Exploitation of Fallen Diaspores by Ants: Are there Ant–Plant Partner Choices?

Alexander V. Christianini[1,4], **Antônio J. Mayhé-Nunes**[2], and **Paulo S. Oliveira**[3]

[1] Universidade Federal de São Carlos, Campus Sorocaba, Rodovia João Leme dos Santos km110, 18052-780, Sorocaba, SP, Brazil

[2] Departamento de Biologia Animal, 23890-000, Universidade Federal Rural do Rio de Janeiro, Seropédica, RJ, Brazil

[3] Departamento de Biologia Animal, C.P. 6109, Universidade Estadual de Campinas, 13083-970, Campinas, SP, Brazil

ABSTRACT

Ants frequently interact with fleshy fallen diaspores (fruits or seeds) not adapted for ant-dispersal. Such interactions are usually considered as opportunistic, but recent evidence has indicated that these ants may differ in their effects on diaspore survival and plant recruitment. We investigated if partner choices are recognizable among genera of ants and plants, and if ant and plant traits may influence such preferences in cerrado (savanna-like vegetation) from southeast Brazil. During a 2-yr period, 521 ant–diaspore interactions were recorded through various methods, yielding 71 ant species and 38 plant species. Exploitation of fallen diaspores was common among several ant genera, and included carnivorous, omnivorous, and fungivorous ants. Contrary to others areas around the world, where true myrmecochory (seed dispersal by ants) is common among shrubs, ants also exploited diaspores from several cerrado trees. Plant life form, diaspore size, and ant body size did not seem to explain the pattern of interactions observed. Two subsets of preferential interactions, however, segregated fungivorous ants from another group composed of carnivorous and omnivorous ants, probably influenced by the chemical composition of the plant diaspores. Omnivorous ants usually remove the fleshy portion of diaspores on spot and probably provide limited benefits to plants. Carnivorous and fungivorous ants usually remove the whole diaspore to the nest. As each of these ant groups may influence the fitness of diaspores in different ways, there are possible subtle pathways for the evolution of partner choices between ants and these non-myrmecochorous diaspores.

Abstract in Portuguese is available in the online version of this article.

MYRMECOCHORY (SEED DISPERSAL BY ANTS) IS CHARACTERIZED BY A LIPID-RICH APPENDAGE called elaiosome covering the seed of myrmecochorous plants. A variety of ants remove these seeds to the nest where the elaiosome is consumed, and the seed is subsequently discarded (usually unharmed) in a midden where it can germinate and recruit to a new plant (Beattie 1985). Myrmecochory is common in the dry sclerophyll shrubs in nutrient-poor soils and fire-prone habitats in Australia (*ca* 1500 species; Berg 1975) and South Africa (*ca* 1300 species; Milewski & Bond 1982), and nearly 300 ant-dispersed herbs are also found in mesic forests in North America, Europe and Japan (*e.g.*, Beattie & Culver 1981).

Seed dispersal by ants may be an important selective force in the evolution and maintenance of plant traits. Seed burial and/or removal by ants may decrease seed loss to rodents and fire (*e.g.*, Christian 2001), reduce parent–offspring conflicts and sibling competition (Higashi *et al.* 1989) and provide directed dispersal to nutrient-enriched microsites (the ant nest) where recruitment is more likely (Hanzawa *et al.* 1988). Myrmecochory occurs in small plants, such as herbs and shrubs, more than expected in relation to other life forms, maybe because in these small plants the short scale of ant seed dispersal (compared with vertebrates such as birds) is enough to remove the seeds from the parent–offspring

conflict zone beneath the parent plant (Giladi 2006). Plants invest relatively little to produce myrmecochorous seeds compared with other biotic ways of dispersal, an advantage for plants growing in poor soils (Hughes *et al.* 1993).

Seed size has been shown to constrain seed removal to a particular suite of ants (Gorb & Gorb 1995). Large ants are able to provide greater distances of dispersal than smaller ants (Ness *et al.* 2004). Elaiosome size, either absolute or relative to seed size (Hughes & Westoby 1992), and its chemical composition (Hughes *et al.* 1994), influence the probability of seed removal as well as the identity of the ant partner. For instance, carnivorous ants are more likely to interact with lipid-rich diaspores probably because these act as chemical analogs of dead insects (Hughes *et al.* 1994). Although myrmecochory is often considered as an opportunistic and diffuse mutualism among many ants and plants in interaction (Beattie 1985), recent evidence pointed out that patterns of interactions may be recognized when multiple sites with distinct ant communities are analyzed (*e.g.*, Garrido *et al.* 2002, Manzaneda & Rey 2009), with each ant species or guild affecting plant fitness in a different way (Hughes & Westoby 1992, Passos & Oliveira 2002). As the outcome of interactions is variable with the identity of the participants, there are probably pathways for the evolution of partner choices among ants and plants (Giladi 2006).

