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**“A FRAGMENTAÇÃO FLORESTAL E A
INTERAÇÃO ENTRE FORMIGAS E
DIÁSPOROS CARNOSOS NA FLORESTA
ATLÂNTICA”**

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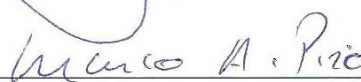
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“Viver é desenhar sem borracha”

Millôr Fernandes

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Quando em meados de 2006, após uma conversa com o Prof. Dr. Paulo Oliveira, decidi vir fazer o doutorado em Campinas, eu apenas tinha dois pontos como certos. Meu tema de estudo teria de envolver interações formiga-planta e teria que, de algum modo, abordar o efeito do homem sobre os ecossistemas. Assim, surgiu-me a idéia de trabalhar com interação formiga-fruto, uma das linhas de pesquisa do grupo, em uma paisagem fragmentada. Desde a época que entrei na Unicamp (2007) até o momento de entregar a tese, passaram-se quase cinco anos. Aqui, passei mais anos do que os dedicados à minha graduação, e mais do que o dobro do meu tempo de mestrado, sempre voltada ‘apenas’ para o mesmo assunto. “Um absurdo”, dirão alguns... Pois, eu direi para vocês que foi um sonho... Não quero com isto dizer que tudo foi perfeito, nem que todo o processo foi fácil, de jeito nenhum! Mas, quero dizer que tive um prazer imenso em desenvolver esta tese, especialmente por abordar temas que sempre me despertaram curiosidade. Espero que, pelo menos nesta seção de agradecimentos, eu seja capaz de transmitir este prazer para minha banca, os meus leitores e os meus amigos.

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RESUMO

Em florestas tropicais, formigas de folhígio são freqüentemente vistas em interação com diásporos vegetais (frutos e sementes). Em alguns casos, esta interação oportunista resulta em um mutualismo. Enquanto formigas se beneficiam ao alimentar-se de partes carnosas nutritivas (i.e., polpa, arilo), elas podem beneficiar a semente, por exemplo, ao aumentar sua chance de germinação ou ao dispersá-la para micro-sítios ricos em nutrientes. Portanto, para algumas espécies de plantas, a perda de interações formiga-diásporo pode implicar numa redução do recrutamento de novos indivíduos. Nesta tese, estudamos os padrões de interação entre formigas e diásporos em dois tipos contrastantes de florestas, representativos do que resta da Floresta Atlântica no Estado de São Paulo: florestas contínuas (CFs) e fragmentos de floresta com vegetação secundária (FFs) (quatro áreas cada). Durante este estudo, quatro abordagens complementares foram adotadas. Primeiramente, registramos as interações entre formigas e diásporos em cada uma das oito áreas durante um ano. As principais famílias de plantas assim como os principais gêneros de formigas registrados correspondem a grupos importantes já listados em estudos prévios realizados neste bioma. Apesar da abundância similar de diásporos considerados atrativos entre os dois tipos de floresta, houve um maior número de interações na floresta contínua. Esta diferença é provavelmente devida à comunidade vegetal depauperada dos fragmentos, composta por espécies menos atrativas para as formigas. Com base no mesmo conjunto de dados, comparamos se a topologia das redes de interação formiga-fruto diferiu entre os dois tipos de floresta. Três das sete métricas calculadas foram afetadas pelo tipo de floresta. A diminuição do número de espécies de plantas nos fragmentos florestais parece ser um fator-chave para justificar os resultados obtidos. Na terceira abordagem, oferecemos um diásporo sintético rico em lipídios em estações de remoção para comparar a visitação e o comportamento das

formigas entre os dois tipos florestais. Em geral, um maior número de espécies de formigas foi atraído às estações das CFs. A frequência de grandes poneríneas (em especial, *Pachycondyla striata*) em interação com diásporos sintéticos foi mais elevada em CFs, estando relacionada com uma maior remoção de diásporos nestas áreas. Por fim, avaliamos experimentalmente se a manipulação prévia por aves (uma condição mais comum em florestas contínuas) afeta a atratividade de diásporos caídos em relação a formigas. Para este procedimento, utilizamos o arbusto *Psychotria suterella* (Rubiaceae), comum no subosque de nossa área de estudo e cujos diásporos são dispersos por aves. Frutos que já tiveram contato com vertebrados apresentaram uma maior chance de interagir com formigas. Este resultado sugere que espécies vegetais em florestas fragmentadas, comumente sujeitas à perda de seus dispersores primários, ainda são afetadas pela diminuição da atratividade de frutos intactos para formigas (dispersores secundários), a despeito da abundância destes insetos no chão da floresta. De forma geral, os resultados desta tese indicam que a fragmentação da Floresta Atlântica afeta negativamente as interações formiga-diásporo. Portanto, é possível que em fragmentos florestais haja uma diminuição dos potenciais benefícios a sementes e plântulas derivados da interação com formigas, podendo repercutir negativamente no recrutamento das plantas.

Palavras-chave: dispersão de sementes, Formicidae, fragmentação florestal, frugivoria, interação formiga-planta, mirmecocoria, *Pachycondyla striata*, redes de interação, vertebrados.

ABSTRACT

In tropical rainforests, ground-dwelling ants opportunistically interact with fleshy diaspores and, in some cases, this interaction can be classified as mutualistic. While ants gain from eating the nutritious fleshy parts, they may benefit the seed in two ways: (1) greater germination success; and (2) directed dispersal to nutrient-rich microsites where seedlings grow better. Thus, for some plant species, the loss of ant-diaspore interactions may negatively affect plant recruitment. Here, we explore ant-diaspore interaction patterns in two divergent forest types, representing what has remained from the Brazilian Atlantic Forest of São Paulo State: continuous old-growth forests (CFs) and secondary forest fragments (FFs) (four sites each). During this study, four complementary approaches were adopted. First, we surveyed ant-diaspore interactions in all forest sites during one year. Main plant families and ant genera registered during our survey correspond to previous studies performed in this biome. In spite of the similar abundance of ant-attractive diaspores on the forest ground, there were striking differences on ant-diaspore interactions between continuous and fragmented forests. Differences are most certainly attributed to the species-poor plant community, composed by less attractive species, found in the fragments. Based on the same dataset, we investigated whether the topology of ant-diaspore interaction networks differed between our two studied forest types. Three out of seven network-level metrics calculated diverged between fragments and continuous forests. The decrease in the number of interacting plant species observed in the fragmented forests appears to be a key-factor for explaining the observed results. Third, we offered a lipid-rich synthetic diaspore in experimental removal stations to compare ant attendance and behavior between forest types. Again, the experiment evidenced differences between the opposing forest types. In general, a higher number of ant species was recorded in CFs. The frequency of large ponerines (mainly *Pachycondyla*

striata) was higher in CFs, corresponding to the higher frequency of diaspore removal and the higher removal distances observed in these sites. Finally, we experimentally evaluated if previous handling by birds (a condition more frequent in continuous forests) would affect ant attendance to fallen fruits. For this approach, we used as a model the bird-dispersed species *Psychotria suterella* (Rubiaceae), a common treelet in the understory of our forest sites. As expected, “feces-embedded” and “mandibulated” *P. suterella* fruits had increased frequencies of ant attendance than “intact” fruits. This result suggests that plant species in fragmented forests, together with the pervasive loss of their primary seed dispersers, may also be affected by the decreased attractiveness of unhandled fruits to ants (secondary dispersers), in spite of the abundance of these insects on the forest floor. Altogether, our results indicate that Atlantic Forest fragmentation negatively affects ant-diaspore interactions with respect to most of the studied parameters. Therefore, we expect that fragments will present a decrease on ant-derived potential benefits to seeds and seedlings.

Key-words: ant-plant interaction, vertebrates, forest fragmentation, Formicidae, frugivory, interaction networks, mirmecochory, *Pachycondyla striata*, seed dispersal.

Capítulo 1. Introdução Geral

Formigas

As formigas pertencem a uma única família de insetos, Formicidae, sendo classificadas, juntamente com abelhas e vespas, dentro da ordem Hymenoptera. Compreendem mais de 12.500 espécies atualmente descritas (<http://www.antbase.org/>; Bolton et al. 2007), que compartilham entre si as seguintes características: vida em colônias (estrutura eusocial), e presença de pecíolo, de glândula metapleural, e de antena geniculada (Hölldobler & Wilson 1990). Porém, a diversidade de espécies existentes atesta que as formigas diferem entre si quanto a inúmeras outras características, como por exemplo: tamanho dos indivíduos e da colônia, local de nidificação, hábito alimentar, grau de comunicação entre membros da mesma colônia, capacidade de colonização de outros ambientes e interações mutualísticas e antagonísticas com outros organismos (Hölldobler & Wilson 1990, Lach et al. 2010).

