

INTERACTION BETWEEN ANTS AND SEEDS OF A NONMYRMECOCHOROUS NEOTROPICAL TREE, *CABRALEA CANJERANA* (MELIACEAE), IN THE ATLANTIC FOREST OF SOUTHEAST BRAZIL¹

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On the forest floor of two Atlantic forest sites in southeast Brazil, we recorded 26 ant species (12 genera) interacting with the seeds of *Cabralea canjerana* (Meliaceae), a typical ornithochorous tree whose seeds are covered by a lipid-rich aril. The ants treat the arillate seeds in three different ways: (1) the large ponerine ants *Pachycondyla striata* and *Odontomachus chelifer* individually remove the seeds to their nests, (2) many species (*Pheidole* spp.) recruit workers to remove the aril on the spot, or (3) *Solenopsis* spp. recruit nestmates and cover the seeds with soil before removing the aril on the spot. The ants remove the aril exceptionally rapidly, and removal greatly facilitates seed germination. Seed predation by insects below fruiting trees is severe, and field experiments using vertebrate exclosures showed that rodents also prey heavily upon seeds found near parent trees. Ponerine ants actively remove seeds from this predation-prone zone. By removing bird-manipulated and naturally fallen seeds, ants can play a key role in the fate of medium-sized seeds like those of *C. canjerana*.

Key words: ant–plant interaction; Atlantic forest; *Cabralea canjerana*; Meliaceae; seed dispersal; seed predation.

Most studies on ant–seed interactions have focused on seed dispersal of typical myrmecochorous plants whose elaiosome-bearing seeds are especially attractive for ants (Beattie, 1985). Tropical forests, however, produce a huge number of fleshy fruits per unit area (Jordano, 1993), and a considerable portion of these may reach the forest floor either spontaneously, or be dropped by vertebrate frugivores (Howe, 1980). In such habitats ant abundance may exceed 8 million individuals per hectare of soil (Hölldobler and Wilson, 1990), comprising nearly one-third of the entire insect biomass (Fittkau and Klinge, 1973; Stork, 1988). Given that seed rain is estimated as 49 seeds·m⁻²·mo⁻¹ in neotropical forests (Denslow and Gomez-Diaz, 1990), and that ants include a broad array of plant material in their diets (Rico-Gray, 1993; Tobin, 1994), these insects are perhaps the most likely organisms to encounter plant diaspores on the forest floor of tropical areas. Therefore, it is surprising that the interactions between ants and seeds from nonmyrmecochorous plants still remain largely unexplored by tropical biologists.

Nearly 90% of shrubs and trees in neotropical forests may depend on vertebrate frugivores for seed dispersal (Frankie, Baker, and Opler, 1974). Recently, however, several authors have shown that ants may markedly affect the postdispersal fates of seeds of nonmyrmecochorous plants in such habitats (Lu and Mesler, 1981; Byrne and

Levey, 1993; Kaspari, 1993; Levey and Byrne, 1993). Through the removal of seeds dropped by primary seed dispersers, ants can alter the original seed shadow produced by such organisms (Roberts and Heithaus, 1986; Kaufmann et al., 1991), and eventually promote seed establishment (Levey and Byrne, 1993). Even fungus-growing ants (Attini), traditionally regarded as plant pests, have recently been recorded facilitating seed germination in the mammal-dispersed tree *Hymenaea courbaril* (Caesalpiniaceae) by removing fruit matter from the surface of the seeds and precluding fungi infestation (Oliveira et al., 1995).

In this paper we investigate the interactions between ants and arillate seeds of a neotropical ornithochorous tree, *Cabralea canjerana* (Mart.) Vell. (Meliaceae), in a humid forest in southeast Brazil. We were especially interested in: (1) determining the ant species that use *C. canjerana* seeds on the forest floor, (2) describing the manner that ants treat these seeds, and (3) evaluating ant effects on seed germination. The study involves both detailed descriptions of ant–seed interactions, as well as field experiments using caged seeds to differentiate seed removal by ants and rodents.

Study sites and the plant species—The study was carried out in two sites located in the Parque Estadual Intervales (hereafter PEI) (24°16' S, 48°25' W), a 49 000-ha reserve located at the Serra de Paranapiacaba mountains of São Paulo State, southeast Brazil. The study sites, Carmo and Saibadela, were located at an altitude of 700 and 100 m, respectively. At both sites the vegetation consists of a primary forest with trees up to 30 m tall, and patches of secondary growth vegetation near human settlements. Extensive areas of pristine forest surround the study sites. The study was conducted from October to December of 1993 and 1995 at Carmo and Saibadela, respectively. Climate is generally wet, with rain or fog occurring frequently. Mean annual temperature during the

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study was 17.6°C at Carmo and 23.6°C at Saibadela. Annual precipitation is ~1600 mm at Carmo, and 4000 mm at Saibadela, with a dry-cold season from April to August, and a wet-hot season from September to March.

