

Interactions between ants, fruits and seeds in a restinga forest in south-eastern Brazil

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Abstract: Fleishy diaspores (fruits, seeds) comprise a large portion of the litter on the floor of tropical forests, and interactions involving litter-foraging ants and diaspores are common in these areas. In this study, the interactions between ants and non-myrmecochorous diaspores (i.e. not adapted to dispersal by ants) were surveyed along a 1.4-km transect in a restinga forest (sandy soil) on the coast of south-eastern Brazil. During 2 y of monthly samplings, 562 interactions involving 48 ant species and 44 species of diaspore (0.02–11.10 g) were recorded. Ant–diaspore associations involved a considerable part of the ground-dwelling ant community. Large ponerine ants individually removed the diaspores up to 13 m, whereas small ants (myrmecines) normally recruited workers and consumed the diaspore on the spot. Ant-derived benefits to diaspores of non-myrmecochorous plants included secondary dispersal (small to medium-sized diaspores), and increased germination success after seed cleaning by ants. Large ponerine ants such as *Odontomachus chelifer* and *Pachycondyla striata* were the main seed vectors. Seedlings of three species were associated with nests of *O. chelifer*. The results indicate that ants play an important role in fruit/seed biology in the restinga forest.

Key Words: ant–fruit/seed interaction, ant–plant interaction, Atlantic forest, fleshy diaspores, seed dispersal

INTRODUCTION

In tropical forests fleshy fruits present a broad range of sizes, shapes, colours and chemical composition of the edible portion (Corlett 1996, Forget & Hammond 2002, van Roosmalen 1985). Diaspores (i.e. any seed, fruit or infructescence that constitutes the unit of dispersal of the plant) can reach the ground spontaneously, dropped by vertebrate frugivores, or in their faeces (Howe 1980, Kaspari 1993, Laman 1996, Leal & Oliveira 1998, Passos & Oliveira 2002, Pizo & Oliveira 1999, 2000). Fallen diaspores constitute a large proportion of the litter on the floor of tropical forests (Denslow & Gomez-Dias 1990, Morellato 1992).

Although the mainstream of studies on seed dispersal of tropical species has focused mostly on fruit consumption and seed deposition patterns generated by vertebrates (Fleming 1986, Wheelwright 1988), recent studies have emphasized the importance of post-dispersal events for the seed fate and demography of plant species in tropical forests (Andresen 1999, Chambers & MacMahon 1994, Levey & Byrne 1993, Passos 2001, Passos & Oliveira 2002, Pizo & Oliveira 1998).

The abundance and diversity of ants in tropical forests are remarkable (Hölldobler & Wilson 1990), and ground-

dwelling ants are perhaps the most likely organisms to encounter diaspores on the forest floor of tropical areas (Kaspari 1993, Pizo & Oliveira, 2000, 2001). Indeed, it has recently been shown that ants interact with a variety of non-myrmecochorous diaspores (i.e. not especially adapted to dispersal by ants). These insects can affect seed fate over a broad range of diaspore sizes, including small (length ≤ 5 mm; Kaspari 1993, Levey & Byrne 1993, Pizo & Oliveira 1999, Roberts & Heithaus 1986), and medium- to large-sized diaspores (≥ 10 mm; Oliveira *et al.* 1995, Pizo & Oliveira 1998, 2001). Moreover, ants can also affect seedling establishment and patterns of recruitment of plant species in tropical ecosystems (Böhning-Gaese *et al.* 1999, Farji-Brener & Silva 1996, Passos & Oliveira 2002).

Despite the growing body of information on the interactions between ants and non-myrmecochorous diaspores (see above), only one study has documented systematically the use of fallen diaspores by the ground-dwelling ant community of a tropical forest (Pizo & Oliveira 2000). Interactions between ants and diaspores are common in lowland forest, involve a diverse assemblage of ants, and may have important consequences for the biology of seeds and seedlings (Pizo & Oliveira 1998, 2000, 2001).

In this paper we document the interactions between ants and diaspores in a restinga forest in south-eastern Brazil.

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Restinga forests are included in the Atlantic forest domain and grow on poor sandy soil along the coast of Brazil (Joly *et al.* 1999, Oliveira-Filho & Fontes 2000). The vegetation is characterized by an open canopy, dominant low-stature trees and abundant epiphytes (Barros *et al.* 1991). We provide a detailed account of the ant fauna exploiting fallen fleshy diaspores, determine the patterns of ant–diaspore interactions, and investigate their possible consequences for seed fate in some plant species. Finally we compare the emerging patterns in restinga forest with those recorded by Pizo & Oliveira (2000) for lowland old-growth forest (*sensu* Clark 1996).