Myrmecochory is uncommon among Neotropical plants, being restricted to a few plant taxa, such as *Calathea* (Horvitz & Beattie 1980) and *Jatropha* (Leal *et al.* 2007). But the absence of

an elaiosome does not preclude the interaction of ants with fallen diaspores (*i.e.*, fruits or seeds, the unit of plant dispersal). Ants were recorded interacting with fallen diaspores adapted for vertebrate dispersal from a number of plant taxa and tropical sites across the world, such as forests in Madagascar (Böhning-Gaese *et al.* 1999), Central (Levey & Byrne 1993) and South America (Pizo & Oliveira 2000, Passos & Oliveira 2003), with possible consequences for seed germination, seedling distribution, and survival (*e.g.*, Passos & Oliveira 2002). In tropical 'cerrado' savannas that grow on fire-prone habitats and nutrient-poor soils of central South America, nearly 65 percent of the shrubs and trees produce fleshy diaspores adapted for dispersal by vertebrates, especially birds and mammals (Gottsberger & Silberbauer-Gottsberger 1983). As most diaspores fall beneath parental plants, they become available to a diverse array of ground-dwelling ants that opportunistically exploit these diaspores, and may influence seed survival and seedling recruitment (Christianini & Oliveira 2010 and references therein). Attendants to fallen diaspores include, fungus-growing ants (Attini) (Leal & Oliveira 1998), carnivorous ants (such as large Ponerinae) (Horvitz & Beattie 1980), seed harvesters (*e.g.*, *Pheidole*, *Solenopsis*) (Levey & Byrne 1993), and many others. The relative importance, however, of different ant taxa differs across plant species (Fig. 1; Christianini & Oliveira 2009, 2010), probably due to differences in the chemical cues of the fleshy portion of the diaspores that makes it more attractive or rewarding to particular guilds of ants (Pizo & Oliveira 2001).

In the present study, we investigated the pervasiveness of fruit and seed use by the general ant community in three vegetation physiognomies within a cerrado reserve in southeast Brazil. We searched for patterns of interactions between ant and plant taxa, and tested whether ant body size, diaspore size, plant life form, or ant foraging guild is correlated with plant species with which the ants interact. We predicted that ant body and diaspore size would segregate genera in interaction, as large ants are more capable to exploit a wider range of diaspore sizes than smaller ants. As diaspore size frequently holds a relationship with plant life form (Westoby *et al.* 1992), and smaller plants are more likely to benefit from the interaction with ants, we expect an effect of life form on the interaction among ants and plants. Finally, we expect that fungus-growing ants would exploit a distinct suite of plant diaspores than that exploited by carnivorous ants due to the specific cues used by each of these ant guilds to utilize diaspores, and that omnivorous ants would show no preference for a particular suite of diaspores.

METHODS

STUDY SITE.—The cerrado occupies more than 2 million km^2, which makes it South America's second largest biome (Oliveira-Filho & Ratter 2002). The study was carried out in the cerrado reserve of Itirapina (22°12′ S, 47°51′ W; altitude 730 m asl), southeast Brazil. Average annual rainfall is 1360 mm, concentrated mostly in the warm/wet season (October–March). A dry/cold season occurs from April to September. Mean annual temperature is 21.8°C (data from 1994 to 2004 from the reserve's

FIGURE 1. An illustration of how ant foraging guild and diaspore size may influence ant–diaspore interactions in the cerrado. (A) Worker of carnivorous *Odontomachus chelifer* (size *ca* 1.8 cm) transporting a diaspore of *Xylopia aromatica* (0.06 g) (Annonaceae) on the leaf litter of cerrado. These large ponerine ants regularly carry diaspores to the nest, where workers and larvae consume the fleshy portion, and the seeds are discarded unharmed. (B) Workers of fungivorous *Acromyrmex coronatus* (size *ca* 0.5 cm) collecting liquids and removing the fleshy portion of a *Calophyllum brasiliense* (Clusiaceae) fruit on the floor of a gallery forest in Brazil. Such large seeds (> 1 g) are not removed, but pieces of fleshy portion are sequentially transported by attine ants that use the material for fungus culturing inside the nest.