Cabralea canjerana is a dioecious tree with a widespread distribution in the neotropics, extending from Costa Rica to southern Brazil and northern Argentina (Pennington, 1981). According to Pennington (1981), it inhabits mainly nonflooded evergreen lowland or lower montane rain forests, being especially common in southeast Brazil. Mature fruits occur from September to January, peaking in November–December, and seeds are dispersed by a diverse assemblage of bird species, which, however, drop hundreds of intact or partially eaten (bits of aril attached) diaspores beneath the parent plants (Pizo, in press). Many seeds also fall spontaneously from fruiting trees of *C. canjerana*. Both bird-manipulated and naturally fallen seeds are heavily attacked by nitidulid and curculionid beetles beneath the canopy of fruiting trees (Pizo, in press). Fruits are globose capsules (mean \pm 1 SD = 36.5 \pm 4.5 mm length, 36.4 \pm 4.0 mm wide; N = 90) that dehisce to expose 1–6 diaspores (4.3 \pm 1.1 diaspores, N = 160). Fruits may contain 1–12 seeds (7.0 \pm 2.6 seeds, N = 160). Each diaspore (18.5 \pm 2.7 mm long, 10.0 \pm 1.0 mm wide; N = 423) contains 1–2 seeds covered by a thin orange aril firmly attached to the seeds. Fresh diaspores weigh 0.98 \pm 0.28 g (N = 45), and the aril corresponds to 22.8% of their mass. The aril of *C. canjerana* has one of the highest lipid contents (70.8% of dry mass) yet described in the literature (Jordano, 1993). Total carbohydrate, protein, and ashes account, respectively, for 16.5, 10.3, and 2.3% of the aril dry mass (Pizo, in press).

MATERIALS AND METHODS

Ant–seed interactions—To determine which ants interact with *C. canjerana* seeds, as well as how ants treat them, we made diurnal (0800–1800) and nocturnal (1900–2200) observations of naturally fallen seeds, and of single seeds placed directly on the forest floor at 5-m intervals along a 50-m transect. Four and 16 transects containing 40 and 160 seeds, respectively, were established at Carmo and Saibadela, respectively. Each transect was established along the trails crossing the study sites. Transects were at least 20 m apart from each other. We inspected the transects continuously during 1 h, recording the ants attracted to the seeds, as well as whether they took seeds away and/or recruited individuals to exploit them on the spot. We followed ants carrying seeds until they entered their nests or disappeared in the leaf litter. The distance of seed displacement was then measured.

Censuses (24 h) and seed cleaning by ants—We made diurnal and nocturnal censuses of the number of ants attending seeds placed on the forest floor at Saibadela. We used 50 arillate seeds set along five transects similar to the ones described above. Seeds were set on transects at 0800 and checked at 4-h intervals during 24 h. We recorded the number of ants present in each census. The percentage of aril removed by ants was estimated visually and categorized into six classes: 0, 1–25, 26–50, 51–75, 76–99, and 100%.

Seed removal by rodents and ants—Seed removal was assessed experimentally at Carmo by placing groups of five seeds along two 20-m transects starting from the trunks of five fruiting trees of *C. canjerana*. Trees used in the removal experiments were at least 50 m apart from each other, and transects starting from the same tree were separated by angles of at least 90°. Seed groups were set out at stations located at

distances of 2, 5, 10, 15, and 20 m from the tree trunk. Experimental seeds were collected from recently opened fruits, and were placed directly on the forest floor inside a 100-cm² square between 1600 and 1800. Seed locations were marked with wooden stakes, and a given seed was considered removed if not found within a 30-cm radius around the seed group. Seed disappearance was recorded after 24 h. Groups of five arillate and nonarillate seeds were set alternately in the transects. After the first trial, a second one was performed changing the sequence of arillate and nonarillate seed groups along the transect. Thus, at the end of the experiment, each experimental tree received 100 seeds divided into 20 seed groups (ten groups with arillate seeds and ten with nonarillate ones).