STUDY SITE

Field work was carried out from January 1998 to April 1999 in the restinga forest of the Parque Estadual da Ilha do Cardoso (hereafter PEIC) (25°03'S, 47°53'W), a 22 500-ha island (altitude 0–800 m asl) located on the coast of São Paulo State, south-east Brazil. At PEIC the well-preserved restinga forest consists of 5–15-m tall trees forming an open canopy, and abundant bromeliads on the ground layer (Barros *et al.* 1991). A cold and drier season occurs from April to August when temperature can drop to nearly 13 °C and rainfall is *c.* 500 mm. A warm and rainier season occurs from September to March when temperature reaches 32 °C and rainfall 1800 mm (Funari *et al.* 1987, Oliveira-Filho & Fontes 2000).

METHODS

Surveys of ant–diaspore interactions

Monthly surveys of ant–diaspore interactions were carried out along a 1.4-km transect from May 1998 to April 2000. Fallen diaspores were searched *c.* 2 m off both sides of the trail (07h30–12h30). Each time ants were found exploiting a diaspore (i.e. contacting the surface of the diaspore apparently collecting liquids, or removing portions of it), an interaction was recorded and the ants were collected for identification. Additional data included the number of ants and the diaspore species. Large ponerines are notably abundant in restinga forest and rapidly remove fallen diaspores (Passos 2001), thereby reducing the chances of recording ant–diaspore interactions. In order to overcome this situation and get a considerable number of records, ant–seed interactions were surveyed monthly through systematic sampling of ants at previously distributed diaspores on the forest floor. Most interactions presented in this study were recorded during systematic sampling. We used ripe diaspores collected on the plant or fresh-fallen diaspores collected on the forest floor. Diaspores were placed on small pieces of white filter paper (4 × 4 cm) to facilitate relocation on leaf litter, at intervals of 10 m to maintain independent discoveries by different

colonies (Byrne & Levey 1993, Kaspari 1993, 1996). Diaspores were set out at 07h30 and 15h00 and checked at 15-min intervals (scan sampling *sensu* Lehner 1979) for 2 h. Vertebrate disturbance was avoided by covering the diaspores with wire cages (25 × 25 × 8 cm, 1.5 cm mesh) closed on the top and staked to the ground (see Kaspari 1993, Roberts & Heithaus 1986).

Sampling ants with baits

We compared the ant community attracted to diaspores with the generalized omnivore community attracted to honey and tuna baits (Pizo & Oliveira 2000). In March 1999, we placed 100 tuna and 100 honey baits distributed 5 m apart along transects established 1–2 m off-trail. Small pieces of white filter paper (4 × 4 cm) were used as substrates for baits to facilitate ant visualization (Pizo & Oliveira 2000). Baits were set out along the transects at 08h00 and number and identity of attracted ants were recorded after 1 h. Voucher specimens of the ants and plants are deposited in the collection of Universidade Federal Rural do Rio de Janeiro (CECL) and at the herbarium of the Universidade Estadual de Campinas (UEC), respectively. We used Spearman's rank correlation to test if the use of fallen diaspores by ants occurred according to their relative frequency on the forest floor.

Ant effects on seeds and seedlings

In order to determine the effects of ants on seed fate, removal-rate experiments and germination tests were performed with eight species typical of the restinga forest (see Tables 3 and 4): *Alchornea triplinervia* (Spreng.) Müll. Arg. (Euphorbiaceae), *Ilex theezans* Mart. (Aquifoliaceae), *Myrcia bicarinata* (O. Berg) D. Legrand and *M. rostrata* DC. (Myrtaceae), *Ocotea pulchella* Mart. (Lauraceae), *Schinus terebinthifolius* Raddi (Anacardiaceae), *Siphoneugenia guilfoyleiana* C. Proença (Myrtaceae), and *Ternstroemia brasiliensis* Cambess. (Theaceae). Diaspore removal by ants was assessed by performing an enclosure experiment. Two marked diaspores (small dot of enamel paint, Testors, Rockford, USA) were set out *c.* 06h00 or 18h00 at baiting stations placed on the forest floor at 10-m intervals along transects established 1–2 m off-trail (*n* = 60 diaspores for each species). Ant response to marked and unmarked diaspores was apparently the same. The diaspores were placed on small pieces (4 × 4 cm) of white filter paper to facilitate visualization on leaf litter, protected from vertebrate disturbance by wire cages. Diaspore removal was recorded after 12 h, and a given diaspore was considered removed if not found within a 30-cm radius around the cage. We abandoned every trial subjected to rains. Data are expressed as the mean percentage of diaspores removed per station.

