and because the location where seeds land has an enormous influence on seed-to-seedling transition probabilities (Schupp & Fuentes 1995). However, spatial patterns of seed fall, seedling emergence and survival are typically extremely heterogeneous both in space and time (Hampe *et al.* 2008). Because most plants rely on animals for seed dispersal (Jordano 2000), evaluating how animals (especially frugivores) influence this process (and its variable outcomes) is crucial to understanding plant recruitment and population dynamics. For instance, the distance to which seeds are carried away from parent plants and deposited on soil

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should produce a template of offspring dispersion and plant recruitment (Nathan & Muller-Landau 2000; Wang & Smith 2002).

The fruit crop size hypothesis states that plants producing large fruit crops are likely to attract a greater number and variety of frugivores (and thus have increased seed dispersal success) compared to plants with small fruit crops (Snow 1971; McKey 1975; Howe & Estabrook 1977). However, having large fruit crops also frequently goes hand in hand with an increased waste of fruits that are dropped under the plant crown by illegitimate seed dispersers or that fall naturally if not removed from the plant canopy (Howe 1980). A dispersal vector can markedly increase plant fitness by 'rescuing' such apparently wasted seeds from beneath the parent plant, where recruitment is unlikely due to distance- as well as density-dependent mortality factors (see Harms *et al.* 2000). Water may transport away some fallen seeds deposited under parents on slopes or near streams after heavy rains (Hampe 2004), but animals such as rodents (Forget & Milleron 1991) and ants (Roberts & Heithaus 1986) are more likely to rescue fallen seeds from under the plant canopy and carry them elsewhere, even at the cost of some seed loss due to predation. However, the contribution of such alternative ways of dispersal to plant regeneration is not obvious. Most studies do not compare the amount of crop size removed away from canopy versus the amount that falls passively or that is dropped by primary dispersers, and then is removed from beneath the parent plant (but see Böhning-Gaese, Gaese & Rabemanantsoa 1999; Passos & Oliveira 2002; Hampe 2004; Christianini & Oliveira 2009). Since primary dispersal is usually carried out by highly mobile vertebrate frugivores such as birds and since most animals that rescue fallen seeds beneath the canopy probably provide only local dispersal (but see Fragoso 1997), a contrasting spatial pattern of seed distribution may be produced by each of these dispersal agents. However, the distances to which seeds are transported by each type of vector are seldom reported (e.g. Böhning-Gaese, Gaese & Rabemanantsoa 1999; Christianini & Oliveira 2009), although different dispersal modes may have distinct consequences for the spatial pattern of plant recruitment and dispersal (Horvitz & Le Corff 1993), and for the genetic structure of populations (Jordano *et al.* 2007).

Usually, seeds carried away directly from a plant canopy by vertebrate frugivores during primary dispersal are deposited in soil as droppings. Such feces-embedded seeds are frequently subject to another subsequent stage of dispersal known as secondary dispersal. For instance, dung beetles (Andresen 2002), rodents (Vander Wall, Kuhn & Gworek 2005) and ants (Passos & Oliveira 2002) frequently remove the seeds from vertebrate feces or move the whole fecal portion with seeds embedded. When primary and secondary stages of dispersal are performed by different dispersal agents, the process is known as diplochory. Vander Wall & Longland (2004) described five ways through which seeds are primarily removed from plant canopy and subsequently scattered by animals on the ground: wind dispersal followed by scatter-hoarding by animals (usually rodents), ballistic dispersal followed by dis-

persal by ants, and endozoochory followed by removal of feces-embedded seeds by dung beetles, scatter-hoarding rodents or ants. Such secondary dispersers may markedly influence the fate of seeds and their probability of recruitment, because they may scatter the seeds and reduce sibling competition, or move seeds to sites where recruitment is more likely (e.g. Vander Wall & Longland 2004). Due to their remarkable abundance and feeding habits, ants are among the animals with the highest probability to act in seed-rescuing and secondary dispersal. Indeed, the role of ants in the regeneration of primarily vertebrate-dispersed species of plants has increasingly been recognized (reviewed in Rico-Gray & Oliveira 2007), suggesting that plant regeneration patterns are frequently more complex than previously acknowledged (Wang & Smith 2002). This gap in our understanding of the role of different seed dispersal vectors in plant regeneration may be due to the complexity of seed dispersal systems and the difficulties of gathering empirical data to link frugivore behaviour with seed dispersal patterns, and thus dispersal with recruitment patterns (Fragoso 1997; Wang & Smith 2002). The concept of seed dispersal effectiveness may help to disentangle the role that different seed vectors play in plant regeneration.