Two sets of experiments designed as described above were performed to differentiate seed removal by ants and rodents. In the first one, rodents were excluded by placing the seed groups under wire cages (25 \times 25 \times 8 cm, 1.5-cm mesh) closed on the top and staked to the ground (see also Roberts and Heithaus, 1986; Kaspari, 1993). In the second experiment (next day), no enclosure was provided, thus permitting free access by ants and rodents to the seeds. The nonenclosure experiment included five trees, three of which were also used in the enclosure experiment.

Data from the seed removal experiments were analyzed using factorial analysis of variance. The dependent variable was the number of seeds removed after 24 h. The independent variables were tree number, distance from tree trunk, aril treatment (arillate vs. nonarillate), and caging (caged vs. uncaged). We performed $\log(x + 1)$ transformations on the number of seeds removed to stabilize treatment variances for the statistical analysis.

Germination—Germination rates were recorded under greenhouse conditions for 115 cleaned seeds (i.e., aril removed by ants) and 92 arillate seeds. All seeds were collected beneath fruiting trees of *C. canjerana*. Germination tests were performed under natural temperature and light conditions. Seeds were kept in petri dishes with moistened filter paper. We checked for radicle protrusion at 2-d intervals. We used chi-square tests with Yates' correction (Zar, 1984) to evaluate seed germination.

RESULTS

The ant assemblage and ant behavior toward seeds—

A total of 26 ant species from 12 genera were attracted to arillate seeds of *C. canjerana* at PEI (Table 1). In contrast, none was recorded at nonarillate seeds. The most frequent species recorded at Saibadela was *Pheidole* sp. 7, a tiny myrmicine, followed by *Pachycondyla striata* (Ponerinae), the largest ant species found at PEI (Table 1).

Ants treat the arillate seeds in three different ways: (1) they individually remove the seed to the nest (*Pachycondyla* and *Odontomachus*), (2) they recruit workers and remove the aril on the spot (*Pheidole*), and (3) they recruit workers and cover the seed with soil before removing the aril on the spot (*Solenopsis*) (Table 1). Ponerine ants recruited 1–8 workers to the seed (Fig. 1), while the other species had >100 recruited workers around a seed. *Pachycondyla striata* and *Odontomachus chelifer* were the only species observed carrying seeds to considerable distances (mean \pm 1 SD = 15 \pm 18 cm, range 0–78 cm, N = 20 for *P. striata*; 57 \pm 60 cm, range 0–180 cm, N = 7 for *O. chelifer*). *Ectatomma edentatum*, however, never carried seeds beyond 16 cm (mean \pm 1 SD = 3 \pm 5 cm, range 0–16 cm, N = 11). These figures, however, represent minimum distance estimates, because once *P. striata* and *O. chelifer* have picked up a seed they rapidly

TABLE 1. Ant species attracted to the arillate seeds of *Cabralea canjerana* at Parque Estadual Intervales, southeast Brazil, and ant behavior during ant-seed interactions. Species occurrence in each site is indicated by an "X."

Ant species	Sites		No. of records at Saibadela (N = 160 seeds)	Behavior ^a
	Carmo	Saibadela		
Ponerinae				
<i>Ectatomma edentatum</i>		X	3	A
<i>Gnamptogenys</i> sp.		X	1	B
<i>Heteroponera</i> sp.	X			B
<i>Odontomachus chelifer</i>	X	X	11	A
<i>Odontomachus affinis</i>	X	X	1	?
<i>Odontomachus</i> sp.		X	3	B
<i>Pachycondyla striata</i>	X	X	38	A
<i>Pachycondyla apicalis</i>		X	1	?
Myrmicinae				
<i>Crematogaster</i> sp. 1		X	1	B
<i>Crematogaster</i> sp. 2		X	1	B
<i>Pheidole</i> sp. 1	X	X	9	B
<i>Pheidole</i> sp. 2	X	X	5	B
<i>Pheidole</i> sp. 3	X	X	19	B
<i>Pheidole</i> sp. 4	X			B
<i>Pheidole</i> sp. 5	X			B
<i>Pheidole</i> sp. 7		X	46	B
<i>Pheidole</i> sp. 9		X	12	B
<i>Solenopsis</i> sp. 1	X	X	18	B
<i>Solenopsis</i> sp. 2	X	X	3	B
<i>Solenopsis</i> sp. 4		X	1	C
<i>Solenopsis</i> sp. 5		X	14	C
<i>Acromyrmex subterraneus</i>		X	1	B
Dolichoderinae				
<i>Linepithema</i> sp.		X	2	B
Formicinae				
<i>Brachymyrmex</i> sp.		X	1	B
<i>Paratrechina</i> sp. 1	X			B
<i>Paratrechina</i> sp. 2		X	1	B

^a A = recruit 1–8 workers and remove the seeds to the nest; B = unable to remove the seeds individually; recruit many (5 to >100) workers, which remove portions of the aril on the spot; C = cover the seed with soil particles before removing the aril on the spot.

disappeared into the leaf litter (total of 49 out of 160 seeds; see Table 1).

