The effect of ants on the seed dispersal cycle of the typical myrmecochorous *Ricinus communis*

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Abstract The directed dispersal hypothesis has two components: (1) non-random seed deposition by a predicted vector, which removes greater amounts of seeds to specific sites, and (2) higher seed survival and seedling establishment in these specific sites. Several studies suggest that ants perform both tasks. This study was designed to cover the processes from post-dispersed seeds to established juvenile plants of a typical ant-dispersed species. Our main objective was to determine whether *Ricinus communis* benefits from directed dispersal by ants to maintain its populations in previously colonized habitats. We examined whether there were differences between ant nest pile mounds and their vicinities in the: (1) densities of seeds with and without elaiosome, seedlings and juveniles; (2) performance of post-dispersed seeds (without elaiosome), which may be affected by seed density, a key feature attracting seed predators; (3) nutrient quantities; (4) number of germinated seeds and juvenile biomass measurements; and (5) ant protection of seedlings from herbivores. There were more seeds without elaiosome, seedlings and juveniles in pile mounds, and seeds with elaiosome were equally distributed. There was no difference in the number of non-removed seeds in pile mounds and in their vicinities, and there was no tendency for this difference to increase or decrease with time or with initial seed density. Apparently, there was no difference in nutrient contents in soils of pile mounds and their vicinities. Likewise, there was no difference in the number of seeds germinated and in the biomass measurements of juveniles in both soils. Ants did not provide differential protection for seedlings in pile mounds against potential herbivores. The dispersal of *Ricinus* seeds by ants had a marked effect on the distribution pattern of the seeds, seedlings and juveniles of this species. However, there were no additional advantages for the seeds, seedlings and juveniles in pile mounds and, therefore, *Ricinus* does not benefit from directed dispersal by ants to maintain its populations in the study sites.

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Abbreviations

FM_{root}	Root fresh mass
FM_{stem}	Stem fresh mass
FM_{leaf}	Leaf fresh mass
DM_{root}	Root dry mass
DM_{stem}	Stem dry mass
DM_{leaf}	Leaf dry mass
DM_{total}	Total dry mass
RMR	Root mass ratio
R/AS	Roots/aerial system ratio
SMR	Stem mass ratio
ROB	Stem robustness
SLM	Specific leaf mass
LMR	Leaf mass ratio
LAR	Leaf area ratio

Introduction

Seed dispersal is an important component of plant demography and largely determines the spatial and temporal patterns of recruitment (Harper 1977; Schupp and Fuentes 1995). The reproductive success of an individual plant may be enhanced by seed dispersal in three different ways: (1) by decrease in mortality due to competition, predation and pathogen infestation, which usually occur in sites with great seed density, such as near parental plants (O'Dowd and Hay 1980, Willson 1993); (2) by colonization of new habitats, which are usually rare, unpredictable or ephemeral (Willson 1993; Wenny 2000, 2001; Wang and Smith 2002); and (3) by high seed deposition in micro-habitats that are better suited for seed survival and seedling establishment (Howe and Smallwood 1982; Willson 1993). The latter advantage is the basis of the directed dispersal hypothesis, which has two components: (1) non-random seed deposition by a predicted vector, which removes greater amounts of seeds to specific sites (Willson 1993), and (2) higher seed survival and seedling establishment in these specific sites (Howe and Smallwood 1982; Wenny 2001).

Several studies suggest that ants perform both tasks (e.g. Passos and Oliveira 2002, 2003, 2004;

Leal et al. 2007). First, they carry large amounts of seeds into their nests, eat their pulp or elaiosome and discard the seeds in pile mounds, often in viable conditions (Berg 1975; Davidson and Morton 1981; Beattie 1985). These mounds are part of the exterior section of ant nests where ants deposit rejected material, such as insect corpses, seeds, plant remains and soil particles (Hölldobler and Wilson 1990). Secondly, seeds discarded in these pile mounds are expected to show higher germination success and seedling growth for two different reasons: (1) higher concentration of organic matter and nutrients in the soil, such as elevated quantities of nitrogen that are especially important to trigger seed germination (Davidson and Morton 1981; Salisbury and Ross 1992; but see Horvitz and Schemske 1986 and Rice and Westoby 1986), and (2) patrolling by ants of their nest vicinities (Hölldobler and Wilson 1990). This behaviour potentially renders protection for both seeds and established plants in pile mounds: seeds may be protected against post-dispersal predation or further removal to less suitable sites by other dispersal vectors, while established plants may gain protection against herbivory (Davidson and Epstein 1989; Passos and Oliveira 2004).