Dispersal effectiveness includes two components: a quantitative component linked to the number of seeds removed from the plant, and a qualitative component related to the fate of dispersed seeds and their probability to reach maturity (Schupp 1993). In this study, we compared the effectiveness of seed dispersal by vectors acting in the plant crown (birds) and on the ground (ants) for plant regeneration in the largest neotropical savanna known as 'cerrado' in Brazil (Oliveira-Filho & Ratter 2002). We dedicated special attention to the quantitative component of disperser effectiveness. Although most trees in the cerrado are adapted for seed dispersal by vertebrates (Gottsberger & Silberbauer-Gottsberger 1983), current evidence suggests that ants remove great numbers of fallen fruits and seeds from beneath fleshy fruited plants (Leal & Oliveira 1998, 2000; Christianini, Mayhé-Nunes & Oliveira 2007) and may ultimately affect plant recruitment (Christianini & Oliveira 2009). We studied the interaction between the tree *Xylopia aromatica* (Lam.) Mart. (Annonaceae) and its bird and ant seed dispersers in the Brazilian cerrado. We addressed the following questions: (i) Does the crop size hypothesis account for among-plant variation in the amount of crop removed away from the plant crown? (ii) What are the spatial scales at which bird and ant seed dispersal operate? (iii) What is the role of each dispersal vector for plant regeneration?

Materials and methods

STUDY SITE

Field work was carried out from February 2004 to March 2006 in the reserve of the Estação Experimental de Itirapina (22°12′ S, 47°51′ W), a *c.* 200-ha fragment of cerrado in south-east Brazil. Average annual rainfall is 1360 mm, concentrated in the warm and wet season (December–March). A dry and cold season occurs from April to November, when occasional frost may occur. Mean annual temperature is 21.8 °C (data from 1994 to 2004 from the reserve's

climatological station). The vegetation at the study site is the cerrado *sensu stricto*, the typical fire-prone savanna-like formation that grows on sandy, nutrient-poor soils characterized by 50–80% of ground cover by herbs, small palms, shrubs and trees (Oliveira-Filho & Ratter 2002). Additional details of the flora of the study site are given by Giannotti & Leitão Filho (1992).

THE PLANT SPECIES

Trees of *X. aromatica* (hereafter *Xylopia*) usually have a lozenge-shaped canopy. Measures of canopy length and width centred on tree trunk are 3.8 ± 1.3 and 2.9 ± 0.9 m, respectively (mean $\pm$ SD, $N = 11$ trees). *Xylopia* reaches a density of 300 individuals ha^{-1} at the study site (Miranda-Melo, Martins & Santos 2007). *Xylopia* grows in patches exposed to full sun and is susceptible to topkill and occasional death by frost or intense fires (Silberbauer-Gottsberger, Morawetz & Gottsberger 1977; Miranda-Melo, Martins & Santos 2007). Fruiting occurs mainly from March to July, when multiple fruits (divided in follicles) open to expose *c*. 60 arillate seeds per fruit. Each seed is coated with a thin bluish fleshy layer and an aril that covers a quarter of the seed, forming the diaspore (i.e. the unit of dispersal). Each diaspore is a 0.6-cm arillate seed that weighs 0.06 g fresh mass ($N = 30$). The diaspore is composed of 32.9% lipids, 50.3% carbohydrates, 16.4% proteins and 2.1% ash on a dry-mass basis (A. V. Christianini & P. S. Oliveira, unpubl. data). The inner portion of the follicle is reddish when opened, which produces a contrasting display with the bluish diaspores that probably attract avian frugivores (Fig. 1a). Plant reproduction is totally dependent on seeds, which remain viable for up to 2 months (Lorenzi 1992; Miranda-Melo, Martins & Santos 2007). In the study site, the diaspores are consumed predispersal by larvae of three species of wasps (Hymenoptera: Chalcidoidea): an unidentified species of Pteromalidae, *Prodecatoma spermophaga* Costa Lima, and *Bephratelloides* sp. (both Eurytomidae). Holes in the diaspores left upon wasp eclosion allowed us to record pre-dispersal predation.

DIASPORE PRODUCTION AND DISPERSAL

To examine diaspore production and dispersal per tree, we placed three to six fruit traps under the crown of seven trees of *Xylopia* in 2004. Considering that the canopy is lozenge-shaped (where the crown area is equal to length times width divided by 2), traps covered nearly 15% of the area beneath the crown of each tree. Trees were located at least 5 m from other reproductive conspecifics. Traps consisted of 0.14-m^2 plastic trays lined with 0.2-mm nylon mesh kept 20 cm above ground by four stakes, each coated with a sticky resin (Tanglefoot®; The Tanglefoot Company, Grand Rapids, MI, USA) to prevent ants from reaching fallen diaspores. Traps collected fallen follicles, as well as diaspores dropped by birds. We checked the traps every 2–4 weeks throughout the fruiting season. Diaspores were then counted and classified as: (i) ripe (bluish arillate diaspore attached to open follicles), (ii) unripe (diaspores within immature closed follicles, or aborted diaspores in open follicles), (iii) preyed on before dispersal (diaspores with holes indicating wasp eclosion), or (iv) dropped by primary dispersers (diaspores dropped by birds that act as aril consumers and diaspores regurgitated or defecated by legitimate seed dispersers). The latter category may include an unknown number of ripe diaspores detached from open follicles of the same tree, as well as diaspores brought by dispersers from other conspecific trees. We estimated crop size per tree by counting the number of follicles that reached fruit traps under each tree by the end of the fruiting season, when all follicles fall to the ground. Unless diaspores are picked up by