Daily activity on seeds and seed cleaning by ants—Arillate seeds of *C. canjerana* were attended day and night by ants (Fig. 2). There was a constant presence of species recruiting many (>50) workers, especially *Solenopsis* spp. and *Linepithema* sp. The large ponerines *P. striata* and *O. chelifer* removed 46% (23/50) of the seeds during the 24-h period.

Ants were fast at removing the aril from the seeds (median = 8.5 h, $N = 17$). Overall, seeds were completely cleaned in 11.5 ± 4.6 h ($N = 17$). However, this could be an overestimate since records of seed cleaning were made at 4-h intervals. The large *P. striata* cleaned the seeds in 9.3 ± 2.0 h ($N = 9$), but the tiny myrmicine and formicine species could take >24 h to entirely clean a seed.

Seed removal—The mean number of seeds removed in different treatments are presented in Table 2. On average, twice as many arillate seeds were removed per

uncaged than per caged seed station (five seeds per station), indicating that ants were responsible for nearly half of the arillate seeds removed. A few nonarillate seeds were removed in the enclosure experiment (0.4 seeds per station), probably indicating that other small organisms (e.g., harvestmen, grasshoppers) may also remove the seeds, or that rodents may occasionally manage to enter some of the cages. Ants were never seen removing nonarillate seeds. The factorial analysis indicates that seed removal varied significantly with the location of the tree, aril treatment, and caging. Rates of seed removal, however, were not affected by distance from focal trees (Table 2).

Germination—Germination of *C. canjerana* seeds is exceptionally rapid. Most of the nonarillate seeds (64.3%) germinated between 6 and 8 d. The presence of the aril not only reduces the germination success (100% for nonarillate against 42.4% for arillate seeds; $\chi^2 = 86.05$, $P < 0.001$), but also decreases the germination rate (Kolmogorov-Smirnov test, $D_{\max} = 0.34$, $P = 0.01$).

DISCUSSION

The categories of ant behavior toward the arillate seeds of *Cabralea canjerana* at PEI are similar to those found for the interactions between ants and *Calathea* spp. (Maranthaceae) in Mexican rain forests (Horvitz and Beattie, 1980; Horvitz, 1981). Large ponerine ants such as *Pachycondyla* and *Odontomachus* pick up single seeds individually and quickly disappear in the leaf litter, with the aril being consumed by the workers and larvae inside the nest (see also Davidson, 1988, on ant-garden epiphytes). On the other hand, smaller ants such as *Solenopsis* and *Pheidole* recruit many nestmates to the seed and consume the aril on the spot. Since we were unable to follow seed-carrying workers of *Pachycondyla striata* and *Odontomachus chelifer* precisely in the field, our estimates of seed displacement by these ants were much smaller (up to 180 cm) than those reported for other *Pachycondyla* and *Odontomachus* species (up to 10 m) when carrying arillate seeds of *Calathea* (Horvitz and Beattie, 1980). Since forest-dwelling ponerine ants are known to forage relatively far from their nests (see Hölldobler, 1980; Oliveira and Hölldobler, 1989), it is possible that seed displacement by *P. striata* and *O. chelifer* at PEI can cover distances comparable to those reported by Horvitz and Beattie (1980) in Mexican forests. Distance per se, however, probably accounts only for a minor benefit resulting from ant dispersal, since seed displacement by ants frequently covers distances <5 m (e.g., Culver and Beattie, 1978; Andersen, 1988; Higashi et al., 1989; Bond, Yeaton, and Stock, 1991). As stressed by Horvitz (1981), even if not carried all the way to the ant nest, a given seed may benefit from being abandoned by the ant in a safe spot beneath the leaf litter (which frequently occurs; see below) where appropriate microconditions such as moisture, temperature, and nutrients may favor seedling establishment (see Harper, 1977). Moreover, competition between the parent plant and offspring can be reduced even with short dispersal distances (Westoby et al., 1982).