Estes insetos são encontrados naturalmente em quase todos os ecossistemas terrestres do planeta, à exceção da Antártida, de áreas montanhosas acima de 3500 m de altitude e de ilhas oceânicas mais distantes, como os Arquipélagos do Hawaii e dos Açores (Hölldobler & Wilson 1990, Fisher 2010). Apesar de seu pequeno tamanho individual, as formigas são organismos extremamente conspicuos, devido a sua grande abundância e aos papéis essenciais desempenhados (Folgarait 1998, Rico-Gray & Oliveira 2007, Lach et al. 2010). Por exemplo, Fittkau & Klinge (1973) calcularam que apesar das formigas representarem apenas 1,5% das espécies de insetos da floresta amazônica, sua biomassa corresponde a 15% de toda a biomassa animal (incluindo vertebrados) deste ecossistema. Um exemplo especialmente apelativo sobre a importância ecológica de espécies individuais de formigas é a estimativa recente de que cerca de

300 espécies, desde carrapatos até aves, dependem em algum momento de sua vida, da formiga de correição *Eciton burchellii* (Rettenmeyer et al. 2011). Mais ainda, enquanto algumas espécies são consideradas como engenheiras de ecossistema (Farji-Brener & Illes 2000, Folgarait 1998), outras espécies são invasoras vorazes (e.g., *Solenopsis geminata*, *Linepithema humile* e *Wasmannia auropunctata*), sendo tratadas como “inimigas de estado”, devido aos danos causados aos ecossistemas invadidos e, principalmente, ao homem (Lach & Hooper-Bùi 2010; ver também os capítulos 13, 14 e 16 em Lach et al. 2010).

Merecidamente, as formigas estão entre os insetos que, até o momento, têm recebido maior atenção em pesquisas científicas, englobando desde estudos sobre reconhecimento químico entre membros de uma mesma colônia (Chapuisat et al. 2005) e utilização do grupo no monitoramento de áreas degradadas (Majer & Nichols 1998), até sua complexa relação com diversas espécies de microorganismos (i.e., fungos e bactérias; Currie 2001) (ver recente compilação do conhecimento sobre a ecologia de formigas em Lach et al. 2010). Dentre as mais bem estudadas interações de formigas com outros organismos, destacam-se interações formiga-planta como: a ‘herbivoria funcional’ de algumas cultivadoras de fungo (Attini: gêneros *Atta* e *Acromyrmex*), o mirmecofitismo (plantas com domáceas, estruturas especializadas que abrigam formigas), o uso por formigas de nectários extraflorais e de exsudados de hemípteros, e suas interações com diásporos vegetais (ver revisão em Rico-Gray & Oliveira 2007).

Interações entre formigas e diásporos vegetais

Em plantas fanerogâmicas, o termo ‘diásporo’ refere-se à unidade básica de dispersão da planta que pode ser uma semente, um fruto ou uma infrutescência (Van der Pijl 1972). Há dois tipos principais de interação formiga-diásporo, ambos baseados em relações tróficas ou de

consumo, em que a formiga se alimenta de alguma parte do diásporo: a semente ou algum apêndice carnoso do diásporo (Rico-Gray & Oliveira 2007). O hábito de predação de sementes é comum a várias espécies de formigas de vários ecossistemas (Rico-Gray & Oliveira 2007), visto que sementes são estruturas extremamente ricas em nutrientes (Janzen 1971). No entanto, dietas predominantemente granívoras são especialmente frequentes em regiões desérticas, com destaque para os seguintes gêneros: *Messor*, *Monomorium*, *Pheidole* e *Pogonomyrmex* (Hölldobler & Wilson 1990, Rico-Gray & Oliveira 2007). Nestes ambientes, como a oferta de sementes e de outros alimentos é bastante sazonal, as formigas estocam as sementes em seus ninhos, para consumi-las em épocas de escassez de alimento (Rico-Gray & Oliveira 2007). Em geral, esta relação formiga-semente é vista como antagônica, pois as sementes predadas tornam-se inviáveis para a germinação. Contudo, relatos mostram que sementes ainda intactas são ocasionalmente abandonadas no caminho para o ninho ou descartadas próximas ao ninho, recebendo assim o benefício da dispersão (Levey & Byrne 1993, MacMahon et al. 2000)

No segundo tipo de interação formiga-diásporo, as formigas estão interessadas principalmente nos nutrientes presentes em apêndices ligados à semente (como arilos, carúnculas, sarcotestas, epicarpos e pericarpos, dentre outros). Diásporos são considerados mirmecocóricos quando possuem um apêndice carnoso rico em lipídeos, o elaiossomo (nome genérico atribuído a estruturas de origens embrionárias diversas, ver Gorb & Gorb 2003), que os torna extremamente atrativos às formigas (Beattie 1985, Hughes et al. 1994). O elaiossomo é utilizado pela formiga como uma alça que facilita o transporte da semente até o ninho, onde é consumido e as sementes viáveis são abandonadas em lixeiras internas ou descartadas na área externa ao formigueiro (Beattie 1985, Leal et al. 2007, Rico-Gray & Oliveira 2007).

Os benefícios da mirmecocoria, dispersão de diásporos por formigas, para a semente são a dispersão para longe da planta-mãe (Andersen 1988, Gómez & Espadaler 1998), e a chegada a micro-sítios mais ricos em nutrientes (os ninhos; Culver & Beattie 1978, Leal et al. 2007). Além disso, os ninhos ofereceriam uma maior proteção contra roedores, principais predadores de sementes (O'Dowd & Hay 1980), e outros insetos predadores de sementes (Lôbo et al. 2011), assim como contra eventuais queimadas (Beattie 1985, Hughes & Westoby 1992) (para benefícios associados à dispersão de sementes de modo geral ver Howe & Smallwood 1982). Embora esteja presente no mundo todo, a mirmecocoria tem sido registrada principalmente em plantas de ecossistemas não-florestais de clima seco, como os “fynbos” sul-africanos (Bond & Slingsby 1983) e as savanas australianas (Hughes & Westoby 1992), ocorrendo em mais de 350 gêneros pertencentes à cerca de 80 famílias de plantas (Beattie 1983, Gómez & Espadaler 1998, Lengyel et al. 2009). No Brasil, ainda há poucos estudos sobre mirmecocoria. No entanto, o bioma Caatinga no semi-árido Nordeste, uma região brasileira pouquíssimo estudada (Santos et al. 2011), tem apresentado uma extrema diversidade deste tipo de interação, concentrada principalmente na família Euphorbiaceae (Leal et al. 2007, Lôbo et al. 2011).

Por outro lado, em florestas tropicais, os vertebrados são de longe os principais agentes dispersores de diásporos vegetais (Frankie et al. 1974, Howe & Smallwood 1982). No entanto, sabe-se que uma grande quantidade de frutos primariamente dispersos por vertebrados atraem também formigas (Pizo et al. 2005, Rico-Gray & Oliveira 2007). Neste caso, apesar da ausência de um mutualismo estreito entre as duas partes (formigas e frutos carnosos), a abundância dos dois grupos torna esta interação bastante freqüente. Levantamentos realizados em ecossistemas brasileiros (Cerrado, Floresta Atlântica e Caatinga) comprovam que muitas espécies de formigas do solo e do folhíço interagem com um número expressivo de diásporos não-mirmecocóricos

(i.e., dispersos primariamente por vertebrados; Leal & Oliveira 1998, Pizo & Oliveira 2000, Passos & Oliveira 2003, Leal et al. 2007, Bottcher 2010, Christianini et al. 2011). Pesquisas desenvolvidas principalmente nos Neotrópicos (Brasil e Costa Rica) têm contribuído muito para o avanço do conhecimento nesta área nos últimos 25 anos (e.g., Roberts & Heithaus 1986; Levey & Byrne 1993; Kaspari 1993; Oliveira et al. 1995; Pizo & Oliveira 1998, 2001; Passos & Oliveira 2002, 2004; Christianini & Oliveira 2009, 2010; ver também, Böhning-Gaese et al. 1999 e Ohkawara & Akino 2005, para estudos fora dos Neotrópicos).

Formigas são visitantes freqüentes de fezes de frugívoros (principalmente, aves) e seu papel na remoção de sementes em meio às fezes teve grande relevância no início dos estudos sobre interações entre formigas e frutos não-mirmecocóricos (Roberts & Heithaus 1986, Byrne & Levey 1993, Kaspari 1993, Levey & Byrne 1993). Apesar de concluírem que a maioria das sementes removidas eram predadas pelas formigas, estes pesquisadores ressaltaram o papel importante que formigas que nidificam no folhiço (i.e., em galhos caídos e entre folhas) teriam como dispersoras secundárias de sementes (Roberts & Heithaus 1986, Kaspari 1993, Levey & Byrne 1993). Estes ninhos caracterizam-se pela sua efemeridade e por abrigarem colônias pequenas, atributos que confeririam às poucas sementes armazenadas no local uma probabilidade considerável de germinação e estabelecimento (Levey & Byrne 1993). Em especial, os trabalhos de Margaret Byrne e Douglas Levey (ver Byrne & Levey 1993, Levey & Byrne 1993) foram fundamentais para chamar a atenção sobre o papel de formigas *Pheidole* spp. (até então consideradas predadoras de sementes) como dispersoras de uma parcela considerável das sementes carregadas até o ninho.