Fig. 1. Most trees in the Brazilian cerrado savanna produce fleshy diaspores adapted for vertebrate dispersal. (a) A multiple fruit of *Xylopia aromatica* with some open follicles exposing the plant diaspores (arillate seeds) (scale bar = 4 cm). Birds are the primary seed dispersers but may drop many diaspores under parent plants with bits of aril still attached, which attract ant dispersers that 'rescue' the diaspores and carry them away from beneath the canopy. (b) A worker of *Odontomachus chelifer* removing a diaspore to the ant nest, where seedlings are more frequently found (scale bar = 0.6 cm).

birds, they do not detach naturally from follicles. Once removed, each diaspore leaves a scar in the inner wall of the follicle. Thus, the follicles in the traps provide a relative measure of crop size produced and an estimate of the quantity of diaspores removed by birds, enabling comparisons among trees. We estimated the relative number of diaspores removed by birds from the canopy of each tree by subtracting the sum of categories 1–4 sampled in traps from the estimated crop size. Since a fraction of diaspores dropped by birds under the canopy (category 4 above) could come from other conspecific trees, our estimate of the proportion of the fruit crop falling under the parent crown is probably slightly overestimated (but see Plant–frugivore interactions in plant crown: observations of frugivorous birds below). To investigate the influence of crop size on diaspore removal by birds and on the amount of viable diaspores falling under parental plants (the sum of categories 1 and 4 above), we applied linear regressions.

PLANT–FRUGIVORE INTERACTIONS IN PLANT CROWN: OBSERVATIONS OF FRUGIVOROUS BIRDS

Information about diaspore removal by birds and diaspore waste (i.e. dropped under the parent plant) was obtained by focal observations of 16 fruiting trees at the study site, totalling 109.7 tree observation hours (A. V. Christianini, unpubl. data). These data were used to

characterize bird behaviour and to quantify removal rates by birds. We also recorded post-feeding flight distances of birds departing from focal trees until the first landing perch as an estimate of dispersal distance (Jordano & 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. Although birds could not be followed to greater distances due to visual obstruction by the vegetation, diaspore retention time in the gut probably allows longer dispersal distances.

INTERACTIONS ON THE GROUND: ANT ATTENDANCE TO FALLEN DIASPORES

To determine which ants interact with fallen diaspores of *Xylopia*, we recorded all ant–diaspore interactions observed throughout the entire fruiting seasons of 2004 and 2005. Systematic sampling was also carried out by placing marked diaspores at 30 ground stations (10 m apart from each other), 1–2 m away from two transects that crossed the study site, throughout the fruiting season of *Xylopia*. Two diaspores of *Xylopia* were placed per sampling station on white filter paper (4 × 4 cm) to facilitate visualization on the leaf litter. The filter paper had no detectable effect on ant behaviour (e.g. Passos & Oliveira 2003). Diaspores were set at 08:00 and 18:00 hours and checked at 15- to 20-min intervals over 2 h, enabling us to sample subordinate as well as dominant ant species active during day and night. We recorded the ant species attracted and their behaviour towards diaspores. Ant behaviour was classified as follows: (i) remove diaspore to nest (> 5 cm) or (ii) clean fleshy portion at the spot, inspect or manipulate diaspore (no removal). We followed ants carrying diaspores until they entered their nests or disappeared in the leaf litter. The distance of displacement was then measured. Since in a fraction of observations (7 out of 40) the ants carrying diaspores disappeared in the leaf litter, our distances of diaspore displacement by ants are slightly underestimated. Ant voucher specimens are deposited in the collection of the Universidade Federal Rural do Rio de Janeiro (CECL), Brazil.

To evaluate what happens to diaspores that fall under parent plants, we measured diaspore removal rates beneath the crown of focal trees throughout two fruiting seasons (2004 and 2005). We kept a minimum distance of 20 m between replicates to increase the probability of independent discoveries by different ant colonies (Levey & Byrne 1993). The relative contribution of ants and vertebrates to diaspore removal was assessed by performing an exclosure experiment. Vertebrates were excluded from diaspores by a wire cage (17 × 17 × 8 cm), fenced on the top and sides with mesh (1.5 cm) and staked to the ground (Roberts & Heithaus 1986). Pairs of diaspores (arillate seeds) of *Xylopia* were set out at *c.* 08:00 h at five stations placed beneath fruiting trees (*N* = 30). Stations were kept 1–2 m apart from each other so as to sample the entire area under a plant crown and the local variation in diaspore removal. Diaspores used in the exclosure experiments were marked with a small dot of enamel paint (Testors, Rockford, IL, USA) to distinguish them from other fallen diaspores (the paint had no detectable effect on ant behaviour). Each pair consisted of a diaspore placed directly on the floor under a wire cage, and an exposed diaspore (control) placed outside the cage, 15 cm away. After 24 h, we recorded the number of diaspores missing and the ants interacting with the remaining diaspores. A diaspore was considered removed if not found within a 30-cm radius from its original location.