An additional benefit gained through seed removal



Fig. 1. Workers of *Odontomachus chelifer* gathering at an arillate seed of *Cabralea canjerana* (arrow) on the leaf litter of the Atlantic forest of southeast Brazil. The ants eventually carry the seed to the nest, where the aril is consumed by workers and larvae. Bar = 2.0 cm.

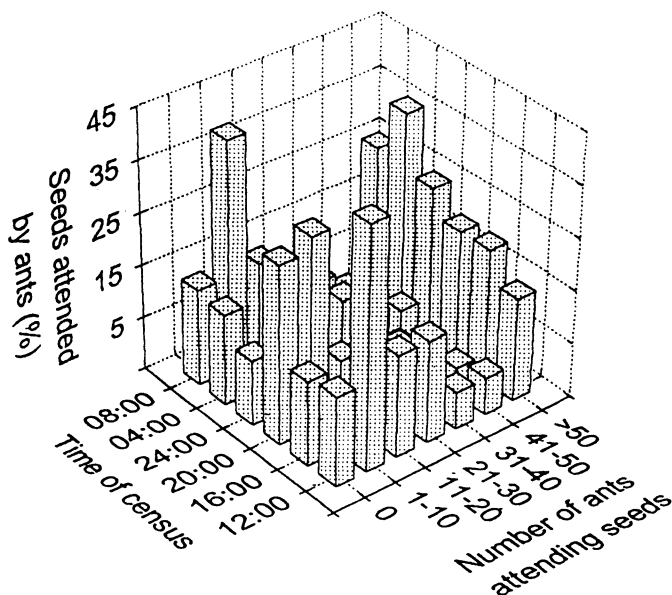


Fig. 2. Number of ants attending 50 arillate seeds of *Cabralea canjerana* during censuses conducted at 4-h intervals (24-h period), in the Atlantic forest of the Parque Estadual Intervales, southeast Brazil.

from exposed areas on the forest floor may be related to avoidance of seed predators, especially insects and rodents (Howe and Smallwood, 1982). *Pachycondyla striata* and *O. chelifer* can remove *C. canjerana* seeds to their nests and occasionally abandon some of them under the leaf litter, thus potentially rendering the seeds the benefit of being safe from rodent predation at PEI (see also Horvitz, 1981). Moreover, *Odontomachus* and *Pachycondyla* can also remove seeds from the proximity of fruiting trees, where predation by insects is severe. In fact, after a 6-d period of exposure, 96% of intact arillate seeds ($N = 200$) experimentally placed beneath fruiting trees of *C. canjerana* are attacked by *Lobiopa* (Nitidulidae) and *Conotrachelus* (Curculionidae) beetles (Pizo, in press). It is therefore possible that, by rapidly removing fallen seeds of *C. canjerana* to safer places, *Odontomachus* and *Pachycondyla* ants decrease the risk of seed predation by beetles beneath parent trees. Avoidance of predation-prone zones resulting from seed dispersal by ants has already been demonstrated for myrmecochores of arid regions (O'Dowd and Hay, 1980; Bond and Slingsby, 1984; Bond and Breytenbach, 1985).

Pachycondyla striata and *O. chelifer* did not concentrate their seed-carrying activities near focal trees. The pattern of spatial exploitation of *C. canjerana* seeds by these ants corresponded to that found by Perry and Fleming (1980) in a Costa Rican deciduous forest, where ants

TABLE 2. Removal rates of arillate and nonarillate seeds of *Cabralea canjerana* in nonenclosure and enclosure experiments carried out at Parque Estadual Intervales, southeast Brazil.

Variable	Uncaged seeds		Caged seeds	
	With aril (N = 50 stations)	Without aril (N = 50 stations)	With aril (N = 30 stations)	Without aril (N = 30 stations)
Mean no. of seeds (± 1 SD) removed per station (5 seeds per station)	2.36 \pm 1.69	0.98 \pm 1.19	1.23 \pm 1.87	0.43 \pm 1.07
Factorial ANOVA Table				
Source	df	SS	F	P
Focal tree	4	7.595	5.78	0.0002
Aril treatment (arillate vs. nonarillate)	1	8.012	24.38	0.0001
Caging (caged vs. noncaged)	1	2.749	8.37	0.0044
Distance from focal tree	4	1.300	0.99	0.4156
Error	149	48.971		

may find and carry seeds irrespective of their distances to parent trees. In fact, ponerines are predominantly carnivorous ants that search the leaf litter for arthropod prey (Horvitz and Beattie, 1980; Hölldobler and Wilson 1990), and their foraging area is mostly determined by the nest location. It is therefore unlikely that *Pachycondyla* and *Odontomachus* set their nests considering fruiting trees like *C. canjerana*, whose arillate seeds probably represent a secondary and ephemeral food source for these ponerines (see also Horvitz and Beattie, 1980; Horvitz 1981).

