UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

ECOLOGIA DA INTERAÇÃO ENTRE FORMIGAS, FRUTOS E SEMENTES EM SOLO DE MATA DE RESTINGA

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Aos meus pais e à Isabela,

que tanto enriqueceram minha vida.

ÍNDICE

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INTRODUÇÃO GERAL

A maior parte das informações sobre as interações entre formigas e sementes é decorrente de estudos realizados com plantas mirmecocóricas típicas, que apresentam adaptações para a dispersão por formigas. Apesar de mirmecocoria ocorrer em certos grupos de plantas nas florestas neotropicais (Horvitz 1981, Passos e Ferreira 1996), plantas mirmecocóricas típicas são especialmente comuns em regiões de solos pobres da Austrália e África do Sul, ou regiões áridas da América do Norte (Berg 1975, Milewski e Bond 1982, Hölldobler e Wilson 1990). Plantas mirmecocóricas possuem sementes com estruturas especiais ricas em lipídeos que são denominadas elaiossomos (Berg 1975, van der Pijl 1982). Estas estruturas atraem formigas que coletam o diásporo (*i. e.* unidade de dispersão, fruto ou semente, veja van der Pijl 1982) e o transportam para o ninho, onde o elaiossomo serve de alimento, sendo a semente descartada no exterior do ninho, onde poderá se estabelecer (Horvitz e Beattie 1980, O'Dowd e Hay 1980).

Nas florestas tropicais, *ca.* 90% das árvores e arbustos têm frutos carnosos e dependem de vertebrados frugívoros para sua dispersão (Frankie *et al.* 1974). Em geral a maior parte dos estudos de dispersão de sementes realizados em florestas tropicais aborda a primeira parte do processo, ou seja, os padrões de consumo dos frutos e deposição de sementes gerados por vertebrados (*e.g.* Fleming 1986, Wheelwright 1988, Jordano 1993). Apesar da reconhecida abundância de frutos carnosos que atingem os solos de florestas tropicais (Jordano 1993), bem como da grande diversidade e abundância de formigas nessas áreas, a ecologia evolutiva e história natural das interações entre formigas e diásporos nesse tipo de ambiente é pouco conhecida (Horvitz 1981, Rico-Gray 1993, Pizo e Oliveira 1998).

A dispersão de sementes é a última etapa do ciclo reprodutivo das plantas, mas é também o início do processo de renovação e recrutamento de populações (Herrera *et al.* 1994). Estudos recentes indicam que nos sistemas de dispersão de espécies tropicais há uma complexa rede de interações, sendo importante considerar os fatores que afetam o destino das sementes após sua dispersão por vertebrados (Chambers e MacMahon 1994, Andresen 1999). Após serem dispersas por vertebrados, as sementes freqüentemente estão sujeitas à ação de predadores e dispersores secundários de sementes, bem como à imprevisibilidade espacial e temporal de micro-sítios favoráveis à germinação. Estes fatores figuram entre os principais determinantes do tamanho, composição e distribuição espacial de populações vegetais (Schupp 1990, Whelan *et al.* 1991, Nathan e Muller-Landau 2000).

Recentemente, diversos autores têm demonstrado que as formigas podem afetar o destino de sementes de plantas primariamente dispersas por vetebrados em regiões neotropicais (Lu e Mesler 1981, Byrne e Levey 1993, Kaspari 1993, Levey e Byrne 1993, Pizo e Oliveira 1998, 1999, 2001 a, b). As formigas interagem com diásporos que chegam ao solo caindo espontaneamente da planta-mãe, derrubados pelos dispersores primários, ou em suas fezes (Howe 1980, Laman 1996, Pizo e Oliveira 1999). Deste modo, as formigas alteram o espectro de deposição de sementes (Roberts e Heithaus 1986, Kaufmann *et al.* 1991, Pizo e Oliveira 1998, 1999), podendo alterar a dinâmica do banco de sementes (Levey e Byrne 1993), facilitar a germinação de sementes (Oliveira *et al.* 1995, Leal e Oliveira 1998, Pizo e Oliveira 1998, 2001b), promover seu estabelecimento (Farji Brener e Silva 1996, Farji Brener e Medina 2000) e afetar a distribuição de plântulas de espécies primariamente dispersas por vertebrados (Böhning-Gaese *et al.* 1999).

O primeiro estudo sistemático das interações entre formigas e diásporos em floresta neotropical (Pizo e Oliveira 2001 a) demonstrou que o uso de frutos e sementes por formigas é bastante comum nessas áreas, e envolve grande número de espécies de plantas (56) e formigas (36). Apesar da relevância das interações entre formigas e diásporos em áreas florestais nos neotrópicos, atualmente pouco se sabe a respeito dos efeitos dessas interações para o recrutamento de espécies vegetais (porém veja Horvitz e Schemske 1986). Com essa perspectiva, o trabalho aqui descrito teve como objetivos gerais:

(1) identificar as espécies de formigas que freqüentemente exploram diásporos em uma área de mata de restinga no sudeste do Brasil, bem como os diásporos por elas explorados;

(2) identificar os padrões de utilização dos diásporos nesta área;

(3) avaliar o impacto da atividade das formigas na demografia das espécies vegetais (*i. e.* distribuição ou sobrevivência de plântulas de espécies vegetais selecionadas), com ênfase especial para *Clusia criuva* e *Guapira opposita* (queira ver a justificativa da escolha das espécies vegetais abaixo, na descrição dos capítulos).

O trabalho foi dividido em três partes representadas pelos capítulos que se seguem. O **Capítulo 1** relata o conjunto de formigas que exploram diásporos no chão da área de estudo, bem como os diásporos por elas explorados. As características dos diásporos (morfológicas e químicas) e a composição local de formigas como fatores determinantes da interação são investigadas nesse capítulo. O estudo do **Capítulo 2** foi delineado para determinar o papel das formigas no destino de sementes e plântulas de uma espécie arbórea primariamente dispersa por aves, *Clusia criuva* (Clusiaceae). Neste estudo foi utilizada uma abordagem observacional/experimental a fim de estimar a probabilidade de transições entre os estágios consecutivos do processo de recrutamento desta espécie (produção de frutos e remoção por aves, interações entre formigas e sementes no solo da floresta, germinação de sementes, e estabelecimento e sobrevivência de plântulas no primeiro ano). Finalmente, o **Capítulo 3** investiga as interações entre formigas e os frutos de *Guapira opposita*

(Nyctaginaceae), espécie arbórea que também é primariamente dispersa por aves. A relevância deste estudo reside no fato de que os efeitos das interações entre formigas e sementes no recrutamento de espécies vegetais eram esperados para frutos ricos em lipídeos (como *Clusia*), especialmente atrativos para formigas (queira ver Pizo e Oliveira 2001 b). *Guapira opposita* é espécie pobre em lipídeos e rica em proteínas, mas seus frutos são especialmente atrativos para formigas no local de estudo. A idéia de verificar se as formigas poderiam afetar a distribuição de plântulas e jovens de uma espécie pobre em lipídeos motivou a investigação.

Ao longo de toda a tese, utilizei o termo diásporo para me referir à unidade de dispersão, ou seja, a semente, fruto, ou infrutescência dispersa pelo vetor animal. No caso de *Clusia criuva*, os frutos do tipo cápsula contêm cinco diásporos, sendo cada diásporo um conjunto de sementes envolvidas por arilo vermelho, rico em óleos. *Guapira opposita* apresenta seus frutos (drupas) reunidos em infrutescências. No caso desta espécie, o diásporo é o fruto (queira ver figuras dos diásporos de *C. criuva* e *G. opposita* nos capítulos 2 e 3, respectivamente).

Os três capítulos que compõe a tese foram redigidos em inglês a fim de agilizar sua publicação.

ÁREA DE ESTUDO

Este estudo foi realizado entre janeiro de 1998 e setembro de 2000 na floresta de restinga do Parque Estadual da Ilha do Cardoso, situado no litoral sul do estado de São Paulo, no município de Cananéia (25°10' S; 47°59' W) (Barros *et al.* 1991). Com área de aproximadamente 22.500 ha e altitudes que vão desde o nível do mar até *ca.* 800 m (a.n.m.), a Ilha do Cardoso apresenta uma amostra de todos os tipos de vegetação ocorrentes na faixa costeira do Brasil: vegetação pioneira de dunas, vegetação de restinga, floresta pluvial tropical de planície litorânea, floresta pluvial tropical da Serra do Mar e vegetação de mangue (figura 1) (Barros *et al.* 1991).

O clima, segundo a classificação de Koeppen, é do tipo Cfa, mesotérmico úmido, sem estação seca, com pluviosidade e umidade relativa elevadas (Pfeifer 1981). A temperatura média anual é de 21,2° C e a precipitação de 3000 mm anuais (figuras 2 e 3) (Barros *et al.* 1991).

A área onde foi desenvolvido o estudo, localmente conhecida como restinga do Pereirinha, é formada predominantemente por floresta de restinga. Esta formação se apresenta em mosaicos com diferentes fisionomias, que vão desde formações arbóreas bastante abertas e baixas, com 4 a 5 m de altura, em solo arenoso (onde as bromélias são abundantes), até as formações arbóreas fechadas, sombreadas no interior e altas, chegando a mais de 15 m de altura, onde a camada de húmus e folhiço no solo é bastante espessa. As famílias vegetais dominantes são Myrtaceae, Arecaceae, Lauraceae, Clusiaceae e Theaceae (veja descrição detalhada da área em Sugiyama 1993). Os solos desta área são do tipo podzol hidromórfico, caracterizando-se pelo alto teor de areia (acima de 90%) e baixa fertilidade (Giulietti *et al.* 1983).

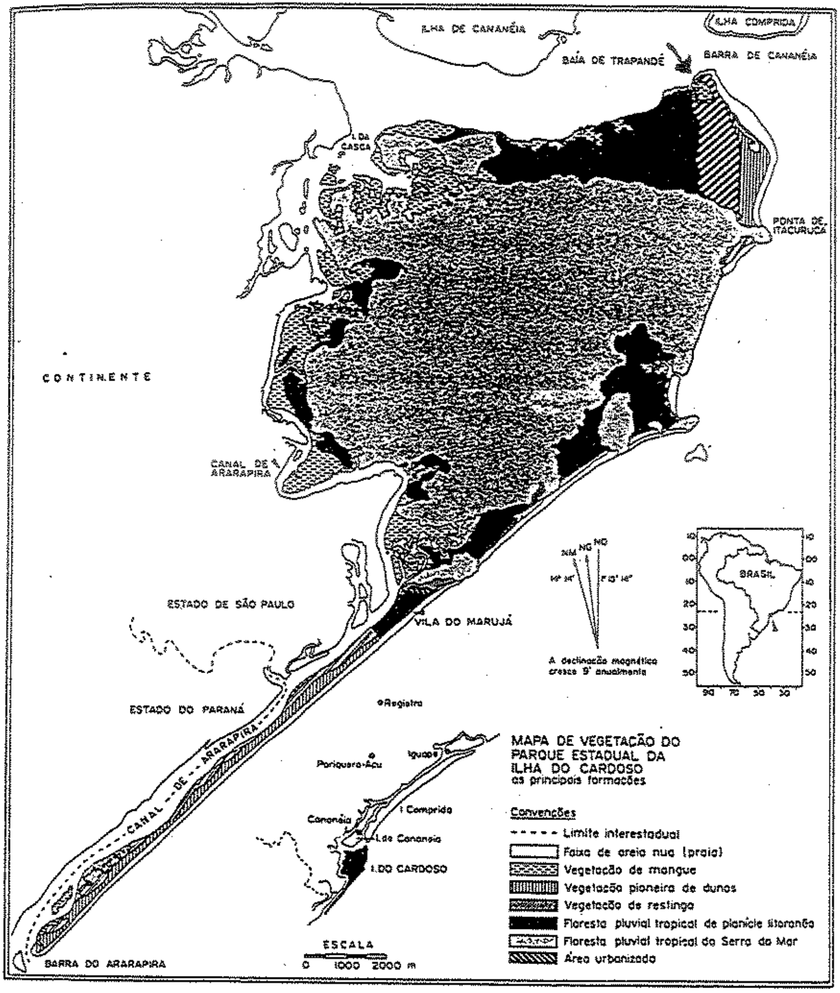

Figura 1. Mapa com a distribuição dos diferentes tipos de vegetação ocorrentes no Parque Estadual da Ilha do Cardoso (PEIC); note a localização da mata de restinga do Pereirinha (seta). No detalhe abaixo, a localização do PEIC, Cananéia, SP (fonte Barros *et al.* 1991).

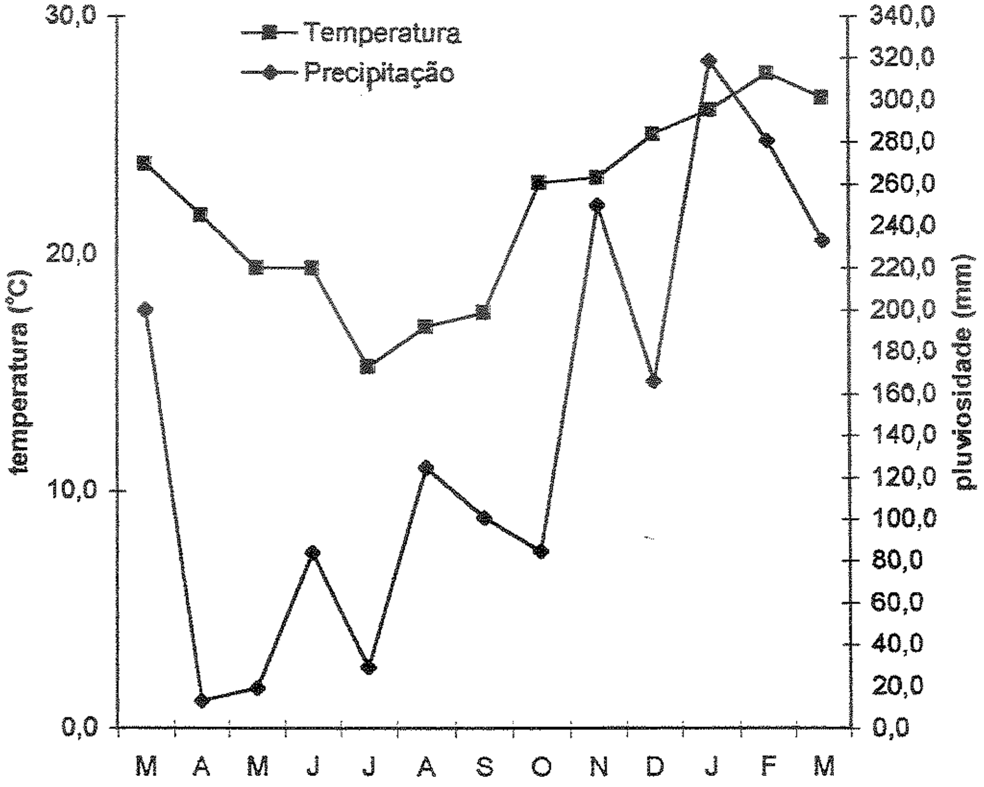

Figura 2. Distribuição da pluviosidade e temperatura (médias mensais) no período de março de 2000 a março de 2001 em base situada no município de Cananéia, SP.

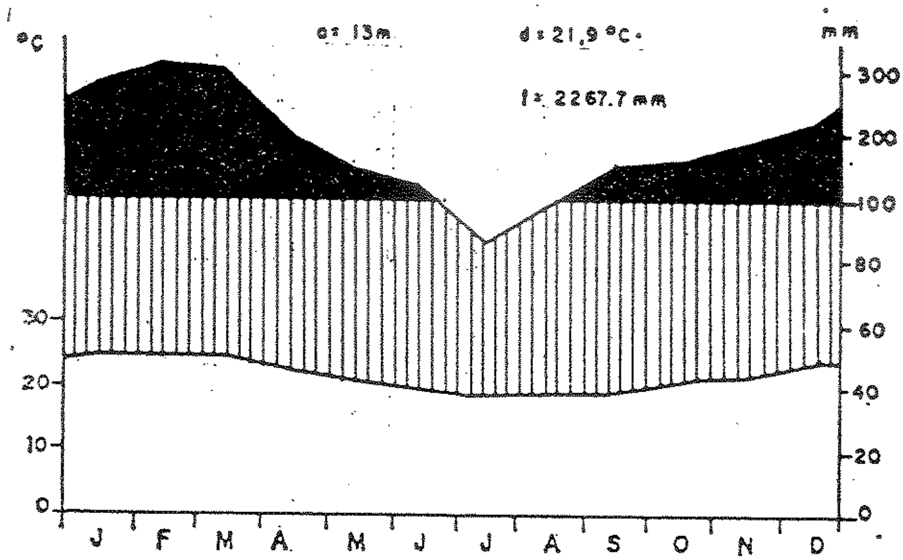

Figura 3. Diagrama climático da região do município de Santos, SP, localidade próxima ao local de estudo, e com clima similar (fonte Nimer 1979).

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CAPÍTULO 1

Interactions between Ants, Fruits, and Seeds in a sandy plain Rainforest: a first assessment*

*Formato e estilo: Biotropica

RESUMO

Em florestas tropicais os frutos carnosos apresentam uma grande variedade de tamanhos e composição química. Diásporos no solo constituem grande parte do folhiço no solo de florestas tropicais, e interações entre formigas e diásporos são freqüentes nessas áreas. Neste trabalho, nós estudamos as interações entre formigas e diásporos não-mirmecocóricos ao longo de um transecto de 1.4 km em uma mata de restinga no sudeste do Brasil. Durante dois anos de amostras mensais, 562 interações entre diásporos e formigas envolvendo 48 espécies de formigas e 44 espécies de diásporos (0.02 – 11.1 g) foram registradas. As associações entre formigas e diásporos envolveram uma parte considerável da comunidade de formigas do solo, e foram generalistas e facultativas. O tamanho e a composição química da porção carnosa de diásporos não-mirmecocóricos são fatores-chave para o resultado das interações entre formigas e diásporos. As categorias de comportamento de formigas em relação aos diásporos encontrados são semelhantes àquelas descritas para interações em outras florestas tropicais. Os benefícios proporcionados pelas formigas aos diásporos de plantas não-mirmecocóricas incluem dispersão secundária (diásporos pequenos a médios), e aumento no sucesso de germinação de sementes limpas. As formigas grandes da subfamília Ponerinae, como *Odontomachus chelifer* e *Pachycondyla striata* foram os principais vetores de sementes. Plântulas de cinco espécies são associadas aos ninhos de *O. chelifer*, e nós sugerimos que estes ninhos podem ser similares aos "jardins de formiga" descritos na literatura. As formigas da subfamília Ponerinae são predominantemente carnívoras, e a disponibilidade de artrópodes no solo da floresta pode determinar os padrões de interação entre formigas e diásporos envolvendo tais espécies. Os resultados indicam que formigas têm um importante papel na biologia de frutos/sementes na mata de restinga no sudeste do Brasil.