climatological station). We selected three vegetation physiognomies that are typical of the Cerrado Biome (see Oliveira-Filho & Ratter 2002): gallery forests, cerrado *sensu stricto* (dense woodland savanna) and campo cerrado (open savanna). Study sites were 1.5 –5 km apart, and comprised of a gradient of tree cover and soil fertility. Gallery forests grow on alluvial organic-rich soils along the drainage in a narrow strip (10–25 m) on both sides of a stream, and are prone to flooding during heavy rains. They have > 80 percent of tree cover, with herbaceous vegetation virtually restricted to the forest edge and gaps. *Calophyllum brasiliense*

Cambess. (Clusiaceae) stands dominate the local plant community, but vines, epiphytes, and mushrooms are also abundant (A. V. Christianini, pers. obs.). Tree canopy is 6–12 m in height. Cerrado *sensu stricto* grows on sandy soils, and is characterized by more than 30 percent cover by trees and bushes, interspaced by grasses (Oliveira-Filho & Ratter 2002). A detailed account of the flora of this site can be found in Giannotti and Leitão Filho (1992). Campo cerrado is a relatively open vegetation growing on sandy nutrient-poor soils, with a dominant grass layer interspaced by palms, bushes, and small trees reaching 1.5–3 m in height (Oliveira-Filho & Ratter 2002). Virtually all plant species found in campo cerrado are also found in cerrado *sensu stricto*, but in the latter trees can reach 4–6 m, with emergent *Dalbergia miscolobium* Benth. (Fabaceae) reaching up to 10 m.

SURVEYS OF ANT–DIASPORE INTERACTIONS.—We established one transect at each physiognomy to search for ant–diaspore interactions. Transects at campo cerrado and cerrado *sensu stricto* were 1-km long, whereas the gallery forest transect was 0.5 km in length due to the small size of the patch with this vegetation. We walked the transects monthly from October 2003 to November 2004, and in January 2005 (a total of 15 mo sampled) looking for ants at fallen diaspores up to 2-m off both sides of the transect. Each time an ant was observed interacting with a diaspore (*i.e.*, in contact with the surface of the diaspore apparently collecting liquids, or removing portions of it), an interaction was recorded and the ants were collected for identification. We also recorded the number of ants present and the portion of the diaspore mediating the interaction (*e.g.*, fruit pulp, seed appendage). Ant–diaspore interactions were surveyed between 0730 and 1300 h, encompassing the overall peak of ant activity at our study site (A. V. Christianini, pers. obs.).

We also placed diaspores of six selected plant species on the floor of the cerrado *sensu stricto* site and recorded the ants attracted to them in diurnal and nocturnal samplings. Diurnal samplings began at 0800 h, and nocturnal ones at 1900 h. Plants selected for these surveys were: *Xylopia aromatica* (Annonaceae), *Erythroxylum pelleterianum* (Erythroxylaceae), *Ocotea pulchella* (Lauraceae), *Miconia albicans* and *Miconia rubiginosa* (Melastomataceae), and *Amaioua guianensis* (Rubiaceae). These species cover a wide range of sizes of fruits/seeds and the chemical compositions of the fleshy portion used by ants (see Christianini *et al.* 2007). The number of diaspores used to attract ants varied according to their availability (from 30 to 100 diaspores), and samplings were carried out during the fruiting period of each species. Fresh diaspores of each species were placed at sampling stations 10 m apart, 1–2 m off the transect. At each sampling station, two diaspores of a single species were placed on a small piece of white filter paper (4 × 4 cm) to facilitate visualization. At each sampling, we walked slowly along the transect for 2 h and recorded all ant–diaspore interactions, following the same procedure described above. Samplings of ant–diaspore interactions were also undertaken during diaspore removal experiments in the cerrado *sensu stricto* site reported in Christianini *et al.* (2007), and Christianini and Oliveira (2009, 2010), and through opportunistic observa

tions at the three sites until September 2005. Voucher specimens of ants and plants are deposited in the entomological collection of the Universidade Federal Rural do Rio de Janeiro (CECL) and at the herbarium of the Universidade Estadual de Campinas (UEC), respectively.