Vários estudos de caso já abordaram o(s) benefício(s) garantido(s) pelas formigas para espécies de plantas (Oliveira et al. 1995; Pizo & Oliveira 1998; Böhning-Gaese et al. 1999;

Passos & Oliveira 2002, 2004; Ohkawara & Akino 2005; Christianini & Oliveira 2009, 2010). Em geral, as formigas são capazes apenas de remover para seu ninho os diásporos de tamanho pequeno a médio (comprimento < 20 mm e peso < 1 g; Pizo & Oliveira 2001). Em especial, as formigas Ponerinae grandes (e.g., *Odontomachus chelifer* e *Pachycondyla striata*) e as formigas cortadeiras da tribo Attini (*Atta* e *Acromyrmex*) são consideradas as principais removedoras de diásporos (Horvitz & Beattie 1980; Pizo & Oliveira 1998, 2001; Passos & Oliveira 2002, 2004; Christianini & Oliveira 2009; Rico-Gray & Oliveira 2007). Por exemplo, *O. chelifer* e *P. striata* respondem juntas por mais de 55% das interações de formigas com frutos de *Guapira opposita* (Nyctaginaceae) em uma área de restinga da Ilha do Cardoso, no litoral Sul paulista (Passos & Oliveira 2004). Em 80% dos registros de *O. chelifer*, esta formiga removeu os frutos para seu ninho, onde a semente já limpa era descartada em área adjacente, resultando numa maior concentração de plântulas de *G. opposita* na vizinhança do formigueiro (Passos & Oliveira 2004). Por fim, Passos & Oliveira (2004) comprovaram que o solo da área adjacente ao ninho de *O. chelifer* apresenta maiores concentrações de alguns nutrientes (Ca, K, e P), assim como maior penetrabilidade, quando comparado ao solo de áreas controle próximas.

No entanto, diásporos maiores que 1 g, assim como certos diásporos pequenos e médios, terão sua polpa e/ou arilo removidos no próprio local de encontro (ver Pizo & Oliveira 2001). Alguns estudos demonstraram que a retirada da parte carnosa que envolve a(s) semente(s), por si só, traz benefícios à planta visto que diminui a incidência de fungos e aumenta a germinação (Oliveira et al. 1995, Leal & Oliveira 1998, Ohkawara & Akino 2005). Por outro lado, sabe-se que a remoção da polpa/arilo diminui a atratividade do diásporo para outras formigas (Guimarães & Cogni 2002, Leal et al. 2007; ver Andersen & Morrison 1998 para diásporos verdadeiramente mirmecocóricos). Desta forma, o atendimento por formigas ‘limpadoras’ (que apenas removem a

parte carnosa) pode ser visto como negativo para certos diásporos (pequenos e médios) potencialmente carregáveis por formigas maiores (e.g. *Odontomachus* spp., *Pachycondyla* spp., *Atta* spp. e *Acromyrmex* spp.).

Até o momento, entretanto, poucos estudos investigaram os benefícios atrelados ao consumo pelas formigas dos apêndices carnosos de diásporos. Sabe-se que colônias de *Aphaenogaster rudis* alimentadas com elaiossomos de *Sanguinaria canadensis* apresentam um desvio no seu esforço reprodutivo para uma maior produção de rainhas virgens em relação a colônias cuja dieta não inclui elaiossomos (Morales & Heithaus 1998). Além disso, Gammans et al. (2005) mostraram que colônias de *Myrmica ruginodis* alimentadas com elaiossomos de duas espécies de *Ulex* produziram larvas 48% mais pesadas do que colônias que não receberam elaiossomos. Quanto a diásporos não-mimecocóricos, de modo geral, formigas são atraídas preferencialmente para diásporos ricos em lipídios (e.g., *Cabralea canjerana*, 70% do arilo são lipídios) e proteínas (e.g. *Guapira opposita*, 28% da polpa são proteínas) (Pizo & Oliveira 2001, Passos & Oliveira 2004; ver também Carroll & Janzen 1973). Esta preferência é semelhante à registrada para formigas que consomem elaiossomos de plantas tipicamente mirmecocóricas (Beattie 1985, Gorb & Gorb 2003). Recentemente, Bottcher (2010) comprovou também haver benefício para as formigas advindos da ingestão de frutos não-mirmecocóricos; o consumo de arilos de *Cabralea canjerana* por *O. chelifer* acarretou num aumento do peso das larvas em relação a uma dieta controle. No caso específico da interação de *O. chelifer* com diásporos de *C. canjerana*, a comprovação dos benefícios tanto para a planta (Pizo & Oliveira 1998) quanto para a formiga (Bottcher 2010) caracteriza a existência de um mutualismo facultativo.

A fragmentação florestal e seus efeitos

Atualmente, a biodiversidade terrestre vem sendo de tal forma ameaçada por distúrbios de origem antrópica, que alguns cientistas chegam a cogitar sobre o início de uma sexta extinção em massa (Dirzo & Raven 2003, Barnosky et al. 2011). Em especial, a destruição e fragmentação das florestas tropicais, ecossistema que abriga mais da metade das espécies atualmente existentes, é considerada como uma das principais ameaças à biodiversidade global (Wilcox & Murphy 1985, Diamond 1989, Turner & Corlett 1996, Laurance & Bierregaard 1997). Associadas à fragmentação florestal, algumas mudanças são impostas ao ecossistema em questão. São elas: perda do habitat original, redução no tamanho das manchas remanescentes, isolamento entre áreas anteriormente conectadas e maior exposição dos fragmentos aos efeitos de borda (Laurance & Bierregaard 1997, Fahrig 2003, Fischer & Lindenmayer 2007).

Boa parte das pesquisas em relação ao efeito da fragmentação sobre a perda de espécies baseou-se na aplicação da teoria de Biogeografia de Ilhas a ambientes terrestres artificialmente fragmentados. Segundo esta teoria (MacArthur & Wilson 1967), que prevê uma relação entre área da ilha e número de espécies existentes, ilhas menores e/ou mais afastadas da área ‘reservatório’ (i.e., o continente) abrigariam menos espécies do que ilhas maiores e/ou mais próximas ao continente. Este efeito seria resultado de um balanço dinâmico entre as taxas de colonização e de extinção. Uma explicação adicional para a relação espécie-área é que além de possuírem uma maior área, as ilhas maiores também possuem uma maior diversidade de habitats (Rosenzweig 1995). Mais ainda, áreas maiores terão maior chance de incluir espécies raras e/ou de distribuição agregada, como o caso de muitas espécies de árvores na floresta Amazônica (Oliveira & Mori 1999).

No entanto, uma das diferenças entre ilhas oceânicas e “ilhas de floresta” é o tipo de matriz que as envolve. Ilhas são circundadas pelo oceano, oferecendo grandes dificuldades para a chegada de espécies incapazes de se dispersar pelo vento ou pela água. Por outro lado, os fragmentos florestais são ilhas de floresta inseridas em uma matriz, cuja permeabilidade à entrada e saída de espécies sempre será maior do que a de um oceano (Gascon et al. 1999). No Brasil, matrizes comumente encontradas ao redor de fragmentos florestais são, em ordem de importância, pastagens, monoculturas de plantas anuais (e.g., cana-de-açúcar e soja) e plantios de árvores exóticas (e.g., plantações de *Eucalyptus* e *Pinus*). Em comum, todas estas matrizes permitem alguma troca de espécies entre as “ilhas de floresta”, porém também funcionam como fonte doadora de espécies que antes não existiam na área florestada, como por exemplo, o cachorro doméstico (Lacerda et al. 2009, Torres & Prado 2010) e a samambaia *Pteridium achilinum* (Silva & Silva-Matos 2006), ambos invasores da Floresta Atlântica. No entanto, o grau de permeabilidade das matrizes difere quanto à sua estrutura e também quanto ao grupo taxonômico em questão (Murcia 1995, Gascon et al. 1999, Banks-Leite & Ewers 2009). Um caso extremo de matriz bastante permeável são cultivos como as agroflorestas de cacau (cabruças), que circundam pequenos fragmentos de floresta Atlântica no sul da Bahia, e são considerados favoráveis à manutenção da biodiversidade nesta região (Schroth et al. 2011). Por outro lado, pastos são matrizes mais inóspitas para espécies estritamente florestais, uma vez que as grandes diferenças estruturais com a floresta (umidade, heterogeneidade de estrutura, quantidade de recursos, luminosidade) fazem com que menos espécies sejam capazes de estabelecer-se e/ou cruzar o pasto (Banks-Leite & Ewers 2009).