LRH: Passos and Oliveira

RRH: Use of fruits and seeds by ants

Interactions between Ants, Fruits, and Seeds in a sandy plain Rainforest: a first assessment

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ABSTRACT

In tropical forests fleshy fruits present a plethora of sizes, and chemical composition. Fallen diaspores (fruits/seeds) constitute a large portion of the litter on the floor of tropical forests, and interactions involving litter-foraging ants and diaspores are common in these areas. In this study, we surveyed the interactions between ants and nonmyrmecochorous diaspores along a 1.4-km transect in a sandy plain Atlantic rainforest in southeast Brazil. During two years of monthly samplings of diaspores, 562 ant-diaspore interactions involving 48 ant species and 44 different species of diaspores (range 0.02 – 11.1 g) were recorded. The ant-diaspore associations involved a considerable part of the ground-dwelling ant community, and were generalized and facultative. The size and the chemical composition of the edible portion of nonmyrmecochorous diaspores are key factors for the outcome of ant-seed interactions. The categories of ant behavior toward the diaspores found were similar to those described for interactions in other tropical forests. Ant-derived benefits to diaspores of nonmyrmecochorous plants included secondary dispersal (small to medium-sized diaspores), and increased germination success by cleaned seeds. Large ponerines such as *Odontomachus chelifer* and *Pachycondyla striata* were the main seed vectors. Seedlings of five species were associated with nests of *O. chelifer*, and we suggest these nests parallel "ant-gardens". These ponerine ants are predominantly carnivorous, and availability of arthropod prey in the forest floor might determine the patterns of ant-diaspore interactions involving such species. The results indicate ants play a significant role in fruit/seed biology in the sandy plain Atlantic rainforest.

Key words: ant fruit/seed interaction; ant-plant interaction; Atlantic forest; Brazil; seed diaspersal.

IN TROPICAL FORESTS FLESHY FRUITS present a broad range of sizes, shapes, colors, and chemical composition of the edible portion (*e.g.* van Roosmalen 1985, Corlett 1996). Diaspores (*i.e.* any seed, fruit, or infrutescence that constitute the unit of dispersal of the plant) can reach the ground spontaneously, dropped by vertebrate frugivores, or in their feces (Howe 1980, Kaspari 1993, Laman 1996, Pizo & Oliveira 1999, chapter 2). Fallen diaspores constitute a large portion of the litter on the floor of tropical forests (Denslow & Gomez-Dias 1990, Morellato 1992).

Although the mainstream of studies on seed dispersal of tropical species has focused mostly on fruit consumption and seed deposition patterns generated by vertebrates (*e.g.* Fleming 1986, Wheelwright 1988), recent studies have emphasized the importance of postdispersal events for the seed fate and demography of plant species in tropical forests (Levey & Byrne 1993, Chambers & MacMahon 1994, Pizo & Oliveira 1998, Andresen 1999, chapters 2, 3).

The abundance and diversity of ants in tropical forests are remarkable (Hölldobler & Wilson 1990), and ground-dwelling ants are perhaps the most likely organisms to encounter diaspores on the forest floor of tropical areas (Kaspari 1993, Pizo & Oliveira 2001a).

Indeed, it has recently been shown that ants interact with a broad range of nonmyrmecochorous (*i.e.* not adapted for ant dispersal) diaspores, and that these insects can affect seed fate of small (Roberts & Heithaus 1986, Kaspari 1993, Levey & Byrne 1993, Pizo & Oliveira 1999), medium-sized (Pizo & Oiveira 1998, 2001a), and large (Oliveira *et* *al.* 1995, Pizo & Oliveira 2001a) diaspores. Moreover, ants can affect seedling establishment (Farji-Brener & Silva 1996), and patterns of recruitment (Böhning-Gaese *et al.* 1999, chapters 2, 3) of plant species in tropical ecosystems. Size categories follow Pizo & Oliveira (2001 a): small (ca. 5 x 5 mm), medium-sized (ca. 15 x 11 mm), and large (ca. 28 x 17 mm) diaspores.

In spite of the growing body of information on the interactions between ants and nonmyrmecochorous diaspores (see literature cited above), only one study has documented systematically the use of fallen diaspores by the ground-dwelling ant community of a tropical forest (Pizo & Oliveira 2001b). Interactions between ants and diaspores are common in lowland forest, involve diverse assemblages of ants, and may render important consequences for the biology of the diaspores (Pizo & Oliveira 2001b).

In this paper we document the ant-diaspore interactions in an area of sandy plain Atlantic rainforest in southeast Brazil. We were especially interested in: (1) providing a detailed account of the ant fauna exploiting fallen fleshy diaspores; (2) determining the patterns of ant-diaspore interactions and their possible consequences on seed fate; (3) comparing the patterns of sandy plain forest with those recorded for a lowland forest studied by Pizo & Oliveira (2001b).

STUDY SITE

Field work was carried out in the sandy plain forest (see Oliveira-Filho 1993, Joly *et al.* 1999) of the Parque Estadual da Ilha do Cardoso (PEIC), a 22,500 ha island (altitude 0 –

800 m a. s. l.) located on the coast of São Paulo State (25° 03' S, 47° 53' W), SE Brazil. The forest grows on poor sandy soil (2 – 3 m a.s.l.), with 5 – 15 m tall trees forming an open canopy, and abundant bromeliads occurring on the ground layer; mean annual temperature and rainfall are 20.9° C and 3000 mm, respectively (Barros *et al.* 1991). A dry-cold season occurs from April to August, and a wet-hot season from September to March (Barros *et al.* 1991).

MATERIALS AND METHODS

The survey of ant-diaspore interactions was carried out following Pizo & Oliveira (2001a). From May 1998 to April 2000, each month we walked a 1.4-km transect looking for ants on fallen diaspores. Diaspores were searched ~ 2 m off both sides of the trail. Each time ants were found exploiting a diaspore (*i. e.* contacting the surface of the diaspore apparently collecting liquids, or removing portions of it), an interaction was recorded and the ants were collected for identification. Additional data included the number of ants and the diaspore species. Ants were censused between 0730 and 1230 h, and the number of ants and the diaspore species were recorded. Ant-diaspore interactions are not commonly observed in the sandy rainforest, probably due to the following factors: (1) fallen diaspores on the floor are less frequent in sandy plain forest than in lowland forest; (2) large ponerines are markedly abundant on sandy plain forest and rapidly remove fallen diaspores, reducing the chances of record of the ant-diaspore interactions. In order to overcome this situation and get a considerable number of records, ant-seed interactions were surveyed through systematic sampling in which we set diaspores on the forest floor before conducting the observations. We performed surveys each month and most interactions presented in this study were recorded during these surveys. We used ripe diaspores collected on the plant or fresh-fallen diaspores collected on the forest floor. Diaspores were placed on small pieces (4 x 4 cm) of white filter paper to facilitate visualization on leaf litter, at intervals of 10 m to maintain independent discoveries by different colonies (Byrne & Levey 1993; Kaspari 1993, 1996). Diaspores were set 0730 h and 1500 h and checked at 15 min intervals ("scan sampling" *sensu* Lehner 1979) during two hours. Vertebrate disturbance was avoided by covering the diaspores with wire cages (25 x 25 x 8 cm, 1.5 cm mesh) closed on the top and stalked to the ground (see Roberts & Heithaus 1986, Kaspari 1993).

We compared the ant community attracted to diaspores with the generalized omnivore community attracted to honey and tuna baits. In March 1999, we placed 100 tuna and 100 honey baits distributed 5 m apart along transects established 1-2 m off-trail. Small pieces (4 x 4 cm) of white filter paper were used as substrates for baits to facilitate ant visualization. Baits were set upon the transects at 0800 h and the number and identity of attracted ants were recorded after one hour. Voucher specimens of the ants and plants are deposited in the collection of Universidade Federal Rural do Rio de Janeiro (CECL) and at the herbarium of the Universidade Estadual de Campinas (UEC), respectively. We used Spearman's rank correlation to test if the use of fallen diaspores by ants occurs according to their relative importance on the forest floor.

In order to determine the effects of ants on seed fate, removal rate experiments and germination tests were performed with eight species typical of the sandy plain forest (see Tables 3, 4): *Schinus terebinthifolius* (Anacardiaceae), *Ilex theezans* (Aquifoliaceae), *Alchornea triplinervia* (Euphorbiaceae), *Ocotea pulchella* (Lauraceae), *Myrcia bicarenata*, *M. rostrata*, *Siphoneugenia guilfoyleiana* (Myrtaceae), *Ternstroemia brasiliensis* (Theaceae). Diaspore removal by ants was assessed by performing an exclosure experiment. Two marked diaspores (small dot of Enamel paint, Testors, Rockford, USA) were set out *ca.* 0600 h or 1800 h at baiting stations disposed on the forest floor at 10 m intervals along transects established 1-2 m off-trail (N= 60 diaspores for each species). Ant response to marked and unmarked diaspores was apparently the same. The diaspores were placed on small pieces (4 x 4 cm) of white filter paper to facilitate visualization on leaf litter, protected from vertebrate disturbance by wire cages. Diaspore removal was recorded after 12 h, and a given diaspore was considered removed if not found within a 30 cm radius around the cage. We interrupted every trial subjected to rains. Data are expressed as the mean percentage of diaspores removed per station. The results concerning two other species, *Clusia criuva* and *Guapira opposita*, will be presentes separately in chapters 2 and 3, respectively.

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

Ponerine ants are the main seed vectors on the floor of neotropical forests (Horvitz & Beattie 1980, Pizo & Oliveira 1998, 2001a, b). *Odontomachus chelifer* is a key species exploiting fleshy diaspores at PEIC, since it accounted for a significant number of ant-seed interactions recorded at the study site and regularly removed diaspores to the nest. The effect of ponerines on plant recruitment (*i.e.* seedlings and juveniles distribution) was determined by censusing recruits growing in *O. chelifer* nests and in control plots without nests. The number of seedlings and juveniles (up to 10 cm high) growing on nests of *Odontomachus chelifer* as compared to control areas was determined in May 2000 by establishing paired experimental plots (0.5 x 0.5 m). Experimental nests were located by following ant workers attracted to tuna baits placed on the forest floor (Horvitz 1981). We tagged 40 nests of *Odontomachus*, and established a control plot 2.5 m far (random direction) from each nest.

Differences in the number of seedlings and juveniles growing in treatment and control plots were analyzed with Mann-Whitney tests. Tests were performed only for plant species represented by abundant seedlings and juveniles on the forest floor.

RESULTS

PATTERNS OF ANT-DIASPORE INTERACTIONS. – We recorded a total of 562 ant-diaspore interactions in the monthly samplings during the two-year study. Fourty-eight ant species (19 genera, 4 subfamilies) and 44 plant species (40 genera, 26 families) were involved in these interactions (Tables 1, 2). The Myrmicinae was the most frequently recorded ant subfamily (36 species), and accounted for 327 interactions (58.19 %), while the Ponerinae with only five species was responsible for 217 interactions (38.61 %). The subfamilies Formicinae (5 species), Dolichoderinae, and Dorylinae (1 species each), together accounted for the remaining 3.20% of the records. The large ponerines *Pachycondyla striata* and *Odontomachus chelifer* are very abundant at study site (Table 1), and were attracted to 31% and 23% of the tuna and 19% and 22% of the honey baits, respectively. The two species together accounted for 35.05% of the ant-diaspore interactions recorded (Table 1). In general, these large ponerines individually removed diaspores (small- or medium-sized) to distances up to 13 m. Large diaspores were usually exploited on the spot, but those bearing small seeds such as *Psidium* could have their seeds removed by ponerines or large attines (*Acromyrmex*) to the nests. The small myrmicines: *Crematogaster* sp. 1, *Pheidole* sp. 1, *Pheidole* sp. 3, and *Solenopsis* sp. 1 were also abundant at the study area (Table 1), and exploited many different species of diaspores (Table 1). In general, small- and medium-sized ants (such as these myrmicines) recruited workers and fed on the diaspore on the spot, although small diaspores were occasionally transported. Ants were recorded on diaspores in a ripe or pre-ripe condition, and the number of workers ranged from 1 to 110. The number of interactions recorded for each non-attine ant species was highly correlated with their frequencies on tuna and honey baits (Spearman's rank correlation, $r_s = 0.60$, $N = 18$, $P = 0.01$), indicating that the use of fallen diaspores by ants occurs according to their relative abundance on the forest floor. All but four ant species attracted to baits were also recorded on diaspores, while 30 of the species recorded on diaspores were not recorded at baits.

Ants exploited diaspores of trees (34 species), shrubs (3 species), herbs (3 species), epiphytes (2 species), lianas, and parasites (1 species each) (Table 2). Myrtaceae is the dominant plant family at the study site (Sugiyama 1993) and was the family with the largest number of species (8) exploited by ants (Table 2). Ants usually exploited the pulp or aril of the diaspore, but were occasionally observed digging on the endosperm of seeds of some species (*e.g. Ternstroemia brasiliensis*). Diaspores varied greatly in size, ranging from 0.02 g (*Pera glabrata* and *Schinus terebinthifolius*) to 11.1 g (*Psidium cattleyanum*), but most of the diaspores exploited by the ants were small- to medium-sized, and only 13.6% were large. Although the aim of the study was to investigate the ant-seed interactions occurring on the forest floor, interactions involving *Crematogaster* spp. and diaspores of the epiphytic *Codonanthe devosiana* and *Aechmea nudicaulis* on tree trunks were also registered. These ants pierced the fruits and recruited nestmates that took the tiny arillate-seeds to their arboreal nests.

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

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

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

DISCUSSION

A diverse assemblage of ants is known to exploit diaspores on a regular basis (Hölldobler & Wilson 1990, Rico-Gray 1993). In neotropical forests this assemblage includes species in the subfamilies Ponerinae, Formicinae, and especially Myrmicinae (Horvitz & Beattie 1980, Kaspari 1996, Pizo & Oliveira 1998, 2001a, b). The ant-diaspore associations at PEIC involved a considerable part of the ground-dwelling ant community, and were generalized and facultative (each plant species was visited by many ant species, as ant species exploited diverse diaspores), being similar to those recorded at the lowland Atlantic forest by Pizo & Oliveira (2001 b). Myrmicinae was the most frequently recorded ant subfamily and accounted for *ca.* 58% of records. The Ponerinae ants were markedly abundant at PEIC, being responsible for *ca.* 39% of the ant-diaspore interactions registered.

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

The categories of ant behavior toward the diaspores at PEIC were similar to those found for interactions in other tropical forests (Horvitz & Beattie 1980, Horvitz 1981, Pizo & Oliveira 1998, 2001a, b). Small ants of the subfamily Myrmicinae (*e.g. Pheidole*, *Solenopsis*) are very abundant on the floor of tropical forests and have a major role exploiting fallen diaspores in such areas (Pizo & Oliveira 1999, 2001 a, b). These ants recruited many nestmates to diaspore and consumed the pulp or aril on the spot. After the cleaning activity by such ants, seeds may meet different fates, depending on their sizes. Myrmicine ants may be beneficial for plant species with medium-sized or large seeds, since they are able to clean those seeds, but not lift or remove them. Consequently, medium to large seeds remain on the spot, and the removal of the pulp or aril itself may reduce fungal attack and increase germination success in some species, as shown by germination tests performed in this study, as well as in other areas (Horvitz 1981, Oliveira *et al.* 1995, Leal & Oliveira 1998, Pizo & Oliveira 1998). On the other hand, myrmicine ants might be simultaneously antagonistic and mutualistic towards small seeds (see Levey & Byrne 1993). Some myrmicine ants (*e.g. Pheidole*) are granivorous that actually eat seeds (Hölldobler & Wilson 1990, Moutinho 1991). After cleaning the small seeds (*e.g. Clusia*), these ants can remove them (chapter 2). Although most retrieved seeds are killed by these ants, seed harvesting is not equivalent to seed predation, and ants may significantly benefit some seeds (see Levey & Byrne 1993).

This study reinforces the idea that ponerines (especially *Odontomachus* and *Pachycondyla*) have an important role as seed vectors on the floor of tropical forests (Horvitz & Beattie 1980, Pizo & Oliveira 1998, 2001a, b, chapters 2, 3). These ponerines can remove small and medium-sized diaspores (see Pizo & Oliveira 1998) to nests. Large diaspores bearing small seeds (*Psidium*) can also have their seeds removed by ponerines and large attines. Other large ants such as large attines (*Atta*, *Acromyrmex*) apparently are not major seed vectors in the Atlantic forests (Pizo & Oliveira 2001a, b, chapters 2, 3, this study), but these ants may play an important role on the seed biology of some plants species in tropical savannas (Farji-Brener & Silva 1996, Leal & Oliveira 1998), and other tropical forests (Moutinho 1998, Dalling & Wirth 1999, Farji-Brener & Medina 2000).

Recent studies have shown that secondary dispersal by invertebrates in tropical forests may benefit seeds by providing a suitable site for germination or establishment (*e.g.* chapters 2, 3), or remove seeds from predation-prone zone (Pizo & Oliveira 1998, Andresen 1999). Removal experiments using diaspores of selected plant species revealed that ants rapidly removed diaspores of some nonmyrmecochorous species, and support the view that seeds of small to medium-sized diaspores may benefit from secondary seed dispersal by ants (see Pizo & Oliveira 2001 a).