CLASSIFICATION OF DIASPORES AND ANT FORAGING GUILDS.—As diaspore size influences ant behavior (*e.g.*, removal of entire diaspore vs. removal of fleshy part on spot; see Fig. 1) and constrains the subset of the ant community that may remove it to the nest, diaspores recorded in interaction with ants were classified as large (*i.e.*, too large to be carried away by ants: > 1 g) or small (*i.e.*, feasibly carried away by ants: < 1 g). Plant life form, which may influence crop size or accessibility to ants, was also recorded. Ants recorded in interaction with plant diaspores were classified into foraging guilds following the classification for ant genera found in Brown (2000), corroborated by observations about the feeding habits of ants in the cerrado (A. V. Christianini & P. S. Oliveira, pers. obs.). Foraging habits were grouped into broad categories for the analyses, and ant genera were classified as carnivores, omnivores or fungivores. For instance, army ants, hypogeic, generalized or specialized predators were grouped in a single category of carnivorous ants, which included Ecitoninae, Ectatomminae, and Ponerinae. Fungus-growing ants (Myrmicinae: tribe Attini) were classified as fungivorous, which included the leaf-cutter ants *Atta* and *Acromyrmex*, and the lower attines (*Cyphomyrmex*, *Mycocepurus*, and *Trachymyrmex*) that cultivate fungus on a diverse array of substrates such as fruits, feces, and insect frass (Leal & Oliveira 2000). Ants with generalized feeding habits, seed harvesters, pollen or plant exudate-feeders were classified as omnivores, including non-Attini Myrmicinae, Dolichoderinae, Formicinae, and Pseudomyrmecinae. Ants were also classified according to total body length into three categories: small (< 0.2 cm), medium (between 0.2 and 1.0 cm) or large (> 1 cm). Body size is linked with several aspects of ant behavior, including seed size selection (Gorb & Gorb 1995), and distance of seed dispersal provided (Ness *et al.* 2004).

STATISTICAL ANALYSIS.—To ascertain what fraction of the expected species pool was sampled, we used the total number of plant and ant species found in interaction, irrespective of plant physiognomy, to build sample-based rarefaction curves in Ecosim (Gotelli & Entsminger 2001). Patterns in ant–diaspore interactions were investigated through correspondence analysis (CA) performed in STATISTICA software, v.5 (STATSOFT, INC., 1996). As species with few records could bias the analysis (Manly 1997), we lumped records by plant and ant genus, and removed those genera with only one record. This procedure may also reduce pseudoreplication due to phylogenetic autocorrelation that generates non-independence among morphologic and physiologic traits within common taxonomic affiliates (*i.e.*, species within genus) that can influence preference patterns, allowing a more conservative analysis (Jordano 1995). The CA was performed on the reduced contingency table of interactions between ants and plants (16 ant × 18 plant genera)

across all study sites. Coordinates for the first two dimensions extracted by CA were used to test differences in plant preferences between a priori defined groups of ants (ant foraging guild, ant body size), and of ant visitor spectra between plant groups (plant life form, diaspore size). One-factorial multiple analysis of variance (MANOVA) was performed for each of these comparisons. Significance levels were adjusted by Bonferroni corrections.

RESULTS

SPATIAL AND SEASONAL PATTERNS.—We recorded a total of 521 ant–diaspore interactions, of which 129 were recorded during transect samplings. The mean number of interactions recorded per km of transect decreased from cerrado *sensu stricto* (4.5 interactions per km) to the campo cerrado and gallery forest (3.1 and 2.3 interactions per km respectively). Overall, ant species richness was almost double that of plant species richness, with 71 ant species recorded interacting with 38 species of plants along the whole study (Appendices S1 and S2; Fig. 2). Our sampling was able to cover most of the expected richness of ants in interaction with fallen diaspores. Estimated ant species richness was 86 (range 76–111); Chao1 estimator from EstimateS (Colwell 2000). However, only 12 ant species had a high frequency (> 10 records) of interaction with diaspores (Appendix S1). Species turnover (beta diversity) of ants recorded in interaction was high, especially between gallery forest and the other physiognomies (Appendix S1). Only three plant species were recorded in interaction with ants in more than one physiognomy (Appendix S2).