The effect of cleaning activity on seed germination was

evaluated through germination tests in the greenhouses of the Universidade Estadual de Campinas. Seeds were set into two categories for the tests: (1) seeds coated with a pulp or aril (diaspore not manipulated by the ants); (2) cleaned seeds (fruit pulp or aril removed by us). Germination tests in the greenhouse followed the same procedure for all plant species. Seeds in each category were placed in separate plastic boxes (40 × 40 cm) containing vermiculite and kept in partial sun. Germination boxes were watered regularly. Seeds were buried 1 cm into the substrate, 3 cm apart from each other, and checked for radicle protrusion at 1-wk intervals until all the seeds had germinated or presented signs of decay (fungal infection). We used chi-square tests to evaluate the effects of cleaning activity on seed germination.

Ponerine ants are the main seed vectors on the floor of neotropical forests (Horvitz 1981, Horvitz & Beattie 1980, Passos & Oliveira 2002, Pizo & Oliveira 1998). *Odontomachus chelifer* is a key species exploiting fleshy diaspores at PEIC, since it accounted for a significant number of ant-seed interactions recorded at the study site and regularly removed diaspores to the nest. The effect of ponerines on plant recruitment (i.e. seedling and juvenile distributions) was determined by censusing recruits growing in *O. chelifer* nests and in control plots without nests. The number of seedlings and juveniles (up to 10 cm high) growing on nests of *Odontomachus chelifer* as compared with control areas was determined in May 2000 by establishing paired experimental plots (0.5 × 0.5 m). Nests were located by following ant workers attracted to tuna baits placed on the forest floor (Horvitz 1981). We tagged 40 nests of *Odontomachus*, and established a control plot 2.5 m (random direction) from each nest. Differences in the number of seedlings and juveniles growing in treatment and control plots were analysed with Wilcoxon paired-sample signed-rank tests. Tests were performed only for plant species represented by abundant seedlings and juveniles on the forest floor.

RESULTS

Patterns of ant–diaspore interactions

We recorded a total of 562 ant–diaspore interactions in the monthly samplings during the 2-y study. Forty-eight ant species (19 genera, four subfamilies) and 44 plant species (40 genera, 26 families) were involved in these interactions (Tables 1 and 2). The Myrmicinae were the most frequently recorded ant subfamily (36 species), and accounted for 327 interactions (58.2%), while the Ponerinae with only five species were responsible for 217 interactions (38.6%). The subfamilies Formicinae (five species), Dolichoderinae and Dorylinae (one species each) together accounted for the remaining 3.2% of the records. The large ponerines *Pachycondyla striata* and *Odontom-*

achus chelifer are very abundant at the study site (Table 1), and were attracted to 31% and 23% of the tuna, and 19% and 22% of the honey baits, respectively. The two species together accounted for 35% of the ant–diaspore interactions recorded (197 out of 562; see Table 1). In general, these large ponerines individually removed diaspores (small- or medium-sized) distances up to 13 m. Large diaspores were usually exploited on the spot, but those bearing small seeds such as *Psidium* had their seeds removed by ponerines or large attines (*Acromyrmex*) to the nests. The small myrmicines *Crematogaster* sp. 1, *Pheidole* sp. 1, *Pheidole* sp. 3 and *Solenopsis* sp. 1 were also abundant at the study area, and exploited many different species of diaspore (Table 1). In general, small- and medium-sized ants (such as these myrmicines) recruited workers and fed on the diaspore on the spot, although small diaspores were occasionally transported. Ants were recorded on diaspores in a ripe or pre-ripe condition, and the number of workers ranged from 1 to 110. The number of interactions recorded for each non-attine ant species was highly correlated with their frequencies on tuna and honey baits (Spearman's rank correlation, $r_s = 0.60$, $n = 18$, $P = 0.01$), indicating that the use of fallen diaspores by ants occurred according to their relative abundance on the forest floor. All but four ant species attracted to baits were also recorded on diaspores, while 30 of the species recorded on diaspores were not recorded at baits.

Ants exploited diaspores of trees (34 species), shrubs (three species), herbs (three species), epiphytes (two species), lianas and parasites (one species each) (Table 2). Myrtaceae are the dominant plant family at the study site (Sugiyama 1993) and were the family with the largest number of species (eight) whose diaspores were exploited by ants (Table 2). Ants usually exploited the pulp or aril of the diaspore, but were occasionally observed digging into the endosperm of seeds of some species (e.g. *Ternstroemia brasiliensis*). Diaspores varied greatly in size, ranging from 0.02 g (*Pera glabrata* and *Schinus terebinthifolius*) to 11.1 g (*Psidium cattleianum*), but most of the diaspores exploited by the ants were small- to medium-sized, and only 13.6% were large. Although the aim of the study was to investigate the ant–seed interactions occurring on the forest floor, interactions involving *Crematogaster* spp. and diaspores of the epiphytic *Codonanthe devosiana* and *Aechmea nudicaulis* on tree trunks were also registered. These ants pierced the fruits and recruited nestmates that took the tiny arillate seeds to their arboreal nests.