Another crucial factor determining the seed fate of nonmyrmecochorous diaspores is the chemical composition of the edible portion. Chemical mediates the behavior of ants toward potential food items (Wilson 1971). Lipids are regarded as the major attractant factor in the interaction between ants and nonmyrmecochorous diaspores (Pizo & Oliveira 2001a), and protein content is also an important factor in the selection of fruits for a variety of ants, particularly ponerines (chapter 3). With respect to chemical composition of the edible portion, our results support the view that lipid-rich (*Alchornea*, *Clusia*, *Ocotea*, *Pera*), and protein-rich (*Guapira*) diaspores do attract a variety of ants especially ponerines (see chapters 2, 3, and Pizo & Oliveira 2001 b for chemical composition of the species cited above). However, carbohydrate-rich diaspores such as those in the Myrtaceae family, *Myrcia rostrata* (lipid 10%, protein 9%, carbohydrate 78%, and ashes 3% of contents, M. A. Pizo, unpublished data), and *Psidium cattleyanum* (lipid 2%, protein 4%, carbohydrate 91%, and ashes 3% of contents, Pizo, M. A. in press) are also attractive to ants, including ponerines, at PEIC and the chemical cues for this attraction should be further investigated.

Ant effects on seedling establishment remain largely unexplored in tropical areas, but it has been shown that ants can markedly affect the distribution of seedlings of some species primarily dispersed by birds (Böhning-Gaese *et al.* 1999, chapters 2, 3). Our results further indicate that seedlings of five species (this study, chapters 2, 3) were significantly associated with nests of *Odontomachus chelifer* at PEIC, and that such nests may parallel "ant-gardens". Restricted to neotropics, ant-gardens are aggregates of epiphytes assembled by ants with arboreal carton nests. Epiphytes benefit from seed dispersal, mineral provisioning, and protection from ants (see Davisdson 1988, Orivel & Dejean 1998). Nests of *O. chelifer* are richer in P and Ca, the ants also increase soil penetrability, what might improve performance of seedlings (chapter 3). Besides that, the association of seedlings with *O. chelifer* nests potentially renders for the plants some protection against herbivores (chapter 3). Data on the regeneration of plant species associated with nests of *O. chelifer* at PEIC would shed light on the consequences of ant-diaspore interactions for plant recruitment in tropical forests.

This study, as that of Pizo & Oliveira (2001b), showed that ants in tropical forests exploit a broad range of diaspores with different sizes/composition (44 plant species, 26 families at PEIC) with no special morphological or chemical device for ant-dispersal. We suggest that ant-diaspore interactions are common in other neotropical forests at <1000 m elevation, presenting high densities of ants.

Although the floristic composition of the sandy plain and the lowland Atlantic rainforests of southeast Brazil are roughly similar (2000), the latter is more diverse and presents greater production of fleshy fruits. Consequently, interactions between ants and fallen diaspores are more common in the lowland than in the sandy forest of PEIC (see Pizo & Oliveira 2001b). The ant assemblage is also different in the two sites, and data obtained using honey baits indicated that the main seed vectors *Odontomachus chelifer* and *Pachycondyla striata* are markedly more abundant at PEIC (22%, and 19%) than in the lowland forest (4%, and 6%, respectively, M. A. Pizo, unpublished data). These differences in the species composition of the ground-dwelling ant assemblage may affect the outcome of ant-seed interactions (see Pudlo *et al.* 1980, chapter 2). Besides that, *O. chelifer* and *P. striata* exploited diaspores differently in the two sites, and used a smaller proportion of dispores available in the lowland forest, concentrating on lipid-rich diaspores such as *Alchornea*, *Cabralea*, and *Virola* (Pizo & Oliveira 2001a, b). *Odontomachus chelifer* and *P. striata* exploited respectively 13, and 21 out of 69 diaspores used by the ant assemblage in the lowland forest. On the other hand, *O. chelifer* and *P. striata* exploited respectively 20, and 35 out of 40 diaspores species exploited by ants in the sandy plain forest of PEIC.

Odontomachus chelifer and *P. striata* of the lowland forest were more selective towards diaspores than those of sandy forest, perhaps reflecting a relatively high biomass of arthropod prey on the forest floor of the former, due to differences in the litter moisture content of the two sites (see Levings 1983, Levings & Windsor 1984 for a discussion on litter arthropod distribution).

Although foraging behavior of ponerine ants has been described as generalist (Déjean & Lachaud 1994, Forcassié & Oliveira 2001), such ants are predominantly carnivorous that feed on arthropod prey and use aril or pulp of fruits as a secondary food source (Horvitz & Beattie 1980, Hölldolbler & Wilson 1990, Pizo & Oliveira 1998). Ants can shift to an alternate food choice, and the distribution of food resources in size, time, space, and quality are among the principal ecological determinants of ant foraging strategy (Traniello 1989, Déjean & Lachaud 1994).

A study combining (1) field experiments on selection of food items by ponerine ants, and (2) the assessment of the availability of arthropod prey in the two sites (*i.e.* the sandy plain Atlantic forest of PEIC, and the lowland Atlantic forest) would be useful to better understand the factors underlying the complex interactions between ants and fruits/seeds in tropical forests.

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Table 1. Ant species recorded exploiting fallen diaspores, and tuna and honey baits, on the forest floor of the Atlantic sandy plain rainforest of Cardoso Island, SE Brazil.

Ant subfamilies/species	Number of diaspore species used (number of records on diaspores)	Records on baits (%)	
		Honey (N= 100)	Tuna (N= 100)
PONERINAE			
1. *Hypoponera* sp.	1 (1)	—	—
2. *Gnamptogenys moelleri*	8 (14)	10	5
3. *Odontomachus chelifer*	20 (51)	22	23
4. *Odontomachus* sp.	5 (5)	6	8
5. *Pachycondyla striata*	35 (146)	19	31
MYRMICINAE			
6. *Cephalotes pusillus*	1 (1)	—	—
7. *Crematogaster* sp. 1	17 (45)	14	38
8. *Crematogaster* sp. 2	3 (5)	—	—
9. *Crematogaster* sp. 3	2 (5)		
10. *Hylomyrma* sp.	—	1	—
11. *Octostruma* sp.	1 (1)	—	—
12. *Oligomyrmex* sp.	1 (1)	—	—
13. *Pheidole* sp. 1	26 (58)	29	25

14. *Pheidole* sp. 2	2 (2)		
15. *Pheidole* sp. 3	17 (33)	45	49
16. *Pheidole* sp. 4	3 (5)	—	—
17. *Pheidole* sp. 5	11 (19)	—	—
18. *Pheidole* sp. 6	2 (2)	—	—
19. *Pheidole* sp. 7	1 (1)	—	—
20. *Pheidole* sp. 8	1 (1)	—	—
21. *Pheidole* sp. 9	1 (1)	—	—
22. *Pheidole* sp. 10	1 (2)	—	—
23. *Pheidole* sp. 11	1 (1)	—	—
24. *Solenopsis* sp. 1	15 (34)	8	5
25. *Solenopsis* sp. 2	3 (3)	—	—
26. *Solenopsis* sp. 3	9 (15)	2	3
27. *Solenopsis* sp. 4	2 (3)	—	—
28. *Solenopsis* sp. 5	1 (1)	—	—
29. *Solenopsis* sp. 6	1 (1)	—	—
30. *Solenopsis* sp. 7	1 (1)	—	—
31. *Solenopsis* sp. 8	3 (3)	—	—
32. *Solenopsis* sp. 9	3 (8)	—	—
33. *Strumigenys* sp.	3 (3)	2	—
34. *Wasmania* sp. 1	3 (4)	—	—
MYRMICINAE (ATTINI)			
35. *Acromyrmex aspersus*	13 (24)	3	—

36. *Acromyrmex coronatus*	2 (5)	—	—
37. *Acromyrmex crassipinus*	5 (7)	2	—
38. *Acromyrmex disciger*	1 (2)	—	—
39. *Acromyrmex subterraneus*	13 (26)	3	1
40. *Acromyrmex* sp. 1	1 (1)	—	—
41. *Acromyrmex* sp. 2	1 (1)	—	—
42. *Apterostigma* sp.	—	1	—
43. *Cyphomyrmex* sp.	1 (2)	—	—
44. *Trachymyrmex* sp.	—	1	—
DOLICHODERINAE			
45. *Linepithema* sp.	2 (2)	1	—
DORYLINAE			
46. *Labidus* sp.	1 (2)	1	—
FORMICINAE			
47. *Brachymyrmex* sp.	1 (1)	3	—
48. *Camponotus* sp.	2 (2)	3	4
49. *Paratrechina* sp. 1	5 (6)	3	3
50. *Paratrechina* sp. 2	4 (4)	—	—
51. *Paratrechina* sp. 3	1 (1)	—	—
PSEUDOMYRMECINAE			
52. *Pseudomyrmex* sp.	—	—	1

Table 2. Plant diaspores exploited by ants on the forest floor of the Atlantic sandy plain rainforest of Cardoso Island, SE Brazil. Data were gathered during monthly surveys (along an 1.4-km transect) of diaspores found naturally being used by ants on the forest floor, as well as fresh diaspores placed by us on the ground. Plant species and families are arranged in alphabetical order. Ant species numbers as in table 1.

Plant families/species	Growth form*	Diaspore length x width (mm)	Diaspore weight (g)	Months	Ant species
ANACARDIACEAE					
Schinus terebinthifolius	T	5.7 x 5.7	0.02	May-Jun	3, 5
Tapirira guianensis	T	14.4 x 11.1	0.5	Feb-Apr	2, 3, 5, 7, 13, 32, 35, 39, 48
ANNONACEAE					
Guatteria australis	T	10.8 x 7.0	0.3	Nov-Dec	13, 15
Xylopia langsdorffiana	T	10.0 x 7.1	0.2	Sep-Feb	2, 3, 5, 7, 12, 15, 17, 24, 26, 34

AQUIFOLIACEAE					
Ilex integerrima	T	6.6 x 6.4	0.1	Apr-Jul	3, 5, 7, 13, 15, 39
Ilex theezans	T	5.1 x 5.7	0.1	Apr-Jul	5, 13, 15, 17, 35
ARACEAE					
Anthurium sp.	B	5.1 x 5.1	0.1	May-Jun	3, 5, 7, 23
ARALIACEAE					
Didymopanax cf. *angustissimo*	T	7.5 x 8.6	0.2	Apr-Ago	5, 24, 37
ARECACEAE					
Euterpe edulis	T	14.3 x 14.0	1.9	Apr-Jul	5, 24, 25, 31
Geonoma shottiana	T	10.2 x 9.2	0.5	Feb-Jul, Nov	5, 13, 24, 39
Syagrus romanziffiana	T	22.0 x 15.7	3.8	Apr	5, 17, 26, 49
BROMELIACEAE					
Aechmea nudicaulis	E	15.6 x 7.7	0.3	Nov-Mar	2, 3, 4, 5, 7, 8, 9, 13, 15, 33, 35, 39, 41, 45, 48, 49

CECROPIACEAE					
Cecropia pachystachia	T	____	____	Feb, May, Dec	2, 3, 4, 5, 7, 13, 17, 49, 50
CELASTRACEAE					
Maytenus robusta	T	10.7 x 10.1	0.4	May-Jul	5, 13, 15, 24, 26
CLUSIACEAE					
Clusia criuva	T	9.8 x 5.5	0.1	Dec-Mar	1, 3, 4, 5, 6, 7, 13, 14, 15, 17, 22, 24, 26, 27, 28, 34, 35, 37, 39, 40, 46, 50
Calophyllum brasiliensis	T	27.2 x 24.6	9.14	Oct	13, 29, 51
DILLENIACEAE					
Doliocarpus cf. *glomeratus*	L	6.2 x 7.1	0.1	Jun-Jul	5, 13
ERICACEAE					
Gaylusacia brasiliensis	S	7.1 x 7.1	0.2	Jan, Feb, Oct	5, 13, 35, 39

ERYTHROXYLACEAE					
Erythroxylum amplifolium	T	8.0 x 5.0	0.1	Jan	3, 13, 35, 37, 39
EUPHORBIACEAE					
Alchornea triplinervia	T	6.3 x 6.3	0.1	Feb-Mar	3, 5, 7, 13, 15, 24, 26, 35
Pera glabrata	T	7.1 x 3.6	0.02	May	2, 5, 13, 15
FABACEAE					
Andira fraxinifolia	T	36.2 X 26.4	9.1	Jul	24
GESNERIACEAE					
Codonanthe devosiana	E	10.0 x 8.7	0.4	Nov-Mar	3, 5, 7, 8, 13, 15, 18, 45
LAURACEAE					
Ocotea pulchella	T	8.4 x 5.2	0.1	Sep-Mar	2, 3, 4, 5, 7, 13, 14, 15, 16, 17, 19, 26, 30, 35, 37, 39
MALPIGHIACEAE					
Byrsonima ligustrifolia	T	10.1 x 12.3	0.9	Mar-Apr	5, 13, 24, 37

MELASTOMATACEAE					
Miconia sp.	T	4.8 x 6.3	0.1	Jun-Oct	5
MYRTACEAE					
Blepharocalyx salicifolius	T	5.8 x 6.9	0.1	Apr-May	5, 13, 24
Eugenia uniflora	T			Jan-Mar	3, 9, 17, 36
Gomidesia cf. *affinis*	T	6.0 x 8.5	0.3	Jun	13
Gomidesia fenzliana	T	6.9 x 9.0	0.3	May-Jul	13, 17, 35
Myrcia bicarenata	T	7.8 x 8.3	0.3	May-Jul	5, 13, 15, 24, 26
Myrcia rostrata	T	9.3 x 7.1	0.3	Jan-Feb	3, 5, 7, 13, 15, 35, 49, 50
Psidium cattleyanum	T	26.0 x 25.3	11.1	Feb-May	2, 3, 5, 7, 13, 17, 24, 35, 39, 47, 50
Siphoneugenia guilfoyleiana	T	9.5 x 9.5	0.5	Nov-Dec	2, 3, 5, 11, 13, 15, 16, 18, 27, 39
NYCTAGINACEAE					
Guapira opposita	T	8.0 x 7.1	0.3	Jan-May	3, 4, 5, 7, 13, 15, 33, 35, 39
RUBIACEAE					
Coccosipsilum cf. *capitatum*	B	7.6 x 8.5	0.1		3, 5

Coccosipsilum sp.	B	13.9 x 9.2	0.3		7
Psychotria cf. *pubigera*	S	6.7 x 8.3	0.2	Mar, Apr, Oct	3, 5, 7, 24, 36
Rudgea villifolia	S	11.7 x 11.9	0.7	Feb-Apr	5, 15, 24
SAPOTACEAE					
Chrysophyllum sp.	T	26.5 x 22.0	6.0	Nov-Jan	7, 8, 17, 21, 24, 26, 31, 32, 33, 38, 43, 49
undetermined 1	T	28.7 x 25.0	8.9	Jan	3, 5, 7, 8, 13, 17, 24, 26, 31, 32, 39
THEACEAE					
Ternstroemia brasiliensis	T	6.3 x 3.8	0.05	Apr-Jun	5, 13, 15, 16, 17, 20, 24, 25, 26, 31, 34, 35
VERBENACEAE					
Aegephyla sp.	T	10.7 x 8.0	0.8		13
VISCACEAE					
Phoradendron crassifolium	P	4.0 x 4.0	0.05	Feb-Apr	5, 39

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*Growth form: T: trees, S: shrubs, B: herbs, E: epiphytes, L: lianas, P: parasites.

Table 3. Removal rates of diaspores by ants on the forest floor of the Atlantic sandy plain rainforest of Cardoso Island, SE Brazil. Marked diaspores were set out *ca.* 0600 h or 1800 h at baiting stations on the forest floor, protected by wire cages, and diaspore removal was recorded after 12 h.

Plant species	No. of Diaspores Set		Removal Rates (%)	
	Day	Night	Day	Night
ANACARDIACEAE				
1. *Schinus terebinthifolius*	30	30	27	27
AQUIFOLIACEAE				
2. *Ilex theezans*	30	30	17	10
EUPHORBIACEAE				
3. *Alchornea triplinervia*	30	30	93	87
LAURACEAE				
4. *Ocotea pulchella*	30	30	90	87
MYRTACEAE				
5. *Myrcia bicarenata*	30	30	0	3
6. *Myrcia rostrata*	30	30	33	60
7. *Siphoneugenia guilfoyleiana*	30	30	63	60
THEACEAE				
8. *Ternstroemia brasiliensis*	30	30	67	13

* Data for diaspore removal of *Clusia criuva* and *Guapira opposita* is provided elsewhere (see chapters 2 and 3).

Table 4. Germination tests of seeds cleaned by the authors (treatment group) and seeds coated by a pulp or aril (control group).

Plant families and Species	No. of Seeds Planted		Germination Success (%)		Signicance of difference (χ^2 tests)
	Treatment	Control	Treatment	Control	
ANACARDIACEAE					
1. *Schinus terebinthifolius*	30	30	100.0	16.7	P<0.001
AQUIFOLIACEAE					
2. *Ilex theezans*	30	30	10.0	0	0.05<P<0.10
EUPHORBIACEAE					
3. *Alchornea triplinervia*	40	40	75.0	22.5	P<0.001
LAURACEAE					
4. *Ocotea pulchella*	70	70	98.6	2.9	P<0.001
MYRTACEAE					
5. *Myrcia bicarenata*	50	50	100.0	38.0	P<0.001

6. *Myrcia rostrata*	35	35	97.1	45.7	P<0.001
7. *Siphoneugenia guilfoyleiana*	40	40	97.5	17.5	P<0.001
THEACEAE					
8. *Ternstroemia brasiliensis*	32	32	96.9	50.0	P<0.001

* Data for germination tests of *Clusia criuva* and *Guapira opposita* is provided elsewhere (see chapters 2 and 3).

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

Plant species*	Mean number of seedlings		U	Significance of difference
	Nests	Control		
ARACEAE				
1. *Anthurium* sp.	3.30	1.48	1086.00	P = 0.004
LAURACEAE				
2. *Ocotea pulchella*	1.70	1.48	804.00	P = 0.968
MYRTACEAE				
3. *Gomidesia fenzliana*	1.15	0.93	853.00	P = 0.583
4. *Myrcia bicarenata*	0.53	0.43	913.00	P = 0.165
5. *Myrcia rostrata*	2.95	0.78	1115.00	P = 0.001
6. *Psidium cattleyanum*	1.00	0.05	965.00	P = 0.011
7. *Siphoneugenia guilfoyleiana*	0.48	0.10	866.00	P = 0.288

*Data for seedling distribution of *Clusia criuva* and *Guapira opposita* is provided elsewhere (see chapters 2 and 3).

