

Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree

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Summary

1 We studied the dispersal system of the tree *Clusia criuva* (Clusiaceae) in a tropical rain forest in south-east Brazil. An observational/experimental approach was adopted to estimate the probability of transitions between consecutive stages in the recruitment process (i.e. fruit production and removal by birds, ant–seed interactions on the forest floor, seed germination, and establishment and early survival of seedlings).

2 *Clusia* trees produce hundreds of capsules with small lipid-rich arillate seeds. Crop size ranges from 393 to 3709 capsules per tree. Birds (14 species) eat 83% of the diaspores on the tree, while the remaining 17% fall to the ground and are removed by ants (16 species).

3 Ants remove 89% of the fallen diaspores and 98% of the seeds found in bird faeces. Ponerine ants (*Odontomachus*, *Pachycondyla*) carry the diaspores to their nests, while small myrmicines (*Pheidole*, *Crematogaster*) remove the aril where found. Aril removal by ants and removal of seeds from bird defecations increase germination success in *C. criuva*.

4 Seedlings are more frequent close to ponerine nests than in control areas without such nests. Early seedling survival (1 year) in nests of *Pachycondyla striata* is greater than in control areas. Soil samples from nests of *P. striata* also had higher concentrations of total nitrogen and phosphorus than random soil samples.

5 This is the first study to demonstrate the combined effects of ants on the distribution and survival of seedlings of a primarily vertebrate-dispersed plant in a tropical forest.

Key-words: ants, birds, Brazil, *Clusia*, Clusiaceae, seed dispersal, seedling survival, tropical rain forest

Journal of Ecology (2002) **90**, 517–528

Introduction

Seeds that are dispersed primarily by frugivorous vertebrates may also be secondarily distributed by ants (reviewed by Böhning-Gaese *et al.* 1999). The ecological consequences of ant activity in such two-phase dispersal systems are still poorly understood (but see Kaufmann *et al.* 1991; Pizo & Oliveira 1998; Böhning-Gaese *et al.* 1999), unlike those of myrmecochorous (i.e. ant-dispersed) species with elaiosome-bearing seeds (e.g. Hanzawa *et al.* 1988; Hughes & Westoby 1992a,b; Garrido *et al.* 2002).

Typical myrmecochorous species occur worldwide but are especially common in arid Australia and South Africa, and temperate forests (Beattie & Culver 1981; Milewski & Bond 1982; Beattie 1985). Although

myrmecochory can be an important dispersal strategy for some plant taxa in neotropical forests (Horvitz & Beattie 1980; Passos & Ferreira 1996), nearly 90% of dicots there have fleshy fruits and rely on vertebrate frugivores for seed dispersal (Frankie *et al.* 1974). Many diaspores are found on the forest floor (Jordano 1993), where they have fallen, been dropped by frugivores (Howe 1980; Laman 1996) or deposited in vertebrate faeces (Kaspari 1993; Pizo & Oliveira 1999), and the abundance of litter-foraging ants (Hölldobler & Wilson 1990) suggests that ant–diaspore interactions may be common. Indeed, a 2-year survey carried out in the Atlantic forest of south-east Brazil recorded 886 ant–diaspore interactions involving 36 ant species and 56 plant species (Pizo & Oliveira 2000). Recent studies in neotropical areas have shown that ants can rearrange the seed shadow generated by vertebrate dispersers (Roberts & Heithaus 1986; Kaspari 1993), affect seed bank dynamics (Levey & Byrne 1993), facilitate seed germination (Oliveira *et al.* 1995; Leal & Oliveira 1998; Pizo & Oliveira 1998) and promote seedling establishment

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(Levey & Byrne 1993; Farji Brener & Silva 1996; Farji Brener & Medina 2000) of primarily vertebrate-dispersed plants. Nevertheless, little is known about how ants affect patterns of recruitment and survival of seedlings of non-myrmecochorous species (but see Böhning-Gaese *et al.* 1999).

This study was designed to assess the effect of ants on seed and seedling fate of a primarily bird-dispersed tree, *Clusia criuva* Camb. (Clusiaceae), in a rain forest in south-east Brazil. Five questions were addressed: (i) How much fruit is removed by birds in the canopy, and how much reaches the forest floor? (ii) What role do ants and/or vertebrates play in the removal of fallen diaspores? (iii) Do ants remove *C. criuva* seeds from bird faeces? (iv) Is germination affected by ingestion by birds, aril removal by ants or removal of seeds from bird faeces? (v) Can ant–seed interactions affect the distribution and survival of *C. criuva* seedlings?

We considered *Clusia*'s dispersal system as a continuous multistep sequence of demographic stages (Herrera *et al.* 1994) and used an observational/experimental approach to assess the predictions for seed fate, from fruit production to germination and seedling establishment.

Methods

STUDY SITE

Fieldwork was carried out from January 1998 to April 1999 in the sandy plain forest (locally called '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 a.s.l.) located off the coast of São Paulo State, south-east Brazil. Sandy plain forests are part of the Atlantic forest domain and frequently adjoin coastal rain forests, from which they differ by having an open canopy, dominant low stature trees and abundant epiphytes (Joly *et al.* 1999; Oliveira-Filho & Fontes 2000). At PEIC the well-preserved sandy plain forest grows on poor sandy soils (2–3 m a.s.l.); trees 5–15 m tall form an open canopy and bromeliads are abundant on the ground. Mean annual temperature and rainfall are 20.9 °C and 3000 mm, respectively (Barros *et al.* 1991). The climate is generally warm and wet throughout the year but may be divided into two seasons: a cold and drier period from April to August when temperature may drop to nearly 13 °C and rainfall is *c.* 500 mm, and a warm and rainier period from September to March when temperature may reach 32 °C and rainfall 1800 mm (Funari *et al.* 1987; Oliveira-Filho & Fontes 2000).