Germination tests with *C. canjerana* seeds showed that aril removal by the ants significantly increases both germination success and speed. Similar results were obtained by Horvitz (1981) with seeds of *Calathea microcephala*. Aril removal per se is known to facilitate germination in tropical plants (Howe and Smallwood, 1982). We do not know whether aril removal by ants also causes scarification of the seed coat in *C. canjerana*. Although scarification of the seed may be a germination cue for some plant species (Howe and Smallwood, 1982), *C. canjerana* seeds do not exhibit dormancy and the seed coat is thin enough to allow germination without scarification.

Unless fruits and seeds dropped on the forest floor by vertebrate frugivores have their fleshy portion removed, infestation by fungal pathogens may rapidly lead them to rot (Augspurger, 1990). Seed cleaning (removal of fruit matter) by attine ants has recently been demonstrated to reduce fungal attack to fallen fruits, facilitating seed germination in the mammal-dispersed tree *Hymenaea courbaril* (Oliveira et al., 1995). In fact, arillate seeds of *C. canjerana* are rapidly infested by fungi on the forest floor at PEI. Although aril removal by the majority of ant species may reduce fungal attack to seeds of *C. canjerana*, such activity may also result in a decreased seed availability to the seed vectors *P. striata* and *O. chelififer* (see Horvitz and Schemske, [1986a] for a similar case).

The interactions between ants and diaspores are probably mediated, among other things, by the chemical cues present in the fleshy portion of the diaspore. Lipids, for example, are either of important nutritional value for some ant species, or function as behavioral releasers to others (Marshall, Beattie, and Bollenbacher, 1979). Elaiosomes often have a high lipid content, which presumably attracts ants (Horvitz, 1981; Lu and Mesler, 1981), and the lipid-rich aril of *C. canjerana* seeds attracted a variety of ants at PEI (see also Davidson and Morton, [1984],

on Australian acacias). Therefore, the high lipid content of the aril may be a key factor accounting for seed attractiveness to ants, leading to a rapid recruitment of nest-mates and a round-the-clock attendance by ants to the food source.

In conclusion, ants that render some benefit to seed dispersal and/or establishment may be attracted by fruit structures other than elaiosomes (Roberts and Heithaus, 1986; Davidson, 1988; Kaufmann et al., 1991; Levey and Byrne, 1993; Oliveira et al., 1995). Since elaiosomes and arils are similar both morphologically (van der Pijl, 1982) and chemically (Hughes, Westoby, and Johnson, 1993), it is not surprising that seeds bearing lipid-rich arils benefit from interacting with ants. One tree of *Cabralea canjerana* may produce up to 4500 fruits, containing over 50000 arillate seeds. The five main bird dispersers of *C. canjerana* remove, on average, 10 diaspores \cdot h⁻¹ \cdot tree⁻¹ at PEI (Pizo, in press). Nearly 30% of the bird-manipulated diaspores may fall beneath *Cabralea* trees with bits of aril that attract ants (Pizo, in press; see also Davidson, 1988, on ant-garden epiphytes). The latter may not only enhance seed germination through aril removal, but also act as secondary seed dispersers. By carrying seeds to potentially safer microsites, ants can increase the survival chances of the seeds that are either dropped by primary vertebrate dispersers or that fall spontaneously from the parent plant. In this case, ants would potentially play a key role in the fate of seeds of many plants in tropical forests, where elaiosome-bearing species are rare but aril-bearing ones are not (Mossop, 1989; Hughes, Westoby, and Johnson, 1993). The interaction between ants and seeds of *Cabralea canjerana* is similar to that reported by other authors for plants that are primarily dispersed by vertebrates, such as fig trees (Roberts and Heithaus, 1986; Kaufmann et al., 1991) and ant-garden epiphytes (Davidson, 1988). Vertebrate-dispersed propagules frequently possess structures which are also especially attractive to ants (i.e., fruit pulp, seed appendages), and some plant species have been domesticated by these insects in a system that parallels human agriculture, as shown for ant-garden epiphytes (Davidson, 1988; Davidson and Epstein, 1989). These findings illustrate the complexity of plant-animal interactions and emphasize the importance of ant-induced movement of seeds in the humid tropics, where ant effects on seed bank demography

and seedling establishment remain largely unexplored (Horvitz and Schemske, 1986b).

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