CAPÍTULO 2

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

*Formato e estilo: Journal of Ecology

RESUMO

Nós estudamos o sistema de dispersão de *Clusia criuva* (Clusiaceae) em uma floresta de restinga no sudeste do Brasil. Uma abordagem observacional/experimental foi adotada a fim de estimar a probabilidade de transições entre estágios consecutivos no processo de recrutamento (produção de frutos e remoção por aves, interações formiga-diásporo no solo da floresta, germinação de sementes, estabelecimento e sobrevivência inicial de plântulas). As árvores de *Clusia* produzem centenas de cápsulas com diásporos constituídos por sementes pequenas envolvidas por um arilo rico em lipídeos. A produção de frutos varia de 393 a 3709 cápsulas por árvore. Aves (16 espécies) consomem 83% dos diásporos na copa das árvores, enquanto os 17% restantes caem no solo e são removidos por formigas (16 espécies). As formigas removem 89% dos diásporos que caem no solo e 98% das sementes contidas nas fezes de aves no solo. Formigas da subfamília Ponerinae (*Odontomachus*, *Pachycondyla*) removem os diásporos para o ninho, enquanto as formigas pequenas da subfamília Myrmicinae (*Pheidole*, *Crematogaster*) removem o arilo no local onde encontram o diásporo. A remoção de arilo por formigas e a remoção de sementes das fezes das aves aumenta o sucesso de germinação de *C. criuva*. As plântulas são mais freqüentes nos ninhos de Ponerinae que em áreas controle sem ninhos. A sobrevivência inicial de plântulas (1 ano) em ninhos de *Pachycondyla striata* é maior que em áreas controle. Amostras de solo de ninhos de *P. striata* também apresentam maior concentração de nitrogênio total que amostras de áreas controle. Este é o primeiro estudo a demonstrar os efeitos combinados das formigas na distribuição e sobrevivência de plântulas de uma espécie primariamente dispersa por vertebrados.

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

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Summary

1. We studied the dispersal system of the tree *Clusia criuva* (Clusiaceae) in a tropical rainforest in SE 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/tree. Birds (16 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 feces. 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 yr) 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 than random soil samples. 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.

Keywords: ants; birds; Brazil; *Clusia*; Clusiaceae; seed dispersal; seed predation; tropical rainforest.

Introduction

In many dispersal systems seeds are dispersed primarily by frugivorous vertebrates and secondarily by ants (Böhning-Gaese *et al.* 1999, and included references). 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). This situation contrasts with that of typical myrmecochorous (i. e., ant-dispersed) species, which present elaiosome-bearing seeds and for whom ant-seed interactions and their consequences have been intensively investigated (e.g. Hanzawa *et al.* 1988, Hughes & Westoby 1992*a*, *b*).

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). In neotropical forests, although myrmecochory can be an important dispersal strategy for some plant taxa (Horvitz & Beattie 1980, Passos & Ferreira 1996), nearly 90% of dicots have fleshy fruits and rely on vertebrate frugivores for seed dispersal (Frankie *et al.* 1974). These diaspores, however, end up reaching the forest floor either spontaneously, dropped by vertebrate frugivores (Howe 1980, Laman 1996), or in vertebrate feces (Kaspari 1993, Pizo & Oliveira 1999). Given the abundance of litter-foraging ants (Hölldobler & Wilson 1990) and fallen fleshy diaspores on the forest floor of tropical forests (Jordano 1993), ant-diaspore interactions should be common in these habitats. Indeed, a two-year survey carried out in the Atlantic forest of southeast Brazil recorded 886 ant-diaspore interactions involving 36 ant species and 56 plant species (Pizo & Oliveira 2000*a*). 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 (Levey & Byrne 1993, Farji Brener & Silva 1996, Farji Brener & Medina 2000) of primarily vertebrate-dispersed plants. In spite of the prominence of such ant-seed interactions, information on how ants can affect patterns of recruitment and survival of seedlings of nonmyrmecochorous species is still scarce (but see Böhning-Gaese *et al.* 1999).

This study was designed to assess the role of ants on seed and seedling fate of a primarily bird-dispersed tree, *Clusia criuva* Camb. (Clusiaceae), in a rainforest in southeast Brazil. Five questions were addressed: (1) How much of *C. criuva*'s fruit crop is removed by birds in the canopy, and how much reaches the forest floor? (2) What is the role of ants *vs*. vertebrates on the removal of fallen diaspores? (3) Do ants remove *C. criuva*'s seeds from bird feces? (4) Is seed germination affected by bird ingestion, aril removal by ants, or removal from bird feces? (5) 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, Jordano & Herrera 1995) and used an observational/experimental approach to assess the predictions for seed fate (from fruit production to germination and seedling establishment). The methods and results of each individual step are presented separately, but the data summarizing the whole sequence of events is presented in a flow chart which allows a quantitative view of the complex dispersal system of *C. criuva*.

THE PLANT AND THE BIRDS

Clusia criuva is a common dioecious tree in the sandy plain forest (see Oliveira-Filho 1993, Joly *et al.* 1999) on the coast of southeast Brazil, and is among the most frequent tree species at the study site (*personal observation*). Mature fruits occur from January to March, and the species presents great annual variation in seed output. Fruits are globular capsules (ca. 30 mm diameter) that dehisce to expose five diaspores (mean ± SD 9.78 ± 1.64 mm length, 5.46 ± 0.90 mm wide, N = 150) containing 0 – 17 seeds each (4.38 ± 3.98 seeds, N = 750 diaspores). The diaspore (i. e., the unit of dispersal) consists of seeds enveloped by a red aril, and its fresh weight is 0.10 ± 0.05 g (N = 150). The aril of *C. criuva* has one of the highest lipid contents (83.4%) 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. Arillate seeds are dispersed by at least 14 bird species: *Turdus albicollis*, *T. rufiventris*, *Turdus* sp. (Turdidae), *Pitangus sulphuratus*, *Myiodynastes maculatus*, *Tyrannus melancholicus*, *Myiozetetes similis*, *Myiarchus* sp., *Pachyramphus castaneus* (Tyrannidae), *Vireo olivaceus* (Vireonidae), *Cacicus haemorrhous*, *Dacnis cayana*, *Tangara seledon* (Emberezidae), *Celeus flavescens* (Picidae). The birds ingest the whole diaspore and defecate intact seeds, acting as legitimate seed dispersers, and occasionally drop intact diaspores beneath the parent plant (M. A. Pizo, *personal communication*).

Study site and Methods

Field work was carried out from January 1998 to April 1999 in the sandy plain 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 on the coast of São Paulo State, southeast Brazil.

The forest grows on poor sandy soil (2 – 3 m a.s.l.), with 5 – 15 m tall trees forming an open canopy, and abundant bromeliads on the ground layer (Barros *et al.* 1991). Mean annual temperature and rainfall are 20.9° C and 3000 mm, respectively. A dry-cold season occurs from April to August, and a wet-hot season from September to March.

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 m^2 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 to 13 traps under each tree, covering 23 -70 % of the area beneath the tree crowns. Since traps caught all fruit debris (capsules, diaspores, and seeds embedded in bird feces) falling under tree crowns, we were able to estimate total fruit production, the crop removed by birds, and the amount of diaspores that reached the forest floor (see Howe & Kerkhove 1981, Blake *et al.* 1990). We removed and counted fruit debris in the traps every two days throughout the entire fruiting season of 1998.

DIASPORE REMOVAL BY ANTS *VS.* VERTEBRATES

Seed removal by ants and vertebrates was assessed by performing an exclosure experiment. Pairs of marked diaspores (small dot of Enamel paint, Testors, Rockford, USA) were set out *ca.* 0800 h at five stations placed radially beneath fruiting trees (N = 40) of *C. criuva* (ant response to marked and unmarked diaspores was apparently the same). Experiments were set in the early morning, when bird activity in *Clusia* trees is greatest, and when most diaspores reach the forest floor. Each pair consisted of (i) one diaspore placed directly on the forest floor under a wire cage (17 x 17 x 8 cm, 1.5 cm mesh) closed on the top and stalked to the ground to exclude vertebrates (see Roberts & Heithaus 1986, Kaspari 1993), and (ii) one diaspore for which no exclosure was provided, thus permitting free access by ants and vertebrates. Diaspore locations were marked with wooden stakes, and a given diaspore was considered removed if not found within a 30 cm radius around the stake. Diaspore removal was recorded after 24 h. We interrupted every trial subjected to rains. Data are expressed as the mean percentage of diaspores removed per tree. Treatments were compared by paired-sample Student's *t*-test, after arcsin transformation of the data.

ANT-DIASPORE INTERACTIONS

To determine which ants interact with *C. criuva*'s fallen diaspores, we recorded all ant-diaspore interactions observed throughout the entire 1998 fruiting season of *C. criuva*. Ant-diaspore interactions were also surveyed through systematic sampling. Two marked diaspores were set out at each of three stations placed radially beneath fruiting trees of *C. criuva* (N = 20). The diaspores were placed on small pieces (4 x 4 cm) of white filter paper to facilitate visualization on leaf litter, protected from vertebrate disturbance by wire cages. Diaspores were set 0730 h and 1500 h and checked at 15 min intervals ("scan sampling" *sensu* Lehner 1979) during two hours. We recorded the ants attracted to the diaspores, 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 which were first discovered by small myrmicine ants were further removed by ponerine ants. Since we wanted to characterize the ultimate fate of seeds, we established two criteria to consider an interaction involving small ants. The interaction was recorded whenever *ca.*

30 individuals have been recruited to the spot, or *ca.* 40% of the aril have been removed. Diaspores meeting these criteria 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 FECES

Bird feces (*ca.* 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 feces and prepared small fecal portions (*ca.* 2 cm long) with 15 seeds each (greater quantities would not result in significant increase in the proportion of seeds removed by ants; see Kaspari 1993). The fecal portions were mounted on small pieces of white filter paper (4 x 4 cm) and placed directly on the leaf litter, protected from vertebrate disturbance by wire cages. One fecal portion was set in a station beneath each of 30 fruiting trees of *C. criuva* at 0800 h (see Kaspari 1993) and the number of seeds remaining in the experimental feces was counted after 24 h. The ant species attracted to the feces, as well as their behavior toward the embedded seeds were recorded in scan samples taken at 15 min intervals from 0800 to 0900 h. We followed ants carrying seeds until they entered their nests or disappeared in the leaf litter. The displacement distance was then measured.

SEED GERMINATION

We carried out a series of field experiments to determine if germination is affected by bird ingestion, aril removal by ants, or removal from bird feces. Seeds in each category were placed in separate 15 cm-spaced germination boxes (11 x 11 cm) containing homogenized soil passed through a 2 mm mesh soil screen. Seeds were placed on the surface of the soil, 2-4 cm apart from each other. Each box received one of the following seed categories: (1) seeds coated by an aril (1-14 seeds in each of 10 diaspores); (2) 20 cleaned seeds (aril removed by ants); (3) four groups of five seeds each embedded in a 1 cm-long fresh fecal portion; (4) 20 seeds isolated by us from bird feces. Fresh diaspores and bird feces were collected on the forest floor. The boxes were covered with nylon mesh to prevent the arrival of other seeds. A barrier of tanglefoot on the external walls prevented ants from entering test boxes. Germination tests were performed at forest locations inhabited by *Clusia* seedlings. We checked for radicle protrusion at two-day intervals. We used chi-square tests to evaluate seed germination.

DISTRIBUTION AND SURVIVAL OF SEEDLINGS

The number of seedlings of *C. criuva* growing on nests of ponerine ants as compared to control areas (without nests) was determined in April 1998 by establishing paired experimental plots (0.5 x 0.5 m). Experimental nests were located by following ant workers attracted to tuna baits placed on forest floor (Horvitz 1981). We tagged 21 nests of *Pachycondyla striata* and 20 nests of *Odontomachus chelifer*, and established a control plot 2.5 m far (random direction) from each nest. These ponerine species were selected since they are very abundant at our study site, and accounted for a significant number of the ant-seed interactions recorded at fresh diaspores and feces containing seeds of *Clusia criuva* (see below). Differences in the number of seedlings growing in treatment and control plots were analyzed with Mann-Whitney *U*-tests. Seedlings within plots were marked and monitored every two months during one year. Survivorship curves of seedlings were constructed and differences between experimental plots were tested using Peto and Peto's

Logrank Test (Pyke & Thompson 1986). The soil composition of experimental plots was compared by collecting soil samples from nests of *P. striata* (N = 15), *O. chelifer* (N = 15), and control plots (N = 15 relative to each ant species). Samples were air-dried and soils were analyzed for total N, macronutrients, micronutrients, pH, texture, and organic matter (Camargo *et al.* 1986). Differences in soil variables between nest and control plots were analyzed with Mann-Whitney *U*-tests (Zar 1999).

Results

FRUIT PRODUCTION AND DIASPORE REMOVAL BY BIRDS

In 1998, *Clusia criuva* fruited for 85 days (from January to March), but individual fruiting periods ranged from 46 – 61 days (54 ± 6 days, N = 10). During this season, birds removed on average 83% of the diaspores per tree, 16.6% reached the forest floor either spontaneously or dropped by birds in the tree, and the remaining 0.4% rot (Table 1). On average 1640 (SD = 810, N = 10 trees) viable seeds embedded in bird feces fall to the ground beneath trees of *C. criuva*, but part of these seeds may have been taken by the birds from other conspecific trees. No pre-dispersal seed predation was recorded at study site.

DIASPORE REMOVAL BY ANTS *VS.* VERTEBRATES

Mean diaspore removal rates within 24 h were similar in exclosure (89 ± 18.1%) and control (91.5 ± 15.6%) treatments ($t = -0.878$, df = 39, $P = 0.385$), indicating that ants are the main removers of *C. criuva*. 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, *ca.* 1800 h (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* account for 34% of ant-diaspore interactions (N = 35 records) and were the main seed vectors among ants. *Pachycondyla striata* and *O. chelifer* (Fig. 1A) displaced seeds in diaspores and seeds within feces (pooled data) to considerable distances (*P. striata*: mean ± 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 nestmates 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

Bird feces found on the ground contained only seeds of *C. criuva*. Sixteen ant species were recorded at bird feces, eleven of which removed seeds (Table 2). Embedded seeds had bits of aril attached and on average 98.5% of the seeds were removed from feces after 24 h (N = 30 experimental feces, 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 feces).

SEED GERMINATION

Germination of *C. criuva* seeds is exceptionally rapid (< 8 d). Although bird ingestion does not affect germination success (71.0% for non-ingested seeds against 67.5% for embedded seeds, $\chi^2 = 0.35$, $P > 0.50$, df = 1), both removal of seeds from bird defecations (82.5% for isolated seeds against 67.5% for embedded seeds, $\chi^2 = 4.80$, $P < 0.05$, df = 1), and aril removal by ants increase significantly the germination success (83.1% for nonarillate against 71.0% for arillate seeds, $\chi^2 = 7.67$, $P < 0.01$, df = 1).

DISTRIBUTION AND SURVIVAL OF SEEDLINGS

Seedlings of *C. criuva* are more abundant in the vicinity of nests of *P. striata* ($U = 404.0$, $P<0.0001$, N = 21) and *O. chelifer* ($U = 282.5$, $P = 0.021$, N = 20) than in areas without nests (Figs 1B and 2). Furthermore, seedling survival is greater near nests of *P. striata* than in control areas ($\chi^2 = 14.18$, $P = 0.0002$). Proximity to *O. chelifer* nests, however, had no effect on seedling performance ($\chi^2 = 1.31$, $P = 0.2526$, Fig. 3). Soil analyses indicate that the concentrations of total nitrogen, iron, and boron are significantly higher at *P. striata* nests than at random locations. Ant-nest samples for *P. striata* also had greater cation exchange capacity and acid potential (H + Al), but no difference was found for other essential plant macronutrients or texture (Table 3). Soil variables did not differ between *O. chelifer* nests and control samples.

THE MULTISTEP DISPERSAL PROCESS IN *CLUSIA CRIUVA*

Figure 4 illustrates through a flow chart the dispersal process in *C. criuva*, summarizing the possible sequential events in the life of the seed. The results obtained for the whole sequence of events indicate that although *Clusia* presents ornithochorous features, being primarily dispersed by birds, the prominence of ant-seed interactions markedly affects seed fate in this species. Eighty-three percent of the diaspores produced are taken by birds, 16.6% fall to the ground, and 0.4% rot. Seeds reach the forest floor in bird feces or in diaspores. On average, 98.5% of the seeds embedded in feces are removed by ants in 24 h. The ant assemblage attracted to *Clusia* seeds includes large ponerines (*Odontomachus* and *Pachycondyla*) that account for 12.2% of seed removal. Approximately 90.3% of the fresh diaspores on the ground surface are removed in 24 h, and ants are responsible for 97.5% of the removal. *Pachycondyla striata* and *O. chelifer* together remove 34.3% of such diaspores. These large ponerines take the diaspores inside the colony, remove the lipid-rich aril and discard the seeds on refuse piles. Feces-embedded seeds and diaspores of *Clusia* are taken to *Pachycondyla* (70.0%), and *Odontomachus* (95.0%) nests. Aril removal by the ants significantly increases germination success in *C. criuva*, as well as the removal of seeds from bird defecations. Dispersal by ponerines of seeds contained in both diaspores and bird defecations had a marked effect on the distribution pattern of seedlings of *C. criuva*, which are more frequent close to ponerine nests than in control areas without such nests. Furthermore seedling survival was also greater in nests of *P. striata* than in control areas, and this is possibly related to a richer soil near the nests.