There was great seasonal variation in the number of interactions recorded within sites. The gallery forest site could not be surveyed all year round due to floods following heavy rains. The interactions were concentrated in the wet season (October–
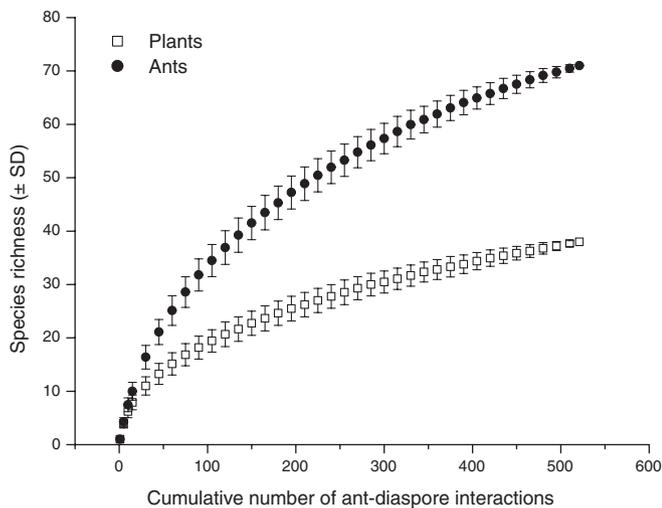

FIGURE 2. Ant (closed circles) and plant (open quadrats) species accumulation curves as a function of the number of records of ants interacting with fallen diaspores in combined data from three cerrado physiognomies.

March). The number of ant–diaspore interactions recorded at a given site along the year was not correlated with records at the other sites (Spearman rank correlations: $r_s \leq 0.48$; $N = 12$; $P \geq 0.11$, for all comparisons), and probably followed distinctive patterns of plant phenology and ant activity at each site.

ANT BEHAVIOR TOWARD DIASPORES, AND PATTERNS OF DIASPORE EXPLOITATION.—Ants exploited diaspores of 18 species of trees, 11 shrubs, 3 palms, 3 lianas, and 3 herbs. Ants interacted with diaspores up to 26 g in weight, such as the fruits of *Dyospyros hispida* (Ebenaceae). Most diaspores had a fleshy portion (either pulp or aril) mediating the interaction, but dry diaspores primarily adapted to wind dispersal (*e.g.*, from Poaceae and Asteraceae), were also exploited by fungivorous ants (Attini) (Appendix S2). *Atta sexdens* was observed removing seeds of *Solanum lycocarpum* (Solanaceae) and *M. rubiginosa* (Melastomataceae) from vertebrate feces, and thus these ants can reshape the seed shadow generated by primary seed dispersers (Christianini & Oliveira 2009). Workers of *Atta* spp. were also frequently observed carrying unripe fruits of *Miconia* spp., which were collected on the floor or directly from the plants. All other ants were observed interacting with ripe fruits only. Fleshy fruits that were partially eaten and dropped to the ground by vertebrate frugivores (*e.g.*, *Hancornia speciosa*, Apocynaceae) attracted many ants that collected liquids from the remains of the juicy pulp.

Myrmicine ants (except Attini) were well represented in interactions with diaspores at all sites, accounting for nearly 47 percent of all interactions recorded (Appendix S1). *Pheidole* ants were observed at all sites cleaning seeds from pulp, removing fruit parts, or carrying diaspores to their nests. Although common in all cerrado physiognomies, accounting for 33 percent of all interactions recorded, Attini ants were best represented in cerrado *sensu stricto*. *Atta sexdens* was the most important species in number of interactions, and the only species recorded at all sites (Appendix S1). Ponerine ants accounted for 13 percent of all observed interactions; these ants were never observed in the gallery forest, but were common in campo cerrado and cerrado *sensu stricto*, and almost always removed diaspores to their nests. Ants in the subfamilies Formicinae, Dolichoderinae, and Pseudomyrmecinae accounted for 7 percent of the interactions recorded, but never removed the diaspores. These figures, however, should be interpreted with caution. Although we used several sampling methods, our records may be biased toward ants that spend more time at the diaspore and recruit foragers to it, rather than ants that rapidly discover the diaspore and remove it to the nest (Fig. 1).

Twelve omnivorous ant genera predominate in interactions with fallen diaspores, followed by carnivorous and fungivorous ants, with five genera each (Appendix S1). Patterns of association between ant and plant taxa were detectable in the ordination analysis. Fungivorous (Attini) ants were significantly segregated from other ants, whereas carnivorous and omnivorous ants appeared together in the ordination space (Table 1; Fig. 3). Plant preferences were not affected by ant body size; neither did plant life form or diaspore size segregate the ants in interaction (Table 1).