THE PLANT AND THE BIRDS

Clusia criuva is a common dioecious tree in the sandy plain forest (see Joly *et al.* 1999) on the coast of south-east Brazil, and is among the most frequent tree species at the study site. Mature fruits occur from January to



Fig. 1 Mature fruit of *Clusia criuva*. Capsules dehisce to expose five diaspores (arrow), each containing 0–17 seeds and enveloped by a lipid-rich aril.

March, and the species presents great interannual variation in seed output. Fruits are globular capsules (*c.* 30 mm diameter, Fig. 1) that dehisce to expose five diaspores (mean \pm SD 9.78 \pm 1.64 mm length, 5.46 \pm 0.90 mm wide, $n = 150$) containing 0–17 seeds each (4.38 \pm 3.98 seeds, $n = 750$ diaspores). The diaspore (i.e. the unit of dispersal) consists of seeds enveloped by a red aril, with an overall fresh weight of 0.10 \pm 0.05 g ($n = 150$). The aril of *C. criuva* has one of the highest lipid contents (83.4%, Passos & Oliveira, unpublished data; method follows Bligh & Dyer 1959) yet described in the literature (Jordano 1993). Total carbohydrate, protein and ashes account for 9.17%, 6.46% and 0.97% of the dry mass, respectively (methods follow AACC 1995; see also Pizo & Oliveira 2001). Arillate seeds are dispersed by at least 14 bird species, which ingest the whole diaspore and defecate intact seeds, and are thus legitimate seed dispersers, and occasionally drop intact diaspores beneath the parent plant (M. A. Pizo, unpublished data).

FRUIT PRODUCTION AND DIASPORE REMOVAL BY BIRDS

Fruit traps were used to evaluate fruit production and diaspore dispersal rates by primary dispersers. Traps were placed under 10 trees of *C. criuva* and consisted of 0.21 m² woody frames covered with fabric. We applied a sticky resin to the borders of the traps to prevent ants from reaching fruit debris. We placed 8–13 traps under each tree, covering 23–70% of the area beneath the tree crowns, to catch fallen capsules and diaspores, as well as seeds embedded in bird faeces. We removed and counted fruit debris in the traps every 2 days throughout the entire fruiting season of 1998. A few capsules contained only three to four (rather than five) well-formed valves with diaspores, or occasionally opened only two to three valves to expose diaspores, but we were always able to record the number of open valves and thus the number of diaspores that were available to animal dispersers. Even if seeds are removed by birds in

the canopy, capsules are left and reach the forest floor intact, thereby allowing us to estimate the number of capsules and diaspores produced by the tree. We also estimated how much of the crop was removed by birds, and the number of diaspores that reached the forest floor (see Howe & Kerckhove 1981; Blake *et al.* 1990).

DIASPORE REMOVAL BY ANTS VERSUS VERTEBRATES

Seed removal by ants and vertebrates was assessed by performing an enclosure experiment. Pairs of diaspores (marked with a small dot of enamel paint, Testors, Rockford, USA) were set out at about 08.00 hours at five stations placed radially beneath fruiting trees ($n = 40$) of *C. criuva* (ants appeared to treat marked and unmarked diaspores similarly). Bird activity in *Clusia* trees is greatest, and most diaspores reach the forest floor, in the early morning. Each pair consisted of a diaspore placed directly on the forest floor under a wire cage ($17 \times 17 \times 8$ cm, 1.5 cm mesh) closed on the top and staked to the ground to exclude vertebrates (see Roberts & Heithaus 1986; Kaspari 1993), and an unenclosed diaspore. Locations were marked with wooden stakes and a given diaspore was considered removed if, after 24 h, it was not found within 30 cm of the stake. We excluded any trial subjected to rain from the analysis. Data on diaspore removal were analysed using nested analysis of variance. The dependent variable was the number of diaspores removed, using tree as nesting factor. The independent variables were tree number and caging (caged versus uncaged). We performed $\log(x + 1)$ transformations on the number of diaspores removed to stabilize treatment variances for the statistical analysis.

ANT-DIASPORE INTERACTIONS

To determine which ants interact with fallen diaspores of *C. criuva*, we recorded all ant-diaspore interactions observed throughout the entire 1998 fruiting season. Systematic sampling was also conducted, whereby two marked diaspores were set out at each of three stations placed radially beneath fruiting trees ($n = 20$). The diaspores were placed on small pieces (4×4 cm) of white filter paper, to facilitate visualization on leaf litter, and protected from vertebrate disturbance by wire cages. Filter paper did not appear to deter any ant species or other potential seed dispersers (see Byrne & Levey 1993; Pizo & Oliveira 2000). Diaspores were set at 07.30 hours and 15.00 hours and checked at 15-min intervals ('scan sampling' *sensu* Lehner 1979) over a period of 2 hours, recording which ants were attracted, as well as whether they removed the diaspores and/or recruited nestmates to exploit them on the spot. We followed ants carrying diaspores until they entered their nests or disappeared in the leaf litter. The distance of diaspore displacement was then measured. Many

diaspores that were first discovered by small myrmicine ants were further dispersed by ponerine ants. Because we wanted to characterize the ultimate fate of seeds, we defined an interaction between diaspores and small ants as having occurred if *c.* 30 ants were recruited, or *c.* 40% of the aril had been removed, at which stage diaspores were no longer removed by ponerine ants.

Voucher specimens of the ants and plant are deposited in the collection of the Universidade Federal Rural do Rio de Janeiro (CECL) and at the herbarium of the Universidade Estadual de Campinas (UEC), respectively.

REMOVAL OF SEEDS FROM BIRD FAECES

Bird faeces (*c.* 2.0 cm long) containing seeds of *C. criuva* with bits of aril attached were abundant in the early morning at the study site. We collected fresh faeces and prepared small faecal portions (*c.* 2 cm long) with 15 seeds each (see Kaspari 1993), which were placed on small pieces of white filter paper (4×4 cm) on the leaf litter and protected by wire cages. One faecal portion was set beneath each of 30 fruiting trees of *C. criuva* at 08.00 hours (see Kaspari 1993) and the number of seeds remaining counted after 24 h. The ant species attracted to the faeces, as well as their behaviour towards the embedded seeds, were recorded in scan samples taken at 15-min intervals from 08.00 to 09.00 hours. We followed ants carrying seeds until they entered their nests or disappeared in the leaf litter. The displacement distance was then measured.