To evaluate if removal rates on the ground were driven by granivores, we performed removal trials using cleaned diaspores (i.e. aril manually removed from diaspores by us) a few weeks later. These removal trials followed the same procedure for whole diaspores (aril-late seeds), using the same individual trees. Data on removal were analysed using two-factor analysis of variance. The dependent variable was the number of diaspores removed per tree, and the independent variables were plant location, year, exclosure treatment (caged versus uncaged) and presence/absence of aril. In the first analysis, data from the 2005 fruiting season included exclosure treatment and aril (presence or absence) as independent fixed factors, and tree location as a block, random effect factor. In a second analysis, fruiting season (2004 or 2005) was entered as a fixed factor to investigate temporal variation in the removal of fallen diaspores (arillate diaspores only) in relation to exclosure treatments. Data were square root-transformed before analyses to improve normality and homoscedasticity.

SEEDLING DISTRIBUTION AND PERFORMANCE

To investigate if ants affect the spatial distribution and performance of seedlings, we compared the number of seedlings of the focal plant species growing on plots (0.5 × 0.5 m) established in ant nests to those in paired controls without nests (random direction, 2 m from each nest). Ant nests were located by following laden ant workers attracted either to diaspores or to tuna baits placed on the ground by day and night (Horvitz 1981). Nests were tagged, and the sampling plot was established centred on the nest entrance. We sampled nests of a subset of local ant species which were known to interact with *Xylopia* in the field (see below) and which were expected to influence seedling distribution based on previous studies (Levey & Byrne 1993; Passos & Oliveira 2002). We sampled 81 ant nests distributed among six ant genera: *Pheidole* (*N* = 22), *Pachycondyla* (*N* = 20), *Odontomachus* (*N* = 13), *Dinoponera* (*N* = 5), *Ectatomma* (*N* = 3) and *Atta* (*N* = 18). Nest and control plots were surveyed in February–March 2005. Seedlings of *Xylopia* (i.e. non-ramified individuals up to 10 cm tall) inside nest and control plots were individually marked with numbered flags and monitored monthly until July 2005, and then every 2 months until February 2006.

Results

DIASPORE PRODUCTION AND DISPERSAL

A high portion of the crop of *Xylopia* was wasted under parent trees as viable diaspores (the sum of 'ripe diaspores' plus 'diaspores dropped by primary dispersers'), comprising a mean of 25% of the total crop in the 2004 fruiting season (Table 1). Birds removed a mean of 32% of the crop from the plant crown (Table 1). These numbers indicate that many viable diaspores are available to predators and dispersers under parent trees each fruiting season. More than a third of the crop was usually lost as unripe diaspores. The number of diaspores preyed on before dispersal was highly variable among plants, and reached a mean of 6% of plant crop size (Table 1). Fruit traps (*N* = 32) set under parental plants were hit by a mean of 15 ± 17 diaspores per 0.14 m^2 (range 1–64).

The fruit crop size hypothesis was rejected for *Xylopia*. There was no relationship between crop size and the number of diaspores removed by birds beyond the plant canopy border (*P* = 0.18), nor between crop size and the proportion of the crop removed away (*P* = 0.90). However, if we consider the sum of categories 'ripe diaspores' plus 'diaspores dropped by

Table 1. Relative measures of diaspore production and dispersal for individual trees of *Xylopia aromatica* in a cerrado savanna in SE Brazil. Trees are depicted in columns arranged by increasing crop size. Diaspore outcome categories show the proportion of each outcome in relation to crop size per plant

	Diaspore production and dispersal for individual trees							Mean ± SD
Estimated crop size	100	121	172	188	282	284	627	253 ± 179
Diaspore outcome categories								
Removed away from crown	0.340	0.496	0.052	0.564	0.117	0.215	0.443	0.318 ± 0.196
Dropped under crown								
Ripe	0.020	0.050	0.140	0.069	0.028	0.113	0.032	0.064 ± 0.046
Unripe	0.400	0.339	0.459	0.186	0.539	0.380	0.242	0.364 ± 0.121
Preyed on before dispersal	0.100	0.008	0.076	0.021	0.078	0.137	0.029	0.064 ± 0.047
Dropped by primary dispersers	0.140	0.107	0.273	0.160	0.238	0.155	0.254	0.189 ± 0.064
Proportion of crop size as viable diaspores under parent plant*	0.160	0.157	0.413	0.229	0.266	0.268	0.286	0.254 ± 0.087
Relative contribution of ant dispersal through rescuing†	0.133	0.130	0.343	0.190	0.221	0.222	0.237	0.211 ± 0.072

*Sum of categories 'ripe diaspore' plus 'dropped by primary dispersers'.