Plant genera associated with fungivorous ants included *Amaioua*, *Copaifera*, *Miconia*, *Myrcia*, *Brachiaria*, and *Stryphnodendron* (Fig. 3), the latter two with dry fruits. Our results should be interpreted with caution as they rely on the reduced matrix of interactions between ant and plant genera, which inevitably reduced the number of groups for comparison (*e.g.*, three genera of fungivorous ants). Our analyses, however, indicated that the partitioning of ant groups among plants was significant, which suggests partner choices between certain groups of ants and plants in interaction.

DISCUSSION

To our knowledge this study sampled the richest assemblage of ants (71 species) recorded in interaction with fallen diaspores so far. Most interactions were opportunistic, and we detected no specific association between particular classes of ants and plants in the cerrado investigated. Nevertheless, some tendencies among ant and plant taxa were found when higher taxonomic levels (genera) were considered.

Plant life form did not segregate genera in ant–plant interactions. Plant size would have a lower influence on diaspore exploitation by ground-dwelling ants compared with ants that forage in the plant canopy (Blüthgen *et al.* 2004), because the influence of plant height is lower when diaspores are collected on the ground. Fallen diaspores may also constitute a more scattered and temporally unpredictable resource (Jordano 2000) compared with nectar or honeydew sources in plant canopy (*e.g.*, Blüthgen *et al.* 2004), which
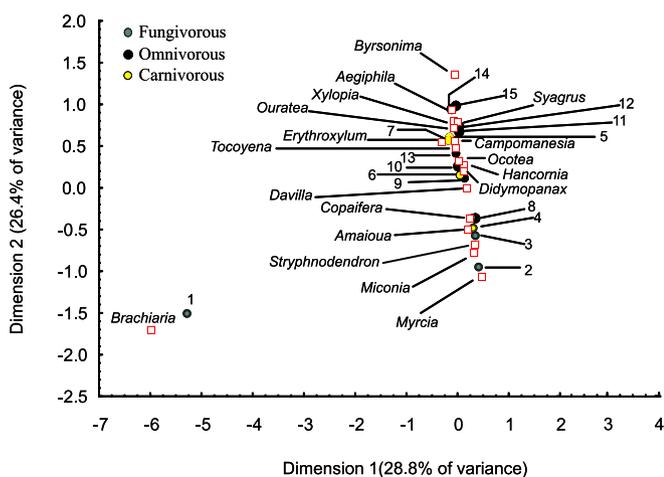
FIGURE 3. Reciprocal ordination of ants and diaspore's genera found in interaction in the cerrado of Itirapina. Squares indicate plant genera whereas colored circles indicate ants according to foraging guild: green circles = fungivorous ants (Myrmicinae: Attini); black circles = omnivorous ants (non-Attini Myrmicinae, Formicinae, and Dolichoderinae); yellow circles = carnivorous ants (Ectatomminae, Ponerinae). Note the segregation among fungivorous ants and a subset of plants from other ants and plants in interaction (see also Table 1). Key for ant genera: (1) *Mycocepurus*; (2) *Atta*; (3) *Trachymyrmex*; (4) *Ectatomma*; (5) *Dinoponera*; (6) *Odontomachus*; (7) *Pachycondyla*; (8) *Brachymyrmex*; (9) *Camponotus*; (10) *Cephalotes*; (11) *Crematogaster*; (12) *Dorymyrmex*; (13) *Pheidole*; (14) *Solenopsis*; (15) *Wasmannia*.

TABLE 1. *Multiple one-way analyses of variance (MANOVA) for effect factors selected a priori on first two dimensions from correspondence analysis (explanatory power: 28.8% and 26.4%, respectively): (a) differences among plants in ant visitation spectra, and (b) among ants in plant preferences (see also Fig. 3). Significant effects after Bonferroni correction in boldface.*

Effect	Wilks	df effect	df error	P
(a) Ants				
Foraging guild	0.349	4	22	**0.0169**
Body size	0.748	4	24	0.458
(b) Plants				
Life form[a]	0.845	2	14	0.308
Diaspore size	0.920	2	15	0.536

[a]Excluding the herb *Brachiaria,* which is an exotic species.