Although directed dispersal is considered common and ecologically important, only a remarkably small number of studies (e.g. Wenny 2000) confirms and quantifies its effects to further steps in the seed dispersal cycle (Wang and Smith 2002), and little is known for typical ant-dispersed seeds. This study was designed to cover the processes from post-dispersed seeds to established juvenile plants of a typical ant-dispersed species. Our main objective was to determine whether *Ricinus communis* L. (Euphorbiaceae) benefits from directed dispersal by ants to maintain its populations in previously colonized habitats.

We hypothesize that: (1) if ants deposit seeds non-randomly in their pile mounds then we expect to find a higher density of post-dispersed seeds, seedlings and juveniles in the pile mounds than in paired control sites; (2) if ants provide protection from potential herbivores near their nests, we expect to find lower seed predation rates and lower plant herbivory near ant nests than in paired control sites; and (3) if the soil of ant nests is nutrient enriched, we expect to find higher germination rates for seeds and higher biomass for seedlings and juveniles in pile mounds than in paired control sites.

Methods

Species studied

Ricinus is an African shrub or small tree which was introduced to all continents as a crop for oil-extraction (Singh 1976; Mabberley 1998). Currently, it occurs worldwide as an invasive species and, in Brazil, is commonly observed in disturbed environments such as urban vacant lots, waste heaps, roadsides and forest edges (V. Martins, 'pers. obs.'). *Ricinus* is monoecious and produces fruits that are an explosive capsule with three seeds, which bear a lipid-rich elaiosome (Singh 1976; Mabberley 1998; Kissmann and Groth 1999; Lorenzi 2000). The species flowers all year long and each plant produces between 1,500 and 150,000 seeds per reproductive period (Hogan 1992). *Ricinus* is also capable of rapid growth and recovery after disturbance, and early maturity (V. Martins 'pers. obs.').

Martins et al. (2006) have shown that *Ricinus* seeds are primarily dispersed by autochory and secondarily dispersed by ants (despite the relative enormous seed weight of about 0.123 g), which are attracted by the elaiosome. Although the interaction between *Ricinus* seeds and ants in Brazil is not naturally co-evolved, it is extremely conspicuous everywhere the plant occurs (V. Martins, 'pers. obs.').

Study sites

Fieldwork was undertaken between April 2005 and January 2006 in the municipality of Campinas, Southeast Brazil (22°54′ S, 47°03′ W). The climate is Koeppen's Cwa, macrothermal temperate with mild dry winter (Camargo et al. 1966). The experiments were performed on vacant lots, i.e. open areas with no considerable shady sites located in urban scenarios. The study sites were dominated by *Brachiaria decumbens* (Poaceae) and *Ricinus*, which occurred in clumped pattern.

Seed, seedling and juvenile densities

In order to find ant nests, we placed a mixture of tuna and honey baits (e.g. Cogni et al. 2003) at a 5 m distance from each other around the *Ricinus* clumps in three study sites. We followed ants visiting baits to their nest entrance and checked for pile mounds in its vicinities. A pile mound is here characterized as an opening in the ground surrounded by rejected material, such as insect corpses, seeds, plant remains and soil particles. We established 30 paired experimental plots of 0.5×0.5 m (Passos and Oliveira 2002, 2003, 2004), an area that encompassed entirely every pile mound in this study. For each pair, one of the plots was placed in the pile mound and the other was a control plot, located 5 m away from its correspondent pile mound. We made sure every control plot was at least 5 m away from any ant nest and at the same distance as its correspondent pile mound to the *Ricinus* clump.

In order to investigate if there were differences between the density of *Ricinus* seeds with and without elaiosome, seedlings and juveniles in pile mounds and in their vicinities, we counted the number of individuals belonging to each of these categories in the plots. We considered as seedling the individual that still retained its first, differentiated leaves and as juvenile the one without these leaves (maximum height found of 47.8 cm).