The experiments performed showed that ants rapidly removed the diaspores of most species during both day and night periods, but some less-attractive species (e.g. *Ilex theezans*, *Myrcia bicarinata*, *Schinus terebinthifolius*) presented low removal rates (Table 3).

Table 1. Ant species recorded exploiting fallen diaspores, and tuna and honey baits, on the floor of the restinga forest at Cardoso Island, SE Brazil.

Ant subfamily and species	No. of diaspore species used (no. of records on diaspores)	Records on baits (%)	
		Honey (n = 100)	Tuna (n = 100)
Ponerinae			
1. <i>Gnamptogenys moelleri</i> (Forel)	8 (14)	10	5
2. <i>Hypoponera</i> sp.	1 (1)	–	–
3. <i>Odontomachus chelifer</i> (Latr.)	20 (51)	22	23
4. <i>Odontomachus</i> sp.	5 (5)	6	8
5. <i>Pachycondyla striata</i> Fr. Smith	35 (146)	19	31
Myrmicinae			
6. <i>Cephalotes pusillus</i> (Klug)	1 (1)	–	–
7. <i>Crematogaster</i> sp. 1	17 (45)	14	38
8. <i>Crematogaster</i> sp. 2	3 (5)	–	–
9. <i>Crematogaster</i> sp. 3	2 (5)	–	–
10. <i>Hylomyrma</i> sp.	–	1	–
11. <i>Octostruma</i> sp.	1 (1)	–	–
12. <i>Oligomyrmex</i> sp.	1 (1)	–	–
13. <i>Pheidole</i> sp. 1	26 (58)	29	25
14. <i>Pheidole</i> sp. 2	2 (2)	–	–
15. <i>Pheidole</i> sp. 3	17 (33)	45	49
16. <i>Pheidole</i> sp. 4	3 (5)	–	–
17. <i>Pheidole</i> sp. 5	11 (19)	–	–
18. <i>Pheidole</i> sp. 6	2 (2)	–	–
19. <i>Pheidole</i> sp. 7	1 (1)	–	–
20. <i>Pheidole</i> sp. 8	1 (1)	–	–
21. <i>Pheidole</i> sp. 9	1 (1)	–	–
22. <i>Pheidole</i> sp. 10	1 (2)	–	–
23. <i>Pheidole</i> sp. 11	1 (1)	–	–
24. <i>Solenopsis</i> sp. 1	15 (34)	8	5
25. <i>Solenopsis</i> sp. 2	3 (3)	–	–
26. <i>Solenopsis</i> sp. 3	9 (15)	2	3
27. <i>Solenopsis</i> sp. 4	2 (3)	–	–
28. <i>Solenopsis</i> sp. 5	1 (1)	–	–
29. <i>Solenopsis</i> sp. 6	1 (1)	–	–
30. <i>Solenopsis</i> sp. 7	1 (1)	–	–
31. <i>Solenopsis</i> sp. 8	3 (3)	–	–
32. <i>Solenopsis</i> sp. 9	3 (8)	–	–
33. <i>Strumigenys</i> sp.	3 (3)	2	–
34. <i>Wasmania</i> sp. 1	3 (4)	–	–
Myrmicinae (Attini)			
35. <i>Acromyrmex aspersus</i> (Fr. Smith)	13 (24)	3	–
36. <i>A. coronatus</i> (Fabr.)	2 (5)	–	–
37. <i>A. crassipinus</i> Forel	5 (7)	2	–
38. <i>A. disciger</i> Mayr	1 (2)	–	–
39. <i>A. subterraneus</i> Forel	13 (26)	3	1
40. <i>Acromyrmex</i> sp. 1	1 (1)	–	–
41. <i>Acromyrmex</i> sp. 2	1 (1)	–	–
42. <i>Apterostigma</i> sp.	–	1	–
43. <i>Cyphomyrmex</i> sp.	1 (2)	–	–
44. <i>Trachymyrmex</i> sp.	–	1	–
Dolichoderinae			
45. <i>Linepithema</i> sp.	2 (2)	1	–
Ecitoninae			
46. <i>Labidus</i> sp.	1 (2)	1	–
Formicinae			
47. <i>Brachymyrmex</i> sp.	1 (1)	3	–
48. <i>Camponotus</i> sp.	2 (2)	3	4
49. <i>Paratrechina</i> sp. 1	5 (6)	3	3
50. <i>Paratrechina</i> sp. 2	4 (4)	–	–
51. <i>Paratrechina</i> sp. 3	1 (1)	–	–
Pseudomyrmecinae			
52. <i>Pseudomyrmex</i> sp.	–	–	1
Total no. of diaspore species used	44		
Total no. of ant–diaspore interactions	562		

Table 2. Plant diaspores exploited by ants on the floor of the restinga forest at Cardoso Island, SE Brazil. Data were gathered during monthly surveys (along 1.4-km transect) of fallen diaspores being used by ants on the forest floor, as well as of fresh diaspores placed on the ground. Plant species and families are arranged in alphabetical order. Key to codes of growth forms: T = tree, S = shrub, B = herb, L = liana, E = epiphyte, H = hemi-epiphyte. Ant species numbers as in Table 1.