Discussion

Ant activity at fallen seeds

Clusia criuva presents copious fruit production and ca. 83% of the diaspores are eaten by birds on the tree, while 17% fall to the ground. Although information on fruit production by trees and fruit removal by vertebrate dispersers is relatively scarce, for many species a considerable portion of the fruits reportedly reaches 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 become available for litter-foraging vertebrates and invertebrates (Pizo & Oliveira 1998, Böhning-Gaese *et al.* 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, since fresh feces containing only seeds of *C. criuva* are abundant in the early morning on the forest floor. The great number of viable seeds found beneath fruiting trees of *C. criuva* (*ca.*1640 seeds), along with the observation of abundant single-seed species feces on the forest floor 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 granivorous and can actually eat seeds (Hölldobler & Wilson 1990, Moutinho 1991). Recent studies, however, have shown that although most of the retrieved seeds are eaten by the ants, some of them escape predation and become established, likely affecting plant recruitment patterns (Byrne & Levey 1993, Levey & Byrne 1993).

Seeds of *C. criuva* reach the forest floor both in diaspores or embedded in bird feces. The attractive diaspores of *C. criuva* are rapidly removed by ants on the forest floor, so the seeds of this species are less likely to be eaten by rodents. The assemblage of ants (16 species) and their behavior toward 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). Large ponerine ants such as *Pachycondyla* and *Odontomachus* transport single diaspores to their nests, where the aril is consumed by workers and larvae before the undamaged seeds are discarded on the colonies' refuse piles. On the other hand, smaller ants such as *Pheidole* recruit many nestmates to the diaspore and consume the aril on the spot. We here emphasize the role of large ponerines because these ants are not only the main removers of *Clusia* seeds, but also because they do not harm the seeds. Our estimates of seed displacement (polled data for fresh diaspores and seeds in bird feces) by ponerine ants are similar to those reported for other *Pachycondyla* and *Odontomachus* species (up to 10 m) at arillate seeds of *Calathea* in Mexican forests (Horvitz & Beattie 1980). Most seeds of *C. criuva* removed by ponerine ants (*P. striata*: 70%; *O. chelifer*: 95%) could be followed until they entered the nest, suggesting both that recorded distances are good estimates of seed dispersal by these ants, and that *P. striata* and *O. chelifer* usually do not abandon *C. criuva* seeds under the leaf litter at the study site (see also Pizo & Oliveira 1998).

Clusia seeds within feces 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 feces are scarce, but it seems that seeds in fruits are more attractive to ants than those embedded in feces (Roberts & Heithaus 1986). Ants of the subfamily Myrmicinae are known to be the prominent removers of seeds from feces of vertebrate frugivores of neotropical forests (e.g. Roberts & Heithaus 1986, Byrne & Levey 1993, Kaspari 1993), and the percent occurrence of ponerines at feces 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 since the behavior of different species may affect not only seed survival, but also their distribution, chance of germination, and establishment (Hughes & Westoby 1992*a*). Therefore, seeds of *C. criuva* may benefit from being exploited by a large ant assemblage of ants, including large ponerines. Although ants belonging to this subfamily are generally regarded as predominantely carnivorous (Hölldobler & Wilson 1990), they also exploit fleshy diaspores and disperse seeds of many plants in different habitats (Horvitz & Beattie 1980, Pizo & Oliveira 1998, Davidson & Morton 1981, Dejean & Lachaud 1994).

Given the differences in behavior of ant species towards seeds (Hughes & Westoby 1992*a*), 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*a*) have shown that the use of fallen diaspores by ants in the Atlantic rainforest of Brazil occurs according to the relative abundance of these insects on the forest floor. *Odontomachus chelifer* 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, and 52% of tuna baits presented at least one species of these ponerines (chapter 1). Besides removing seeds from feces, 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 rainforests species (Chambers & MacMahon 1994). The results showed that birds have no effect on seed germination in this species, and therefore corroborate other studies in which bird ingestion had no consistent effect on percent germination (Traveset 1998). Aril removal by the ants, however, significantly increased germination success in *C. criuva*, as also reported for other species in neotropical areas (Horvitz 1981, Pizo & Oliveira 1998, Leal & Oliveira 1998).

Besides increasing germination success in *C. criuva*, removal of seeds by ants from bird defecation may also affect establishment success 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).

Dispersal of seeds contained in diaspores and bird defecations by ponerine ants had a marked effect on the distribution pattern of seedlings of *C. criuva*. Seedlings were more frequent in the vicinity of nests of *P. striata* and *O. chelifer* than in control areas without nests. Furthermore, seedling survival was also greater in nests of *P. striata* than in control areas. Secondary movement and survivorship of seeds on the floor of tropical areas remain poorly understood, even though they often influence patterns of establishment in other regions (Levey & Byrne 1993, and included references). It has recently been shown that ants can affect seedling recruitment in nonmyrmecochorous tropical species (Farji Brener & Silva 1996, Farji Brener & Medina 2000, Böhning-Gaese *et al.* 1999). Our results with *Clusia* further indicate that ants affect seedling survival, a benefit never been shown for any other nonmyrmecochorous species. Seed rain and seedling establishment seem to be spatially uncoupled for *C. criuva* due to ant activity (see Herrera *et al.* 1994, Jordano & Herrera 1995). While birds disperse a great percentage of *C. criuva* fruit crop (83%) 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 feces (98%), and produce only local seed movements (see Horvitz & Le Corff 1993 for a discussion on scale of bird and ant dispersal).

Ant effects on seedling survival

There is evidence that seedlings can grow better near ant nests because such microsites can be chemically richer than background soils (Beattie 1985, Horvitz & Schemske 1986, Culver & Beattie 1980, Levey & Byrne 1993). However, many studies have also 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, what may improve performance of *C. criuva* seedlings. However, there might be other factors underlying greater survivorship of *C. criuva* in the vicinity of *Pachycondyla* nests and causes of seedling mortality are still to be assessed. Possible factors of seedling mortality 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 1984, Auspurger & Kelly 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 in a primarily vertebrate-dispersed species, and we predict that ant-induced effects on recruitment also hold for other plant species in neotropical forests.

Concluding remarks

Mutualisms involved in dispersal systems are less conspicuous than more tightly coevolved mutualisms (Wheelwright 1982), and one factor contributing to the lack of tight evolutionary interactions between rainforest frugivores and small-seeded fruiting plants is the unpredictable interactions between seeds and ants (Herrera 1986). Although complex dispersal systems may be even less conspicuous mutualisms, such interactions may underly the biotic complexity and high diversity of the tropical ecosystem (see Gilbert 1980). In a recent study, the relative importance of primary and secondary seed dispersal was assessed for a Malagasy tree that presents an unusually simple dispersal system in which primary and secondary seed dispersal are each effectively carried out by a single species (Böhning-Gaese *et al.* 1999). The more complex dispersal ecology of *C. criuva*, with diverse assemblages of both birds and ants, may be a more representative pattern of what is found in tropical rainforests (see Pizo & Oliveira 1998, 2000*a*, *b*).

In spite of the limitations of predicting the fate of dispersed seeds (Byrne & Levey 1993), the contribution of the current study lies precisely at providing a comprehensive picture of the recruitment of a nonmyrmecochorous species, involving several sequentially-connected stages (see Herrera *et al.* 1994). The main conclusion of our investigation is 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). Given that lipid-rich arils of fleshy fruits are attractive both to birds and ants (Böhning-Gaese *et al.* 1999, Pizo & Oliveira, 1998, 2000*a*), numerous vertebrate-dispersed species can actually present complex dispersal systems involving the latter. Considering that the size and lipid-content of nonmyrmecochorous diaspores are major determinants of the outcome of ant-diaspore interactions (Pizo & Oliveira 2000*b*), we predict that the effects of these interactions 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) would be worthwhile.

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Table 1. Diaspore production and fate from 10 *Clusia criuva* trees in the Atlantic rainforest of Cardoso Island, SE Brazil.

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

Table 2. Ant behavior toward fallen diaspores and feces-embedded seeds of *Clusia criuva* in the Atlantic rainforest of Cardoso Island, SE Brazil. Frequency is provided only for records obtained in systematic surveys. Two marked diaspores were set out at three stations beneath fruiting trees of *Clusia* (0730 or 1500 h) under wire cages and checked at 15 min intervals during two hours. One experimental feces was placed in a station beneath a fruiting tree of *Clusia* (0800 h) under wire cages and checked at 15 min intervals for one hour. The ant species attracted to the seeds and their behavior were recorded. Ants are arranged in alphabetical order under each subfamily. Ant species followed by an asterisk were not sampled in systematic surveys.

Ant subfamily and species	Percent - Behavior[a]	
	Diaspore (N = 168)	Feces (N = 58)
Ponerinae		
Gnamptogenys moelleri	8.6 – A	
Hypoponera sp.*	E	
*Odontomachus chelifer**	8.6 – R	E, I, R
Odontomachus sp.	5.7 - E, R	
Pachycondyla striata	25.7 - R	12.2 - R
Myrmicinae		
Acromyrmex aspersus		8.2 – D
Acromyrmex crassipinus		4.1 – D
Acromyrmex subterraneus	8.6 – R	
Acromyrmex sp.*	R	

Cyphomyrmex sp.		2.0 – D
Crematogaster sp	5.7 – S	16.3 - C, D, S
Pheidole sp. 1	5.7 – S	30.6 – C, D
Pheidole sp. 2*	E, C	
Pheidole sp. 3	20.0 - S	6.1 - E, S
Pheidole sp. 4		4.1 – C
Pheidole sp. 5		2.0 – C
Pheidole sp. 6		2.0 – C
Pheidole sp. 10*	C	
Solenopsis sp. 1		4.1 – C
Solenopsis sp. 4*	C	
Wasmannia sp.	5.7 - C, S	2.0 - C, D
Ecitoninae		
Labidus sp.	2.9 – A	2.0 – D
Formicinae		
Paratrechina sp. 1		2.0 - C, D
Paratrechina sp. 2	2.9 – C	2.0 – C
Number of interactions in systematic surveys	35	49
Total number of interactions[b]	79	62
Removal rate (after 24 h)[c]	89%	98.5%

[a] Behavior: A: remove portions of diaspores (aril + seeds) more than 5 cm; C: clean seeds by removing portions of the aril or of the fecal 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.

[b] Include records made during the surveys carried out monthly on the study site, as well as non-systematic records of *Clusia* seeds being explored by ants.

[c] Data obtained in experiments of diaspore removal by ants vs. vertebrates and removal of seeds from bird feces.

Table 3. Comparison of soil variables from nests of *Pachycondyla striata* (N = 15) and *Odontomachus chelifer* (N = 15) to those of random spots on the forest floor (N = 15 for each ant species). Values of K, Ca, Mg, Na, Al, H+Al, and C. E. C. (i. e., 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 (values are means); N in g/kg. Texture values are percentages.

Soil variable	*P. striata*	Random	Mann-Whitney's *U*	*O. chelifer*	Random	Mann-Whitney's *U*
Total Nitrogen	14.3	9.9	127.5*	12.2	10.4	143.0
Phosphorus	18.00	15.67	140.5	16.7	13.3	151.5
Potassium	1.51	1.53	140.0	1.54	1.29	142.0
Zinc	1.31	1.09	148.5	1.46	1.33	132.5
Iron	36.87	24.93	172.0**	38.47	37.20	104.0
Manganese	21.29	19.09	111.0	14.45	11.84	118.5
Cooper	0.11	0.12	104.5	0.14	0.12	133.5
Calcium	1.73	1.60	138.5	3.40	1.40	149.5
Magnesium	4.27	4.40	122.5	4.27	4.40	106.5
Boron	0.26	0.20	168.5*	0.23	0.20	116.5
Fine sand	7.78	6.85	118.5	6.87	5.71	134.0
Coarse sand	83.10	85.43	74.0	86.20	89.03	96.0
Silt	6.16	4.97	145.5	3.55	2.34	133.5
Clay	2.97	2.76	124.5	3.38	2.94	101.5
Organic matter	79.73	70.60	151.0	77.3	67.4	127.5

C. E. C.	137.91	117.53	160.0*	166.87	135.42	127.0
H+ Al	130.20	109.60	160.5*	157.67	128.33	126.5
PH	3.27	3.32	106.0	3.23	3.25	110.5

* $P<0.05$; ** $P<0.01$

Figure Legends

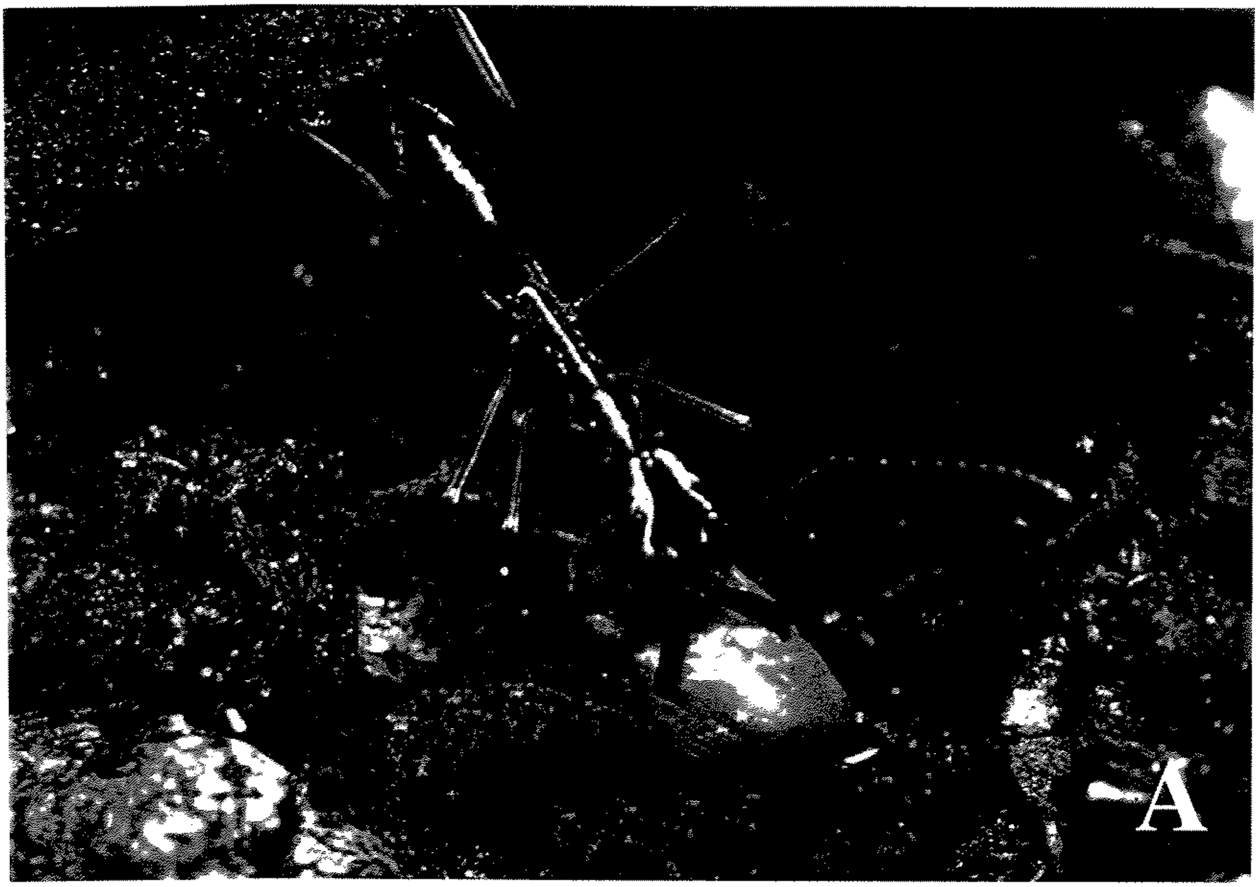
Figure 1. A) Worker of *Odontomachus chelifer* (size ≈ 1.8 cm) removing a diaspore of *Clusia criuva* on the leaf litter of a rainforest in southeast Brazil. The ants regularly carry the diaspores to the nest, where the aril is consumed and the seeds discarded; B) Seedlings of *C. criuva* clumped in the refuse pile of a nest of *O. chelifer*.

Figure 2. Mean number (+ 1 SE) of seedlings of *Clusia criuva* in nests of *Pachycondyla striata* (A) and *Odontomachus chelifer* (B), and in respective adjacent control plots.

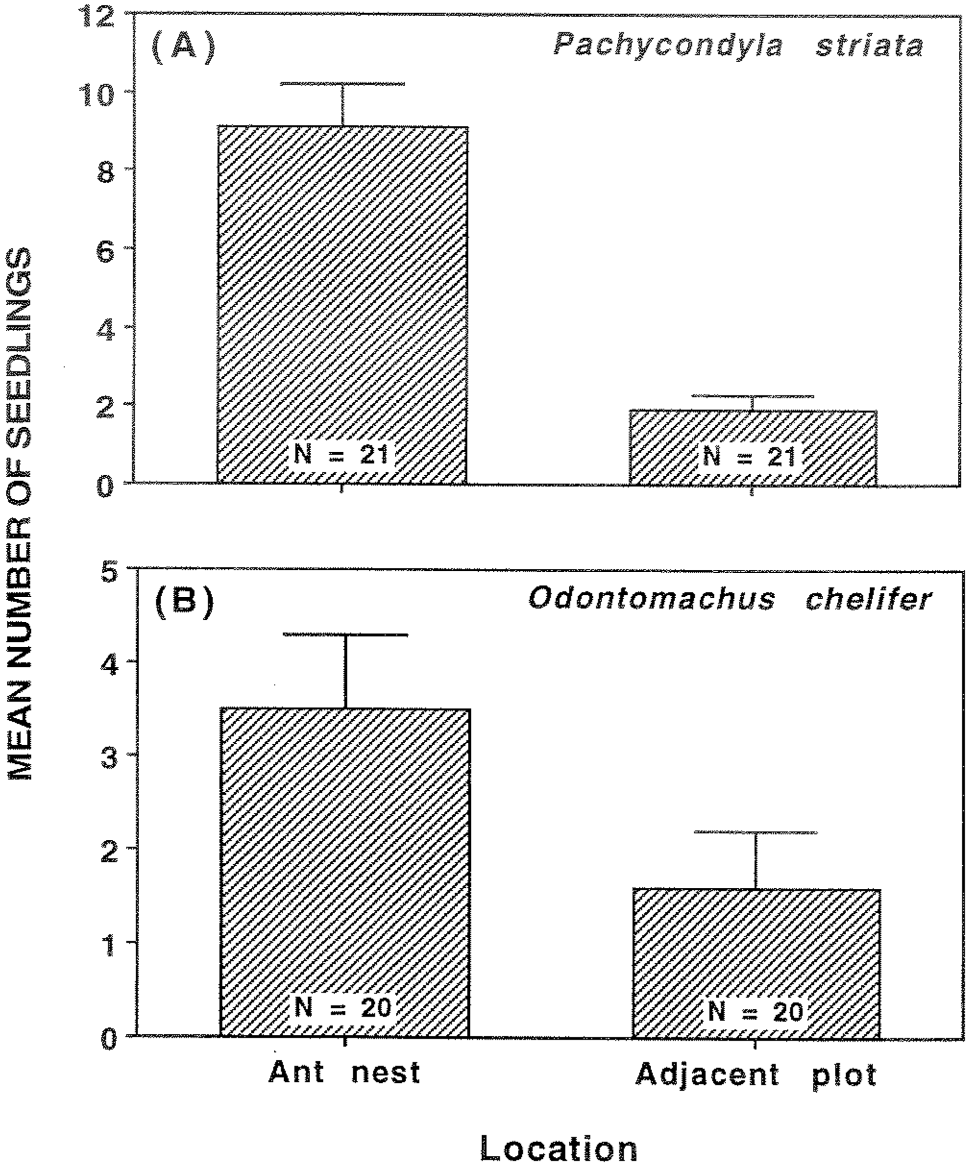
Figure 3. Survivorship curves for *Clusia criuva* seedlings growing in nests of *Pachycondyla striata* (A), *Odontomachus chelifer* (B), and in respective control plots over one year (April 1998 - April 1999). See also Figure 2 for mean number of seedlings in nests and control plots in April 1998.