should make fallen diaspores less prone to monopolization by more aggressive ants. In Australia, South Africa and the Northern Hemisphere myrmecochory is common among shrubs and herbs, while in the cerrado ants also interacted with fallen diaspores from many trees. Life-form spectrum, however, is biased toward smaller life forms in the cerrados, especially in the more open physiognomies (Batalha & Martins 2002). Prevalence of vertebrate seed dispersal is positively related to plant size in the cerrado, with most herbs and shrubs adapted to dispersal by wind or by ballistic means (Gottsberger & Silberbauer-Gottsberger 1983). As most records were of ants interacting with plant diaspores that are readily dispersed by vertebrates, ants probably play a complementary role in tree seed dispersal together with birds and mammals (Christianini & Oliveira 2010), rather than an exclusive one as seen for most true myrmecochores elsewhere. Mean distances of seed removal by ants in the cerrado are five times greater than mean global estimates of seed dispersal by ants (Gómez & Espadaler 1998, Christianini *et al.* 2007), which may increase benefits of dispersal by ants in cerrado compared with other sites around the world, including savannas in Australia (Andersen & Morrison 1998).

Ant body size did not segregate genera in ant–plant interactions in this study. Although antagonistic encounters can be observed while ants exploit fallen diaspores in cerrado (*e.g.*, large *Dinoponera* displacing smaller ants, or mass recruiting myrmicines expelling larger ants), such interactions are usually restricted to the nest vicinity of the more aggressive species, and are unlikely to determine the whole interaction pattern. Large diaspores can also be cleaned on spot rather than transported to the ant nest by smaller ants (Fig. 1B), which may increase seed germination (Oliveira *et al.* 1995), but at the cost of a decreased probability of seed removal by other ants or vertebrates (Christianini & Oliveira 2010). All these aspects may contribute for the widespread use of fallen diaspores irrespective of ant size, and for the absence of segregation of interacting genera in relation to diaspore size.

The CA analysis indicated that a subset of the cerrado plants interacted mainly with carnivorous and omnivorous ants (see Table 1; Fig. 3). This subset includes plant genera primarily dispersed by birds that produce lipid-rich diaspores such as *Ocotea*, *Xylopia*, and *Erythroxylum* (32%, 33%, and 68% of lipids in

dry mass, respectively) (A. V. Christianini & P. S. Oliveira, unpubl. data). This result corroborates early findings in the Atlantic forest of Brazil suggesting that carnivorous ants prefer lipid-rich fruits (Pizo & Oliveira 2001), similar to what was found for true myrmecochorous diaspores elsewhere (Hughes *et al.* 1994). Lipids are an important resource for ants, serving for nutrition, physiologic constituents, and behavioral releasers (reviewed in Rico-Gray & Oliveira 2007). In the cerrado, lipid-rich diaspores show higher removal rates than lipid-poor ones (Christianini *et al.* 2007), and attract a high quality dispersal guild of large Ponerinae ants that increase seedling recruitment (Christianini & Oliveira 2010). Myrmicine ants (other than Attini) account for a large number of interactions with fallen diaspores in the cerrado, a common result of other studies investigating the interaction of ants with non-myrmecochorous diaspores elsewhere (Levey & Byrne 1993, Böhning-Gaese *et al.* 1999, Pizo & Oliveira 2000, Passos & Oliveira 2003). As opportunistic feeders, these omnivorous ants are probably just taking advantage of the availability of the rich food source represented by fallen diaspores. Contrary to areas in the Old World where true myrmecochory is common (Christian 2001, Garrido *et al.* 2002), omnivorous ants seem to provide no strong benefits to the plants with which they interact in the cerrado, although some taxa such as *Pheidole* behave mainly as seed predators (A. V. Christianini & P. S. Oliveira 2009, Ferreira *et al.* 2011). In addition, seedlings are not usually found around the nests of omnivorous ants in the cerrado (Christianini & Oliveira 2010).