Plant family and species	Growth form	Diaspore length × width (mm)	Diaspore fresh weight (g)	Months	Ant species
Anacardiaceae	T	5.7 × 5.7	0.02	May–Jun	3, 5
<i>Schinus terebinthifolius</i> Raddi					
<i>Tapirira guianensis</i> Aubl.	T	14.4 × 11.1	0.5	Feb–Apr	2, 3, 5, 7, 13, 32, 35, 39, 48
Annonaceae					
<i>Guatteria australis</i> A. St.–Hil.	T	10.8 × 7.0	0.3	Nov–Dec	13, 15
<i>Xylopia langsdorfiana</i> St. Hilaire & Tulasne	T	10.0 × 7.1	0.2	Sep–Feb	2, 3, 5, 7, 12, 15, 17, 24, 26, 34
Aquifoliaceae					
<i>Ilex integerrima</i> Reissek	T	6.6 × 6.4	0.1	Apr–Jul	3, 5, 7, 13, 15, 39
<i>I. theezans</i> Mart.	T	5.1 × 5.7	0.1	Apr–Jul	5, 13, 15, 17, 35
Araceae					
<i>Anthurium</i> sp.	B	5.1 × 5.1	0.1	May–Jun	3, 5, 7, 23
Araliaceae					
<i>Didymopanax</i> cf. <i>angustissimum</i> March.	T	7.5 × 8.6	0.2	Apr–Aug	5, 24, 37
Areaceae					
<i>Euterpe edulis</i> Mart.	T	14.3 × 14.0	1.9	Apr–Jul	5, 24, 25, 31
<i>Geonoma schottiana</i> Mart.	T	10.2 × 9.2	0.5	Feb–Jul, Nov	5, 13, 24, 39
<i>Syagrus romanzoffiana</i> (Cham.) Glassm.	T	22.0 × 15.7	3.8	Apr	5, 17, 26, 49
Bromeliaceae					
<i>Aechmea nudicaulis</i> (L.) Griseb.	E	15.6 × 7.7	0.3	Nov–Mar	2–5, 7–9, 13, 15, 33, 35, 39, 41, 45, 48, 49
Cecropiaceae					
<i>Cecropia pachystachya</i> Trécul	T	–	–	Feb, May, Dec	2–5, 7, 13, 17, 49, 50
Celastraceae					
<i>Maytenus robusta</i> Reissek	T	10.7 × 10.1	0.4	May–Jul	5, 13, 15, 24, 26
Clusiaceae					
<i>Calophyllum brasiliense</i> Cambess.	T	27.2 × 24.6	9.14	Oct	13, 29, 51
<i>Clusia criuva</i> Cambess.	T	9.8 × 5.5	0.1	Dec–Mar	1, 3–7, 13–15, 17, 22, 24, 26–28, 34, 35, 37, 39, 40, 46, 50
Dilleniaceae					
<i>Dolioscarpus</i> cf. <i>glomeratus</i> Eichler	L	6.2 × 7.1	0.1	Jun–Jul	5, 13
Ericaceae					
<i>Gaylussacia brasiliensis</i> (Spreng.) Meisn.	S	7.1 × 7.1	0.2	Jan, Feb, Oct	5, 13, 35, 39
Erythroxylaceae					
<i>Erythroxylum amplifolium</i> (Mart.) O. E. Schulz	T	8.0 × 5.0	0.1	Jan	3, 13, 35, 37, 39
Euphorbiaceae					
<i>Alchornea triplinervia</i> (Spreng.) Müll. Arg.	T	6.3 × 6.3	0.1	Feb–Mar	3, 5, 7, 13, 15, 24, 26, 35
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	T	7.1 × 3.6	0.02	May	2, 5, 13, 15
Fabaceae					
<i>Andira fraxinifolia</i> Benth.	T	36.2 × 26.4	9.1	Jul	24
Gesneriaceae					
<i>Codonanthe devosiana</i> Lem.	E	10.0 × 8.7	0.4	Nov–Mar	3, 5, 7, 8, 13, 15, 18, 45
Lauraceae					
<i>Ocotea pulchella</i> Mart.	T	8.4 × 5.2	0.1	Sep–Mar	2–5, 7, 13–17, 19, 26, 30, 35, 37, 39
Malpighiaceae					
<i>Byrsonima ligustrifolia</i> St. Hilaire	T	10.1 × 12.3	0.9	Mar–Apr	5, 13, 24, 37
Melastomataceae					
<i>Miconia</i> sp.	T	4.8 × 6.3	0.1	Jun–Oct	5
Myrtaceae					
<i>Blepharocalyx salicifolius</i> (Knuth) O. Berg	T	5.8 × 6.9	0.1	Apr–May	5, 13, 24
<i>Eugenia uniflora</i> L.	T			Jan–Mar	3, 9, 17, 36
<i>Gomidesia</i> cf. <i>affinis</i> (Cambess.) D. Legrand	T	6.0 × 8.5	0.3	Jun	13
<i>G. fenliana</i> O. Berg	T	6.9 × 9.0	0.3	May–Jul	13, 17, 35