Estudos realizados principalmente a partir da década de 90 têm descrito as alterações sofridas por diversos grupos taxonômicos utilizando abordagens diversas que vão desde a

descrição e comparação da riqueza de espécies abrigadas em fragmentos (e.g., Chiarello 1999, Vasconcelos et al. 2006, Dixo & Metzger 2009), a estudos sobre estrutura genética de metapopulações (e.g., Galbusera et al. 2004, Dixo et al. 2009), bem como permeabilidade da matriz quanto ao movimento de espécies (e.g., Gascon et al. 1999, Awade & Metzger 2008, Lees & Peres 2009). Apesar de diferenças marcantes entre florestas fragmentadas e florestas contínuas quanto aos padrões observados de riqueza, composição e abundância de vários grupos taxonômicos, em muitos casos os resultados não apontam para um efeito da perda de área tão grande quanto anteriormente imaginado (Pardini et al. 2005, Vasconcelos et al. 2006, Uehara-Prado et al. 2007, Dixo & Metzger 2009, Filgueiras et al. 2011; ver também Debinski & Holt 2000). Dois processos distintos podem estar influenciando os padrões encontrados: uma demora na resposta das espécies à perda de área florestal como também a outros efeitos da fragmentação (Brooks et al. 1999, Metzger et al. 2009), e/ou uma influência maior do efeito de borda do que da perda de área *per se* (Ewers & Didham 2006, Ewers et al. 2007, Fletcher et al. 2007, Banks-Leite et al. 2010).

Considerando que as espécies de um ecossistema conectam-se por meio de diversos tipos de interações (como predação, competição, parasitismo, polinização e dispersão de sementes; Begon et al. 2006), ao alterar as condições abióticas locais e os padrões de ocorrência das espécies, a fragmentação florestal tenderá a afetar também as interações entre as espécies (Terborgh et al. 2001, Bruna 2004; ver também Tylianakis et al. 2010). Em uma retro-alimentação positiva, a perda de interações mutualísticas envolvendo a reprodução e o recrutamento de plantas pode trazer drásticas consequências para o funcionamento do ecossistema como um todo (Howe 1984, Christian 2001, Terborgh et al. 2001). Devido à maior dificuldade inerente ao estudo das interações, a maioria dos estudos existentes aborda o efeito da fragmentação sob o ponto de vista

de uma única espécie, como, por exemplo, ao comparar a polinização ou a dispersão de sementes de uma dada espécie entre fragmentos florestais (e.g., Rao et al. 2001, Cordeiro & Howe 2003, Lopes & Buzato 2007; mas, ver Bruna et al. 2005 e Tylianakis et al. 2007, para abordagens ao nível da comunidade).

No quesito mutualismos planta-animal, os principais focos de estudo quanto aos efeitos da fragmentação de habitats são a polinização (e.g. Aizen & Feinsinger 1994, Lopes & Buzato 2007, Pauw 2007) e a dispersão de sementes por vertebrados (e.g., Cordeiro & Howe 2003, Farwig et al. 2006, Cramer et al. 2007). No caso das interações mutualísticas, assim como relatado anteriormente para estudos da diversidade de grupos taxonômicos, a resposta à fragmentação também diverge bastante entre as espécies e os ecossistemas. Por exemplo, em estudo na Amazônia, Cramer e colaboradores (2007) observaram que a dispersão de duas espécies zoocóricas em uma mesma paisagem era afetada diferentemente pela fragmentação. Para *Bocageopsis multiflora* (Annonaceae), cujas sementes são dispersas por aves, a fragmentação não afetou nem a quantidade de frutos removidos nem a distância de remoção. Por outro lado, para *Duckeodendron cestroides* (Moraceae), primariamente dispersa por primatas, os mesmos parâmetros avaliados sofreram um decréscimo significativo nos fragmentos (Cramer et al. 2007). Outro estudo com resultados interessantes, desta vez em uma paisagem fragmentada no Quênia, mostrou haver mais visitas por aves frugívoras e maior remoção de frutos de *Prunus africana* (Rosaceae) em áreas fragmentadas do que na floresta contínua (Farwig et al. 2006).

Efeito da fragmentação florestal sobre formigas e sua interação com diásporos

Em geral, considera-se que os insetos, com pequena massa corpórea e ocupando níveis tróficos inferiores, não sejam tão afetados pela perda de área florestal, mas sim por efeitos de borda (Didham *et al.* 1996, Gascon *et al.* 1999; ver também Laurance & Bierregaard 1997). Dentre estes invertebrados, a família Formicidae é um dos grupos cuja resposta à alteração e fragmentação de habitats foi mais bem estudada (e.g., Majer *et al.* 1997, Suarez *et al.* 1998, Carvalho & Vasconcelos 1999, Vasconcelos 1999, Vasconcelos *et al.* 2000, Gibb & Hochuli 2002, Brühl *et al.* 2003, Sobrinho & Schoereder 2007). Numa pesquisa recente na *ISI Web of Science*, Crist (2009) encontrou um total de 75 trabalhos envolvendo formigas e fragmentação de habitats. De forma geral, estudos sobre a comunidade de formigas de folhiço mostram que a fragmentação afeta principalmente a composição de espécies encontrada, embora em alguns casos os fragmentos apresentem também uma menor riqueza total de formigas (Carvalho & Vasconcelos 1999, Brühl *et al.* 2003, Bieber *et al.* 2006, Vasconcelos *et al.* 2006; ver também Crist 2009). Sabe-se que um fator importante para esta mudança na composição de espécies é a entrada de espécies exóticas a partir da matriz circundante (Suarez *et al.* 1998, Holway *et al.* 2002). Por exemplo, a invasão da formiga *Solenopsis invicta* em florestas e campos dos E.U.A. alterou profundamente a estruturação das comunidades invadidas ao diminuir a riqueza local de formigas nativas e mudar os padrões de co-ocorrência das espécies restantes (Gotelli & Arnett 2000).

Apesar do alto número de estudos abordando a resposta da comunidade de formigas à fragmentação, até o momento poucos estudos avaliaram como a fragmentação de habitats afeta as várias interações mutualísticas entre formigas e plantas. No caso específico das interações formiga-diásporo, Crist (2009) cita cinco trabalhos que investigaram como a perda de habitats e a

fragmentação podem interferir neste mutualismo. Por exemplo, ao comparar fragmentos de floresta temperada decídua de dois tamanhos (<25 ha e >200 ha) e com diferentes históricos de uso de terra (alto e baixo uso), Mitchell et al. (2002) encontraram respostas díspares das comunidades de herbáceas mirmecocóricas e de formigas dispersoras. Houve uma maior abundância e riqueza de formigas dispersoras em fragmentos pequenos e com alto grau de perturbação, contrastando com a menor abundância e riqueza de herbáceas encontrada nestes ambientes quando comparados a fragmentos maiores e com menor histórico de perturbação. Assim, outros fatores, que não a ausência de formigas dispersoras, estariam determinando a baixa representatividade de herbáceas mirmecocóricas nos pequenos fragmentos (Mitchell et al. 2002). No mesmo tipo de habitat, Ness (2004) demonstrou que nas bordas florestais as formigas carregavam sementes de *Sanguinaria canadensis* (Papaveraceae) mais frequentemente no sentido oposto à borda florestal, sugerindo que este viés na dispersão estaria por trás da raridade de plantas mirmecocóricas em bordas e florestas mais jovens. Além disto, a presença da formiga invasora *Solenopsis invicta* afetou negativamente a distância de dispersão de sementes de *S. canadensis*, que caiu de 100 cm para 40 cm nos locais invadidos, onde esta formiga torna-se a principal espécie a interagir com as sementes nas estações.

Alterações na taxa e distância de remoção de sementes mirmecocóricas são efeitos frequentemente atribuídos a formigas invasoras em ecossistemas onde a mirmecocoria é comum (Bond & Slingsby 1984, Christian 2001, Ness 2004; ver também Holway et al. 2000 e Lach & Hooper-Bùi 2010). Nos “fynbos” sul-africanos, Christian (2001) demonstrou efeitos drásticos causados pela formiga invasora *Linepithema humile* a sementes mirmecocóricas grandes, cuja dispersão recai sobre poucas espécies de formigas que estão ausentes dos locais invadidos por *L. humile*. A alta densidade de colônias destas formigas nas áreas invadidas resulta em maior

predação destas sementes por roedores e no estabelecimento de uma comunidade alterada de plantas, com o predomínio de Proteaceae com sementes pequenas (Ness 2004, Lach & Hooper-Bùi 2010). Quanto a interações de formigas com diásporos não-mirmecocóricos, há até o momento apenas um trabalho abordando os efeitos da fragmentação (Guimarães & Cogni 2002). Estações experimentais no interior de uma floresta apresentaram maior quantidade de sementes de *Cupania vernalis* (Sapindaceae) cujo arilo foi removido por formigas do que estações na borda, sendo a retirada do arilo fundamental para a germinação da semente (Guimarães & Cogni 2002).

De modo geral, se comparadas a outros tipos de interações formiga-planta, como o mirmecofitismo, as interações formiga-diásporo são mutualismos pouco especializados, onde várias espécies de formigas são capazes de interagir com a mesma planta (Guimarães et al. 2007, Rico-Gray & Oliveira 2007). Esta falta de especialização por parte das espécies envolvidas pode ser um fator positivo para sua manutenção em longo prazo, em vista das modificações da paisagem impostas pelo homem (Blüthgen 2012). Sabe-se, entretanto, que tanto na mirmecocoria típica (Andersen & Morrison 1998, Cuautle *et al.* 2005) como nas relações entre formigas e diásporos carnosos (Horvitz & Beattie 1980, Passos & Oliveira 2002), diferentes espécies de formigas provêem diferentes serviços à semente (e.g., remoção do elaiossomo/polpa/arilo *in situ*; local de deposição do diásporo; taxa e distância de remoção do diásporo; e desfolha de plântulas, no caso das formigas cortadeiras). Assim, além de colocar em risco serviços essenciais fornecidos às sementes por determinadas espécies de formigas, a fragmentação do habitat facilita ainda a entrada de espécies exóticas que são potencialmente prejudiciais a estas relações mutualísticas.

