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# Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic Forest of southeastern Brazil

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ABSTRACT. The seed dispersal system of a neotropical tree, *Cabralea canjerana* (Meliaceae), was studied in two forested areas in southeastern Brazil. The first study site, Parque Estadual Intervales (PEI), is a 49,000-ha reserve composed mostly of old-growth Atlantic rain forest. The second site, Mata de Santa Genebra (MSG), is a 250-ha fragment of old-secondary semideciduous forest whose present bird fauna differs markedly from the original, in part as a consequence of forest fragmentation. At PEI 35 bird species ate the diaspores of *C. canjerana*. Black-tailed tityra (*Tityra cayana*, Tyrannidae) was the main seed disperser, but several other species were also important seed dispersers. In contrast, at MSG *C. canjerana* diaspores were eaten by 14 bird species. At this area, the red-eyed vireo (*Vireo olivaceus*, Vireonidae) was the most important seed disperser, but it was also a 'waster' which dropped seeds beneath parent plants, or carried them to sites unsuitable for germination. At PEI, exposed seeds on the forest floor were heavily preyed upon by rodents and insects. Insects destroyed mainly seeds deposited near to parent plants. Insect predation was less intense at MSG than at PEI. The rodent density at MSG was unusually small, and part of the post-dispersal seed predation may be done by terrestrial birds, such as doves and tinamous, which are especially common at MSG. Some of the differences recorded between the seed dispersal systems of *C. canjerana* at PEI and MSG may have been the result of the fragmentation and isolation of the latter area.

KEY WORDS: Atlantic forest, Brazil, *Cabralea*, forest fragmentation, Meliaceae, ornithochory, seed dispersal, seed predation.

## INTRODUCTION

Recent studies on plant/disperser interactions frequently have focused on the spatially and temporally variable nature of these interactions (Guitián *et al.* 1992; Jordano 1993a, 1995; Keeler-Wolf 1988, Sallabanks & Courtney 1993, Traveset 1994, Willson & Whelan 1990). Such studies help to identify factors affecting the evolution of mutualistic interactions between plants and their seed dispersers (Jordano 1995), and point out some possible consequences of variability in space and time to plant and frugivore populations (Jordano 1993a, Keeler-Wolf 1988).

For plants whose seeds are dispersed by birds, much of the variability is a consequence of the differential contribution of bird species to the removal and efficient dispersal of seeds (Guitián *et al.* 1992, Jordano 1995). However, seed predators and secondary seed dispersers influence the post-dispersal fate of seeds, affecting the effectiveness (*sensu* Schupp 1993) of primary dispersers, and adding unpredictability to seed establishment. Events occurring between seed dispersal and germination, such as post-dispersal seed predation, can have a major impact on plant recruitment (Schupp 1990, Whelan *et al.* 1991).

Habitat changes can affect the interactions between plants and their seed dispersers and predators (Mittelbach & Gross 1984, Pudlo *et al.* 1980). Forest fragmentation, for example, may alter the composition of bird seed-disperser assemblages and the relative contribution of some species as seed dispersers (Galetti *et al.* 1994). Such alterations may prove to be important for the demography and spatial distribution of plant populations (Howe 1984).

Although the number of studies involving the spatial variability of plant-disperser interactions is growing rapidly, similar studies focusing on the interaction between plants and seed predators are relatively scarce. In the present study I investigate the seed dispersal system (*sensu* Howe 1984) of *Cabralea canjerana* (Mart.) Vell. (Meliaceae) in a 250-ha forest fragment, and in a 49,000-ha reserve, both located in southeastern Brazil. I was especially concerned with: (1) the composition of bird disperser assemblages in the two areas and the 'quantity of seed dispersal' they provided (see Schupp 1993), and (2) the impact of seed predators on seeds dropped under and away from parent plants.

## STUDY SITES AND SPECIES

### *Study sites*

The study was conducted in two Atlantic forest sites (*sensu lato*), Parque Estadual Intervales (PEI) (24°16′S, 48°25′W) and Mata de Santa Genebra (MSG) (22°49′S, 47°06′W), both in São Paulo State, southeastern Brazil, and separated by *c.* 180 km. PEI is a 49,000-ha reserve surrounded by three other reserves encompassing a total of 120,000 ha of continuous forest. PEI ranges in elevation from 60 to 1100 m a.s.l.. The study site was located at an elevation of 700 m in an area of old-growth (*sensu* Clark 1996) Atlantic rain forest (*sensu strictu*) with trees reaching up to 30 m, and patches of second growth vegetation near human settlements. Extensive areas of old-growth forest surround the study site. Climate is generally wet, with frequent rain or fog. Mean annual precipitation between 1990–93 was 1558 mm, with a dry-cold season from April to August (winter), and a wet-hot season from September to March. Mean annual temperature during the study was 17.6 °C.

Approximately 345 bird species occur at PEI, and 25% of them include fruits in their diets. Large frugivorous birds (e.g. cracids, toucans, trogons) are common at PEI.

MSG is a 250-ha forest fragment at an elevation of 640 m a.s.l.. It is surrounded by urban areas and plantations (see aerial photograph in Chiarello & Galetti 1994). According to Willis (1979), the forested area was reduced to its present size in 1969 following the logging of 145 ha. Selective logging continued until 1984 when the reserve was created. The vegetation can be classified as old-secondary (*sensu* Clark 1996) semideciduous forest (Leitão-Filho & Morellato 1994). The canopy reaches 15 to 20 m, the understory is dense, and lianas are plentiful, particularly at the forest edge. The mean annual temperature and rainfall between 1956–93 was respectively 22.4 °C and 1360 mm, with a rainy season extending from November to February, and a marked dry season from May to August.

Willis (1979) studied the avifauna of MSG between 1975 and 1978 and recorded 143 species, but noted that many of the 230 species that once constituted the original avifauna of the area had been lost from the reserve. Large frugivorous birds such as the solitary tinamou (*Tinamus solitarius*), macaws (*Ara* spp.), and the black-necked aracari (*Pteroglossus aracari*) were among those species that had disappeared from MSG by the time of Willis' study. A recent survey (Wesley R. Silva *et al.* unpubl. data) noted the disappearence of 40 species recorded by Willis, and registered 70 new occurrences, mostly insectivorous and omnivorous species occupying the forest edge. As in PEI, aproximately 25% of the bird species presently found at MSG are partially frugivorous.