†Expressed as the proportion of total crop size that may be influenced by diaspore-rescuing ants, calculated as follows: proportion of arillate diaspores displaced by ants in removal experiments (mean = 0.83) times the proportion of crop size that falls as viable diaspores under the parent plant.
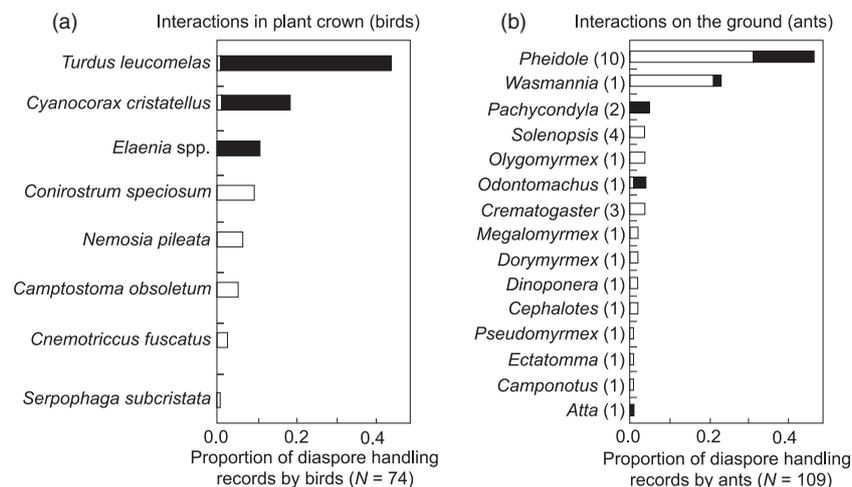

Fig. 2. Frugivorous bird and ant assemblages recorded in interaction with diaspores (arillate seeds) of *Xylopia aromatica* in the plant crown and on the floor, respectively, in a cerrado savanna in SE Brazil. (a) Relative importance of different species of birds interacting with diaspores in plant canopy. Birds may drop diaspores beneath the canopy (white bars), or swallow and defecate seeds away from fruiting trees (black bars). (b) Relative importance of different ant genera (30 species) interacting with diaspores on the floor. The number of species in each genus is given in parentheses. Ants may remove seed aril at the spot (white bars) or carry the diaspore to the nest (black bars). (See Fig. 3, for distances of diaspore displacement in each phase of dispersal.)

primary dispersers' from plant canopy (see Table 1), absolute dispersal failure (i.e. the number of viable diaspores that fall under parent plants) increased linearly with crop size (number of diaspores wasted = 1.93 + 0.95 log(crop size); $F_{1,5}$ = 45.5, R^2 = 0.88, P = 0.001). Thus, trees producing larger crop sizes retain a higher number of diaspores beneath the plant canopy.

FRUGIVOROUS BIRDS

We observed eight species of birds feeding on diaspores of *Xylopia* (Fig. 2a). The following birds of distinct body sizes acted as legitimate dispersers by ingesting the whole diaspore, and afterwards defecating or regurgitating intact seeds: resident Pale-breasted trush (*Turdus leucomelas*; 67 g) and Curl-crested jay (*Cyanocorax cristatellus*; 134 g), and the migratory Elaenia flycatchers (*Elaenia* spp.; 14–29 g) (bird weights from Marini *et al*. 1997). Many diaspores, however, were also dropped beneath the parent plant by birds that act as aril consumers and provide no dispersal away from the parent plant (e.g. Chestnut-vented conebill *Conirostrum speciosum*; 9.4 g). We observed that birds dropped 28% of the diaspores they manipulated in the canopy (Fig. 2a), and many of them fell with portions of the aril still attached. Diaspores removed by
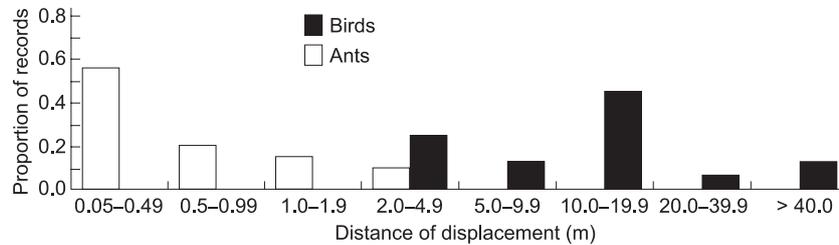
Fig. 3. Birds and ants displace diaspores of *Xylopia aromatica* to complementary distances in the Brazilian cerrado savanna. Comparative distances of dispersal achieved by diaspores carried by birds in their first flight from focal feeding trees (16.3 ± 11.8 m, mean $\pm$ SD; $N = 16$) or by ants after the diaspores reached the ground (0.8 ± 0.9 m; $N = 40$). Data of diaspores cleaned on the spot by ants with no displacement, or dropped under the plant crown by birds, are shown in Fig. 2.

birds in the canopy travelled 16.3 ± 11.8 m ($N = 16$) until dispersers made the first landing perch (mean $\pm$ SD; see Fig. 3).