Objetivos da tese

Em vista da importância das interações mutualísticas envolvendo formigas e diásporos e da atual escassez de estudos abordando como estas interações são afetadas pela fragmentação, trataremos aqui da interação mutualística facultativa entre formigas e diásporos carnosos em florestas tropicais fragmentadas. Esta tese apresenta quatro capítulos originais (capítulos 2 a 5) organizados como manuscritos a serem enviados para revistas científicas indexadas, estando, portanto, escritos em língua inglesa. Além destes capítulos, a tese conta com a presente introdução geral e um capítulo conclusivo, onde são ressaltados os principais resultados do trabalho e suas implicações (capítulo 6). Em conjunto, os manuscritos tentam responder várias das questões acima levantadas envolvendo a fragmentação florestal e a interação entre formigas e diásporos carnosos na Floresta Atlântica. A abordagem adotada consistiu de observações e experimentos realizados em campo, em uma área de Floresta Atlântica no Estado de São Paulo, onde estudamos quatro fragmentos florestais e quatro áreas dentro de uma floresta contínua.

O primeiro manuscrito (Capítulo 2) trata da observação *in loco* das interações entre formigas e frutos carnosos. Este capítulo traz a listagem das espécies de formigas e de plantas encontradas em interação, bem como a descrição de padrões gerais que podem estar afetando a interação (variação sazonal, diferença na quantidade de frutos disponíveis). Além disso, o comportamento das formigas em relação aos frutos é descrito. No Capítulo 3, buscamos responder se, ao ignorarmos a composição das espécies, fragmentos diferem de florestas contínuas quanto à topologia das redes de interações entre formigas e frutos.

No Capítulo 4, utilizamos como ferramenta de estudo um fruto sintético, elaborado a partir de uma massa similar à composição da polpa de frutos ricos em lipídios. Nosso intuito foi verificar

se a fragmentação da floresta afeta a interação das formigas com frutos caídos, empregando um fruto sintético como modelo. A possibilidade de oferecer uma quantidade igual de frutos, bem como a certeza de não haver frutos similares nas proximidades, tornam mais robustas as inferências sobre como a fragmentação florestal influencia as formigas atraídas, o seu comportamento em relação ao fruto, bem como a distância de remoção do mesmo.

Finalmente, no Capítulo 5, nosso interesse foi descobrir se o estado do fruto no chão da floresta pode afetar a sua atratividade para as formigas. Em outras palavras, será que um fruto maduro intacto tem a mesma chance de interagir com formigas do que um fruto que foi anteriormente aberto por um vertebrado ou, ainda, um fruto consumido cujas sementes encontram-se embebidas nas fezes de vertebrados? Esta questão tem efeitos importantes na conservação das funções de um ecossistema, pois se sabe que fragmentos florestais pequenos e médios abrigam uma fauna depauperada de vertebrados (Redford 1992, Terborgh et al. 2001) e portanto, espera-se que mais frutos intactos cheguem ao solo sob a planta-mãe em fragmentos do que em áreas contínuas.

A Floresta Atlântica

Grande parte da pesquisa brasileira sobre fragmentação florestal vem sendo desenvolvida no âmbito do projeto de longa duração intitulado ‘Projeto Dinâmica Biológica de Fragmentos Florestais’ (PDBFF). O PDBFF está em curso desde 1979, quando uma paisagem anteriormente contínua foi propositadamente fragmentada, a cerca de 80 km ao norte da cidade de Manaus, no Estado do Amazonas. Os fragmentos, espalhados por três antigas fazendas de gado, possuem formato em geral quadrado e tamanhos pré-determinados, e situam-se nas proximidades de uma

floresta verdadeiramente contínua (Laurance et al. 2011). Levantamentos de diversos grupos taxonômicos (*e.g.*, árvores, aves de subosque, pequenos mamíferos, primatas, sapos, vários grupos de invertebrados) foram feitos antes da fragmentação (Laurance et al. 2011). Desde então, pesquisadores vêm acompanhado como vários grupos taxonômicos, bem como a estrutura da floresta e certos fatores abióticos, respondem à fragmentação (ver Bierregaard et al. 1992, Gascon et al. 1999, Laurance et al. 2002, Laurance et al. 2011 e literatura incluída). No entanto, o processo de fragmentação como encontrado nas áreas do PDBFF difere bastante do que, de fato, ocorre em outras áreas amazônicas e, mais ainda, na Floresta Atlântica (Laurance et al. 2011; para a Floresta Atlântica ver Tabarelli et al. 2010). Sendo assim, embora a maioria das paisagens fragmentadas estudadas no Brasil não ofereça condições de trabalho tão ideais quanto o PDBFF (incluindo informações pré-fragmentação), estudar estas áreas é extremamente importante já que seu processo de fragmentação seria mais fiel à realidade dos remanescentes florestais brasileiros.

A Floresta Atlântica originalmente ocupava cerca de 1,5 milhão de km², estendendo-se ao longo da costa brasileira desde os brejos de altitude no Ceará até o Rio Grande do Sul, além de em alguns trechos se expandir para o interior e atingir também dois países vizinhos, o Paraguai e a Argentina (Ribeiro et al. 2009). Devido ao histórico de ocupação do Brasil desde o período colonial, cerca de 70% da população brasileira vive dentro dos domínios originais deste Bioma, com consequências irreversíveis para a sua biodiversidade (Tabarelli et al. 2010). Atualmente, restam menos de 13% da floresta original, sendo que grande parte dos fragmentos possuem uma área inferior a 50 ha (Ribeiro et al. 2009). Além disso, uma parcela considerável das florestas restantes é formada por vegetação secundária e está sujeita a várias pressões antropogênicas, tais como o avanço das fronteiras agrícola e urbana, a caça, a retirada seletiva de madeira e palmito, o uso de pesticidas nas lavouras adjacentes e a invasão de espécies exóticas (Galetti & Aleixo

1998, Cullen et al. 2001, Tabarelli et al. 2005). Ou seja, os remanescentes de Floresta Atlântica não estão sujeitos apenas à perda de habitat e ao efeito de borda, mas a uma constante degradação florestal impingida pela presença próxima de atividades agrárias e/ou agrupamentos urbanos. Desta forma, a enorme devastação, aliada a um alto grau de endemismo de espécies de plantas e de vertebrados encontrados neste ecossistema, fazem da Floresta Atlântica um dos ecossistemas mais importantes e ameaçados do planeta, sendo, portanto, incluída nos chamados ‘hotspots’ de biodiversidade (Myers et al. 2000).

A paisagem estudada

A paisagem utilizada neste estudo faz parte de um projeto cooperativo delineado para estudar questões relacionadas ao limiar de fragmentação nas florestas do Planalto Atlântico Paulista (‘Biodiversity conservation in fragmented landscapes on the Atlantic Plateau of São Paulo’, BioCAPSP), que incluiu vários cientistas e instituições. O projeto, coordenado pelos Prof. Dr. Jean Paul Metzger (USP) e Dr. Christoph Knogge (UFZ - *Helmholtz-Zentrum für Umweltforschung*), abrangeu três paisagens com diferentes graus de cobertura florestal remanescente: Ribeirão Grande (com apenas 10% de vegetação restante), Caucaia (com 30% restante) e Tapiraí (com 50% restante) (para informações sobre este grande projeto e a escolha das áreas ver Banks-Leite 2009). Apesar de ter contado com parte da estrutura oferecida pelo projeto, a presente tese não esteve oficialmente vinculada ao mesmo.

A área mais bem conservada dentre as três paisagens acima citadas situa-se nos municípios de Tapiraí e Piedade (23° 50' S, 47° 20' O) e foi a paisagem escolhida para o desenvolvimento desta tese (Figura 1). O clima da região apresenta um verão quente e ausência de período seco no inverno (tipo Cfa, segundo a classificação climática de Koeppen), com temperatura média mensal

variando entre 15° e 22°C (temperatura anual média de 19° C) e precipitação média de 1808 mm/ano (www.cpa.unicamp.br). A estação chuvosa vai de outubro a março, meses que concentram aproximadamente 65% da precipitação anual. A altitude na região varia de 700 a 1100 m acima do nível do mar. Assim, a vegetação original na área é classificada como floresta ombrófila baixo-montana (Veloso et al. 1991, Oliveira-Filho & Fontes 2000).