Table 2. Continued.

Plant family and species	Growth form	Diaspore length × width (mm)	Diaspore fresh weight (g)	Months	Ant species
<i>Myrcia bicarinata</i> (O. Berg) D. Legrand	T	7.8 × 8.3	0.3	May–Jul	5, 13, 15, 24, 26
<i>M. rostrata</i> DC.	T	9.3 × 7.1	0.3	Jan–Feb	3, 5, 7, 13, 15, 35, 49, 50
<i>Psidium cattleyanum</i> Sabine	T	26.0 × 25.3	11.1	Feb–May	2, 3, 5, 7, 13, 17, 24, 35, 39, 47, 50
<i>Siphoneugenia guilfoyleana</i> C. Proença	T	9.5 × 9.5	0.5	Nov–Dec	2, 3, 5, 11, 13, 15, 16, 18, 27, 39
Nyctaginaceae					
<i>Guapira opposita</i> (Vell.) Reitz	T	8.0 × 7.1	0.3	Jan–May	3–5, 7, 13, 15, 33, 35, 39
Rubiaceae					
<i>Coccocypselum</i> cf. <i>capitatum</i> Willd. ex DC.	B	7.6 × 8.5	0.1		3, 5
<i>Coccocypselum</i> sp.	B	13.9 × 9.2	0.3		7
<i>Psychotria</i> cf. <i>pubigera</i> Schldtl.	S	6.7 × 8.3	0.2	Mar, Apr, Oct	3, 5, 7, 24, 36
<i>Rudgea villiflora</i> Schumm. ex Standl.	S	11.7 × 11.9	0.7	Feb–Apr	5, 15, 24
Sapotaceae					
<i>Chrysophyllum</i> sp.	T	26.5 × 22.0	6.0	Nov–Jan	7, 8, 17, 21, 24, 26, 31–33, 38, 43, 49
Undetermined 1	T	28.7 × 25.0	8.9	Jan	3, 5, 7, 8, 13, 17, 24, 26, 31, 32, 39
Theaceae					
<i>Ternstroemia brasiliensis</i> Cambess.	T	6.3 × 3.8	0.05	Apr–Jun	5, 13, 15–17, 20, 24–26, 31, 34, 35
Verbenaceae					
<i>Aegiphila</i> sp.	T	10.7 × 8.0	0.8		13
Viscaceae					
<i>Phoradendron crassifolium</i> (Pohl ex DC.) Eichler	H	4.0 × 4.0	0.05	Feb–Apr	5, 39

Germination

Pulp or aril removal significantly increased germination success in seven out of eight species. Greenhouse conditions apparently were not adequate for germination of *Ilex theezans* (Table 4).

Distribution of seedlings and juveniles

At the beginning of the dry season (May 2000) at the study site, seedlings and juveniles of three out of seven species were more abundant in nests of *Odontomachus chelifer* than in areas without nests (Table 5).

Table 3. Removal rates of diaspores by ants on the floor of the restinga forest at Cardoso Island, SE Brazil. Marked diaspores were set out at 06h00 (day) and at 18h00 (night) at baiting stations on the forest floor, protected by wire cages. Thirty diaspores were set in each period. Diaspore removal was recorded after 12 h. See text for further details.

Plant species	Removal rates (%)	
	Day	Night
1. <i>Alchornea triplinervia</i>	93	87
2. <i>Ilex theezans</i>	17	10
3. <i>Myrcia bicarinata</i>	0	3
4. <i>M. rostrata</i>	33	60
5. <i>Ocotea pulchella</i>	90	87
6. <i>Schinus terebinthifolius</i>	27	27
7. <i>Siphoneugenia guilfoyleana</i>	63	60
8. <i>Ternstroemia brasiliensis</i>	67	13

DISCUSSION

A diverse assemblage of ants is known to exploit diaspores on a regular basis (Hölldobler & Wilson 1990, Rico-Gray 1993, Rico-Gray *et al.* 1998). In neotropical forests this assemblage includes species in the subfamilies Ponerinae, Formicinae and especially Myrmicinae (Horvitz & Beattie 1980, Kaspari 1996, Pizo & Oliveira 1998, 2000, 2001). The ant–diaspore associations at PEIC involved a considerable part of the ground-dwelling ant community, and were generalized and facultative (each plant species was visited by many ant species, as ant species exploited diverse diaspores; see also Pizo & Oliveira 2000).