ANT ATTENDANCE AT FALLEN DIASPORES AND SECONDARY DISPERSAL

Ants belonging to 30 species in 15 genera were attracted to fallen diaspores (Fig. 2b). We also occasionally observed unknown species of cockroaches, grasshoppers and flies at fallen diaspores, but they were never seen removing diaspores. Small myrmicine ants (mainly *Pheidole* spp. and *Wasmannia auropunctata*) accounted for 68% of the records at diaspores, whereas ponerines (*Pachycondyla*, *Odontomachus* and *Dinoponera*) comprised 10% of the interactions seen, but were responsible for a third of seed removal (Figs 1b and 2b). Many ant foragers (e.g. *Solenopsis*, *Olygomyrmex* and *Crematogaster*) typically did not displace fallen diaspores and instead recruited nestmates to collect liquids or remove the aril on the spot (Fig. 2b); thus, did not behave as 'rescuers'. The large ants *Pachycondyla*, *Odontomachus* and *Atta* removed most diaspores they interacted with (Fig. 1b), whereas the small *Pheidole* and *Wasmannia* mainly removed the aril on the spot, but sometimes also transported diaspores (Fig. 2b). Ants displaced diaspores to 0.8 ± 0.9 m (mean $\pm$ SD; Fig. 3). Considering the lozenge-shaped canopy of *Xylopia*, ants may remove at least some fallen diaspores beyond the area beneath the plant canopy of an average tree (i.e. displace diaspores to distances larger than half the length or half the width of plant crown; see species description).

Presence of an aril covering *Xylopia* diaspores caused an almost twofold increase in removal compared to cleaned diaspores, with ants removing a mean of 83% of the arillate diaspores against 42% of the cleaned diaspores in experimental depots (Fig. 4), but removal varied with plant location (block effect, Table 2). There was no effect of fruiting season on the removal of arillate diaspores (2004–05; Table 2). The exclosure treatment had no effect on removal of *Xylopia* diaspores over two fruiting seasons, indicating that ants are the major diaspore removers on the ground. No interaction between exclosure treatment and presence of aril was found. Taken together these results suggested that some ants are interested in the seed itself and thus might act chiefly as granivores rather than dispersers of *Xylopia*.
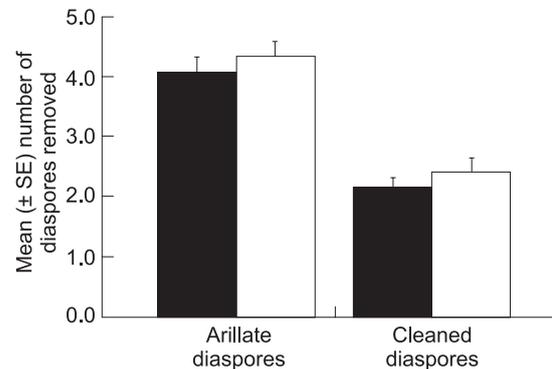

Fig. 4. Removal of fallen diaspores of *Xylopia aromatica* by ants and vertebrates in the cerrado savanna in SE Brazil. Caged treatments were accessible to ants only (black bars), whereas the paired open controls were accessible to ants and vertebrates (white bars). Data are mean $\pm$ SE number of diaspores out of five removed from beneath fruiting trees ($N = 30$ trees) in 2005 fruiting season.

Table 2. Analysis of variance of the diaspore removal experiments in a cerrado savanna in SE Brazil. The first analysis included each fruiting tree as a block, random effect factor, and exclosure treatment (access to ants only, or open to all animals) and presence of aril (arillate diaspore versus cleaned diaspore) as fixed factors. The second analysis included fruiting season (2004 or 2005) and exclosure treatment as fixed factors, and was performed with arillate diaspores only. Significant differences are in bold ($P < 0.05$)

Effect	d.f.	MS	F	P-value
Analysis 1				
2005 fruiting season				
Block	29	3.361	3.26	**< 0.001**
Exclosure	1	2.133	2.07	0.15
Aril	1	112.13	108.72	**< 0.001**
Exclosure × Aril	1	0.000	0.00	1.00
Error	87	1.031		
Analysis 2				
2004 and 2005 fruiting seasons (arillate diaspores only)				
Fruiting season	1	0.003	0.033	0.86
Exclosure	1	0.141	1.480	0.23
Fruiting season × Exclosure	1	0.001	0.009	0.92
Error	116	0.095		

SEEDLING DISTRIBUTION AND PERFORMANCE

Seedlings of *Xylopia* were found in small numbers, close to the refuse piles of nests of the large ponerines *Odontomachus* (0.2 ± 0.6 plants, mean ± SD), *Pachycondyla* (0.1 ± 0.2) and *Dinoponera* (0.2 ± 0.5), and of leaf-cutting *Atta* ants (0.1 ± 0.3). No seedlings were found close to the nests of *Pheidole* and *Ectatomma* ants. In total, sampled ant nests ($N = 81$) had a mean of 0.1 ± 0.3 (range 0–2) *Xylopia* seedlings, whereas no seedling was found in paired control plots (Wilcoxon paired-sample sign rank tests: $Z = 2.2$; $P = 0.028$). Seedling survival after 1 year was 57%.