Performance of post-dispersed seeds

We investigated whether the performance of seeds discarded from ant nests (without elaiosome) differed between seeds in pile mounds and in their vicinities. This performance may be affected by seed density, which is a key feature attracting seed predators. We carefully removed each *Ricinus* seed, seedling and juvenile from the 30 previously established plot pairs, trying to prevent considerable disturbances in the soil. We placed *Ricinus* seeds without elaiosome on bare ground at five different densities: 1, 3, 9, 27 and 81 seeds/plot. The two plots within a pair had the same seed density and there were six pairs for each density. We manually removed the elaiosome of the seeds used in this experiment, which enables it to be fully detached from the seed without damaging the seed coat (V. Martins, 'pers. obs.'). The number of seeds placed in each plot pair was randomly determined and the seeds were equidistantly placed in the plots.

We recorded the number of removed seeds and emerged seedlings in each plot twice a week for 6 weeks. A seed was considered to be removed when it was no longer in the plot. We took every seed or

seedling not provided by us off the plots and we did not add any new seed during the experiment.

Ant collection, soil analysis, seed germination and juvenile biomass

In order to determine if pile mound soils were nutrient enriched, we established 10 new paired experimental plots, as previously described, in only one study site. This time, we collected ants interacting with the baits using a soft brush and preserved the specimens in 70% ethanol. The collection was performed in the morning and voucher specimens were identified by an ant taxonomist and deposited in the Museum of Zoology at University of São Paulo (MZUSP). We collected approximately 200 g of soil from each pile mound for macro- and micro-nutrients analysis. In each pile mound plot, we cleared the soil surface in order not to collect any rejected materials from the ant nests. Then we scooped up the superficial portion of the soil encompassed in the entire 0.5×0.5 m plot. The collected soil was transferred into a bag, which we closed and sent to a specialized soil analysis laboratory. We also collected approximately 20 g of soil from each control plot, using the same procedure described above. We mixed the soil samples of control plots for only one chemical analysis, as we were interested in comparing individual pile mound soils to an average, non-ant-nest, vicinity soil.

In order to compare the number of germinated *Ricinus* seeds in the two types of soil, we scooped up more soil from the 10 new established plot pairs in order to fill a plastic box (11 cm each side and 3.3 cm depth), in a total of 20 boxes (half with pile mounds soil and half with control plots soil). Then we equidistantly placed 10 *Ricinus* seeds without elaiosome (manually removed) in each box. The boxes were placed inside a germination cabinet with four 20 W fluorescent regular tube lights and alternating temperatures of 20 and 30°C. We adjusted the cabinet for uninterrupted 12-h light and 12-h darkness to simulate day and night periods, and the dark period was coincident with the 20°C period. The boxes were wetted with distilled water whenever necessary. After 3 weeks in the cabinet, we counted the number of seeds germinated in each box. We considered a seed germinated when the hypocotile-radicle axis started to protrude.

In order to compare the biomass of *Ricinus* juveniles growing in the two types of soil, we reduced

the plant density to only three individuals in each of the boxes used in the previous experiment. This was the lowest number of germinated seeds we recorded in the germination experiment and, so as to avoid differences in biomass due to intraspecific competition, we discarded the exceeding plants in the boxes with more than three individuals. We randomly determined which plants to pull up and were very careful during this procedure in order not to damage the root system of the remaining individuals. We placed the boxes under natural conditions and exposed to sunlight. We believe that the temperature, humidity and light regime were very similar to those found by natural populations of *Ricinus*, as the distance from them and the experiment site was not greater than 8 km. The boxes were watered four times a day.

One week after the last seedling had progressed to juvenile, we performed biomass measurements. We gently removed all the content of the plastic boxes and washed away the soil from the roots. We measured the root length and the stem length of each plant with a millimetric ruler. For the whole plant set of each box, we obtained the fresh masses of roots (FM_{root}), stems plus leaf petioles (hereafter called just stems; FM_{stem}) and leaf blades (hereafter called just leaves; FM_{leaf}) using an analytical scale. We also counted the number of leaves and obtained the leaf area with a leaf area meter (LI-COR, Inc., model LI-3100, Lincoln, Nebraska, USA). Roots, stems and leaves were dehydrated in an 80°C cabinet for more than 2 days, and then weighed on an analytical scale to determine their dry masses (DM_{root}, DM_{stem} and DM_{leaf}). We calculated the total dry mass (DM_{total}), root mass ratio (RMR), roots/aerial system ratio (R/AS), stem mass ratio (SMR), stem robustness (ROB), specific leaf mass (SLM), leaf mass ratio (LMR) and leaf area ratio (LAR) as follows (Hunt 1982; Lee et al. 1996):