The size of non-myrmecochorous diaspores is a key factor for their dispersal by ants (Pizo & Oliveira 2001). Indeed, diaspore size determines which ants are physically able to lift and carry a diaspore, which may affect seed fate since different behaviours may have relevant effects on seed survival, distribution, chance of germination, and establishment (Hughes & Westoby 1992a, b).

The categories of ant behaviour toward the diaspores at PEIC were similar to those found for interactions in other tropical forests (Horvitz 1981, Horvitz & Beattie 1980, Passos & Oliveira 2002, Pizo & Oliveira 1998). Small myrmicine ants (e.g. *Pheidole*, *Solenopsis*) recruited many nestmates to diaspores and consumed the pulp or aril on the spot. After the cleaning activity by such ants, seeds may meet different fates depending on their sizes.

Table 4. Greenhouse germination tests of seeds cleaned by the authors (treatment group) and seeds coated by a pulp or aril (control group). See text for further details.

Plant species (n for treatment and control)	Germination success (%)		Significance (P) (χ^2 tests)
	Treatment	Control	
1. <i>Alchornea triplinervia</i> (n = 40)	75.0	22.5	< 0.001
2. <i>Ilex theezans</i> (n = 30)	10.0	0	ns
3. <i>Myrcia bicarinata</i> (n = 50)	100.0	38.0	< 0.001
4. <i>Myrcia rostrata</i> (n = 35)	97.1	45.7	< 0.001
5. <i>Ocotea pulchella</i> (n = 70)	98.6	2.9	< 0.001
6. <i>Schinus terebinthifolius</i> (n = 30)	100.0	16.7	< 0.001
7. <i>Siphoneugenia guilfoyleiana</i> (n = 40)	97.5	17.5	< 0.001
8. <i>Ternstroemia brasiliensis</i> (n = 32)	96.9	50.0	< 0.001

ns, not significant

Table 5. Distribution of seedlings and juveniles of plant species in nests of *Odontomachus chelifer* (n = 40) and in random spots (n = 40), on the floor of the restinga forest at Cardoso Island, SE Brazil.

Plant species	Mean no. of seedlings and juveniles		Z	Wilcoxon's P
	Nests	Control		
1. <i>Anthurium</i> sp.	3.30	1.48	-2.85	0.004
2. <i>Gomidesia feniziana</i>	1.15	0.93	-0.52	0.604
3. <i>Myrcia bicarinata</i>	0.53	0.43	-1.12	0.264
4. <i>Myrcia rostrata</i>	2.95	0.78	-3.49	0.000
5. <i>Ocotea pulchella</i>	1.70	1.48	-0.59	0.555
6. <i>Psidium cattleianum</i>	1.00	0.05	-2.49	0.013
7. <i>Siphoneugenia guilfoyleiana</i>	0.48	0.10	-1.47	0.142

Medium to large seeds remain on the spot, and the removal of the pulp or aril itself may reduce fungal attack and increase germination success in some species, as shown by germination tests performed in this study and in other areas (Horvitz 1981, Leal & Oliveira 1998, Oliveira *et al.* 1995, Pizo & Oliveira 1998). On the other hand, some myrmicine ants (e.g. *Pheidole*; Moutinho 1991) are granivores, and after cleaning small seeds these ants can remove them (Passos & Oliveira 2002). Although most retrieved seeds are killed by myrmicines, seed harvesting is not necessarily equivalent to seed predation, and ants may significantly benefit some seeds (see Levey & Byrne 1993).

This study reinforces the idea that ponerines (especially *Odontomachus* and *Pachycondyla*) have an important role as seed vectors on the floor of tropical forests (Horvitz & Beattie 1980, Passos & Oliveira 2002, Pizo & Oliveira 1998, 2001). Although large attines (*Atta*, *Acromyrmex*) apparently are not important seed vectors in the Atlantic coastal forests (Passos & Oliveira 2002, Pizo & Oliveira 2000, 2001), they may affect seed biology in other tropical forests (Dalling & Wirth 1999, Farji-Brener & Medina 2000, Moutinho 1998) and savannas (Farji-Brener & Silva 1996, Leal & Oliveira 1998, 2000).