SEED GERMINATION

To determine whether germination is affected by ingestion of diaspores by birds, aril removal by ants or removal from bird faeces, seeds were placed in 11×11 cm boxes containing homogenized soil collected locally and passed through a 2-mm mesh soil screen. Seeds were placed on the surface of the soil, 2–4 cm apart from each other with a box receiving either: (i) seeds coated by an aril (1–14 seeds in each of 10 diaspores); (ii) 20 cleaned seeds (aril removed by ants); (iii) four groups of five seeds each embedded in a 1-cm-long fresh fecal portion; or (iv) 20 seeds isolated by us from bird faeces. Fresh diaspores and bird faeces were collected on the forest floor. The boxes were covered with nylon mesh to prevent influx of other seeds, and a barrier of tanglefoot on the external walls prevented ants from entering. To control for unknown effects of light and temperature, germination tests were performed at four forest locations where *Clusia* seedlings occurred naturally. We checked for radicle protrusion at 2-day intervals. We used the CATMOD procedure of SAS (SAS Institute 1988) to detect variation in the proportion of seeds that germinated as a function of site (the four locations), seed treatment and site-by-treatment interaction. This procedure is designed to analyse data when the response variable is categorical,

and its interpretation is analogous to an analysis of variance.

DISTRIBUTION AND SURVIVAL OF SEEDLINGS

The number of seedlings of *C. criuva* growing on nests of ponerine ants as compared with control areas (without nests) was determined in April 1998 by establishing paired experimental plots (0.5 × 0.5 m). Nests were located by following ant workers that had been attracted to tuna baits placed on the forest floor (Horvitz 1981): *Pachycondyla striata* and *Odontomachus chelifer* nests (21 and 20, respectively) were tagged and a control plot was established 2.5 m in a random direction from each nest. These two ponerine species are very abundant at our study site and accounted for a significant number of the ant–seed interactions recorded at fresh diaspores and faeces containing seeds of *Clusia criuva* (see below). Seedlings within plots were marked and monitored every 2 months for a year. Differences in the number of seedlings growing in nest and control plots were analysed with Wilcoxon paired-sample sign rank tests (Zar 1999). Survivorship curves of seedlings were constructed and differences analysed using Peto and Peto's logrank test (Pyke & Thompson 1986). Soil samples were collected from nests of *P. striata* ($n = 15$), *O. chelifer* ($n = 15$) and from control plots ($n = 15$ relative to each ant species), air-dried and analysed for total N, macronutrients, micronutrients, pH, organic matter (Sparks *et al.* 1996) and texture (Day 1986). Differences in soil variables between nest and control plots were analysed with Wilcoxon paired-sample sign rank tests.

Results

FRUIT PRODUCTION AND DIASPORE REMOVAL BY BIRDS

In 1998, the fruiting period of *C. criuva* extended over 85 days (January–March), but values for individual trees ranged from 46 to 61 days (54 ± 6 days, $n = 10$). During this season, birds removed an average of 83% of the diaspores from each tree, while most of the remainder fell to forest floor (spontaneously or dropped by birds) (Table 1). On average, 1640 (SD = 810, $n = 10$ trees) viable seeds embedded in bird faeces were found beneath trees of *C. criuva*, but some of these may have

originated from other conspecific trees. No pre-dispersal seed predation was recorded at the study site.

DIASPORE REMOVAL BY ANTS VERSUS VERTEBRATES

Mean diaspore removal rates within 24 h were similar in enclosure ($89 \pm 18.1\%$) and control ($91.5 \pm 15.6\%$) treatments ($F_{1,319} = 0.828$, $P = 0.363$), indicating that ants are primarily responsible. Diaspore removal, however, varied significantly with tree location ($F_{(78, 319)} = 1.896$, $P = 0.0001$). Ants rapidly discovered the diaspores of *C. criuva* on the forest floor. Interactions took place mainly during daytime and most experimental diaspores had been removed or cleaned by the end of the day, *c.* 18.00 hours (77% of caged and 77.5% of uncaged diaspores; $n = 200$ for each treatment). Sixteen ant species were attracted to the diaspores (Table 2). Results from systematic surveys show that the ponerines *Pachycondyla striata* and *Odontomachus chelifer* accounted for 34% of ant–diaspore interactions ($n = 35$ records) and were the main seed vectors among ants. *Pachycondyla striata* and *O. chelifer* (Fig. 2a) displaced seeds in diaspores and seeds within faeces (pooled data) to considerable distances (*P. striata*: mean \pm SD = 1.50 ± 2.15 m, range = 0.10–10.10 m, $n = 20$; *O. chelifer*: 2.33 ± 1.33 m, range = 0.80–6.00 m, $n = 20$). The two ponerines carried seeds into their nests in 70% and 95% of the records ($n = 20$ for each species), respectively. Large attines (*Acromyrmex*) removed diaspores to a mean distance of 2.40 m (SD = 2.01, range = 0.40–5.30, $n = 7$). Other ants, mainly *Pheidole*, *Crematogaster* and *Solenopsis*, typically recruited nest-mates to remove the aril on the spot, without displacing the seeds from beneath the parent plant ($n = 79$ records, including non-systematic observations).

REMOVAL OF SEEDS FROM BIRD DEFECATIONS

The only seeds in bird faeces found on the ground were those of *C. criuva*. Sixteen ant species were recorded at bird faeces, 11 of which removed seeds (Table 2). Embedded seeds had bits of aril attached and on average 98.5% of the seeds were removed from faeces after 24 h ($n = 30$ experimental faeces, each containing 15 seeds). Ponerine ants (mainly *P. striata*) accounted for 12% of the ant records at embedded seeds ($n = 49$ ant records in 30 experimental faeces).