### *Plant species*

*Cabralea canjerana* is a dioecious tree with a widespread distribution in the Neotropical region, extending from Costa Rica to southern Brazil and northern Argentina (Pennington 1981). According to Pennington (1981), it inhabits mainly non-flooded evergreen lowland or lower montane rain forests, being specially common in southeastern Brazil. Although it is not a dominant species at both study sites, where it occurs as a canopy tree, it is reasonably common. Reproductive individuals reach 22 and 16 m height at PEI and MSG, respectively.

Fruit and fruiting characteristics of *C. canjerana* were investigated at both study sites (Pizo 1994) and are summarized here. Pooled data are presented when no between-site differences were found. Fruit crops surveyed between 1992 and 1994 at PEI ranged from zero to 4500 fruits (mean ± SD = 85.5 ± 468.3, n = 93) with most of them (68.7%) bearing fewer than 50 fruits. At MSG, only five individuals produced fruits during the study (mean = 613.0 ± 530.3). Mature fruits occur from September to January, with a peak in abundance in November–December, a period that also corresponds to the fruiting period of many other fleshy-fruited species at the study sites (Morellato 1991, Pizo 1994). Fruits are globose capsules that dehisce to expose between 1 and 6 diaspores (mean = 4.4 ± 1.0, n = 200). Each diaspore corresponds to one or two seeds enveloped by a thin orange aril, which on average corresponds to 22.8 and 27.5% of the diaspore fresh mass at PEI and MSG, respectively. The diaspores sampled at PEI had a larger weight (means = 1.4 ± 0.1 g and 0.4 ± 0.2 g, range 0.6–2.2 g and 0.2–0.8 g, n = 54 and 15 for PEI and MSG,

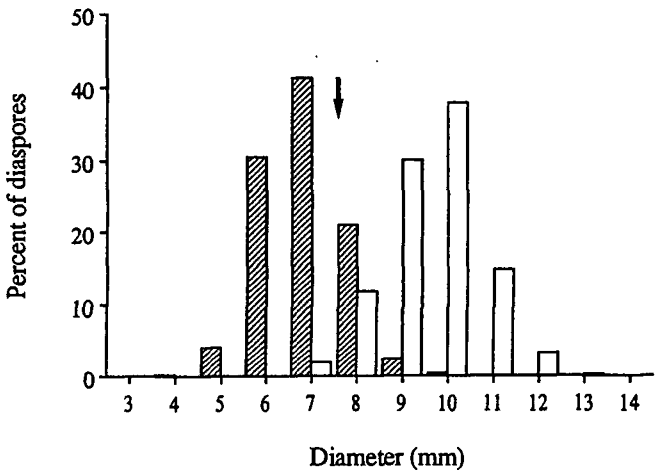

Figure 1. Diameter of *Cabralea canjerana* diaspores sampled at Mata de Santa Genebra (MSG, hatched bars) and Parque Estadual Intervales (open bars). Sample sizes were 287 and 423, respectively. The arrow indicates the mean gape width (7.6 mm) of *Vireo olivaceus*, the main seed disperser at MSG.

respectively; $t = 11.82$, $P < 0.001$) and diameter (means 10.0 ± 1.0 mm and 7.3 ± 0.9 mm, ranges 7.0–13.0 mm and 4.5–11.1 mm, $n = 423$ and 287 for PEI and MSG , respectively; $t = 38.37$, $P < 0.001$; Figure 1) than those sampled at MSG. Seeds are soft and covered by a thin coat which makes them vulnerable to predation by rodents.

The aril of *C. canjerana* has one of the highest lipid contents yet described in the literature (73.4% of dry mass, see Jordano 1993b). Total carbohydrate, protein and ashes account respectively for 15.5, 8.8 and 2.3% of the aril dry mass. Details of chemical analysis are in Pizo (1994).

## METHODS

### *Seed dispersal*

Bird visitation and feeding behaviour at three trees at each study site was monitored between October and December 1992/93 at PEI, and between October and December 1993 at MSG. In order to avoid trees with few fruits that usually render low visitation rates (Howe & Vande Kerckhove 1979, Herrera & Jordano 1981) only trees bearing more than 1000 fruits were selected for observation. Total observation time (70.2 and 45.4 h at PEI and MSG, respectively) was divided into observation sessions that lasted between 1 and 3 h at PEI (32 observation sessions), and between 20 min and 2 h at MSG (34 observation sessions). The observation sessions were concentrated between 06:00 and 10:00 h, the period of highest feeding activity of birds at *C. canjerana* trees. After 10:00 h open capsules often were depleted of their diaspores and birds rarely visited the trees. During each observation session, all bird visits were recorded whether the visiting birds took diaspores or not. When they did, the methods employed to handle the diaspores, and whether the diaspores were effectively swallowed or dropped, were also noted. Feeding rates of selected bird species were obtained whenever possible by recording the number of diaspores taken during entire visits of some individuals to the trees.

Germination times were recorded for seeds regurgitated by birds (i.e. seeds without arils, n = 115 and 60 for PEI and MSG, respectively) and arilate seeds (n = 92 and 40 for PEI and MSG, respectively) collected beneath the trees, and exposed to 12 h-light period and natural ambient temperature in Petri dishes with regularly moistened filter paper. The protrusion of the radicle was verified each other day.

Although bats seldom feed on fruits adapted for dispersal by birds such as those of *C. canjerana* , this possibility does exist (see Whittaker & Turner 1994). Thus, sporadic nocturnal observations were made during the period of peak fruit maturation. These observations were conducted between 19:00 and 22:00 h, when bats concentrate their foraging activity (Coates-Estrada & Estrada 1986, Fleming & Williams 1990).

Gape widths (i.e. external distance between commissural points) of bird species seen feeding on *C. canjerana* were measured with calliper to the nearest 0.1 mm from ten museum specimens collected in southeastern Brazil. Bird scientific names used here followed Ridgely & Tudor (1989, 1994).