Recent studies have shown that secondary dispersal by invertebrates in tropical forests may benefit seeds by providing a suitable site for germination or establishment (Passos 2001, Passos & Oliveira 2002), or remove seeds from zones of high predation risk (Andresen 1999, Pizo &

Oliveira 1998). Our experiments in restinga forest revealed that ants rapidly removed diaspores of some non-myrmecochorous species, and support the view that seeds of small to medium-sized diaspores may benefit from secondary seed dispersal by ants (Pizo & Oliveira 2001).

Another crucial factor determining seed fate of non-myrmecochorous diaspores is the chemical composition of the edible portion. Chemicals mediate the behaviour of ants toward potential food items (Wilson 1971). Lipids are regarded as the major attractant factor in the interaction between ants and non-myrmecochorous diaspores (Pizo & Oliveira 2001), and protein content is also an important factor in the selection of fruits for a variety of ants, particularly ponerines (Passos 2001). Our results and other studies in neotropical forests support the view that lipid-rich (*Alchornea*, *Cabralea*, *Calathea*, *Clusia*, *Ocotea*), and protein-rich (*Guapira*) diaspores do attract a variety of ants, especially ponerines (Horvitz 1981, Passos & Oliveira 2002, Pizo & Oliveira 1998, 2000). Moreover, the study at PEIC also showed that species bearing carbohydrate-rich fruits such as *Myrcia rostrata* (carbohydrates 78% of pulp content; M. A. Pizo, unpubl. data), and *Psidium cattleianum* (carbohydrates 91% of pulp content; Pizo 2002) can be highly attractive to ants as well, including large ponerines (Tables 2 and 5).

It has recently been shown that ants can markedly affect the distribution of seedlings of primarily bird-dispersed species (Böhning-Gaese *et al.* 1999, Passos & Oliveira 2002). Although some species present special features for

dispersal systems involving both vertebrates and ants (Davidson 1988, Kaufmann *et al.* 1991), the lack of structures for ant-dispersal does not preclude secondary removal of seeds. Our results further indicate that seedlings of three species were significantly associated with nests of *Odontomachus chelifer* at PEIC. Such a spatial association is analogous to epiphyte ant-gardens in which the plants grow principally on arboreal ant nests. The epiphytes benefit from seed dispersal, mineral provisioning and protection by ants (Davidson 1988, Orivel & Dejean 1998). Nests of *O. chelifer* are rich in P, K and Ca, and the ants also increase soil penetrability, that might improve seedling performance (Passos 2001). Moreover, the association of seedlings with *O. chelifer* nests potentially provides some protection against herbivores for the plants (Passos 2001).

The current study in restinga forest, and that of Pizo & Oliveira (2000) in lowland Atlantic rain forest, showed that ants in tropical forests exploit a broad range of diaspores with different sizes and chemical characteristics (44 plant species at PEIC; 56 plant species in lowland forest). Interactions between ants and fallen diaspores are more common in the lowland (886 cases; Pizo & Oliveira 2000) than in the restinga forest of PEIC (562 cases; this study). Data obtained using honey baits indicated that the main seed vectors *Odontomachus chelifer* and *Pachycondyla striata* are markedly more abundant at PEIC (22% and 19% of records) than in the lowland forest (4% and 6% of records, respectively; M. A. Pizo, unpubl. data). *Odontomachus chelifer* and *P. striata* were apparently more selective towards diaspores in the lowland forest than in the restinga forest. In lowland forest these two ants exploited 13 and 21 diaspore species, representing respectively 23% and 38% of all plant species used by ants in the study area (56 species; Pizo & Oliveira 2000). In contrast, in the restinga forest *O. chelifer* and *P. striata* utilized 20 and 35 diaspore species, accounting respectively for 45% and 80% of all plant species used by ants at PEIC (44 species; Table 1). Ponerine ants feed predominantly on arthropod prey and use seed arils or fruit pulp as a secondary food source (Dejean & Lachaud 1994, Fourcassié & Oliveira 2002, Horvitz & Beattie 1980, Pizo & Oliveira 1998). The tendency towards a more frugivorous diet in *O. chelifer* and *P. striata* at PEIC is possibly related with a lower biomass of arthropod prey associated with a thinner and drier leaf litter in the restinga forest than in the lowland forest (see Levings 1983, Levings & Windsor 1984, for a discussion on litter arthropod distribution). Thus ants can shift to alternative food items, and the distribution of food resources in size, time, space and quality are among the principal ecological determinants of ant foraging strategies (Dejean & Lachaud 1994, Traniello 1989). Future work in Brazilian coastal forests will investigate spatial variation in the relative importance of arthropod prey vs. fleshy diaspores within the diet of

ponerine ants of particular interest (*Odontomachus* and *Pachycondyla*), taking into account the availability of alternate food resources across different areas. This approach should clarify the factors underlying ant-fruit/seed interactions in tropical forests, and also cast further light on the dispersal ecology of tropical plants.

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