Ao longo deste estudo, optamos por realizar nossas comparações com base no contraste entre dois tipos de floresta. O primeiro tipo é a floresta sob efeito da fragmentação, representada por quatro fragmentos de tamanhos considerados relativamente grandes (ver Banks-Leite et al. 2010, Laurance et al. 2011), entre 91 e 146 ha, cuja matriz circundante era pasto ou cultivos de herbáceas (como inhame e gengibre; Tabela 1 e Figura 2). Além dos processos diretamente relacionados à fragmentação (e.g., perda do habitat original e aumento da área remanescente sob efeito de borda), estes fragmentos são em geral constituídos por floresta secundária em diversos estádios de regeneração (de 20 a mais de 100 anos; Banks-Leite et al. 2010). No entanto, dado o panorama geral da Floresta Atlântica (Ribeiro et al. 2009), estes fragmentos podem ainda ser considerados em bom estado de conservação. Já o segundo tipo florestal considerado foi a floresta preservada (ou controle) situada dentro do Parque Estadual de Jurupará (PEJU) e constando de mais de 26 mil hectares ainda em grande parte conectados à Serra de Paranapiacaba (maior trecho de Floresta Atlântica atualmente existente; Ribeiro *et al.* 2009). Esta floresta é composta predominantemente por uma floresta secundária bastante antiga, com histórico de corte seletivo para extração de madeira de lei (Develey & Metzger 2006). Para a obtenção de réplicas na área contínua, dentro do PEJU foram escolhidas quatro áreas, distando pelo menos 1,5 quilômetros entre si (Tabela 1 e Figura 3; ver Banks-Leite 2009). Esta distância mínima permitiu que as amostragens dentro da área contínua fossem consideradas como espacialmente independentes. O

tipo de desenho experimental adotado, em que agrupamos fragmentos com históricos diferentes numa mesma categoria, é freqüentemente usado em estudos de interações ecológicas sob o ponto de vista da fragmentação (ver, por exemplo, Cramer et al. 2007), visto que a amostragem simultânea de interações requer um esforço amostral considerável.

Para esta tese, foram demarcadas três transecções de 300 m em cada uma das oito áreas estudadas. As transecções dentro de uma mesma área não foram idealizadas para serem paralelas entre si, devido à topografia bastante irregular da região e à nossa impossibilidade de amostrar as interações em áreas muito inclinadas. No entanto, foi mantida uma distância mínima de 50 m entre quaisquer dois pontos pertencentes a transecções diferentes. Porém, como em alguns casos dois pontos de transecções diferentes estarão mais próximos entre si do que os pontos extremos da mesma transecção, as transecções dentro de uma mesma floresta foram agrupadas na maioria das análises realizadas. As metodologias específicas para os diferentes objetivos do trabalho estão detalhadas nos respectivos capítulos desta tese.

Tabela 1: Características das oito áreas usadas para o estudo dos efeitos da fragmentação florestal sobre as interações entre formigas e diásporos, municípios de Piedade e Tapiraí, no Planalto Atlântico do Estado de São Paulo. Os fragmentos pertencem a proprietários particulares e as áreas não-fragmentadas encontram-se dentro do Parque Estadual de Jurupará.

Local (código)	Tipo de habitat	Latitude	Longitude	Área (ha)*	Perímetro (m)*	Altitude (m)
Cristo (FF1)	Fragmento	23°51,027' S	047°28,501' O	103,54	12.012	999
Médico (FF2)	Fragmento	23°54,731' S	047°28,791' O	91,41	8.055	957
Odorico (FF3)	Fragmento	23°52,859' S	047°26,142' O	146,00	10.525	990
Theomar (FF4)	Fragmento	23°49,851' S	047°26,967' O	115,87	11.980	1024
Cobrinha (CF1)	Floresta contínua	23°57,718' S	047°24,321' O	26.250,47	93.250	703
Criss-Cross (CF2)	Floresta contínua	23°57,721' S	047°23,045' O	26.250,47	93.250	697
Piramba (CF3)	Floresta contínua	23°57,139' S	047°24,496' O	26.250,47	93.250	736
Porteira (CF4)	Floresta contínua	23°56,731' S	047°23,710' O	26.250,47	93.250	738

*os valores de área e perímetro dos fragmentos foram disponibilizados pela equipe do *Laboratório de Ecologia da Paisagem e Conservação* (LEPAC-USP). Valores para a área não-fragmentada foram retirados do site http://www.iflorestal.sp.gov.br/unidades_conservacao/index.asp



Figura 1. Localização da área de estudo no Estado de São Paulo, municípios de Piedade e Tapiraí. A área pontilhada destaca a paisagem fragmentada em que foram escolhidos os quatro fragmentos. Localizados a sudeste da área pontilhada, ficam os quatro pontos dentro da floresta contínua, no PEJU. A área clara situada entre os quatro pontos de floresta contínua representa a barragem de Jurupará, de propriedade da CBA (Companhia Brasileira de Alumínio). Modificado a partir de Banks-Leite et al. (2010).



Figura 2. (A) Aspecto da paisagem fragmentada ao redor do fragmento ‘Theomar’ (FF4), e (B) interior do fragmento ‘Odorico’ (FF3), ambos no município de Piedade, Planalto Atlântico do Estado de São Paulo.



Figura 3. (A) Aspecto da paisagem contínua utilizada na presente tese, Parque Estadual de Jurupará, no Planalto Atlântico do Estado de São Paulo, e (B) interior da área contínua ‘Cobrinha’ (CF1).

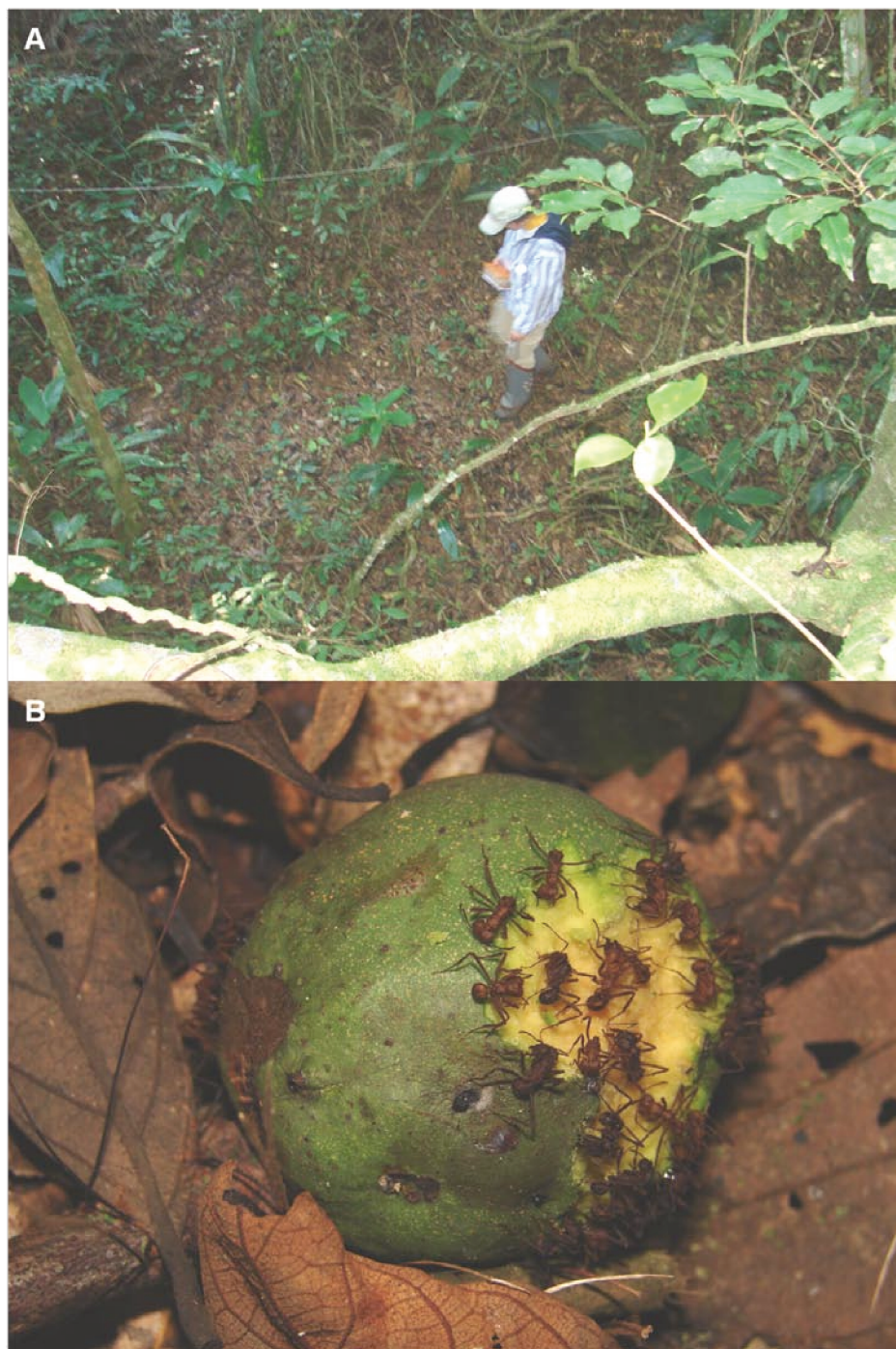


Figura 4. (A) Transecção percorrida durante a amostragem de interações formiga-fruto no fragmento ‘Cristo’ (FF1), município de Piedade, no Planalto Atlântico Paulista. (B) Formigas *Acromyrmex* sp. removendo pedaços da polpa de fruto de *Couepia venosa* (Chrysobalanaceae) na área contínua ‘Piramba’ (CF3), em maio de 2009.