$$DM_{total} = DM_{root} + DM_{stem} + DM_{leaf}$$

$$RMR = DM_{root}/DM_{total}$$

$$R/AS = DM_{root}/(DM_{stem} + DM_{leaf})$$

$$SMR = DM_{stem}/DM_{total}$$

$$ROB = DM_{stem}/Stem\ length$$

$$SLM = DM_{leaf}/Leaf\ area$$

$$LMR = DM_{leaf}/DM_{total}$$

$$LAR = Leaf\ area/DM_{total}$$

Ant protection of seedlings from herbivores

In order to evaluate whether *Ricinus* seedlings growing near ant nests can gain protection from ants against herbivory, we performed an experiment using termites to simulate the presence of herbivores on the plants. The predation of termites by ants indicates their patrolling of the plants growing near their nests and the removal of potential herbivores (Freitas and Oliveira 1996). In 30 paired experimental plots established as previously described, one live termite worker (*Neocapritermes opacus*, Termitidae) was glued to a leaf of a *Ricinus* seedling growing in every plot. The termites were glued to the first leaves by their dorsum using white glue (Tenaz®). In each plot, we randomly sorted which seedling and which of its leaves would receive the termite. In order to allow free access by ants and exclude vertebrates, the seedlings were protected with wire cages (20 × 20 × 30 cm, 1 cm mesh) closed at the top and staked to the ground. We recorded whether termites were attacked by ants at 30-min intervals from 8 a.m. to 10 a.m. (Passos and Oliveira 2004).

Data analyses

The differences in the number of *Ricinus* seeds with and without elaiosome, seedlings and juveniles between pile mounds and control plots were analyzed with Wilcoxon paired-sample sign rank tests. At the end of the experiment where we investigated the performance of post-dispersed seeds, we computed the difference in final seed densities between the two plots within a plot pair. We used a general linear model to measure the effects of time and initial seed density on the difference in final seed densities within plot pairs. Initial seed density was defined as fixed factors, whereas time was used as a repeated measure. Initial seed density was $\log_3$-transformed to improve normality (Zar 1999). Emerged seedlings were not included in this analysis due to their low number.

In order to test for differences in the number of *Ricinus* plants growing in pile mound soils and in control soils in the germination experiment, we used paired *t* test. In order to determine differences in the 18 biomass measurements obtained for the juveniles growing in pile mound soils and in control soils, we first obtained a mean per box of every measure for the plants that survived until the end of the experiment.

Then we used paired *t* tests or Wilcoxon paired-sample sign rank tests, when data showed no normality, to compare the means of juveniles growing in ant nest pile mound soils and in control soils. Finally, we used a chi-square test to compare the number of termites attacked by ants in *Ricinus* seedlings growing pile mound plots and in control plots (Zar 1999).

Results

Seed, seedling and juvenile densities

There was a greater number of *Ricinus* seeds without elaiosome ($Z = -2.968$, $P = 0.003$), seedlings ($Z = -2.216$, $P = 0.034$) and juveniles ($Z = -3.852$, $P < 0.001$) in pile mounds than in control plots. Seeds with elaiosome were equally distributed between the plot pairs ($Z = -0.941$, $P = 0.347$; Fig. 1).

Performance of post-dispersed seeds

After 6 weeks, more than half of the seeds ($54.0 \pm 31.9\%$) remained, on average, in each plot. There is no evidence that post-dispersed seeds gain protection in ant nests against predation or further removal: across plot pairs, there was no difference in the number of non-removed seeds in pile mounds and in control plots (mean difference = 1.3 ± 6.7 seeds) after 12 observations ($t = 1.03$, $N = 30$ plot pairs, $P = 0.15$). In addition, there was no tendency for pile mound—control plot difference to increase or decrease with time ($F = 0.32$, $P = 0.97$) or with initial seed density ($F = 0.34$, $P = 0.56$; Fig. 2).