Table 1 Production and fate of diaspores from 10 *Clusia criuva* trees in the Atlantic rain forest of Cardoso Island, SE Brazil

| Fate | Number of diaspores | | Percentage of diaspores | |
|----------------------|---------------------|-----------------|-------------------------|------|
| | Range | Mean \pm SD | Range | Mean |
| Produced | 1890–18264 | 5795 \pm 4892 | – | – |
| Removed by birds | 1446–15632 | 4901 \pm 4279 | 72–91 | 83.0 |
| Fallen to the ground | 307–2627 | 876 \pm 668 | 9–26 | 16.6 |
| Rotten | 0–56 | 19 \pm 19 | 0–1.6 | 0.4 |

Table 2 Ant behaviour toward fallen diaspores and faeces-embedded seeds of *Clusia criuva* in the Atlantic rain forest of Cardoso Island, SE Brazil. Frequency is provided only for data obtained in systematic surveys (in which species marked * were not recorded); values are percentage of records for each ant species relative to the total number of interactions observed at diaspores (35) and faeces (49). Behaviour: A = ants remove portions of diaspores (aril + seeds) and displace them over more than 5 cm; C = clean seeds by removing portions of the aril or of the faecal mass on the spot, no displacement; D = remove seeds (> 5 cm) isolated from bird defecations; E = inspect or manipulate diaspore or defecation, no removal; I = ignore defecation; R = remove diaspores or portions of bird defecations with seeds; S = clean aril on the spot and then remove seeds. Total interactions also include non-systematic records of *Clusia* seeds being explored by ants

| Ant subfamily and species | Percentage (behaviour) | |
|--|----------------------------|-------------------------|
| | Diaspore (<i>n</i> = 168) | Faeces (<i>n</i> = 58) |
| Ponerinae | | |
| <i>Gnamptogenys moelleri</i> | 8.6 (A) | |
| <i>Hypoponera</i> sp.* | (E) | |
| <i>Odontomachus chelifer</i> * | 8.6 (R) | (E, I, R) |
| <i>Odontomachus</i> sp. | 5.7 (E, R) | |
| <i>Pachycondyla striata</i> | 25.7 (R) | 12.2 (R) |
| Myrmicinae | | |
| <i>Acromyrmex aspersus</i> | | 8.2 (D) |
| <i>Acromyrmex crassipinus</i> | | 4.1 (D) |
| <i>Acromyrmex subterraneus</i> | 8.6 (R) | |
| <i>Acromyrmex</i> sp.* | (R) | |
| <i>Cyphomyrmex</i> sp. | | 2.0 (D) |
| <i>Crematogaster</i> sp. | 5.7 (S) | 16.3 (C, D, S) |
| <i>Pheidole</i> sp. 1 | 5.7 (S) | 30.6 (C, D) |
| <i>Pheidole</i> sp. 2* | (E, C) | |
| <i>Pheidole</i> sp. 3 | 20.0 (S) | 6.1 (E, S) |
| <i>Pheidole</i> sp. 4 | | 4.1 (C) |
| <i>Pheidole</i> sp. 5 | | 2.0 (C) |
| <i>Pheidole</i> sp. 6 | | 2.0 (C) |
| <i>Pheidole</i> sp. 10* | (C) | |
| <i>Solenopsis</i> sp. 1 | | 4.1 (C) |
| <i>Solenopsis</i> sp. 4* | (C) | |
| <i>Wasmannia</i> sp. | 5.7 (C, S) | 2.0 (C, D) |
| Ecitoninae | | |
| <i>Labidus</i> sp. | 2.9 (A) | 2.0 (D) |
| Formicinae | | |
| <i>Paratrechina</i> sp. 1 | | 2.0 (C, D) |
| <i>Paratrechina</i> sp. 2 | 2.9 (C) | 2.0 (C) |
| Number of interactions in systematic surveys | 35 | 49 |
| Total number of interactions | 79 | 62 |
| Removal rate (after 24 h) | 89% | 98.5% |

SEED GERMINATION

Germination of *C. criuva* seeds is exceptionally rapid (< 8 d). Although ingestion of diaspores by birds does not affect germination success (71.0% for non-ingested seeds against 67.5% for embedded seeds), both removal of seeds from bird defecations (82.5% for isolated seeds against 67.5% for embedded seeds) and aril removal by ants (83.1% for nonarillate against 71.0% for arillate seeds) increase the germination success significantly (Table 3).

DISTRIBUTION AND SURVIVAL OF SEEDLINGS

Seedlings of *C. criuva* are more abundant in the vicinity of nests of *P. striata* ($Z = -3.869$, $P < 0.0001$, $n = 21$) and *O. chelifer* ($Z = -2.964$, $P = 0.003$, $n = 20$) than in areas without nests (Figs 2b and 3). Seedling survival is

greater near nests of *P. striata* than in control areas ($\chi^2 = 14.18$, $P = 0.0002$) but is not affected by proximity to *O. chelifer* nests ($\chi^2 = 1.31$, $P = 0.2526$) (Fig. 4). Soil analyses indicate that the concentrations of total nitrogen, phosphorus, iron and boron are significantly higher at *P. striata* nests than at random locations, but no difference was found for other essential plant macronutrients (Table 4). Soil variables did not differ between *O. chelifer* nests and control samples.