### *Seed predation by rodents*

Post-dispersal seed removal was experimentally assessed between October and December 1993 by placing groups of five non-arilate seeds along two 20 m-line transects starting from the trunks of three fruiting and four non-fruiting trees at PEI, and from two fruiting and three non-fruiting trees at MSG. All the fruiting trees had more than 1000 fruits, which is a quantity enough to guarantee the presence of naturally-fallen seeds beneath the trees. All the non-fruiting trees were located more than 50 m away from any fruiting tree. Transects were separated by angles no less than 90°, and seed groups were set out at stations located at 2, 5, 10, 15 and 20 m from the trunk. Seeds were collected from recently opened fruits, and placed direct on the forest floor at the corners of a 10 cm × 10 cm square, with the fifth seed in the center. Seed locations were marked with wooden stakes, and seed disappearence was censused at 2, 4 and 6 d after placement, when most seeds start germination (see below). Seeds were considered to have been removed if they were not found within 30 cm of the seed group.

Immediately after the seed removal experiment, in an effort to capture rodents a total of 13 live-traps of two sizes (42 cm × 20 cm × 18 cm and 27 cm × 12 cm × 13 cm) were set beneath the experimental trees. Traps were baited with arilate and non-arilate *C. canjerana* seeds and were checked every 24 h. A total of 91 and 260 trap-nights were performed at PEI and MSG, respectively.

### *Seed predation by insects*

Post-dispersal insect predation of *C. canjerana* seeds was checked during the censuses conducted for the seed removal experiments described above, when seeds in the transects were checked for the typical hole left by insect larvae entering them. This procedure has the potential to underestimate the total insect predation because insect damage may have passed unnoticed in a seed removed before the first census day. However, all comparisons involving insect predation remain unaffected because all the transects were subjected to the same potential bias.

In order to evaluate the amount of insect predation on seeds naturally found under fruiting trees at PEI, all the seeds found beneath the canopy of nine trees were collected on a monthly basis. These seeds were opened and inspected to detect the presence of insect predators. The scarcity of fruiting trees together with the need for seeds in the seed removal experiments, meant that few seeds could be inspected at MSG.

The pre-dispersal seed predation by insects was verified by examination of fruits collected directly from the trees throughout the study.

### *Data analysis*

No between-station significant differences (Kruskal-Wallis non-parametric one-way analysis of variance, all $P>0.10$) in the proportion of seeds removed by rodents was deteced for any censuses in any treatment (i.e. seeds near [$\leq 20$ m] fruiting trees and seeds farther than 50 m away from fruiting trees, placed near non-fruiting trees). So, results for all stations on a transect were pooled. For all analyses the results of both transects per tree were summed, and the total number of seeds removed by rodents or preyed upon by insects per treatment was considered in chi-squared analysis of predation by rodents and insects, respectively. Yates' correction was used in all 2 × 2 contingency tables. All tests followed Zar (1984).

## RESULTS

### *Bird visiting and feeding behaviour*

A taxonomically and biologically diverse assemblage of birds visited *C. canjerana* trees, including predominantly frugivorous species (e.g. trogons) and predominantly insectivorous ones (e.g. most of tyrannid species; Table 1). Some species predominantly use wing-powered manoeuvres to take diaspores (e.g. tyrannid flycatchers) whereas others almost exclusively take them while perched (e.g. toucans and woodpeckers). Birds visiting *C. canjerana* ranged in weight from 15 g (*Mionectes rufiventris*) to aproximately 500 g (*Ramphastos dicolorus*). Bats were not observed visiting *C. canjerana* trees. In fact, Galetti & Morellato (1994) and Sazima *et al.* (1994) did not record this plant species in the diet of the large fruit-eating bat (*Artibeus lituratus*), the most common frugivorous bat at MSG.

Birds treat the diaspores in three different ways: (1) swallowing diaspores whole and regurgitating intact seeds without arils, thereby acting as legitimate seed dispersers; (2) consuming only portions of the aril and dropping partially arilate seeds under the parent plant; and (3) cracking and eating the seeds. Hereafter I shall refer to these birds as seed dispersers, aril consumers, and seed predators, respectively.

*Parque Estadual Intervales.* Thirty-five bird species made 1021 visits to the *C. canjerana* trees observed at PEI (Table 1). Twenty-seven species, responsible for 74% of the visits, acted as seed dispersers, and six species acted as aril consumers (16% of the visits). The latter species are either morphologically constrained by their narrow gape widths (*Mionectes rufiventris* and *Pipraedea melanonota*, mean gape widths = 7.7 ± 0.7 mm, and 7.5 ± 0.4 mm, respectively), or are species that typically eat fruits piecemeal (*Cacicus haemorrhous*, *C. chrysopterus*, *Cyclarhis gujanesis*, and *Pitylus fuliginosus*; see Levey 1987, Trainer & Will 1984). The yellow-fronted Woodpecker (*Melanerpes flavifrons*), one of the main seed dispersers (Table 2), was the only species to employ two feeding techniques, eating diaspores whole or piecemeal. The reddish-bellied parakeet (*Pyrrhura frontalis*) was the only avian seed predator recorded.

The most important seed disperser was the black-tailed tityra (*Tityra cayana*; mean gape width = 18.0 ± 1.6 mm), which was responsible for 12.6% of the visits recorded, and removed the highest number of diaspores from the trees (44% of the diaspores removed by the top-five dispersers; Table 2). Moreover, it was observed in all the study trees, and during 72% of the observation sessions, thus indicating reliability in attending the trees. *Tityra cayana* usually visited the trees in pairs, flying distances of 50 m or more after a feeding bout.

Aggressive encounters between visitors were rarely observed despite the occurrence of several birds concomitantly visiting the same tree. Only eight apparent chases were recorded.

*Mata de Santa Genebra.* A total of 443 visits by 14 bird species were recorded in the *C. canjerana* trees at MSG, a feeding assemblage wholly composed by passerines (Table 1). The proportion of visits made by the three types of frugivores (seed dispersers, aril consumers, and seed predators) differed significantly from that observed at PEI ($\chi^2 = 57.3$, df = 2, $P<0.001$), with seed dispersers being more frequently recorded at MSG (74 versus 97% of the visits). The blue dacnis (*Dacnis cayana*), responsible for 3.4% of the visits, was the only aril-consumer observed. Constrained by its narrow gape width (mean = 4.7 ± 0.2 mm), this species pecked portions of the aril and dropped the seeds.