Discussion

Our data on diaspore removal by birds do not support the fruit crop size hypothesis for *Xylopia*. Diaspore removal from plant canopies is usually subject to other sources of variation than just crop size, such as spatial and temporal variation in disperser abundance, plant neighbourhood and alternative food sources (Ortíz-Pulido & Rico-Gray 2000; García *et al*. 2001; Saracco *et al*. 2005). Nevertheless, a higher number of mature diaspores reach the ground beneath parent trees as crop size increases in *Xylopia* (mean of 25% of estimated crop size, expressed as 'ripe diaspores' plus 'diaspores dropped by primary dispersers'; see Table 1). Indeed, a great proportion of plant crops usually fall under parent plants, irrespective of dispersal mode (e.g. Clark *et al*. 2005). Ants may compensate for such waste by potentially rescuing many *Xylopia* diaspores from under parent plants within 24 h. Surprisingly, the trend found for *Xylopia* suggests that diaspore-rescuing ants can have a contribution to the quantitative component of disperser effectiveness as high as that of birds, at least for some trees. If removal rates by ants of diaspores fallen under parent plants (mean of 4.1 diaspores per exclusion treatment, or 83%) are balanced against the amount of viable diaspores that fall under parents (mean of 25% of total plant crop size), we realize that ants may affect the fate of 21% of the total plant fruit crop. For comparison, birds affected the fate of 32% of total plant crop of *Xylopia*. However, there was substantial variation between the relative contribution of birds and ants to diaspore fate among individual trees (see Table 1). Thus, using diaspore removal by primary dispersers as a surrogate of plant fitness may be misleading, since the rescue of diaspores under canopy by ants can have a considerable effect on the quantitative component of disperser effectiveness for species like *X. aromatica* in the cerrado.

Determining the fate of each seed is a hard task, and our experimental design did not allow us to track the fate of diaspores once they were removed by animals. We assume that removal of fallen diaspores beneath the parent plants may increase the chance of seedling establishment, but our results should be interpreted with caution. Since some of the ant groups recorded removing diaspores behave mainly as granivores (e.g. *Pheidole*), removal of diaspores from beneath the plant canopy will not always mean true 'rescuing'. Nevertheless, we found seedlings of *Xylopia* growing only in refuse piles

of ant nests, especially of large ponerines and leaf-cutting ants, an evidence of the importance of these ants in the regeneration cycle of *Xylopia*. It has been suggested that diffuse mutualisms may depend largely on the identity of particular partners (Gove, Majer & Dunn 2007), and our data indicate that the identity of participants may influence the outcome of interactions among *Xylopia* and its bird and ant partners in different ways (see below).

In this study, we considered dispersal vectors in a broad sense; that is, our approach simplifies the complexity of the outcomes of the plant–animal interactions inherent to each group of animals (birds or ants) which are composed of several species interacting with the diaspores. For instance, it is obvious that the effect of birds on the regeneration of *Xylopia* will vary according to the species involved, since bird foraging behaviour may determine the outcome of the bird–diaspore interaction (see Fig. 2a). Differences in habitat use and home ranges may influence the places and distances where plant diaspores may be deposited by bird dispersers (Jordano & Schupp 2000). For instance, migratory *Elaenia* spp. feeding on *Xylopia* may carry diaspores across their migration routes (Jordano 1982). Large birds such as the Curl-crested Jay may deposit *Xylopia* diaspores farther than small birds, since body size is usually correlated with home range and bird movements (e.g. Spiegel & Nathan 2007). The same is valid for the ants interacting with diaspores (see Fig. 2b). For instance, with the aid of an artificial seed shadow and a controlled exposition of seeds to ant colonies, Avgar, Giladi & Nathan (2008) demonstrated that two species of granivorous ants with contrasting foraging strategies (social *Messor ebeninus* and solitary forager *Messor arenarius*) may produce, respectively, hump-shaped and gradually declining patterns of distribution of surviving seeds by responding differently to seed density gradients. Similarly, our observations indicated that different species of ants do not have the same effect on the distribution of diaspores and seedlings of *Xylopia*. Many ants just cleaned the aril of fallen diaspores at the spot, without removing the diaspore to the nest (see Fig. 2b). Although seed cleaning may increase germination rate for some plants, minimizing the time diaspores are exposed to predators and pathogens (Christianini, Mayhé-Nunes & Oliveira 2007 and references therein), cleaned diaspores have a lower chance of subsequent removal (see Fig. 4), decreasing the potential of distance-related benefits (Giladi 2006) that seem to be more important for the regeneration of *Xylopia* (see below). A considerable portion of diaspores of *Xylopia* is removed by small group-foraging ants such as *Pheidole* that behave mainly as granivores (but see Levey & Byrne 1993), displace diaspores to short distances and have short-living nests in the cerrado (or arboreal nests, such as *Wasmannia*; A. V. Christianini pers. obs.). All these traits may constrain the probability of seedling establishment in the nests of these ants, as noted for *Pheidole* in this study. Although large solitary-foraging ponerine ants play only a minor role in diaspore removal, they displace diaspores twofold farther than smaller ants (mean of 1.6 vs. 0.6 m, respectively). Indeed, the distance of diaspore dispersal by ants is correlated with ant body size (Ness *et al*. 2004), and records of seed removal up to

25 m by large ants are available for the cerrado (Christianini, Mayhé-Nunes & Oliveira 2007). Diaspore displacement by large ponerines depends largely on diaspore size (Pizo & Oliveira 2001), and our data show that at least some of the removal distances of small *Xylopia* diaspores were great enough to surpass the parent plant crown (see Fig. 3 and study species description). Ponerines are also known to remove plant diaspores from bird feces and provide high quality dispersal (reviewed by Giladi 2006; Rico-Gray & Oliveira 2007).