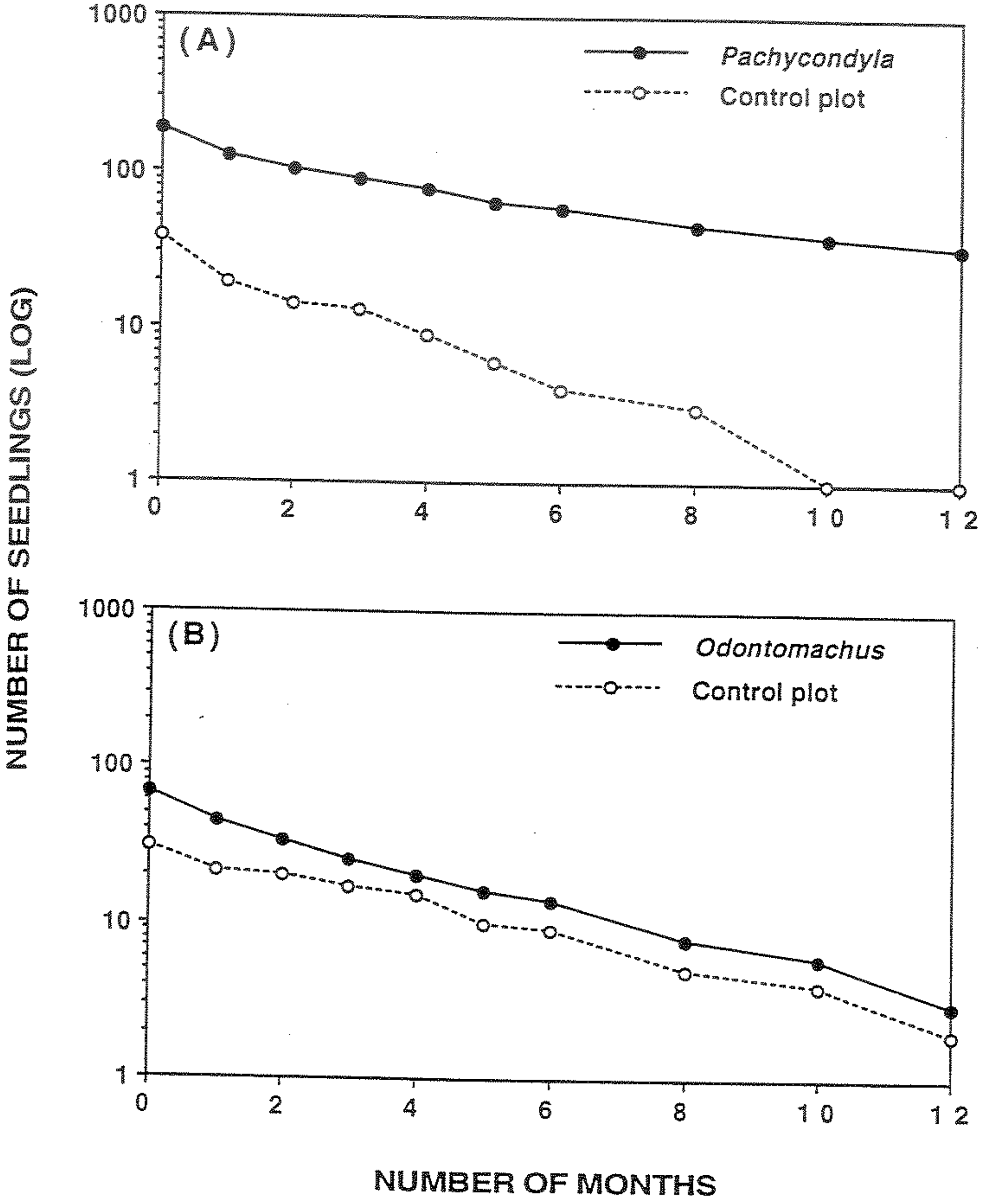
Figure 4. Illustration of the seed dispersal process in *Clusia criuva* for the fruiting period of 1998. The starting point is 100.0% diaspores produced of which on average 83.0% are taken by birds, 16.6% fall to the ground, and 0.4% rot. Seeds reach the forest floor in bird feces (A) or in diaspores (B). On average, 98.5% of the seeds embedded in feces are removed by ants in 24 h, and *P. striata* and *O. chelifer* 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. chelifer* together remove 34.3% of the diaspores. Feces-embedded seeds and diaspores (the diaspore consists of seeds

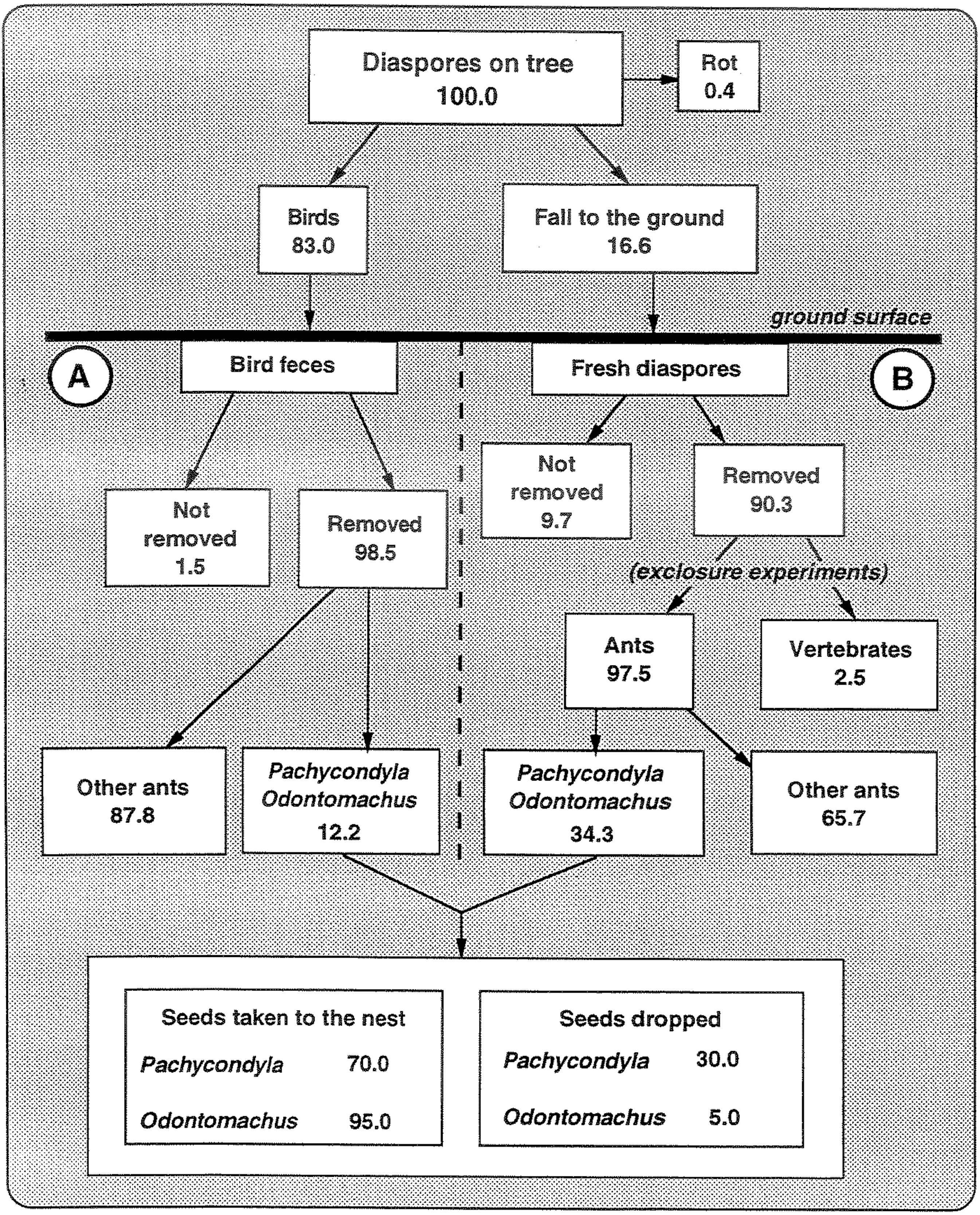
enveloped by a red aril) of *Clusia* are taken by *Pachycondyla* to nests in 70.0%, and by *Odontomachus* in 95.0% of the records. See Table 1 and text for further details.


A


B


MEAN NUMBER OF SEEDLINGS
(A)
Pachycondyla striata
0
2
4
6
8
10
12
N = 21
N = 21
(B)
Odontomachus chelifer
0
1
2
3
4
5
N = 20
N = 20
Ant nest
Adjacent plot
Location


(A)
Pachycondyla
Control plot
1000
100
10
1
0
2
4
6
8
1 0
1 2
(B)
Odontomachus
Control plot
1000
100
10
1
0
2
4
6
8
1 0
1 2
NUMBER OF SEEDLINGS (LOG)
NUMBER OF MONTHS


Diaspores on tree
100.0
Rot
0.4
Birds
83.0
Fall to the ground
16.6
ground surface
A
Bird feces
Not removed
1.5
Removed
98.5
Other ants
87.8
Pachycondyla
Odontomachus
12.2
B
Fresh diaspores
Not removed
9.7
Removed
90.3
(exclosure experiments)
Ants
97.5
Vertebrates
2.5
Pachycondyla
Odontomachus
34.3
Other ants
65.7
Seeds taken to the nest
Pachycondyla 70.0
Odontomachus 95.0
Seeds dropped
Pachycondyla 30.0
Odontomachus 5.0

CAPÍTULO 3

Interaction between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian sandy plain rainforest: ant effects on seed and seedlings*

*Formato e estilo: Functional Ecology

RESUMO

Este estudo examina o sistema de dispersão de *Guapira opposita* em uma floresta de restinga no sudeste do Brasil. As árvores de *Guapira* produzem frutos pequenos com polpa rica em proteínas (28.4%) e baixo teor de lipídeos (0.3%), que são primariamente dispersos por aves. Os frutos no solo da floresta são rapidamente removidos por formigas (93% após 12 h). Formigas da subfamília Ponerinae (*Odontomachus, Pachycondyla*) são os principais vetores de sementes, sendo cada espécie responsável por 29% das interações registradas. Operárias de *O. chelifer* e *P. striata* transportam individualmente o fruto de *Guapira* para seus ninhos, onde a polpa é consumida por operárias e larvas. A remoção da polpa aumenta o sucesso de germinação de sementes de *Guapira.* Plântulas e jovens de *Guapira* são mais freqüentes nos ninhos de *Odontomachus* que em áreas controle sem ninhos. Amostras de solo de ninhos de *Odontomachus* apresentaram uma maior concentração de Ca e P, e maior penetrabilidade que amostras de locais sem ninho. Experimentos de campo sugerem que a associação de plântulas de *G. opposita* com ninhos de *O chelifer* pode potencialmente proteger a planta contra herbívoros. Os resultados sugerem que o conteúdo de proteínas dos frutos é importante para a atração de formigas da subfamília Ponerinae no solo da floresta, e ilustram a complexidade da ecologia de dispersão de espécies arbóreas tropicais.

Interaction between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian sandy plain rainforest: ant effects on seeds and seedlings

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Running headline: Seed dispersal of *Guapira*

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Abstract

1. This study examines the dispersal system of *Guapira opposita* in a tropical rainforest in SE Brazil. *Guapira* trees produce small fruits with high protein-content (28.4%) and low lipid-content (0.3%), and the plant is primarily dispersed by birds.

2. Fruits on the ground are rapidly removed by ants (93% after 12 h). Ponerine ants (*Odontomachus*, *Pachycondyla*) are the main seed vectors, and each species account for 29% of the interactions recorded. Individual workers of *O. chelifer* and *P. striata* transport single fruits to their nests, where the pulp is consumed by workers and larvae. Pulp removal by ants increases germination success in *Guapira*.

3. Seedlings and juveniles of *Guapira* are more frequent close to *Odontomachus* nests than in sites without such nests. Soil samples from nests of *Odontomachus* had higher concentration of Ca and P, and greater penetrability, than random soil samples. Field experiments suggest that the association of *G. opposita* seedlings with nests of *O. chelifer* can potentially render the plant some protection against herbivores.

4. Results indicate that the protein-content of fruits may be relevant for the attraction of ponerine ants on the forest floor, and illustrate the complex nature of the dispersal ecology of tropical tree species.

Introduction

In tropical forests nearly 90% of the trees and shrubs bear fleshy fruits and rely on vertebrate frugivores such as birds, bats, or monkeys for seed dispersal (Frankie *et al.* 1974, Jordano 1993 and references therein). However, recent studies have shown that interactions between ants and diaspores (*i.e.*, any seed, fruit, or infrutescence that constitute the unit of dispersal of the plant) are common on the floor of tropical forests, and involve about 40 ant species and 50 plant species in rainforests in southeast Brazil (Pizo & Oliveira 2001a). These ant-seed interactions can modify the fate of seeds (*e.g.*, Roberts & Heithaus 1986, Kaspari 1993, Levey & Byrne 1993, Pizo & Oliveira 1998), and affect patterns of recruitment (distribution and survival of seedlings) in primarily vertebrate-dispersed species that lack special adaptations for ant-dispersal (Böhning-Gaese *et al.* 1999).

Fleshy fruits of tropical forests present a plethora of sizes, shapes, colours, and chemical composition of the edible portion (*e.g.*, van Roosmalen 1985, Corlett 1996, Galetti 1996). Consequently, ants in tropical forests interact with a broad range of fruits differing in morphology and nutrient content (Pizo & Oliveira 2001a). It has recently been suggested that the outcome of the interaction between ants and diaspores in tropical forests can be largely determined by the size and lipid content of the latter (Pizo & Oliveira 2001b). Lipids are an important food resource for ants, serving a variety of purposes that include nutrition, physiological constituents, and behavioural releasers (Beattie 1985 and references therein). According to Pizo & Oliveira (2001b), lipid-rich diaspores are more attractive to ants than diaspores with low lipid content, or rich in carbohydrates (see Jordano 1993 for main fruit composition patterns), and ant-effects in seedling recruitment have been shown for two lipid-rich tropical species (Böhning-Gaese *et al.* 1999, chapter 2).

Proteins are an essential food source for social insects such as ants and bees. Colonies must get the adequate protein intake to meet the dietary requirements of larvae and functional queens (Michener 1974, Hölldobler & Wilson 1990). Comparative studies of nutrient contents of fleshy fruits have revealed that in general fruits are poor in protein in comparison with leaves and insects, and that protein-rich fruits are not common (Herrera 1987, Jordano 1993, 1995). However, protein-rich fruits are attractive to ants, especially those in the predominantly carnivorous subfamily Ponerinae (Hölldobler & Wilson 1990). Ponerines search the leaf litter for arthropod prey and use the aril or pulp of fruits as a secondary food source (Horvitz & Beattie 1980, Hölldobler & Wilson 1990, Pizo & Oliveira 1998). Protein-rich fruits can be regarded as mimics of arthropod-type prey (see Carroll & Janzen 1973), and therefore complement the adequate protein intake of the colonies. Ponerine ants are the main seed vectors on the floor of neotropical forests (Horvitz & Beattie 1980, Pizo & Oliveira 1998, 2001a, b), and *Odontomachus chelifer* and *Pachycondyla striata* are key species determining the outcome of ant-seed interactions in the Atlantic rainforests in Brazil (Pizo & Oliveira 1998, 2001a, b). The activity of these large ponerines can markedly affect recruitment patterns in lipid-rich species (chapter 2), but there is no information on ant-induced effects on species with protein-rich fruits.

The present study examines the ant effects on seed fate in *Guapira opposita* (Vell. & Reitz) (Nyctaginaceae), a primarily bird-dispersed tree producing protein-rich fruits (see below), and their possible influence on plant recruitment in a sandy plain forest in southeast Brazil. Three questions were addressed: (1) What ant species use *G. opposita* fruits on the forest floor? (2) How do ants behave towards the fruits? (3) Can ant-fruit interactions affect recruitment (*i.e.*, distribution of seedlings and juveniles) in *G. opposita*?