Ant collection, soil analysis, seed germination and juvenile biomass

We found five ant species in our collection, four from the Myrmicinae subfamily and only *Dorymyrmex brunneus* from Dolichoderinae subfamily. Soil analysis showed great heterogeneity and apparently there was no difference in the macro- and micro-nutrient contents between pile mound soils and control soils (Table 1). Likewise, there was no difference in the number of seeds germinated in pile mound soils and
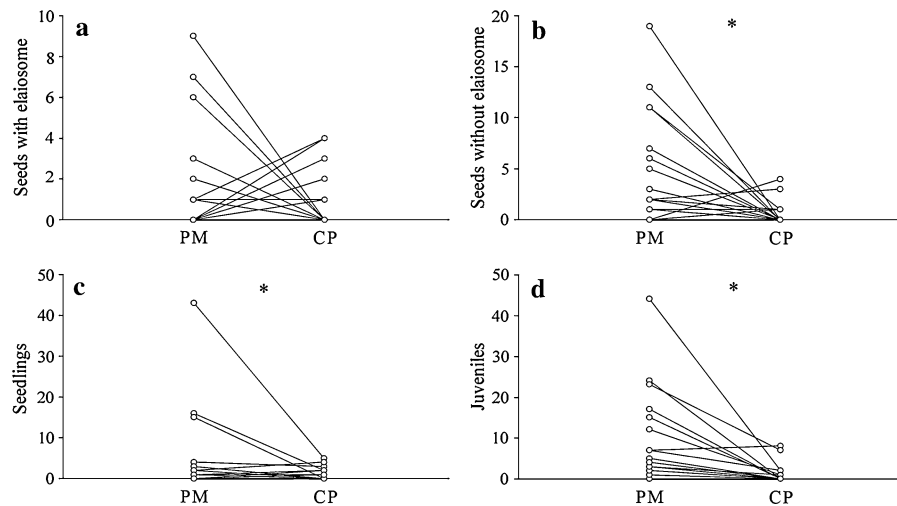
Fig. 1 Contrasts between the number of *Ricinus communis* **a** seeds with elaiosome, **b** seeds without elaiosome, **c** seedlings and **d** juveniles in paired ant nest pile mound plots (PM) and in control plots (CP) within the same experimental pair (*lines*).* $P < 0.05$
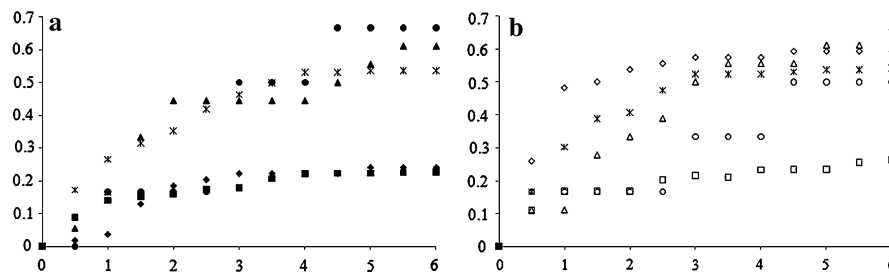
Fig. 2 Proportion of *Ricinus communis* seeds without elaio-some removed from **a** ant nest pile mound plots (*full markers*) and from **b** control plots (*empty markers*) in 12 observations

during 6 weeks. Each symbol represents an initial seed density in the plots: ○ 1, △ 3, ◇ 9, * 27 and □ 81

in control soils ($t = 1.103$, df $= 9$, $P = 0.299$). Juveniles growing in pile mound soils presented lower R/AS (median $= 0.293$, 95% upper limit $= 0.500$, 95% lower limit $= 0.108$) than those growing in control soils (median $= 0.416$, 95% upper limit $= 0.560$, 95% lower limit $= 0.291$) ($Z = 2.240$, $P = 0.025$). The other vigour measurements did not differ among juveniles growing in the plot pairs ($P > 0.05$). Please refer to the electronic appendix to view the biomass data.

Ant protection of seedlings from herbivores

There was no difference in the number of termites attacked by ants in *Ricinus* seedlings growing in pile mound plots and in control plots ($\chi^2 = 0.100$, df $= 1$, $P > 0.999$).

Discussion

As expected, we found higher densities of *Ricinus* post-dispersed seeds, seedlings and juveniles in pile mounds, which are in accordance with the findings for other plant species (e.g. Passos and Oliveira 2002, 2003, 2004). The equal distribution of seeds with elaiosome between pile mounds and their vicinities may be an outcome of the primary ballistic seed dispersal mechanism of the plant.