Discussion

THE MULTISTEP DISPERSAL PROCESS IN *CLUSIA CRIUVA*

This study shows that the dispersal ecology of *Clusia criuva* involves complex interactions between the plant, its guild of bird primary dispersers and its many ant

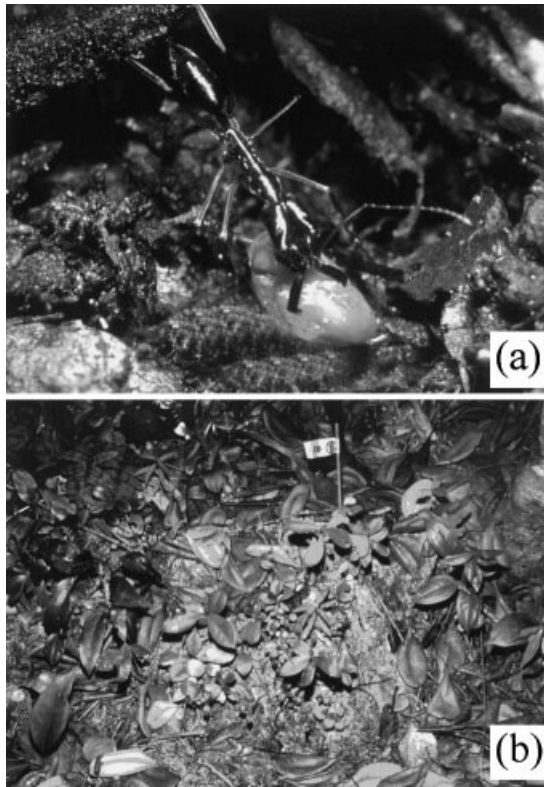


Fig. 2 (a) Worker of *Odontomachus chelifer* (size *c.* 1.8 cm) removing a diaspore of *Clusia criuva* on the leaf litter of a rain forest in south-east Brazil. The ants regularly carry the diaspores to the nest, where the aril is consumed and the seeds discarded. (b) Seedlings of *C. criuva* clumped in the refuse pile of a nest of *O. chelifer*.

secondary dispersers. Figure 5 summarizes the possible sequential events in the life of the seed, and indicates that ant–seed interactions markedly affect seed fate in this primarily bird-dispersed species. Eighty-three per cent of the diaspores produced are taken by birds, and seeds reach the forest floor either in bird faeces or as fallen fresh diaspores. Most seeds embedded in faeces are removed by ants within 24 h, and large ponerines (*Odontomachus* and *Pachycondyla*) account for *c.* 12% of seed removal. Approximately 90% of the fresh diaspores on the ground surface are also removed in 24 h, and ants are responsible for 97.5% of this removal (*c.* 34% due to *P. striata* and *O. chelifer*). Inside the colony, these ants remove the lipid-rich aril and

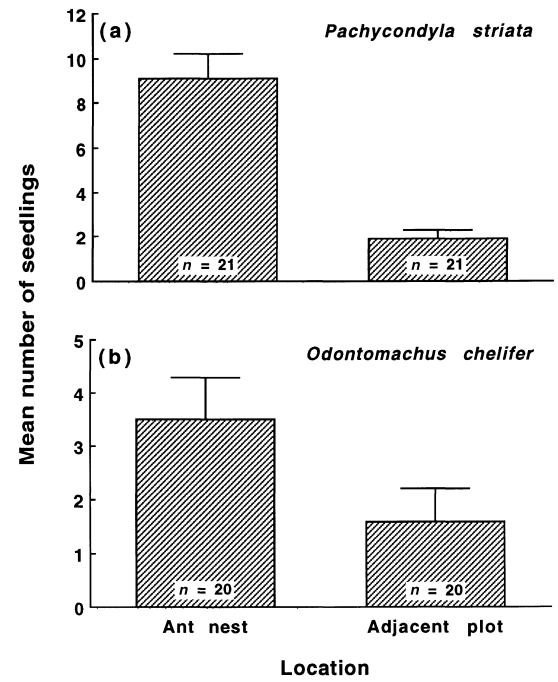


Fig. 3 Mean number (\pm SE) of seedlings of *Clusia criuva* on nests of *Pachycondyla striata* (a) and *Odontomachus chelifer* (b), and in adjacent control plots.

discard the seeds on refuse piles. Aril removal and separation from bird defecations increase germination success and this, together with the secondary dispersal, markedly affects the distribution of *C. criuva* seedlings. Furthermore, seedling survival is also greater in nests of *P. striata* than in control areas, and this is possibly related to a richer soil near the nests.

ANT ACTIVITY AT FALLEN SEEDS

Although information on fruit production by trees and fruit removal by vertebrate dispersers is relatively scarce, a considerable portion of the fruits is often reported to reach the floor either spontaneously or dropped by vertebrate frugivores (e.g. Howe & Kerckhove 1981; Masaki *et al.* 1994; Laman 1996). Once on the ground, such fleshy diaspores (in *C. criuva* 17% of the copious production) become available for litter-foraging vertebrates and invertebrates (Pizo & Oliveira 1998; Böhning-Gaese *et al.* 1999).

Table 3 Categorical analysis of the probability of seed germination in *Clusia criuva* at four forest locations. All significant sources of variation are shown in bold

| Source | d.f. | Treatment categories | | | | | |
|-------------------------|------|----------------------|---------------|------------------------------|---------------|----------------------|---------------|
| | | Ingestion by birds | | Removal of seeds from faeces | | Aril removal by ants | |
| | | χ^2 | <i>P</i> | χ^2 | <i>P</i> | χ^2 | <i>P</i> |
| Intercept | 1 | 29.97 | 0.0000 | 31.88 | 0.0000 | 90.14 | 0.0000 |
| Site | 3 | 14.49 | 0.0023 | 29.14 | 0.0000 | 3.60 | 0.3075 |
| Treatment | 1 | 0.00 | 0.9975 | 4.14 | 0.0420 | 7.71 | 0.0055 |
| Site \times treatment | 3 | 18.89 | 0.0003 | 3.41 | 0.3327 | 8.22 | 0.0417 |