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Capítulo 2:

Interaction between ants and non-myrmecochorous fleshy diaspores in the Atlantic Forest – natural history and patterns in a fragmented landscape

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Running head: Ant-fruit interactions in the Atlantic forest

Keywords: anthropogenic disturbance, ant-seed interaction, diplocory, Formicidae, frugivory, myrmecochory, seed dispersal, vertebrate loss

Abstract: The ongoing process of rainforest fragmentation is one of the most pervasive threats to present-day biological diversity. Together with the loss of species diversity, changes in the frequency and importance of species interactions may also result from habitat fragmentation. A particular interaction type, still poorly studied, has an enormous potential to increase in frequency in fragmented landscapes: ant attendance to non-myrmecochorous fleshy diaspores, followed or not by seed dispersal by ants. Here, we compared how this opportunistic and generalized interaction varied between two contrasting forest types (continuous and fragmented forests) in a lower montane region of the Atlantic forest in São Paulo State, Southeast Brazil. Our selected landscape included four continuous forest sites and four large-sized fragments (ca. 100 ha each) surrounded by an agricultural matrix. Once a month, during one year, transects in each forest site were walked, looking for fruits and for ant-fruit interactions on the forest ground. Nearly 1,000 ant-diaspore interactions were recorded, unevenly distributed along months, transects, and sites. Although the abundance of ant-attractive diaspores on the ground did not vary between forest types, the number of interactions was higher in continuous forests than in fragmented forests. This difference is attributed mostly to the different plant species found in each forest type, with fragments presenting species-poor floras of ant-attractive diaspores whose fruiting period is concentrated mainly in the summer. We strongly encourage further case studies to confront the complementary roles played by primary seed dispersers (vertebrates) and by secondary seed dispersers (ants) between these two forest types. It is possible that in fragments the role of ants in the dispersal and recruitment of certain plant species will increase, especially for winter fruiting species and those producing lipid-rich diaspores.

Introduction

Ant-plant interactions are extremely diverse, ranging from mutually dependent relations between ants and myrmecophytes to more opportunistic interactions involving ants and plants bearing extrafloral nectaries. Among the most studied types of interactions are those involving ants, fruits and seeds (Beattie 1985; Rico-Gray & Oliveira 2007). Plant species dispersed by ants are mostly herbaceous, occur in sclerophyll vegetations and, most importantly, produce diaspores with a distinct lipid-rich appendage (i.e., the elaiosome; Rico-Gray & Oliveira 2007). Nonetheless, recent studies claim that interactions involving animals and plant diaspores are not as straightforward as predicted earlier (Wang & Smith 2002; Vander Wall & Longland 2004), and that a given seed species may be effectively dispersed by two or more agents (Forget & Milleron 1991; Böhning-Gaese et al. 1999; Andresen 2002; Vander Wall et al. 2005; Christianini & Oliveira 2009, 2010). Ants are known to interact with a wide variety of non-myrmecochorous fleshy diaspores (Leal & Oliveira 1998; Pizo & Oliveira 2000; Passos & Oliveira 2003; Christianini et al. 2011), providing real benefits (i.e., dispersal distance, directed dispersal to favorable micro-sites, decrease in fungal infection) to several plant species whose primary dispersal is associated with vertebrates (Oliveira et al. 1995; Pizo & Oliveira 1998; Böhning-Gaese et al. 1999; Passos & Oliveira 2002, 2004; Ohkawara & Akino 2005; Christianini & Oliveira 2009, 2010)

The ongoing process of tropical rainforest fragmentation has multifaceted effects on species composition and abundance of many taxonomic groups, including plants (Laurance et al. 1998a; Laurance et al. 2000; Oliveira et al. 2004; Santos et al. 2008), invertebrates (Didham 1997; Carvalho & Vasconcelos 1999; Uehara-Prado et al. 2007; Filgueiras et al. 2011), and vertebrates (Stouffer & Bierregaard 1995; Chiarello 1999; Dixo & Metzger 2009; Dixo et al.

2009; Banks-Leite et al. 2010). Following these changes, diverse key plant-animal mutualistic interactions such as pollination and seed dispersal are also affected (Cordeiro & Howe 2003; Cramer et al. 2007; Lopes & Buzato 2007; see also Aizen & Feinsinger 1994 and Ness 2004, for non-tropical studies). Most of the existing studies on how fragmentation affects mutualistic interactions are focused on the species-level; for example, the seed dispersal of one or few plant species (Pizo 1997; Cordeiro & Howe 2003; Cramer et al. 2007). Indeed, this approach is much easier than studying all interactions occurring in one community. Nonetheless, there are also some studies that tracked interaction modifications among a large group of organisms (Aizen & Feinsinger 1994; Mitchell et al. 2002; Galetti et al. 2003; Bruna et al. 2005). In such studies, the investigator does not focus on specific interactions but rather evaluates the ‘whole’ assemblage of, say, seed dispersers.

The objective of the present study is to investigate how ant interactions with fleshy diaspores change after rainforest fragmentation. The relevance of the study is supported by (1) the predicted scenarios of vertebrate loss due to forest fragmentation and the consequent low recruitment of vertebrate-dispersed species (Silva & Tabarelli 2000; Cordeiro & Howe 2001); (2) the opportunistic interactions between ants and diverse species of fleshy diaspores (e.g., Pizo & Oliveira 2000; Passos & Oliveira 2003); and (3) the importance of ants in the dispersal/establishment of some plant species (e.g., Oliveira et al. 1995; Pizo & Oliveira 1998; Böhning-Gaese et al. 1999; Dausmann et al. 2008). On one side of this interaction there are the ground-dwelling ants, an extraordinarily abundant invertebrate group living in the leaf-litter (Fittkau & Klinge 1973). Ant species composition and abundance are known to be affected by anthropogenic disturbances of the forest habitat (Carvalho & Vasconcelos 1999; Brühl et al. 2003; Vasconcelos et al. 2006; see also review in Crist 2009). For instance, these insects may

directly be influenced by abiotic changes at edge habitats (Carvalho & Vasconcelos 1999). Moreover, interference competition with invasive ant species from the surrounding matrix changes ant species communities (Suarez et al. 1998; Gotelli & Arnett 2000) and their interactions with true myrmecochorous diaspores (Christian 2001; Ness 2004).

On the other side, there are the huge amounts of fleshy diaspores unremoved by vertebrates and ‘wasted’ on the forest ground (Howe 1980; Christianini & Oliveira 2009). The availability of fleshy fruits on the forest ground may differ between continuous forests and forest fragments as a consequence of various non-mutually excluding processes. First of all, the process of fragmentation causes important changes in plant species composition and functional groups (Laurance et al. 1998b, 2000; Oliveira et al. 2004; Santos et al. 2008; Tabarelli et al. 2010a). Studies in different ecosystems show that fruit production in several species consistently changes after habitat fragmentation due to differences in: pollination success (Aizen & Feinsinger 1994; Cunningham 2000; Duncan et al. 2004), presence of floral herbivores and pathogens (Matsumura & Washitani 2000; Duncan et al. 2004), inbreeding levels (Mavraganis & Eckert 2001), and availability of abiotic resources (e.g., water, light, nutrients) needed to develop flowers, seeds and fruits (Laurance et al. 2003). Finally, changes in fruit/seed consumption by early seed predators (Steffan-Dewenter et al. 2001) and primary seed dispersers (Santos & Tellería 1994; Farwig et al. 2006; Cramer et al. 2007) will also affect the availability of fruits that reach the forest ground.

Here, we applied a standardized sampling protocol to sample ant-diaspore interactions in two contrasting forest types in the highly fragmented Brazilian Atlantic forest, one of the most threatened world’s ecosystems (Mittermeier et al. 2005; Tabarelli et al. 2010b). We surveyed four sites in old-growth continuous forests within a protected reserve, representing the original ‘undisturbed’ condition of the Brazilian Atlantic Forest. For comparison, we selected four forest

fragments of secondary growth vegetation, embedded within an agricultural matrix, similar to most remnants of the Atlantic forest (see Ranta et al. 1998; Ribeiro et al. 2009). Describing the interactions in these two different forest types should not only help us to better understand the opportunistic relation between ants and fleshy non-myrmecochorous diaspores, but also how other opportunistic interactions may change in disturbed forest fragments.

Methods

Study site

Our study landscape encompassed two neighboring municipalities (Piedade and Tapiraí; S23°59'49" - 23°57'48", W47°22'52" - 47°28'47"), located within the Atlantic Plateau of São Paulo State, Brazil. Altitudinal variation is from 700 to 1100 m above sea level, and the native vegetation in this area is classified as lower montane rainforest (*sensu* Veloso et al. 1991). The climate is characterized by a wet and warm summer and by the absence of a true dry season during the winter period. Monthly mean temperatures vary from 15° to 22° (mean annual temperature, 19°C) and rainfall is *ca.* 1800 mm yr⁻¹ (<http://www.ciiagro.sp.gov.br/ciiagroonline/>). The rainy season is from October to March, concentrating nearly 65% of annual precipitation. Additional information on the study site may be found in Banks-Leite et al. (2010).