A striking characteristic of the visitor assemblage recorded at MSG was the overall importance of migratory species, which were much more frequent at MSG than at PEI (72 and 44% of the visits recorded at MSG and PEI, respectively; $\chi^2 = 89.5$, $P<0.001$; Table 1).

The main disperser of *C. canjerana* seeds at MSG was the red-eyed vireo (*Vireo olivaceus*), which was responsible for almost 50% of the visits, and removed the

Table 1. Diet, migratory status, and number of visits of bird species visiting *Cabralea canjerana* trees at the Parque Estadual Intervales (PEI) and Mata de Santa Genebra (MSG), southeastern Brazil

| | | Migratory status[c] | | Number of visits (% of all visits) | |
|---|---|---|---|---|---|
| Bird species[a] | Frugivore type[b] | PEI | MSG | PEI | MSG |
| PSITTACIDAE | | | | | |
| *Pyrrhura frontalis* | SP | R | | 4 (0.4) | |
| TROGONIDAE | | | | | |
| *Trogon rufus* | SD | R | | 2 (0.2) | |
| *Trogon surrucura* | SD | R | | 3 (0.3) | |
| RAMPHASTIDAE | | | | | |
| *Selenidera maculirostris* | SD | R | | 1 (0.1) | |
| *Baillonius bailloni* | SD | R | | 12 (1.2) | |
| *Ramphastos dicolorus* | SD | R | | 7 (0.7) | |
| PICIDAE | | | | | |
| *Melanerpes flavifrons* | SD/AC | R | | 94 (9.2) | |
| COTINGIDAE | | | | | |
| *Carpornis cucullatus* | SD | R | | 3 (0.3) | |
| PIPRIDAE | | | | | |
| *Chiroxiphia caudata* | SD | R | R | 22 (2.2) | 11 (2.5) |
| *Manacus manacus* | SD | | R | | 15 (3.4) |
| *Schiffornis virescens* | SD | R | | 4 (0.4) | |
| TYRANNIDAE | | | | | |
| *Tyrannus savana* | SD | | M | | 3 (0.7) |
| *Tyrannus melancholicus* | SD | | R | | 5 (1.1) |
| *Empidonomus varius* | SD | M | M | 40 (3.9) | 3 (0.7) |
| *Legatus leucophaius* | SD | M | | 14 (1.4) | |
| *Megarhynchus pitangua* | SD | R | O | 12 (1.2) | 3 (0.7) |
| *Myiodynastes maculatus* | SD | M | M | 88 (8.6) | 74 (16.7) |
| *Myiozetetes similis* | SD | R | | 6 (0.6) | |
| *Pitangus sulphuratus* | SD | R | R | 29 (2.8) | 28 (6.3) |
| *Attila rufus* | SD | R | | 54 (5.3) | |
| *Atilla phoenicurus* | SD | R | | 66 (6.5) | |
| *Myiarchus ferox* | SD | | R | | 30 (6.8) |
| *Myiarchus* sp. | SD | M | | 6 (0.6) | |
| *Mionecks rufiventris* | AC | R | | 44 (4.3) | |
| *Pachyramphus validus* | SD | M | O | 140 (13.7) | 3 (0.7) |
| *Tityra cayana* | SD | M | | 129 (12.6) | |
| *Tityra inquisitor* | SD | M | | 10 (1.0) | |
| OXYRUNCIDAE | | | | | |
| *Oxyruncus cristatus* | SD | R | | 29 (2.8) | |
| TURDIDAE | | | | | |
| *Platycichla flavipes* | SD | M | | 34 (3.3) | |
| *Turdus rufiventris* | SD | R | | 13 (1.3) | |
| *Turdus leucomelas* | SD | | R | | 30 (6.8) |
| *Trudus albicollis* | SD | R | | 30 (2.9) | |
| VIREONIDAE | | | | | |
| *Cyclarhis gujanensis* | AC | R | | 7 (0.7) | |
| *Vireo olivaceus* | SD | M | M | 2 (0.2) | 219 (49.4) |
| EMBERIZIDAE-ICTERINAE | | | | | |
| *Cacicus haemorrhous* | AC | R | | 32 (3.1) | |
| *Cacicus chrysopterus* | AC | R | | 48 (4.7) | |

Table 1. Continued.

| Bird species[a] | Frugivore type[b] | Migratory status[c] | | Number of visits (% of all visits) | |
|---|---|---|---|---|---|
| | | PEI | MSG | PEI | MSG |
| EMBERIZIDAE-COEREBINAE | | | | | |
| *Dacnis cayana* | AC | | O | 15 (3.4) | |
| EMBERIZIDAE-THRAUPINAE | | | | | |
| *Pipraeidea melanonota* | AC | R | | 13 (1.3) | |
| *Cissopis leveriana* | SD | R | | 2 (0.2) | |
| EMBERIZIDAE-EMBERIZINAE | | | | | |
| *Saltator similis* | SD | R | R | 1 (0.1) | 6 (1.3) |
| *Pitylus fuliginosus* | AC | R | | 20 (1.9) | |
| Total | | | | 1021 | 443 |

[a] Scientific names and phylogenetic sequence follow Ridgely & Tudor (1989, 1994).
[b] SD = seed disperser, AC = aril consumer, SP = seed predator. See Results for definitions.
[c] R = resident, M = migrant, O = occasional (i.e. sporadically present at the study site, not following a regular pattern of migration). Based on personal observations and on Aleixo & Vielliard (1995).