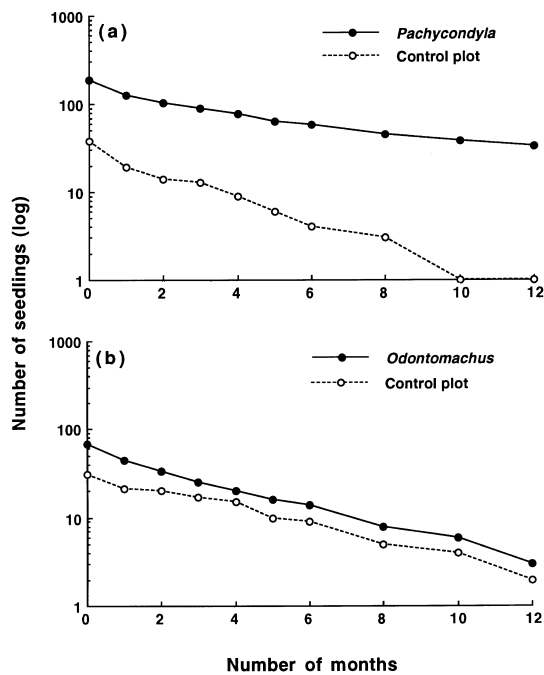


Fig. 4 Survivorship curves for *Clusia criuva* seedlings growing on nests of *Pachycondyla striata* (a), *Odontomachus chelifer* (b), and in control plots between April 1998 and April 1999.

Fourteen bird species feed on *C. criuva* diaspores in the early morning when there is plenty of fruit available (M.A. Pizo, personal communication). Seeds are likely to pass rapidly through the digestive tract of birds, as fresh seed-containing faeces are abundant in the early morning on the forest floor. The great number of viable seeds found in faeces beneath fruiting trees (c. 1640 seeds), and the absence of seeds of other species, suggest that *C. criuva* is an important food source for birds in years of massive fruit production.

We have never seen *C. criuva* seeds attacked by beetles or any other predators, but some of the ant genera (e.g. *Pheidole*) found in the study site are known to eat seeds (Hölldobler & Wilson 1990; Moutinho 1991). Recent studies, however, have shown that although most of the retrieved seeds are eaten by such ants, some of them escape predation and become established, which is likely to affect plant recruitment patterns (Byrne & Levey 1993; Levey & Byrne 1993).

Seeds of *C. criuva* thus reach the forest floor both in diaspores and embedded in bird faeces. The attractive diaspores are rapidly removed by ants and are thus less likely to be eaten by rodents. The assemblage of ants (16 species) and their behaviour towards lipid-rich diaspores of *C. criuva* at PEIC are similar to those found for other arillate species (Horvitz & Beattie 1980; Horvitz 1981; Pizo & Oliveira 1998). Our estimates of seed displacement (pooled data for fresh diaspores and seeds in bird faeces) by ponerine ants are also similar to those reported for other *Pachycondyla* and *Odontomachus* species (up to 10 m) with arillate seeds of *Calathea* in Mexican forests (Horvitz & Beattie 1980). Not only are large ponerines the main removers of *Clusia* seeds, but their importance is enhanced because they do not harm the seeds.

Clusia seeds within faeces are also rapidly removed by ants on the forest floor and the removal rate (98%) is among the highest yet described in the literature (Roberts & Heithaus 1986; Kaspari 1993; Pizo & Oliveira 1999). This is possibly due to the bits of aril that remain attached to the seeds and to the small size of the seeds allowing displacement by a large assemblage of ants (Davidson 1977). Studies that examine ant–seed interactions in both fruits and faeces are scarce but it seems that seeds in fruits are more attractive to ants than those embedded in faeces (Roberts &

Table 4 Comparison of soil variables from nests of *Pachycondyla striata* ($n = 15$) and *Odontomachus chelifer* ($n = 15$) with those of random spots on the forest floor ($n = 15$ for each ant species). Mean values of K, Ca, Mg, Na, Al, H + Al, and C.E.C. (cation exchange capacity) are given in mmol dm^{-3} ; P, S, B, Cu, Fe, Mn, and Zn in mg dm^{-3} ; organic matter in g dm^{-3} ; N in g kg^{-1} and texture as percentages

| Soil variable | <i>P. striata</i> | Random | Wilcoxon's <i>P</i> | <i>O. chelifer</i> | Random | Wilcoxon's <i>P</i> |
|----------------|-------------------|--------|---------------------|--------------------|--------|---------------------|
| Total nitrogen | 14.3 | 9.9 | 0.003 | 12.2 | 10.4 | 0.198 |
| Phosphorus | 18.00 | 15.67 | 0.030 | 16.7 | 13.3 | 0.191 |
| Potassium | 1.51 | 1.53 | 0.248 | 1.54 | 1.29 | 0.139 |
| Zinc | 1.31 | 1.09 | 0.093 | 1.46 | 1.33 | 0.060 |
| Iron | 36.87 | 24.93 | 0.011 | 38.47 | 37.20 | 0.955 |
| Manganese | 21.29 | 19.09 | 0.820 | 14.45 | 11.84 | 0.955 |
| Cooper | 0.11 | 0.12 | 0.414 | 0.14 | 0.12 | 0.461 |
| Calcium | 1.73 | 1.60 | 0.729 | 3.40 | 1.40 | 0.048 |
| Magnesium | 4.27 | 4.40 | 0.677 | 4.27 | 4.40 | 0.783 |
| Boron | 0.26 | 0.20 | 0.006 | 0.23 | 0.20 | 0.650 |
| Fine sand | 7.78 | 6.85 | 0.044 | 6.87 | 5.71 | 0.427 |
| Coarse sand | 83.10 | 85.43 | 0.532 | 86.20 | 89.03 | 0.706 |
| Silt | 6.16 | 4.97 | 0.061 | 3.55 | 2.34 | 0.675 |
| Clay | 2.97 | 2.76 | 0.164 | 3.38 | 2.94 | 0.629 |
| Organic matter | 79.73 | 70.60 | 0.132 | 77.3 | 67.4 | 0.187 |
| C.E.C. | 137.91 | 117.53 | 0.156 | 166.87 | 135.42 | 0.281 |
| H + Al | 130.20 | 109.60 | 0.363 | 157.67 | 128.33 | 0.426 |
| pH | 3.27 | 3.32 | 0.440 | 3.23 | 3.25 | 0.861 |