Our study points out the importance of considering complementary dispersal (*sensu* Spiegel & Nathan 2007) as part of the strategies of plant regeneration. The dispersal kernel of *Xylopia* suggests that a plant with two broad groups of dispersers (birds and ants) may not only spread diaspores farther, but also have a larger variance in seed rain across distances than plants with a single mode of dispersal. For instance, if we remove the records of seed displacement by birds from the dispersal kernel of *Xylopia* in the cerrado, the range and variance of distance records would drop sharply; while the exclusion of ants as dispersers would affect more the variance of distances achieved by diaspores (see Fig. 3). The importance of the recognition of the scale at which seed dispersal and granivory operate was emphasized by models and simulations by Nathan & Casagrandi (2004), who demonstrated that variation in these two parameters may be enough to explain several spatial patterns of plant recruitment. For *Xylopia*, Santos (1991) recorded a leptokurtic pattern of the seed shadow in two localities of the cerrado. Although establishing juveniles were found at various distances from adult plants, at least in one locality seedlings were found in smaller numbers within 4 m from parent trees than expected by the seed shadow, which suggests a reduced probability of diaspore survival, germination or seedling establishment close to the parent trees. Nevertheless, even within this small spatial scale the probability of seedling recruitment is slightly enhanced as the distance to the parent plant increases (Santos 1991). Thus, removal of diaspores from the immediate vicinity of the parent plant should increase the probability of diaspore survival. Birds, which deliver diaspores to distances over 40-fold greater than do ants, are more effective in removing diaspores from near the parent tree, in providing new sites for plant colonization and recruitment, and in influencing metapopulation dynamics (Jordano *et al.* 2007; Calviño-Cancela, He & Lamont 2008). This effect should be even more pronounced, since gut retention time of diaspores may be much longer than the flight duration to the first perch, enabling birds to carry seeds to longer distances. Bird dispersal may be crucial for long-term survival of metapopulations of *Xylopia* facing large-scale fires or frost, and habitat fragmentation (all of which are common in the cerrado; see Silberbauer-Gottsberger, Morawetz & Gottsberger 1977; Hoffmann & Moreira 2002; Oliveira-Filho & Ratter 2002). Santos (1991), however, also found that seedling distribution and abundance at increasing distances from adult plants were not good predictors of juvenile establishment, which showed two peaks of recruitment in the same locality: one

at 1–2 m and another at 5–6 m from adult plants. Conflicting selective pressures are common for plants at different stages (Schupp 1995). While seed survival seems to be higher away from parent plants of *Xylopia*, seedling recruitment peaks near adult plants. This is compatible with the redistribution of diaspores near the parent plant and directed dispersal by ants (see below), at least in the case of greater juvenile recruitment at 1–2 m from adult plants (see Fig. 3). Diaspore rescuing by ants may reduce parent–offspring competition and produce a distribution of recruits that mostly match the spatial distribution of adult plants of *Xylopia* at broad scales. Compared to birds, ants should play a greater role in local population dynamics and genetic structuring of *Xylopia* (Kalisz *et al.* 1999). This dual seed dispersal system suggests that birds and ants act as complementary seed dispersers as a function of spatial scale: while ants redistribute most seeds within the vicinity of the parent plant, birds have the premier role of displacing diaspores from the parent plant to 5 m and beyond (see Fragoso 1997; Spiegel & Nathan 2007, for examples of complementary seed dispersal in other systems).

When ants act as secondary dispersers by removing seeds from bird feces, they may also increase the chance of successful establishment of *Xylopia* (Vander Wall & Longland 2004). Tropical plants are frequently establishment-limited as well as seed-limited (Hubbell *et al.* 1999; see Hoffmann 1996, for examples in the cerrado). Although data on seed rain away from parent trees suggest that regeneration of *Xylopia* is not constrained by limited dispersal (Santos 1991; A. V. Christianini pers. obs.), small-seeded species like *Xylopia* have much lower seed-to-seedling transition probabilities than do large-seeded species in forests (Harms *et al.* 2000) and savannas (Lahoreau *et al.* 2006). Because the seed aril of *Xylopia* is not fully removed in the digestive tract of birds (M. R. Francisco, pers. comm.), the diaspores remain attractive to ants after defecation. Indeed, the fact that *Xylopia* seedlings were only found growing in refuse piles of ant nests (mostly of ponerines) suggests that ants act as secondary directed dispersers and drive diaspores to their nests following long-distance dispersal by birds (see Passos & Oliveira 2002, 2004). Ant nests in poor soils are usually nutrient-rich sites that increase seedling growth and survival (Passos & Oliveira 2002; Giladi 2006; Rico-Gray & Oliveira 2007; Farji-Brener & Ghermandi 2008). Thus, the combined effect provided by two vectors in subsequent stages of dispersal (i.e. diplochory) should increase the chance of a diaspore of *Xylopia* hitting a safe site in patchy environments such as savannas, with birds removing diaspores to longer distances from the parent plant followed by a fine-tuning and directed dispersal by ants.

Acknowledgements

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