Table 2. Foraging behaviour, number of diaspores taken and number of diaspores effectively removed from the trees by the five main bird dispersers of *Cabralea canjerana* seeds at the Parque Estadual Intervales and Mata de Santa Genebra, southeastern Brazil. Values are mean ± SD. Sample sizes are presented between parentheses

| Bird species | Individuals/ visit | Diaspores taken/visit | % of diaspores | | N | Number of diaspores removed[a] |
|---|---|---|---|---|---|---|
| | | | removed | dropped | | |
| Parque Estadual Intervales | | | | | | |
| *Tityra cayana* | 1.6 ± 0.5 (122) | 4.8 ± 4.0 (17) | 100 | | 39 | 990 |
| *Melanerpes flavifrons* | 1.4 ± 0.5 (82) | 4.5 ± 4.4 (4) | 86.7 | 13.3 | 15 | 513 |
| *Pachyramphus validus* | 1.3 ± 0.6 (132) | 2.6 ± 2.3 (8) | 100 | | 29 | 473 |
| *Myiodynastes maculatus* | 1.1 ± 0.3 (84) | 1.5 ± 1.2 (7) | 100 | | 18 | 145 |
| *Attila phoenicurus* | 1.1 ± 0.3 (61) | 1.5 ± 1.3 (8) | 100 | | 21 | 109 |
| Mata de Santa Genebra | | | | | | |
| *Vireo olivaceus* | 1.2 ± 0.5 (170) | 0.7 ± 0.7 (15) | 70.2 | 29.8 | 57 | 129 |
| *Myiodynastes maculatus* | 1.0 ± 0.2 (42) | 1.6 ± 0.6 (13) | 100 | | 26 | 118 |
| *Pitangus sulphuratus* | 1.4 ± 0.6 (20) | 2.0 ± 1.2 (5) | 100 | | 8 | 78 |
| *Turdus leucomelas* | 1.0 ± 0.0 (5) | 1.6 ± 0.5 (3) | 100 | | 5 | 48 |
| *Myiarchus ferox* | 1.1 ± 0.4 (27) | 1.0 ± 0.6 (6) | 100 | | 4 | 33 |

[a] Given by number of visits (Table 1) × number of individuals/visit × number of diaspores taken/visit × percentage of diaspores removed.

highest amount of diaspores from the trees (Tables 1 and 2). *Vireo olivaceus* and the streaked flycatcher (*Myiodynastes maculatus*) were together responsible for 66% of all visits, making the overall visitation pattern quite different from that registered at PEI (Figure 2). *Vireo olivaceus* was recorded in all the study trees, and during 97% of the observation sessions. However, this species was also responsible for dropping almost 30% of the diaspores it pecked (Table 2). Two reasons accounted for its apparent inefficiency as a seed disperser: (1) the gape width of *V. olivaceus* (mean = 7.6 ± 0.7 mm) renders the bird unable to swallow some of the diaspores occurring at MSG (Figure 1), and trying to do so the

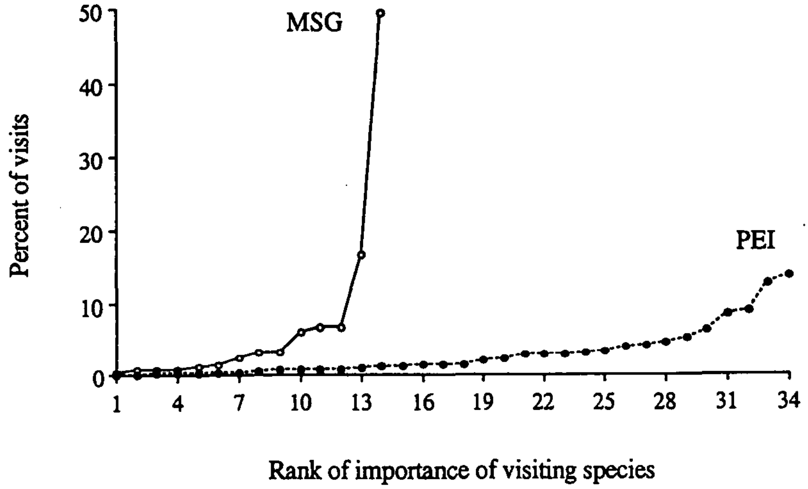

Figure 2. Proportion of visits made by birds species at the *Cabralea canjerana* trees observed at Mata de Santa Genebra (MSG) and Parque Estadual Intervales (PEI). Bird species are ranked in the horizontal axis from the least to the most frequently recorded.

birds often dropped the diaspores; and (2) aggressive encounters were commonly observed at MSG, and *V. olivaceus* was the most chased species (Table 3). Chased individuals often dropped the diaspores they had just picked.

### *Germination*

Germination was exceptionally rapid, with most of the regurgitated seeds (64 and 52% for PEI and MSG, respectively) germinating after 6 to 8 d. The presence of the aril not only reduced the final percentage germination ($\chi^2 = 107.47$, df = 1, $P<0.001$), but also decreased the germination rate (Kolmogorov-Smirnov $D_{max} = 0.27$, $P<0.01$).

### *Seed predation*

*Parque Estadual Intervales* – Besides *Pyrrhura frontalis*, which cracked the seeds on the tree (see above), pre-dispersal predation of *C. canjerana* seeds at PEI was

Table 3. Agonistic interactions among bird species visiting *Cabralea canjerana* trees at Mata de Santa Genebra, southeastern Brazil

| Dominant species[a] | Attacked species[a] | | | | | | |
|---|---|---|---|---|---|---|---|
| | Tl | Ps | Mm | Ev | Pv | Ts | Vo |
| Tl | 33 | 3 | 16 | 3 | | 2 | 11 |
| Ps | | 2 | 1 | | 1 | | 2 |
| Mm | | 3 | | | | | 4 |
| Ev | | | 1 | 1 | | | |
| Cc | | | | | | | 1 |
| Vo | | | | | | | 24 |
| Dc | | | | | | | 2 |

[a] Tl–*Turdus leucomelas*, Ps–*Pitangus sulphuratus*, Mm–*Myiodynastes maculatus*, Ev–*Empidonomus varius*, Cc–*Chiroxiphia caudata*, Vo–*Vireo olivaceus*, Dc–*Dacnis cayana*, Pv–*Pachyramphus validus*, and Ts–*Tyrannus savana*.

done by an unidentified curculionid larvae, which superficially ate the endosperm of immature seeds. However, its action seems to be highly variable in space, as only two of the seven trees sampled had their seeds damaged by these beetles.