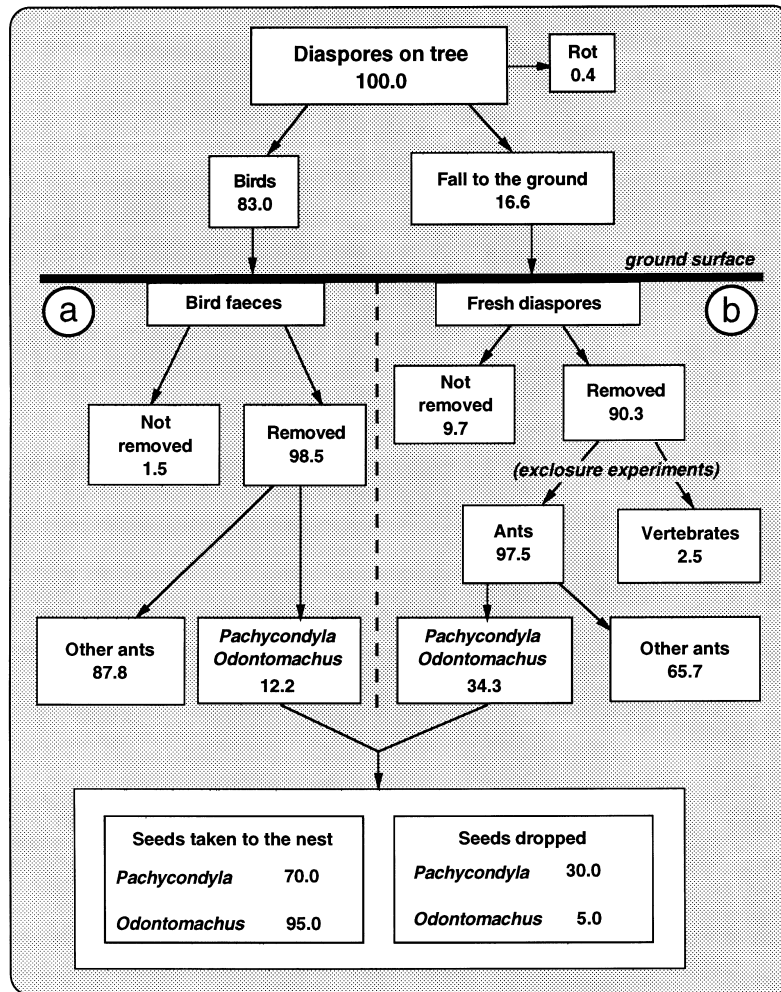


Fig. 5 Illustration of the seed dispersal process in *Clusia criuva* for the fruiting period of 1998. The starting point is 100% diaspores produced, of which on average 83.0% are taken by birds, 16.6% fall to the ground and 0.4% rot. Seeds reach the forest floor in bird faeces (a) or in diaspores (b). On average, 98.5% of the seeds embedded in faeces are removed by ants in 24 h, and *P. striata* and *O. chelififer* account for 12.2% of seed removal. Approximately 90.3% of fresh diaspores on the ground surface are removed in 24 h, and ants are responsible for 97.5% of removal. *P. striata* and *O. chelififer* together remove 34.3% of the diaspores. Faeces-embedded seeds and diaspores (the diaspore consists of seeds enveloped by a red aril) of *Clusia* are taken by *Pachycondyla* to nests in 70.0%, and by *Odontomachus* in 95.0%, of the records. See Table 1 and text for further details.

Heithaus 1986). Ants of the subfamily Myrmicinae are known to be the prominent removers of seeds from faeces of vertebrate frugivores of neotropical forests (e.g. Roberts & Heithaus 1986; Byrne & Levey 1993; Kaspari 1993) and the percentage occurrence of ponerines at faeces with *C. criuva* seeds is much higher (12%) than that recorded for other plant species (see Kaspari 1993; Pizo & Oliveira 1999).

Ant species is a key factor determining the fate of seeds because the behaviour of different species may affect not only seed survival, but also their distribution, chance of germination and establishment (Hughes & Westoby 1992a). Therefore, seeds of *C. criuva* may benefit from being exploited by a wide ant assemblage, including large ponerines. Although ants belonging to this subfamily are generally regarded as predominantly carnivorous (Hölldobler & Wilson 1990), they also exploit fleshy diaspores and disperse seeds of many plants in different habitats (Horvitz & Beattie

1980; Davidson & Morton 1981; Déjean & Lachaud 1994; Pizo & Oliveira 1998; Fourcassié & Oliveira 2002).

Given the differences in behaviour of ant species towards seeds (Hughes & Westoby 1992a), the composition of the ground-dwelling ant assemblage could be an important factor determining the fate of a seed on the forest floor. Pizo & Oliveira (2000) have shown that the use of fallen diaspores by ants in the Atlantic rain forest of Brazil occurs according to the relative abundance of different ants on the forest floor. *Odontomachus chelififer* and *Pachycondyla striata* are very abundant at our study site and were attracted to 23% and 31% of the tuna baits placed on the ground, respectively, with 52% of baits attracting at least one of these species (Passos & Oliveira, unpublished data). Besides removing seeds from faeces, these large ponerines also accounted for 34% of the ant records at *C. criuva* diaspores.

ANT EFFECTS ON SEED BIOLOGY

Germination in *C. criuva* is rapid, a common trait of tropical rain forest species (Chambers & MacMahon 1994). Ingestion of diaspores by birds may have a positive, neutral or negative effect on seed germination (Traveset 1998). Although birds have no effect on seed germination in *C. criuva*, aril removal by the ants significantly increased germination success, as in other neotropical species (Horvitz 1981; Leal & Oliveira 1998; Pizo & Oliveira 1998). Removal of seeds from faeces, besides enhancing germination may also affect establishment by rearranging the seed shadow generated by vertebrate dispersers (Roberts & Heithaus 1986; Pizo & Oliveira 1999) and/or by decreasing sibling competition (Howe 1989; Loiselle 1990).