THE PLANT SPECIES

Guapira opposita is a tree or treelet distributed in forested areas of tropical South America, extending from Amazonia to Southeast Brazil, being especially common in the Atlantic forest (Furlan 1996). Fruits of *Guapira* (January to May) are consumed by a diverse assemblage of bird species. Infrutescences bear drupes that are black when mature (mean ± SD 8.02 ± 0.84 mm length, 7.09 ± 0.49 mm wide, $N = 30$), weigh 0.25 ± 0.04 g ($N = 30$), and contain one seed each. The pulp of *G. opposita* has one of the highest protein contents (28.4%, Passos & Oliveira, unpublished) yet described in the literature (Jordano 1993), and a negligible amount of lipids (0.5%). Total carbohydrate and ashes account for 66.2% and 4.9% of the dry mass, respectively.

STUDY SITE AND METHODS

Field work was carried out in the sandy plain forest (see Oliveira-Filho 1993, Joly *et al.* 1999) of the Parque Estadual da Ilha do Cardoso (PEIC), a 22,500 ha island (altitude 0 – 800 m a. s. l.) located on the coast of São Paulo State (25° 03' S, 47° 53' W), SE Brazil. The forest grows on poor sandy soil (2 – 3 m a.s.l.), with 5 – 15 m tall trees forming an open canopy, and abundant bromeliads occurring on the ground layer (Barros *et al.* 1991). Mean annual temperature and rainfall are 20.9° C and 3000 mm, respectively. A dry-cold season occurs from April to August, and a wet-hot season from September to March.

ANT-FRUIT INTERACTIONS

Interactions between ants and fruits were surveyed through systematic sampling. Single fruits were placed on the forest floor at 10 m intervals along an 800 m transect at the study site. Fruits were set on small pieces (4 x 4 cm) of white filter paper to facilitate visualization on leaf litter. Fruits were distributed at 0700 h and 1500 h and checked at 15 min intervals ("scan sampling" *sensu* Lehner 1979) during two hours (*N* = 90 fruits). We recorded the ants attracted to the fruits, as well as whether they removed the fruits and/or recruited nestmates to exploit them on the spot. We followed ants carrying fruits until they entered their nests or disappeared in the leaf litter. The distance of fruit displacement was then measured.

Fruit removal by ants was experimentally assessed by distributing marked fruits (small dot of Enamel paint, Testors, Rockford, USA) along a transect, at intervals of 10 m to maintain independent discoveries by different ant colonies (Byrne & Levey 1993, Kaspari 1993). Ant response to marked and unmarked fruits was apparently the same. Each fruit was placed directly on the forest floor under a wire cage (17 x 17 x 8 cm, 1.5 cm mesh) closed to the top and stalked to the ground to permit free access by ants and exclude vertebrates (see Roberts & Heithaus 1986). Fruits were set out ca. 1800 h, and their removal was checked after 12 h. A given fruit was considered removed if not found within a 30 cm radius around the cage (*N* = 30 fruits). We interrupted every trial subjected to rains.

SEED GERMINATION

To test if fruit cleaning (*i.e.*, pulp removal) had any effect on seed germination of *G. opposita*, we sowed intact fruits (control), as well as fruits having their pulp removed by us (treatment), in plastic trays (40 x 40 cm) containing regularly moistened vermiculite. A total of 40 fruits were used in each treatment. Fruits in both treatments were placed in separate trays that were kept in the greenhouse of the Universidade Estadual de Campinas. Fruits were buried 1 cm into the substrate, 3 cm apart from each other, and checked for germination at 7-day intervals until seeds germinate or present decay signs. We used chi-square tests to evaluate seed germination. Given that some ants may secrete fungicidal substances from their metapleural glands (Beattie *et al.* 1986), thus potentially rendering an additional benefit for seed germination, cleaning of fruits by us may represent in fact a conservative simulation of the services provided by the ants (see Pizo & Oliveira 2001b).

DISTRIBUTION OF SEEDLINGS AND JUVENILES

Ponerine species, in particular *Odontomachus chelifer*, are very abundant at the study site, and accounted for a great number of the ant-seed interactions recorded for *Guapira opposita* (chapter 1). The number of seedlings and juveniles of *G. opposita* growing on nests of *Odontomachus chelifer* as compared to control areas (without ant nests) was determined in May 2000 by establishing paired experimental plots (0.5 x 0.5 m). Throughout this paper "juvenile plant" refers to a plant that no longer has cotyledons (see Gatsuk *et al.* 1980 for definition of age states of plants). Experimental nests were located by following ant workers attracted to tuna baits placed on the forest floor (Horvitz 1981). We tagged 40 nests of *Odontomachus*, and established a control plot 2.5 m far (random direction) from each nest. Seedlings and juveniles were counted at the end of the fruiting period of *G. opposita* (May), when they are abundant at study site. Since drought stress can be a factor of seedling mortality in this species, the same experimental plots were re-checked for the number of seedlings and juveniles at the end of the dry season (September). Early seedling mortality is often exceedingly high and rates of survivorship increase as seedlings become larger (Lieberman 1996). Differences in the number of seedlings and juveniles growing in treatment and control plots in May and September 2000 were analyzed with Mann-Whitney tests. The soil composition of experimental plots was compared by collecting soil samples from nests of *O. chelifer* (*N* = 40) and control plots (*N* = 40). Samples were air-dried and soils were analyzed for total N, macronutrients, pH, and organic matter (Camargo *et al.* 1986). Since physical soil properties such as drainage and aeration may be modified locally by ant nests (Farji-Brener & Medina 2000), and may likely affect seedling establishment and growth, we evaluated soil penetrability in refuse piles of *O. chelifer* nests and adjacent plots (*N* = 40). At each location we released a sharpened wire stake (30 cm long) from the inside top of a 1.5 m high plastic PVC tube. The depth reached by the stake into the ground was the estimate of soil penetrability for that location. Differences in soil variables between nest and control plots were analyzed with Mann-Whitney tests (Zar 1999).

Ant-derived protection against herbivores has been demonstrated for numerous plant species (see Oliveira *et al.* 1999, and references therein), and there is evidence that seedlings associated with ant nests may receive a similar benefit (see Davidson & Epstein 1989). In order to evaluate if seedlings and juveniles growing in the vicinity of nests of *Odontomachus chelifer* can gain protection from ants against herbivores, we performed an experiment using dipteran larvae. We pinned one live larvae on each of two seedlings growing on an ant nest, and on an adjacent plot without nest (*N* = 30 nests) under wire cages (17 x 17 x 8 cm, 1.5 cm mesh) closed to the top and stalked to the ground to permit free access by ants and preclude vertebrate disturbance. The number of larvae attacked by *O. chelifer* ants, or by other ant species, in either experimental plot was recorded at 30-min intervals. Experiments were performed from 0700 to 0930 h.

Results

ANT-FRUIT INTERACTIONS

A total of 11 ant species were attracted to fruits of *Guapira opposita* at PEIC (Table 1). The most frequent species recorded on fruits were the large ponerines *Odontomachus chelifer* and *Pachycondyla striata* that together accounted for 56% of the ant-fruit interactions, and were the main seed vectors among the ants (Table 1). *Odontomachus chelifer* (Fig. 1) and *P. striata* displaced fruits to considerable distances (*O. chelifer*: mean ± SD = 2.18 ± 1.18 m, range 0.90 - 4.00 m, $N = 8$; *P. striata*: 1.28 ± 0.58 m, range 0.50 - 2.30 m, $N = 10$). The two ponerines carried fruits into their nests in 87.5 and 40.0% of records, respectively. Large attines such as *Acromyrmex subterraneus* may occasionally remove fruits. Other ants (mainly *Pheidole* and *Crematogaster*) typically recruited nestmates to remove the pulp on the spot, without displacing seeds (Table 1). Ants removed 93% of the fruits used in removal experiments performed during the 12-h night period.

SEED GERMINATION

Germination of *Guapira opposita* is rapid, pulp removal increased germination speed in this species (pers. obs.) and all the cleaned seeds germinated in 10 d. The presence of pulp reduces the germination success in this species (100% for cleaned seeds against 45% for intact fruits; $\chi^2 = 30.34$, $P < 0.001$).

DISTRIBUTION OF SEEDLINGS AND JUVENILES

By the end of the fruiting period (May) seedlings ($U = 1419.00$, $P < 0.0001$, $N = 40$) and juveniles ($U = 1151.50$, $P < 0.0001$, $N = 40$) of *G. opposita* are more abundant in the vicinity of nests of *O. chelifer* than in random plots without nests. Seedlings ($U =$

1321.00, $P<0.0001$, $N = 40$) and juveniles ($U = 1241.00$, $P<0.0001$, $N = 40$) are also more frequent in nests of *O. chelifer* by the end of the dry season in PEIC (September) (Fig. 2). Soil analyses indicate that the concentrations of phosphorus and calcium are significantly higher at *O. chelifer* nests than at random locations. Soil samples from *O. chelifer* nests also had greater pH, while random locations had more organic matter, and higher cation exchange capacity, and acid potential (H + Al) (Table 2). Soil penetrability was greater in nests of *O. chelifer* than in random plots without nests (Table 2).

Live larvae placed on seedlings growing in the vicinity of *O. chelifer* nests were attacked by ants in greater numbers than those in control plots without nests (Fig. 3; $\chi^2 = 15.42$, $P < 0.001$). Furthermore, *O. chelifer* accounted for virtually all attacks to larvae recorded in ant nests, while attacks by small myrmicines (other ants) were more common in the control plots.

Discussion

The fruits of *G. opposita* are rapidly removed by ants on the forest floor, and the species composition of the ant assemblage exploiting the protein-rich fruits of this species is similar to that found for lipid-rich arillate species (Horvitz & Beattie 1980, Horvitz 1981, Pizo & Oliveira 1998). However, the percent occurrence of ponerines (*Odontomachus chelifer* and *Pachycondyla striata*) at fruits of *G. opposita* is much higher (27.8% for each species) than that recorded for other plant species (Pizo & Oliveira 1998, chapter 2; but see Horvitz & Schemske 1986). Chemicals mediate the behaviour of ants toward potential food items (Wilson 1971), and lipids are the major attractant factor in the interactions between ants and diaspores of myrmecochorous species (*i.e.*, adapted to ant-dispersal; see Marshall *et al.* 1979, Skidmore & Heithaus

1988, Brew *et al.* 1989). Lipid content also underlies ant-attraction to non-myrmecochorous diaspores in tropical forests and, together with diaspore size, comprises the main determinants of the outcome of such interactions (Pizo & Oliveira 2001b). The results presented here suggest that protein content is also an important factor in the selection of fruits by a variety of ants, especially ponerines. Ants in this subfamily are predominantly carnivorous (Hölldobler & Wilson 1990), and the lipid-rich elaiosome (*i.e.*, food reward of myrmecochorous plants) can be regarded as arthropod-prey mimics (Carroll & Janzen 1973, Horvitz & Beattie 1980). Results suggest that protein-rich fruits may be important food items in the diet of ponerines, and thus complement the protein intake of the colonies. We predict that protein-rich fruits would be important food items in areas with scarce animal resources (arthropod prey), such as the sandy plain forest of PEIC. Individual workers of *Odontomachus chelifer* and *P. striata* transport single fruits to their nests, where the pulp is consumed by the workers and larvae. The estimates of displacement of *Guapira* fruits by *Odontomachus* and *Pachycondyla* are similar to those reported for plants bearing lipid-rich diaspores (Horvitz & Beattie 1980, Horvitz & Schemske 1986, chapter 2; but see Pizo & Oliveira 1998).

Small myrmicine ants such as *Pheidole* do not displace fruits, but recruit nestmates and consume the pulp on the spot. Pulp removal increases both germination success and speed in *G. opposita*. Seed cleaning by ants may reduce fungal attack to fallen fruits, facilitating germination in some species (Horvitz 1981, Oliveira *et al.* 1995, Leal & Oliveira 1998, Pizo & Oliveira 1998). *Guapira opposita* seedlings emerge shortly before the dry season, thus drought stress greatly contributes to seedling mortality in this species (see Figure 2). Seed cleaning in *G. opposita* may be advantageous because early emergence maximizes the length of the first growing season and allows time for the development of a potentially large root system, which might ensure survival through the first dry season (see Garwood 1983, Traveset 1998). The data on number of seedlings and juvenile plants before and after the dry season indicate that although seedlings suffered a heavy mortality during this period due to desiccation, juvenile plants survived much better. These results are in agreement with the observed pattern that rates of survivorship improve as seedlings become larger and older (Lieberman 1996, Whitmore 1996, Traveset 1998).

Dispersal of *G. opposita* by *O. chelifer* had a marked effect on the distribution pattern of seedlings and juveniles of this species, supporting the view that large ponerines are key species mediating ant-seed interactions in tropical forests. Although some plant species bear diaspores morphologically adapted for sequential dispersal by vertebrates first and then by ants (Davidson 1988, Clifford & Moneith 1989, Kaufmann *et al.* 1991), the effect of ants on seed recruitment found here is devoid of any morphological specialization by the plant for ant-dispersal. It has recently been suggested that the importance of primary dispersal by vertebrates for plants bearing fleshy fruits greatly exceeds that of secondary dispersal by ants (Böhning-Gaese *et al.* 1999). The distribution patterns of seedlings and juveniles of *G. opposita*, however, suggest that dispersal by ants strongly affects recruitment in this species (but see Horvitz & Le Corff 1993, for a discussion on scale of bird and ant dispersal). The association between ants and diaspores could have arisen without special adaptations on the part of the plants or ants. Considering that ant-diaspore interactions are common on the forest floor of tropical forests (Pizo & Oliveira 2001a), we predict that ant-induced effects on recruitment will probably hold for other tropical species, particularly those presenting small and nutritious diaspores (*i.e.*, with high lipid or protein content).

Seed dispersal, germination, and early seedling growth/survival are the most critical stages in determining where plants recruit within a landscape (Herrera *et al.* 1994, Schupp 1995). Ant nests are known to have specific temperature, moisture, texture, and nutrient characteristics (Wilson 1971, Moutinho 1998, Farji-Brener & Medina 2000) that may be important conditions for seed germination and seedling establishment (Horvitz 1981, chapter 2, but see Bond & Stock 1989). Nests of *O. chelifer* are significantly richer in phosphorous and calcium, and the ants also increase soil penetrability, what might improve performance of *G. opposita* seedlings (see Horvitz 1981, Levey & Byrne 1993, chapter 2). Moreover, our data suggest that the association of *G. opposita* seedlings with nests of *O. chelifer* can potentially render the plant some protection against herbivores, as expressed by the attack rates by ants toward dipteran larvae. Indeed, ant-derived protection of seedlings growing in ant nests has already been demonstrated (Davidson & Epstein 1989). Given that herbivore-induced injury was seen in many seedlings and juveniles of *G. opposita*, an anti-herbivore role of *O. chelifer* deserves further investigation. Drought stress and herbivory seem to be relevant sources of seedling mortality in *G. opposita*, as reported for other tropical species (Turner 1990, Steven 1994, Lieberman 1996, Basset 1999). However, since *G. opposita* seedlings are strongly clumped at *O. chelifer* nests, additional density-related mortality factors should also be considered, as well as other possible factors affecting establishment and survivorship (Auspurger & Kelly 1984, Howe & Schupp 1985, Schupp 1988, Howe 1989, Schupp 1990, Whitmore 1996).

Location of "suitable" sites is unpredictable (Schupp 1988, Whelan *et al.* 1991), but some sites are associated with higher probabilities of survival than others (Schupp 1993). The nests of *O. chelifer* seem to be suitable sites for seedlings/juveniles of *G. opposita*, but previous results (chapter 2) suggest that the quality of such microsites may vary with the requirements of the plant species involved (see also Schupp 1993, Denslow *et al.* 1987).

Recent studies on seed dispersal ecology in the tropics emphasize the role of secondary dispersers and their impact on seed-fate of primarily vertebrate-dispersed species (*e.g.*, Levey & Byrne 1993, Chambers & MacMahon 1994, Pizo & Oliveira 1998, 1999, 2001b, Andressen 1999, chapter 2). This study also illustrates the complex nature of the dispersal ecology of tropical tree species. Untangling the complexity of such dispersal systems is crucial for understanding the evolutionary relationship between frugivores and fruiting plants (Byrne & Levey 1993, Herrera *et al.* 1994), as well as its role in determining the spatial structure of plant populations (Nathan & Muller-Landau 2000).

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Table 1. Ant behavior toward fallen fruits of *Guapira opposita* in the Atlantic rainforest of Cardoso Island, SE Brazil. Frequency is provided for records obtained in systematic surveys ($N = 90$ fruits). Single fruits were placed on the forest floor at 10 m intervals, along a transect at study site. Fruits were set on leaf litter at 0700 h and 1500 h, and checked at 15 min intervals during two hours ($N = 90$ fruits). The behavior of the ant species attracted to the fruits is also indicated. Ants are arranged in alphabetical order under each subfamily.

Ant subfamily and species	Percent - Behaviour[a]
	Fruits ($N = 90$)
Ponerinae	
Odontomachus chelifer	27.8 (R, T)
Odontomachus sp.	2.8 (E)
Pachycondyla striata	27.8 (R)
Myrmicinae	
Acromyrmex aspersus	2.8 (C)
Acromyrmex subterraneus	8.3 (E, R)
Crematogaster sp. 1	5.5 (C)
Crematogaster sp. 2	2.8 (C)
Pheidole sp. 1	8.3 (C)

Table 1 (continued)

Pheidole sp. 3	8.3 (E)
Solenopsis sp. 1	2.8 (E)
Strumigenys sp.	2.8 (E)
Total number of interactions	36

[a] Behaviour: C: clean seeds by removing portions of the pulp on the spot, no displacement; E: inspect or manipulate diaspore, no removal; R: remove diaspores more than 5 cm; T: try to remove diaspores, displacement < 5 cm.

Table 2. Comparison of soil variables from nests of *Odontomachus chelifer* ($N = 40$), and random spots on the forest floor. Values of total N is given in g/kg; K, Ca, Mg, H+Al, and C. E. C. (*i.e.*, cation exchange capacity) are given in mmol/dm^3; P, in mg/dm^3; organic matter in g/dm^3 (values are means). Soil penetrability is given in cm.