The removal of *Ricinus* post-dispersed seeds was similar for those deposited in pile mounds and in their surroundings. Therefore, seeds neither gained protection from ants against post-dispersal seed predators nor did they become unavailable for further removal by other dispersal vectors. Since such reallocation was density independent, it may be performed by ants: some authors have shown that they either do not

Table 1 Macro- and micro-nutrient quantities in soils of 10 ant nest pile mound samples and of a control sample (a mix of one non-ant nest soil sample to every ant nest pile mound sample)

| Soil from | Macronutrients | | | | | | | | | | | | | | Micronutrients | | | | | | |
| | pH | Organic matter | P | K | Ca | Mg | H + Al | H | SB[a] | CEC[b] | V | N | Ca/Mg | Mg/K | S | Na | Fe | Mn | Cu | Zn | B |
	CaCl$_2$	g/dm^3	mg/dm^3	mmolc/dm^3							%				mg/dm^3						
Control	6.4	46	54	6.5	100	19	18	16	125.5	143.5	87.4	0.36	5.26	2.92	36	1	29	9.5	3.6	5.3	0.54
Dorymyrmex brunneus	6.4	29	22	6.3	80	19	16	16	105.3	121.3	86.8	0.19	4.21	3.01	16	1	20	11.3	3.8	3.4	0.01
Pheidole gertrudae	6	44	130	5.2	72	15	22	22	92.3	114.3	80.7	0.25	4.8	2.88	14	3	112	5.9	5.7	12.1	0.21
Pheidole gertrudae	6.4	36	140	9.8	100	24	16	16	134.2	150.2	89.3	0.26	4.16	2.44	18	10	48	14.5	5.8	10.5	0.46
Pheidole sp. 1	6.4	29	60	7.6	62	17	15	15	86.7	101.7	85.2	0.2	3.64	2.23	14	3	41	9.1	3.2	4.9	0.27
Pheidole sp. 2	6.3	84	130	9.1	100	19	20	20	128.2	148.2	86.5	0.47	5.26	2.08	22	4	26	11.5	3.6	8.9	0.41
Pheidole sp. 2	5.8	96	90	10.8	100	22	34	34	132.8	166.8	79.6	0.65	4.54	2.03	22	1	69	10.6	2.9	13.3	0.39
Pheidole sp. 2	6.1	44	38	5.2	76	16	20	20	97.2	117.2	82.9	0.28	4.75	3.07	14	1	44	11.1	4.1	6.8	0.16
Solenopsis sp. 1	6.1	30	61	10.3	60	22	20	19	92.4	112.4	82.2	0.22	2.72	2.13	20	3	109	8.2	5.7	4.4	0.04
Solenopsis sp. 1	5.9	27	63	11.8	45	15	20	19	72	92	78.2	0.25	3	1.27	18	5	29	17	3.6	3.5	0.02
Solenopsis sp. 1	7.5	30	50	3.9	95	8	8	8	107.7	115.8	93	0.2	11.87	2.05	22	19	11	5.8	4.8	16.9	0.71

[a] Sum of basis

[b] Cation exchange capacity

respond to fruit and seed density or exploit them at an inverse density-dependent fashion (e.g. Hulme 1997; Mull and MacMahon 1997). Nevertheless, we did not observe a single event of post-dispersed seed removal by ants (or other animals) and we are not aware of any species capable of feeding from *Ricinus* seeds, since they are highly toxic (Windsor 2004). Moreover, stochastic events, such as rain, did not result in seed rearrangement, contrary to examples described in literature (e.g. Hampe 2004). Therefore, the removal agents of *Ricinus* post-dispersed seeds are not yet clear and deserve further investigation. The reallocated seeds that do not suffer predation and the post-dispersed seeds that remain in the site where they were first deposited may either germinate if conditions are satisfactory or be incorporated into soil seed banks.

Myrmicinae ants often feed on seeds and/or their appendages (Hölldobler and Wilson 1990) and the discarded, viable seeds could germinate and benefit from higher nutrient availability in the pile mounds (O'Dowd and Hay 1980; Davidson and Morton 1981; Passos and Oliveira 2002, 2004; Leal et al. 2007). Although our soil collection methods are not usual and do not provide an analysis of the natural variation in soil nutrients present at our study site, they do enable the comparison of individual pile mound soils to an average, non-ant-nest, vicinity soil. In this study, we did not find any evidence of nutrient-enrichment in the pile mounds and so, our results are in agreement with Horvitz and Schemske (1986) and Rice and Westoby (1986). Therefore, there was no additional advantage for seeds discarded in pile mounds: not only did they not gain protection by ants, but they were also not provided with a nutrient-enriched environment. Besides, the higher abundance of post-dispersed seeds in pile mounds than in their vicinities (Fig. 1b) may result in further higher seedling competition.