Ants also affect the distribution of seedlings of *C. criuva*, which were more frequent near *P. striata* and *O. chelififer* nests and survived better close to *P. striata* nests. Secondary movement and survivorship of seeds on the floor of tropical forests remain poorly understood, even though they often influence patterns of establishment in other regions (Levey & Byrne 1993). Seed rain and seedling establishment seem to be spatially uncoupled for *C. criuva* due to ant activity (see Herrera *et al.* 1994). While birds disperse a great percentage of *C. criuva* fruit crop (83%) well away from the parent tree (Table 1), vertebrate exclusion experiments indicate that ants remove virtually all seeds reaching the forest floor in fresh diaspores (89%) or within faeces (98%), but produce only local seed movements (see Horvitz & Le Corff 1993 for a discussion on scales of bird and ant dispersal).

ANT EFFECTS ON SEEDLING SURVIVAL

Although seedlings can grow better near ant nests because such microsites can be chemically richer than background soils (Culver & Beattie 1980; Beattie 1985; Horvitz & Schemske 1986; Levey & Byrne 1993), many studies have rejected the nutrient-enriched microsite hypothesis (Rice & Westoby 1986; Bond & Stock 1989; Higashi *et al.* 1989; Hughes 1990). Our results show that ponerine nests are significantly richer in total nitrogen and phosphorus, which may improve performance of *C. criuva* seedlings, but other factors may underlie the greater survivorship of *C. criuva* in the vicinity of *Pachycondyla* nests. Causes of seedling mortality are still to be assessed and may include physical damage from litterfall, herbivory, pathogens and drought stress (see Turner 1990; Steven 1994; Lieberman 1996). The association of seedlings with ant nests could confer some protection against herbivores (Davidson & Epstein 1989), but intra- or interspecific seedling competition and microenvironmental characteristics, such as light conditions, distance from parent or conspecific plants, also have to be considered (Auspurger & Kelly 1984; Auspurger 1984; Schupp 1988; Howe

1989; Schupp 1990; Whitmore 1996). Whatever the causes promoting better seedling performance near *Pachycondyla* nests, and whether or not this can affect adult plant population, ant–seed interactions are certainly an important component in the recruitment dynamics of *C. criuva*. The importance of ant effects on seedling establishment remains largely unexplored in the humid tropics (Horvitz & Schemske 1986). To our knowledge this is the first study to demonstrate that ants affect seedling survival through time in a primarily vertebrate-dispersed species in tropical forests, and we predict that ant-induced effects on recruitment also hold for other plant species in these areas.

CONCLUDING REMARKS

Mutualisms are less conspicuous in dispersal systems than in more tightly co-evolved systems (Wheelwright & Orians 1982). Interactions between seeds and ants are unpredictable and variable (Herrera 1986) but mutualism in complex dispersal systems may underlie the biotic complexity and high diversity of the tropical ecosystem (see Gilbert 1980). The relative importance of primary and secondary seed dispersal has been assessed for a Malagasy tree that presents an unusually simple dispersal system (primary and secondary seed dispersal are each effectively carried out by a single species, Böhning-Gaese *et al.* 1999) but the diverse assemblages of both bird and ant dispersers of *C. criuva* may be more representative of tropical rain forests (see Pizo & Oliveira 1998, 2000, 2001).

In spite of the difficulty of predicting the fate of dispersed seeds (Byrne & Levey 1993), this study provides a comprehensive picture of the recruitment of a non-mymecochorous species, involving several sequentially connected stages (Fig. 5, see Herrera *et al.* 1994), and suggests that ant–seed interactions may markedly affect patterns of recruitment in primarily vertebrate-dispersed species in tropical forests. Although some species present special structures for complex dispersal systems involving both vertebrates and ants (Davidson 1988; Clifford & Monteith 1989; Kaufmann *et al.* 1991), the lack of structures for ant-dispersal does not preclude secondary removal of seeds (Roberts & Heithaus 1986; Aronne & Wilcock 1994), especially where lipid-rich arils of fleshy fruits are attractive both to birds and ants (Pizo & Oliveira 1998, 2000; Böhning-Gaese *et al.* 1999). The size and lipid-content of non-mymecochorous diaspores are major determinants of the outcome of ant–diaspore interactions (Pizo & Oliveira 2001) and we therefore predict that any effects on seed fate will be more clear-cut for species presenting small, lipid-rich diaspores. Furthermore, the species composition of the ground-dwelling ant assemblage may also affect the outcome of ant–seed interactions, and studies concerning different spatial scales and regions (see Thompson 1999; Garrido *et al.* 2002) would be worthwhile.

Acknowledgements

We thank K. Böhning-Gaese, P. Jordano, D. Levey, A.T. Oliveira-Filho and M.A. Pizo for discussions and helpful suggestions on the manuscript. The final version was improved by the comments of two anonymous referees and by the careful editing of L. Haddon. We also thank H.C. Menezes and A.E. Koon for chemical analyses of the fruits, M. de Abreu and S.C. F. Dechen (Department of Soil, Instituto Agronômico de Campinas) for soil analyses, and A. Mayhé-Nunes and I.R. Leal for ant identification. We are indebted to M.A. Pizo and G. Machado for help during fieldwork, and to A.X. Linhares, L.B. Klaczko, F.M. Santos, E. Sujii, and T. Quental for statistical advice. We are particularly grateful to M.A. Pizo for giving us access to his data on the bird assemblage at *Clusia* fruiting trees. Financial support to L. Passos was provided by a doctoral fellowship, and to P.S. Oliveira by a research grant, both from the Brazilian Research Council (CNPq). We are grateful to the Instituto Florestal de São Paulo for permission to work at Parque Estadual da Ilha do Cardoso.

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Received 13 August 2001

revision accepted 4 February 2002