Soil variable	*O. chelifer*	Random	Mann-Whitney's *U*
Total Nitrogen	1.21	1.40	698.0
Phosphorus	13.88	11.20	1012.5*
Potassium	1.45	1.24	929.5
Calcium	5.13	2.26	1288.5***
Magnesium	2.95	2.58	909.5
Organic matter	43.98	58.40	510.0**
C. E. C.	72.16	137.05	425.0***
H+ Al	62.55	131.08	404.5***
PH	3.88	3.24	1326.5***
Soil penetrability[a]	10.21	6.21	1402.0***

*P<0.05; **P<0.01; ***P<0.001

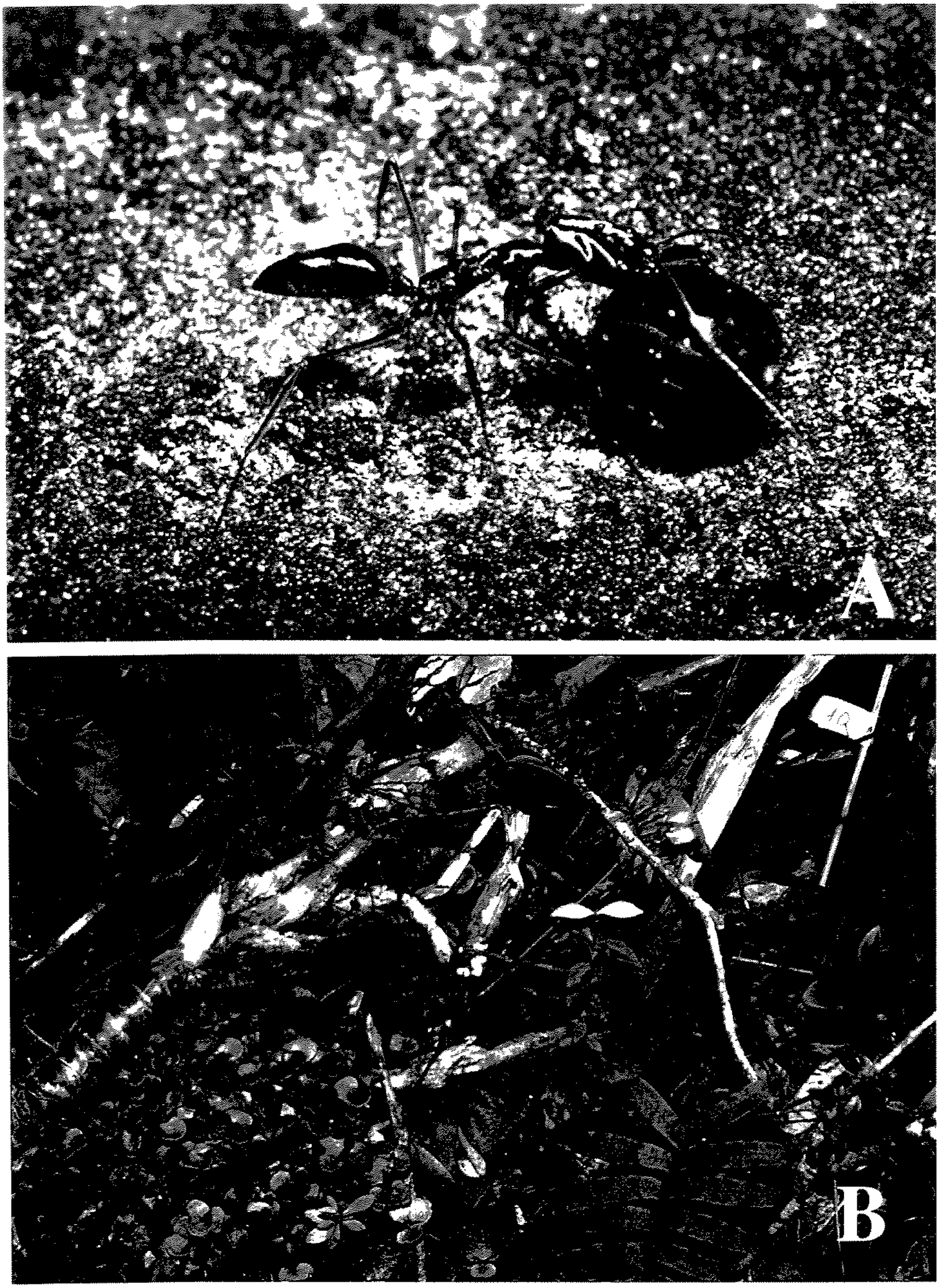
[a] Data obtained in experiments to assess penetrability of the soil in refuse piles of *O. chelifer* nests and adjacent plots.

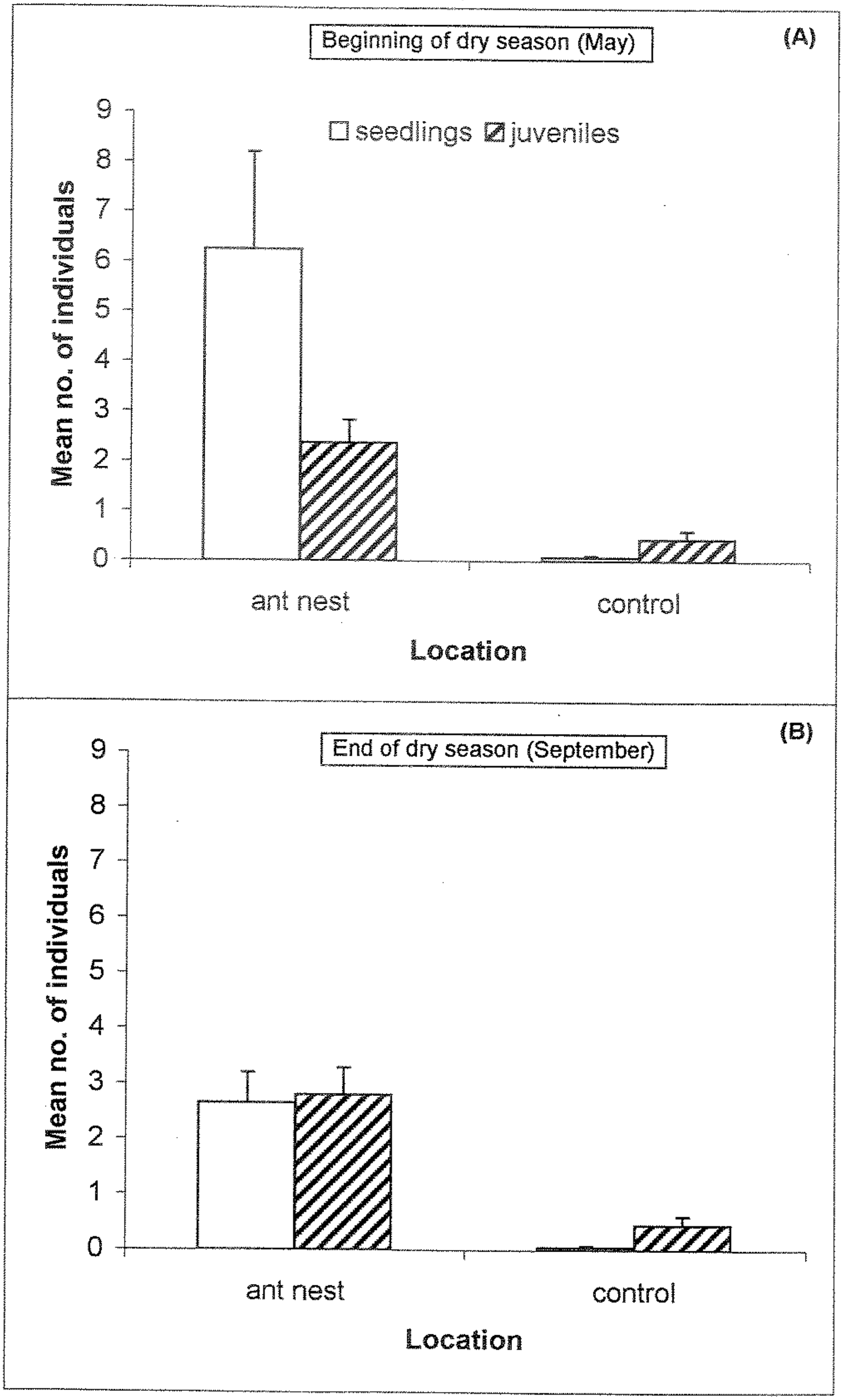
Figure Legends

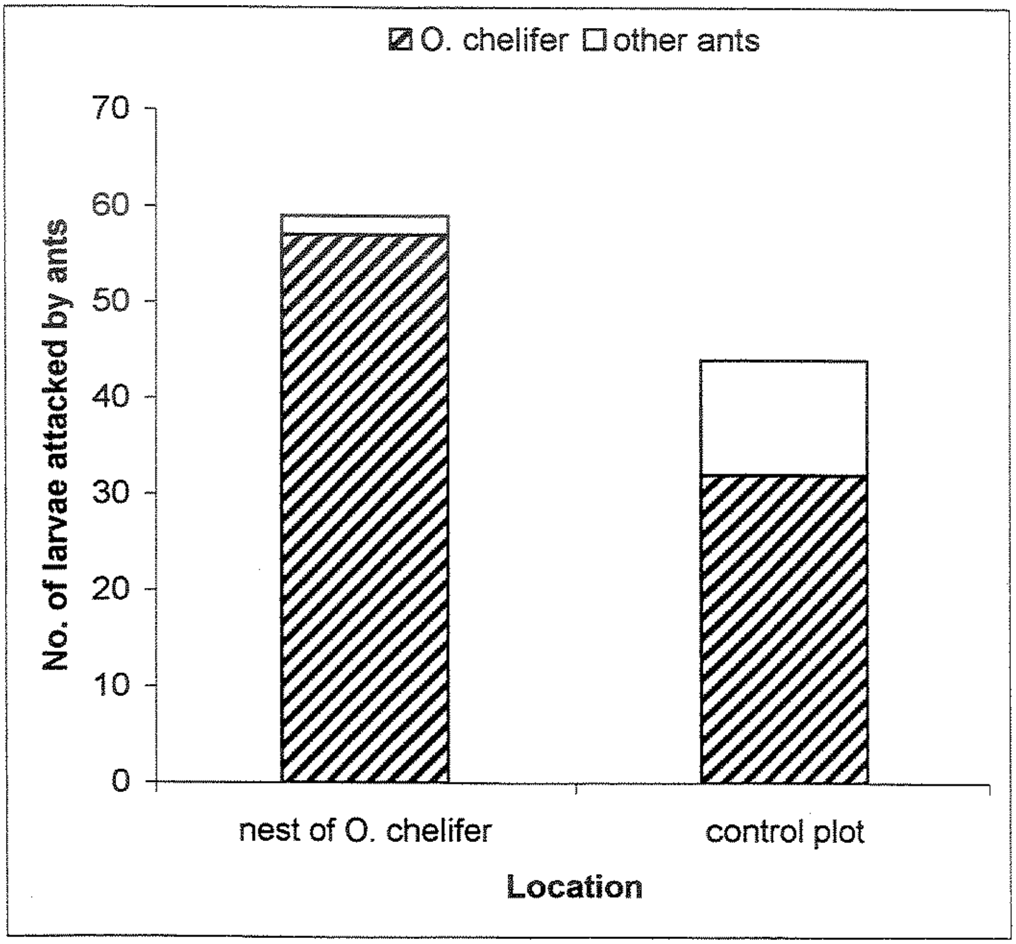
Figure 1. A) Worker of *Odontomachus chelifer* removing a fruit of *Guapira opposita* in a rainforest in southeast Brazil. The ants regularly carry the fruits to the nest, where the pulp is consumed and the seeds discarded; B) Seedlings of *G. opposita* clumped in the refuse pile of a nest of *O. chelifer* at the end of the fruiting season (May 1998).

Figure 2. Mean number (+ 1 SE) of seedlings and juveniles of *Guapira opposita* in nests of *Odontomachus chelifer*, and in respective adjacent control plots, in May (A) and September (B) 2000.

Figure 3. Distribution of attacks by ants on dipteran larvae-baits placed on seedlings growing in *O. chelifer* nests and respective control plots. Thirty experimental pairs (nest and control) were used. Two larvae were placed simultaneously on experimental pairs (two larvae per location, $N = 60$ larvae) under wire cages. The number of larvae attacked by *Odontomachus* ants or other ant species in either experimental plot was recorded in snapshots at 30-min intervals. Experiments were performed from 0700 to 0930 h. The distribution of attacks of ants is statistically different between treatments; ($\chi^2 = 15.42$, $P < 0.001$).


A
10
B


Beginning of dry season (May)
(A)
☐ seedlings ▨ juveniles
Mean no. of individuals
0
1
2
3
4
5
6
7
8
9
ant nest
control
Location
End of dry season (September)
(B)
Mean no. of individuals
0
1
2
3
4
5
6
7
8
9
ant nest
control
Location


▨ O. chelifer ☐ other ants
70
60
50
40
30
20
10
0
No. of larvae attacked by ants
nest of O. chelifer
control plot
Location

DISCUSSÃO GERAL

A dispersão de sementes tem grande influência na aptidão das plantas, pois determina os locais nos quais as sementes e, subseqüentemente, as plântulas irão viver ou morrer (Nathan e Muller-Landau 2000, Wenny 2001). Embora a maior parte dos estudos de dispersão enfoque apenas uma etapa do processo, o recrutamento de plântulas é composto por muitas etapas (veja Herrera *et al.* 1994, capítulo 2). Os estudos recentes realizados em florestas tropicais indicam que os sistemas de dispersão são complexos nessas áreas, sendo que a dispersão por vertebrados é freqüentemente apenas a primeira etapa da dispersão. Sementes que atingem o solo diretamente, em diásporos, ou em fezes de vertebrados frugívoros são posteriormente removidas por formigas, roedores ou besouros (capítulo 1, 2, 3, Roberts e Heithaus 1986, Kaspari 1993, Levey e Byrne 1993, Fragoso 1997, Andresen 1999, Pizo e Oliveira 1998, 1999). Embora os dispersores secundários possam agir principalmente como predadores de sementes, o efeito benéfico que conferem às sementes que dispersam pode influenciar consistentemente o recrutamento de plântulas (*p.e.* Levey e Byrne 1993, Wenny 2001).

O presente estudo avança por demonstrar claramente que as interações entre formigas e diásporos no solo de uma floresta de restinga afetam o recrutamento, ou seja, padrão de distribuição e sobrevivência inicial de plântulas de diversas espécies (capítulos 1, 2 e 3).

Foi sugerido recentemente que a importância da dispersão primária por vertebrados em plantas com frutos carnosos excede grandemente a importância da dispersão secundária por formigas (Böhning-Gaese *et al.* 1999). Entretanto os padrões de distribuição de plântulas encontrados para *Clusia criuva* e *Guapira opposita* (capítulos 2 e 3) sugerem que a dispersão por formigas afeta fortemente o recrutamento nestas espécies (mas veja Horvitz e Le Corff 1993 para uma discussão sobre a escala de dispersão por aves e formigas). A mata de restinga onde foi realizado este estudo reúne características como: (1) solo arenoso muito pobre com áreas sem cobertura vegetal, (2) grande abundância de formigas da sub-família Ponerinae (*Odontomachus* e *Pachycondyla*) e (3) pequena disponibilidade de artrópodes no folhiço (em comparação com a floresta ombrófila) que certamente contribuem para a relevância das interações formigas-diásporos neste ambiente, bem como para a ocorrência de efeitos marcados das formigas nos padrões de distribuição e sobrevivência de plântulas/jovens.

Ao compararmos o conjunto de informações disponíveis atualmente para interações entre formigas e diásporos envolvendo (1) plantas mirmecocóricas típicas ou (2) plantas não-mirmecocóricas, fica claro que para plantas mircocóricas os padrões gerais já foram determinados e os estudos recentes enfocam questões específicas ou suas conseqüências para o sistema (*p.e.* Hughes e Westoby 1992, Hananza *et al.* 1988).

Por outro lado, os estudos acerca das interações entre formigas e plantas mirmecocóricas estão em outro patamar: ainda estamos na fase exploratória; onde os levantamentos das interações (Pizo e Oliveira 2001a, capítulo 1) são importantes. Entretanto, já são sugeridos alguns padrões mediando estas interações (*p.e.* Pizo e Oliveira 2001b). Nesse contexto o presente estudo vem colaborar para a maior compreensão das interações entre formigas e diásporos não-mirmecocóricos e determinação dos fatores mediando estas interações. Com base nos resultados obtidos neste estudo, e em outros trabalhos sobre a interação formiga-diásporo não-mirmecocóricos citados ao longo do texto, podemos concluir que:

(1) Conforme assinalado por Pizo e Oliveira (2001b) o tamanho é relevante para as interações, sendo seus efeitos mais nítidos para espécies com diásporos pequenos ou médios (ou diásporos grandes contendo sementes pequenas);

(2) A composição química do diásporo é um fator importante, mas além dos lipídios (Pizo e Oliveira 2001b), as proteínas também podem ter papel relevante na atração de formigas, e estudos mais elaborados são necessários antes que possamos estabelecer padrões consistentes;

(3) O contexto é muito importante na determinação do resultado das interações entre formigas e diásporos não-mirmecóricos. Características locais (*p.e.* abundância de formiga Ponerinae e disponibilidade de artrópodes) podem ser determinantes para o tipo de interação, bem como suas conseqüências para o recrutamento das plantas (queira ver capítulo 1 para discussão).

Perspectivas:

Estudos comparando os padrões de utilização de diásporos não mirmecocóricos por formigas (e suas conseqüências) em diferentes áreas (queira ver capítulo 1) seriam úteis a fim de compreender os fatores mediando as relações complexas entre formigas e frutos/sementes em florestas tropicais.

O presente estudo, ao determinar os efeitos das formigas no recrutamento de plântulas, sugere uma frente promissora de investigação, abordando as seguintes perguntas: (1) Quais são de fato as características relevantes no microambiente dos ninhos de formigas (queira ver Wenny 2001 para discussão sobre dispersão direta); (2) Como esses fatores influenciam a sobrevivência de plântulas/jovens nestes locais?; (3) O efeito das formigas na distribuição de plântulas/jovens vai se refletir na distribuição de plantas adultas?

Estudos enfocando os aspectos descritos acima irão seguramente contribuir para nossa compreensão dos sistemas de dispersão complexos de espécies vegetais nos trópicos.

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