A distinct subset of the cerrado plant community interacted mainly with fungivorous ants (see Table 1; Fig. 3). This subset includes several plant genera that produce lipid-poor, carbohydrate-rich diaspores such as *Myrcia* (75% water and 75% carbohydrates in dry mass of fleshy portion), *Copaifera* (75% and 87%), and *Miconia* (76% and 86%), which are primarily dispersed by birds (Galetti 1996, Christianini & Oliveira, unpubl. data). Such diaspores may provide water and essential nutrients to the ant workers, and/or compose a more balanced and better substrate for fungus growth when combined with other plant material (De Fine Licht & Boomsma 2010 and references therein). As lipids are hydrophobic, there is often a trade-off between lipid and water/carbohydrate content in fruit pulp (Jordano 1995), which may constrain water availability for optimal fungus growth inside nests. It is well known that the chemical composition of plant matter usually plays a role in the selection by leaf-cutter ants (*e.g.*, Howard *et al.* 1988, Farji-Brener 2001, Wirth *et al.* 2003, Mundim *et al.* 2008). Leaf-cutters may also prefer to harvest fleshy fruits because of the toxic compounds, high toughness, and/or poor nutrient content of plant leaves in cerrado (Marquis *et al.* 2001, but see Costa *et al.* 2008). Indeed, terpenoids that are toxic to leaf-cutter ants and their fungus (Howard *et al.* 1988) are common in some plant clades from the cerrado (*e.g.*, Gottlieb *et al.* 1975). Attine ants collect many diaspores in cerrado whose fleshy part is easily colonized by opportunistic fungi, for instance, during seed germination experiments (Leal & Oliveira 1998, Christianini *et al.* 2007). Thus by removing the fleshy material from seeds, leaf-cutter ants may benefit plants through positive effects on germination, and by delivering seeds to specific micro-habitats, such as vegetation gaps around nest mounds, they may positively impact the recruitment of certain plants with pioneer habits (Christianini & Oliveira 2009, Meyer *et al.* 2011).

This study indicates that interactions between ants and fallen fleshy diaspores may be not as diffuse as once suspected. Geographic variation in ant assemblages and diaspore traits have obscured the recognition of partner choices among ants and plants at local scales (Garrido *et al.* 2002, Gove *et al.* 2007). Intensive sampling, however, and the consideration of higher taxonomic levels (genera) among local taxa might also reveal partner choices among plants and ants in interaction, as shown by this study. As the two broad types of ants interacting with diaspores in the cerrado (fungivorous vs. carnivorous and omnivorous ants) provide different outcomes to the interaction, there may be different pathways for the evolution of diaspore traits that influence plant fitness (Hughes & Westoby 1992, Hughes *et al.* 1994). The shifts in species composition faced by plant communities invaded by exotic ant species—that are not seed dispersers and replace native seed-dispersing ants—are a dramatic example that redundancy in seed dispersal services among ant species are far from true in the Old World (Christian 2001). This study suggests that redundancy is unlikely also for ants interacting with non-myrmecochorous diaspores elsewhere.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1. Ant species observed in interaction with fallen diaspores in cerrado in southeast Brazil.
APPENDIX S2. Plant diaspores exploited by ants in cerrado in southeast Brazil.

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Mundim, F. N., A. N. Costa, and H. L. Vasconcelos. 2008. Leaf nutrient content and host plant selection by leaf-cutter ants, *Atta laevigata*, in a Neotropical savanna. Ent. Exp. Appl. 130: 47–54.

Ness, J. H., J. L. Bronstein, A. N. Andersen, and J. N. Holland. 2004. Ant body size predicts dispersal distance of ant-adapted seeds: implications of small ant invasions. Ecology 85: 1244–1250.

Oliveira, P. S., M. Galetti, F. Pedroni, and L. P. C. Morellato. 1995. Seed cleaning by *Mycocepurus goeldii* ants (Attini) facilitates germination in *Hymenea courbaril* (Caesalpiniaceae). Biotropica 27: 518–522.

Oliveira-Filho, A. T., and J. A. Ratter. 2002. Vegetation physiognomies and woody flora of the cerrado biome. *In* P. S. Oliveira, and R. J. Marquis (Eds.). The cerrados of Brazil: ecology and natural history of a neotropical savanna, pp. 91–120. Columbia University Press, New York.

Passos, L., and P. S. Oliveira. 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., and P. S. Oliveira. 2003. Interactions between ants, fruits, and seeds in a restinga forest in south-eastern Brazil. J. Trop. Ecol. 19: 261–270.

Pizo, M. A., and P. S. Oliveira. 2000. The use of fruits and seeds by ants in the Atlantic forest of southeast Brazil. Biotropica 32: 851–861.

Pizo, M. A., and P. S. Oliveira. 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.

Rico-Gray, V., and P. S. Oliveira. 2007. The ecology and evolution of ant–plant interactions. The University of Chicago Press, Chicago.

Westoby, M., E. Jurado, and M. Leishman. 1992. Comparative evolutionary ecology of seed size. Trends Ecol. Evol. 7: 368–372.

Wirth, R., H. Herz, R. J. Ryel, W. Beyschlag, and B. Hölldobler. 2003. Herbivory of leaf-cutting ants: a case study on *Atta colombica* in the tropical rainforest of Panama, Vol. 164. Springer Verlag, Berlin.