Seed dispersal and germination, and early seedling growth/survival are the most critical stages in determining where plants recruit within a landscape (Herrera et al. 1994; Schupp 1995). Though we found no specific nutrient characteristics for the soils of pile mounds, ant nests are known to have specific temperature, moisture and texture. Since ant nests present higher moisture and penetrability (Hölldobler and Wilson 1990; Farji-Brener and Medina 2000; Leal et al. 2007), such characteristics may account for the lower roots/aerial system ratio of plants growing

in pile mound soils than in control soils. However, we do not believe that there is such a greater advantage for plants growing in pile mound soils, since we did not observe differences in the number of germinated seeds and only one out of 18 juvenile vigour measurements differed between the two types of soil. Besides, there was no difference in the total dry mass of plants growing in pile mound soils and in control soils, indicating that biomass gain, which is the ultimate importance of a nutrient-enriched soil, was similar independent of where the plant is established.

Ants also did not bring any benefits to seedlings growing in pile mounds with a differential protection against herbivory. This result is contrary to many findings in literature, such as those of Davidson and Epstein (1989) and Passos and Oliveira (2004) for other plant species. In our study sites, ants are abundant and widespread, and are commonly observed visiting *Ricinus* plants, probably because of the presence of extra-floral nectaries (EFNs) on leaf petioles and nerves (V. Martins, 'pers. obs.'). The non-differential patrol of ants regarding the location of the seedlings may be due to such structures, which are active even in the early developmental stages of the species (V. Martins, 'pers. obs.'). Since the same ant species can act as seed disperser and consume extra-floral nectar (Boulay et al. 2005; Cuautle et al. 2005), ants in our study sites may patrol the plants in order to collect this substance and, as a result, attack herbivores as a defence of their resource (as explained by e.g. Beattie 1985 and Beattie and Hughes 2002) anywhere the plant is established. If this is true, we may predict that any plant species whose seedlings grow near ant nests and have active EFNs may not rely as much on directed dispersal as do species which do not have EFNs, at least in the earliest developmental stages. Besides the EFNs, *Ricinus* also has high quantities of toxic compounds (Windsor 2004), and the interaction between this plant and the foraging ants deserves further investigation.

We did not observe *Atta* or other leaf-cutting ants in any of the experiments carried out in this study. Moreover, Martins et al. (2006) demonstrated that leaf-cutting ants rarely interact with *Ricinus* seeds. The establishment of seedlings in cutting-ant nest pile mounds could potentially be negative to the plant, since its great proximity to the nest could result in a higher chance of having its leaves cut by the ants. Therefore, we assumed that the interaction between

ants and *Ricinus* plants in the pile mounds were not negative concerning herbivory in the plants viewpoint.

It is well known that ant species vary greatly in their dispersal behaviour, seed dispersal distance, nutrient enrichment of the nest soil, patrolling and predation of potential herbivores (Hölldobler and Wilson 1990), all of which may result in different outcomes for the plant species they disperse. In this sense, the effects of *Ricinus* seed dispersal may differ according to the disperser ant species. Studies that separately analyze the outcomes of the interaction with each individual species are needed to provide a better understanding of the effects of *Ricinus* seed dispersal by ants.

This study shows that the dispersal of *Ricinus* seeds by ants had a marked effect on the distribution pattern of the seeds, seedlings and juveniles of this species. However, there were no additional advantages for seeds, seedlings and juveniles in pile mounds. In spite of the suggestion that seed dispersal by ants affects recruitment in many species (Passos and Oliveira 2002 and 2004; Leal et al. 2007), we found no evidence to support this hypothesis for *Ricinus*. Therefore, this plant does not benefit from directed dispersal by ants to maintain its populations in the study sites, where it may rely on other characteristics, such as high seed production (Hogan 1992) and germination success in a wide range of conditions (Martins et al. 2006, 2009) to do so. It is probable that *Ricinus* populations from other geographical regions benefit from the interaction with ants. However, large geographical studies of interactions are complicated and this is the first attempt to quantify the outcome of an extremely conspicuous interaction involving a widely distributed plant species.

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