Three individuals of the Atlantic forest rat *Delomys dorsalis* (Cricetidae) were captured under fruiting trees. When seeds were offered to one of these rodents in captivity, it ate and entirely destroyed them. Only two of the 70 seed groups had no seeds removed after 6 d on the forest floor. Overall, 82.6% of the seeds ($n = 350$) had been removed by the end of the experiment. Seed survival was inconsistent between treatments through the experiment (Figure 3A). After 2 d, seeds placed near fruiting trees were significantly more removed than those placed near non-fruiting trees ($\chi^2 = 4.4$, $P < 0.05$). However, the opposite was true after 4 and 6 d ($\chi^2 = 5.2$ and 4.2, both $P < 0.05$) (Figure 3A), indicating that rodents found and ate seeds irrespective of the distance from fruiting trees.

Insect predation on seeds under fruiting trees was intense. Eighty-four percent of the seeds collected ($N = 986$) under nine trees during the study presented signs of predation by insects. The beetles *Lobiopa insularis* (Nitidulinae, Nitidulidae) and *Conotrachelus* sp. (Molytinae, Curculionidae) accounted for 84.4 and 13.9% of the seeds infested by insects, respectively. Their larvae fed on the endosperm of the seeds invariably leading them to rot. Adults of both beetle species also commonly ate the endosperm of the seeds. In contrast to seed predation by rodents, seeds placed near fruiting trees were significantly more infested by insects than those deposited near non-fruiting trees ($\chi^2 = 6.40$, 14.70, and 5.42, $P < 0.01$, 0.001, and 0.01 for 2, 4, and 6-d censuses, respectively; Figure 4A).

*Mata de Santa Genebra*— No pre-dispersal insect predation was recorded at MSG. However, capuchin monkeys (*Cebus apella*) were observed eating the diaspores of one tree in a way indicating seed predation (but see Galetti & Pedroni 1994). The monkeys picked one by one all the diaspores of open capsules and appeared to chew them. During this study no intact seeds were observed in capuchin faeces.

Two individuals of the grass mouse (*Akodon* aff. *cursor*) were captured at the edge of MSG forest with traps baited with *C. canjerana* seeds. Four of the 50 seed groups had no seeds removed after 6 d on the forest floor. Overall, 67% of the seeds ($n = 300$) had been removed by the end of the experiment. Seeds placed near fruiting trees were removed significantly more often than those placed near non-fruiting ones ($\chi^2 = 14.1$, 13.2, and 21.8, all $P < 0.001$; Figure 3B).

The nitidulid beetle *Lobiopa insularis* also infested *C. canjerana* seeds at MSG. All four seeds inspected at this site contained the larvae of this beetle. Insect predation on *C. canjerana* seeds at MSG was much less intense than at PEI (Figure 4B). In addition, insects infested seeds independently of the distance

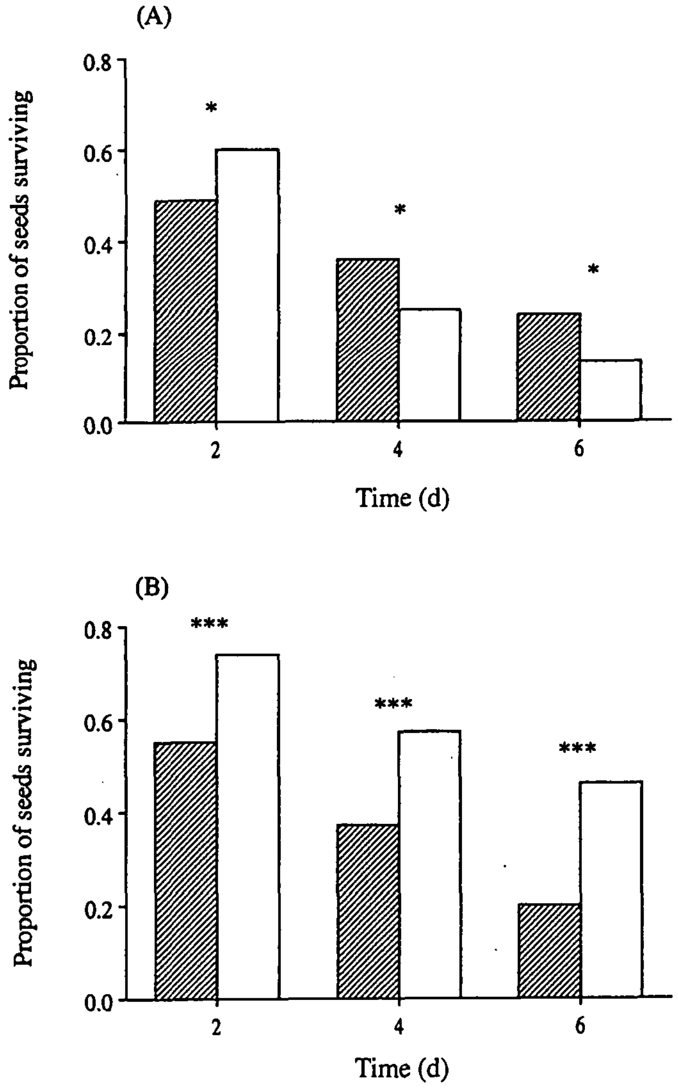

Figure 3. Proportion of *Cabralea canjerana* seeds surviving over the 6-d seed removal experiment at (A) Parque Estadual Intervales (PEI) and (B) Mata de Santa Genebra (MSG). Hatched bars refer to the seeds placed near (within 20 m) fruiting trees (n = 150 and 100 for PEI and MSG, respectively), and open bars to those placed farther than 50 m away, near non-fruiting trees (n = 150 and 200 for PEI and MSG, respectively). Significance of chi-squared tests using Yates' correction: ** $P \leq 0.05$, *** $P \leq 0.001$.

from fruiting trees. Either seeds deposited in close proximity to fruiting trees, or those deposited near non-fruiting ones were equally preyed upon ($\chi^2 = 0.66$, 0.05, 0.07, all $P > 0.40$; Figure 4B).

## DISCUSSION

### *Seed dispersal*

*Cabralea canjerana* fruits provide food for a large assemblage of birds at PEI. The high lipid content of the aril of *C. canjerana* might be a key factor account-

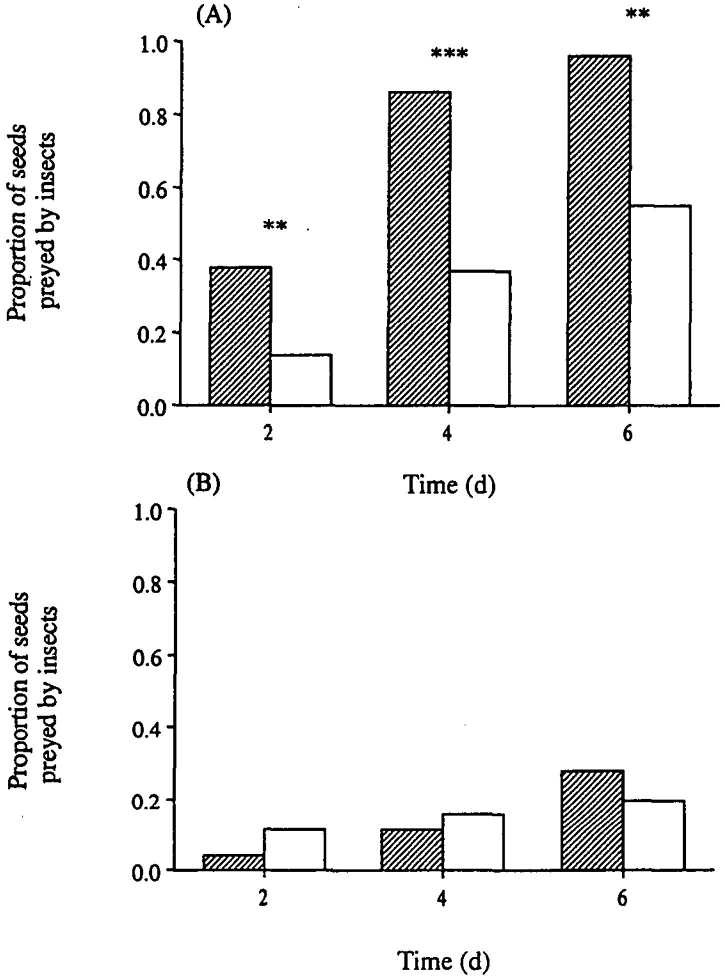

Figure 4. Proportion of *Cabralea canjerana* seeds preyed upon by insects on transects during the 6-d seed removal experiment at (A) Parque Estadual Intervales (PEI) and (B) Mata de Santa Genebra (MSG). Hatched bars refer to the seeds settled near (up to 20 m) fruiting trees (n = 150 and 100 for PEI and MSG, respectively), and open bars to those placed farther than 50 m away, near non-fruiting trees (n = 150 and 200 for PEI and MSG, respectively). Significance of chi-squared tests using Yates' correction: ** $P \leq 0.01$, *** $P \leq 0.001$.

ing for the attractiveness of this fruit to birds, since lipids constitute an important indicator of nutritional quality of fruits, which can influence food preferences of frugivorous birds (Johnson *et al.* 1985, Martin 1985, Stiles 1993).The nutritional quality of the aril of *C. canjerana* diaspores emphasizes the status of the Meliaceae as a plant group with high energy-rewarding fruits (Jordano 1993b).

As is typical for a large seed disperser assemblage (Schupp 1993), the main seed disperser at PEI, *T. cayana*, was responsible for a relatively low proportion of visits, and several other bird species accounted for a similar proportion of visits (see Figure 2). Based on data from several studies on avian seed dispersal, Schupp (1993) showed that the proportion of visits is positively correlated with the proportion of seeds dispersed by each bird species (see also Greenberg *et* *al.* 1995). Thus, given that most of the feeding assemblage recorded at PEI was comprised of legitimate seed dispersers, one can assert that several bird species contributed to the dispersal of a great proportion of *C. canjerana* seeds at this site. In contrast, at MSG only two species (*Vireo olivaceus* and *Myiodynastes maculatus*) were responsible for the bulk of visits, and the remaining bird visitors were probably relatively minor seed dispersers. Considering that each bird species is likely to produce a different seed shadow (Herrera & Jordano 1981, Izhaki *et al.* 1991, Jordano 1982), *C. canjerana* seeds probably reach a more diverse array of microhabitats at PEI than they do at MSG.

*Vireo* species may efficiently exploit arilate diaspores and act as seed dispersers (Greenberg *et al.* 1995). The overall importance of *V. olivaceus* as a seed disperser at MSG, however, seems to be highly influenced by its high frequency of visitation rather than to its diaspore handling efficiency. *Vireo olivaceus* is among the most common birds at both study sites from September to February, when it reaches PEI and MSG for reproduction (Aleixo & Vielliard 1995, M. A. Pizo, *pers. obs.*). Such high abundance could have influenced its high frequency of visitation observed at MSG. The larger diaspores of *C. canjerana* at PEI, however, probably precluded its exploitation by the relatively small-gaped *V. olivaceus* (see Figure 1), which was observed visiting the trees at that area only twice.

Although legitimate seed dispersers made the bulk of visits at both study sites, aril consumers at PEI, and *V. olivaceus* at MSG dropped many seeds beneath parent plants. Moreover, as a medium-sized seed that is invariably regurgitated by birds, *C. canjerana* seeds are likely to pass rapidly through the digestive tract of birds (Hoppes 1987, Levey 1987), thus increasing the opportunity for seeds to be regurgitated under the canopy during successive visits of legitimate seed dispersers to the same tree. Rodent and insect predators can act freely upon these seeds reducing their survival chances.

### *Seed predation*

Pre-dispersal seed predation was negligible at both study areas during the study period. Damage caused by insects on fruits in the canopy was low and extremely variable from one tree to another. *Pyrrhura frontalis* was a pre-dispersal seed predator at PEI, but it made few visits to only one tree and its impact on seed crops seems to be low. At MSG, the most common psittacid, the scaly-headed Parrot (*Pionus maximiliani*), was never observed eating *C. canjerana* diaspores (Galetti 1993). Capuchin monkeys (*Cebus apella*), however, due to their high density at MSG (M. A. Pizo, *pers. obs.*) can have a major impact on individual crops of *C. canjerana*. Troops of this primate at MSG are made of up to 22 individuals (Rodrigues *et al.* 1994) which can rapidly consume all the diaspores of several *C. canjerana* fruits.

The pattern of post-dispersal seed predation verified at PEI corresponds to the pattern found in other studies in tropical forests, i.e. insect predation concentrated under and in the immediate vicinity of fruiting trees (Howe *et al.* 1985, Janzen 1972, Ramirez & Arroyo 1987, Traveset 1990), and rodents preying on seeds irrespective of their distances to fruiting trees (Perry & Fleming 1980, Terborgh & Wright 1994, Terborgh *et al.* 1993; but see Coates-Estrada & Estrada 1988). The Atlantic forest rat *Delomys dorsalis* is the most abundant rodent at PEI (Olmos 1991), and probably is the main rodent predator of *C. canjerana* seeds there. Because insect predation is concentrated near fruiting trees, the survival probability of dispersed seeds is greater than that of seeds regurgitated or dropped beneath fruiting trees, where seeds have a negligible chance of escaping from rodent and insect predation before germination, which occurs 6 to 8 d after landing on soil surface.

Post-dispersal seed predation at MSG was less intense than at PEI, and somewhat different because insect predators did not concentrate their activities under or near fruiting trees. The higher rodent predation recorded near fruiting trees may be a consequence of the location of those trees near the forest edge, where rodents are likely to be especially common due to the proximity of plantations and human residences (Wilcove *et al.* 1986). We can thus expect that either seeds dropped under the trees by *V. olivaceus* and *D. cayana*, or those carried away may experience a similar chance of survival, which may be higher than at PEI. However, an unassessed factor may decrease the survival chance of *C. canjerana* seeds at MSG. The thin-coated seeds have to escape desiccation in the relatively drier climate of MSG where, in fact, desiccated seeds were commonly found on the leaf litter.

Rodent populations seem to have unusually low densities at MSG. During the study, only two grass mice, (*Akodon* aff. *cursor*), were captured in traps placed at the forest edge. In addition, a rodent survey involving 360 night-traps previously conducted at MSG yielded only opossums (*Didelphis* spp.) and no rodents (H. Bergallo, *pers. com.*). Such low densities may have accounted for the relatively low removal of seeds recorded at MSG. Nonetheless, terrestrial frugivorous birds, such as the tataupa tinamou (*Crypturellus tataupa*) and the white-tipped dove (*Leptotila verreauxi*) may have eaten some seeds and contributed to the final 67% removal. Both bird species have gape widths (mean = 6.9 ± 0.4 mm, and 5.2 ± 0.5 mm, respectively) large enough to swallow some of the *C. canjerana* diaspores at MSG, and presently are among the most common birds at MSG (Aleixo & Vielliard 1995).

### *Effects of fragmentation*

There is some evidence to indicate that habitat changes can alter dispersal systems (Howe 1984, Janzen 1972, Jordano 1995, Pudlo *et al.* 1980). Unfortunately, however, studies specifically designed to address this issue are lacking, mainly due to the absence of comparable studies carried out before and after the fragmentation of a given area. The present study conducted at MSG suffers the same constraint, but some of the results obtained deserve comment because they may have been influenced by the presently, and relatively welldocumented, altered state of the MSG fauna (Aleixo & Vielliard 1995, Chiarello & Galetti 1994, Galetti *et al.* 1994, Willis 1979).

The present avifauna of MSG is largely comprised of passerine species typical of disturbed habitats, which was reflected in the feeding assemblage recorded at this site. For instance, the five main seed dispersers of *C. canjerana* at MSG (Table 2) often frequent urban areas surrounding the reserve (M. A. Pizo *pers. obs.*), where they probably regurgitate some of the seeds they ingest. Thus, some of the seeds that leave the trees, especially from trees located in the forest edge, are likely to be lost in urban areas where the seeds have no chance of establishment (see Janzen 1983).

A striking characteristic of the MSG feeding assemblage is the overall dominance of migratory species. Willis (1979) noticed a higher abundance of summering migrants at MSG compared to two other forest fragments in southeastern Brazil. Although such species are generally insectivorous, they can include a great array of fruits in their diets and act as seed dispersers (Blake & Loiselle 1992). However, disperser assemblages dominated by migrant bird species are affected by temporal unpredictability (Jordano 1995, Martin & Karr 1986). Populations of migratory bird species are especially prone to high annual fluctuations due to events occurring in their breeding and winter grounds (see references in Hagan & Johnston 1992), which make them relatively unreliable seed dispersers. Thus, given the smaller feeding assemblage dominated by migratory species, we might expect a temporally more variable seed disperser assemblage at MSG than at PEI, with unknown long-term consequences for seed removal and seed dispersal efficiency (but see Guitián *et al.* 1992, Jordano 1995). It is important to notice that the feeding assemblage recorded at MSG is more complete than at PEI. With the exception of the red-crowned ant-tanager (*Habia rubica*) and the ruby-crowned tanager (*Tachyphonus coronatus*), all of the most common bird species including fruits as part of their diets in MSG were recorded at *C. canjerana* trees. At PEI, in contrast, some common frugivorous species (e.g. dusky-legged guan [*Penelope obscura*], white-tailed trogon [*Trogon viridis*], bare-throated bellbird [*Procnias nudicollis*], and cinnamon-vented piha [*Lipaugus lanioides*]) were not recorded at the fruiting trees.

The low density of rodents cited above may be a result of fragmentation as well. Fonseca & Robinson (1990) suggested that forest fragments are likely to suffer a reduction in small mammal populations. This may decrease the predation pressure on the seeds, with consequences for the structure and spatial distribution of plant populations (Mittelbach & Gross 1984). Similarly, the unusual high abundance of ground frugivorous birds such as *C. tataupa* and *L. verreauxi* may prove to have an impact on seed establishment. Although conclusive studies are lacking, tinamous and doves are generally considered seed predators (Érard & Sabatier 1986, Lambert 1989). Willis (1979) had already noticed an unusual increase in the abundance of both these species at MSG as a consequence of fragmentation.

Further investigations are needed to test the consequences of the presently altered fauna of MSG on the population dynamics of *C. canjerana*. Additionally, a promising future study should investigate the influence of such likely altered biotic inter-relations on *C. canjerana* fruit traits and its evolutionary differentiation (see Keeler-Wolf 1988).

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