We selected four fragments embedded in a fragmented landscape (municipalities of Piedade and Tapiraí) with *ca.* 50% of remaining forest cover. The selected fragments varied in size from 91 to 146 ha, which are commonly viewed as large fragments (see Banks-Leite et al. 2010), and were surrounded mainly by herbaceous cropland, such as ginger and yam, and by pastures (Banks-Leite *et al.* 2010, AGD Bieber pers. observation). Vegetation in the fragments

consists mostly of secondary regrowth forest in various successional stages, from 20 to more than 100 years (Banks-Leite et al. 2010). As continuous forest sites or control areas, we selected four sites inside the Parque Estadual de Jurupará (PEJU; municipalities of Ibiúna and Piedade), adjacent to the fragmented landscape. PEJU's total area is 26,000 ha, mainly composed by old-growth secondary forests in a late successional stage (Banks-Leite et al. 2010). The replicated areas for the continuous forest are at least 1.5 km apart from each other. This minimum distance allowed us to consider the four areas inside the park as spatially independent (see Banks-Leite et al. 2010).

Sampling Protocol

In each of the eight sites, three 300-m transects (1.5 m width) were established. Transects were not parallel due to the irregular topography of the region. Nonetheless, a minimum distance of 50 m was kept for any point at two different transects. Once a month, during one year (June 2008 to May 2009), transects in each site were carefully searched (*ca.* 225m/hour) for fleshy diaspores (hereafter referred simply as 'fruits' or 'diaspores') on the forest floor and for ant-diaspore interactions. Similar methods for documenting ant-diaspore interactions have already been employed by other studies (Pizo & Oliveira 2000; Christianini *et al.* 2011; Bottcher 2010). Each time a fruit spot (*i.e.*, one or more fruits of the same species on the ground) was found, its relative location in the transect was annotated. In addition, the following characteristics of the spot were recorded: fruit species (or morphospecies), number of fruits, ontogenetic state (unripe, ripe or rotten), possible previous manipulation by vertebrates (with beak/teeth marks, or already opened fruits), and fruit size. Each fruit on the spot was carefully inspected for ant presence either before

(for large fast-moving ants) or while counting the fruits. Every time ants were seen attending fruits or fruit parts, it was counted as an ant-fruit interaction. All ant-fruit interactions were described in relation to: number of ants present, ant behavior (either carrying, outside the fruit, inside the fleshy part of the fruit, or consuming the seed), fruit ontogenetic state, seed state (whether predated or not), previous manipulation by vertebrates and presence of invertebrates other than ants. Since sometimes it was not possible to state the identity of the diaspore present in vertebrate feces, this kind of interaction was not systematically registered and, therefore, is not included in our analyses.

Due to logistical limitations, two forest sites were visited each day (from 8.00 h to 17.00 h). To control for differences in the time of sampling, each forest site was alternatively visited in successive months in the morning or in the afternoon. Samplings were normally performed in sunny or cloudy days. Only light rains were tolerated since these did not seem to disturb the ants (see Pizo & Oliveira 2000). Total sampling effort for the eight areas was 384 hours (4 h x 8 areas x 12 months).

Data analyses

Total diaspore abundance (number of fruits and fruit spots), abundance of ant-attractive diaspores (i.e., diaspore species seen at least once in interaction), and abundance of ant-diaspore interactions per transect and per month were compared between the two forest types (continuous and fragmented) using the four sites as a random factor nested within each forest type through nested ANOVAs with repeated measures. This procedure was based on Sokal and Rohlf (1995), and performed in the software Statistica 7.1 (Statsoft 2005).

Total ant species richness in the different forest sites was compared by estimating species richness using the Jackknife I procedure (see Krebs 1998) in the program EstimateS (Version 7.5, R. K. Colwell, <http://purl.oclc.org/estimates>). This procedure was applied for estimating species richness per site in the following cases: all ant-attractive diaspore species found on the ground, diaspore species found in interactions and ant species found in interactions. For these estimations, transects were subdivided in 10m-plots and all records made in the 12-month survey were summed. Thus our sampling unit was the accumulated occurrence of diaspores or ants per 10m-plot (N=90 sampling units per site). Based on the richness estimates and the standard errors, we calculated the corresponding 95% confidence intervals.

To evaluate whether the species composition of ant-attractive diaspore species differs between fragmented and continuous forests, we adopted two complementary procedures. First, we performed a non-metric multi-dimensional scaling (MDS) ordination of all eight sites based on the Jaccard similarity matrix of species presence-absence (Krebs 1998). As species with few records may bias the analysis (Manly 1997), we removed from the analysis the singletons, i.e. diaspore species which were recorded in only one spot during the whole survey. To examine if forest type significantly affects the species similarity between sites, we performed an ANOSIM test using habitat type as a factor (see Clarke & Gorley 2001). Both analyses were performed in the software PRIMER (Clarke & Gorley 2001).

To explain the variation in the (1) number of ant-diaspore interactions, (2) number of interacting diaspore species, and (3) number of interacting ant species seen in different types of forests and different sampling months, we used multiple linear regressions, testing the effect of the following independent variables: forest type (all fragments together and all continuous sites together), monthly precipitation, mean temperature, number of ant-attractive diaspores, number

of ant-attractive diaspore species, and number of ant-attractive diaspore spots. To choose the best subset among these variables, we used a forward stepwise procedure that allows the selection of the “best model” from a number of possible models (Sokal & Rohlf 1995). The best model should present the lowest number of predictor variables with a significant P and the lowest Akaike information criterion (AIC) (see Sokal & Rohlf 1995; Burnham & Anderson 2002). The normality of samples was tested a posteriori via Lilliefors test. These analyses were performed using the JMP software (SAS-Institute 2002).

Results

Plant diaspores available on the ground

Considering all eight studied sites, a total of 13,303 plant diaspores were found during one-year of monthly samplings. Fruits were found scattered in 1,598 diaspore spots (i.e., a concentration of one or more diaspore of the same species in the ground) unevenly distributed along transects, forest sites, and months. Out of this total, we considered as ripe 9,750 diaspores (distributed in 1,146 spots), belonging to 155 species/morphospecies. There was no difference between fragments and continuous forests regarding the number of ripe fleshy diaspores found per transect ($F = 0.001$; $P = 0.97$), nonetheless there were significant differences among sites within forest types ($F = 6.48$; $P < 0.002$) and among sampling months ($F = 4.47$; $P < 0.0001$; Fig. 1A).

General description of ant-fruit interactions

A total of 998 ant-diaspore interactions were registered during surveys, comprising 105 plant diaspore species and 66 ant species. From this total, 37 interactions were with fruits whose seeds were somehow unviable (*i.e.*, immature, or seeds predated by other animals, or by the ants themselves) and 48 involved fruit parts without any seed. Considering that on few occasions more than one ant species were recorded simultaneously exploring a single diaspore, ants were recorded in 904 sound diaspores, or 6.8% of the 13,303 diaspores available.

The most important plant families with ant-attractive diaspores were: Myrtaceae (19 spp.), Lauraceae (8 spp.), Annonaceae, Araceae and Rubiaceae (5 species each). Among the 74 species found in interaction with ants in continuous forests (CFs), the five most frequent were: *Cryptocaria mandioccana*, *Protium heptaphyllum*, *Tetrastylidium grandiflorum*, *Eugenia cerasiflora* and *Couepia venosa* (Appendix 1). In fragmented forests (FFs), the most important ones were: *Psychotria suterella*, *Cupania vernalis*, *Prunus myrtifolia*, *Solanum cinnamomeum* and *Buchenavia* sp. (Appendix 1). Twenty-six species (24.8% of the 105 species) were recorded only once in interactions.

Considering all studied sites together, species in the genera, *Pheidole*, *Solenopsis*, and *Wasmannia* were the ones most frequently recorded, and interacted with the highest number of plant species (Appendix 2). Among the 54 ant species collected in CFs, the five most frequent were in the genera *Pheidole* and *Solenopsis*. In FFs, the five most common ones were *W. affinis*, *Brachymyrmex* sp. 2, two species of *Pheidole* and one of *Solenopsis*. Of the 998 interactions recorded, in 14 cases the ants were clearly preying on the seeds. On only 18 occasions ants were registered carrying the whole diaspore, seeds, or fruit parts. Finally, the majority of the observed

interactions involved ants exploring diaspores on the spot: whereas in 306 interactions the ants were registered in the outer part of the diaspore, probably ingesting liquids, on 660 occasions the ants were in direct contact with the fleshy part. Ant individuals attending the fallen diaspores varied from one to 65 individuals, but in nearly 90% of the cases less than five ants were present.

Comparisons between CFs and FFs

To compare the availability of ant-attractive diaspores, we considered only species found at least once in interaction with ants. We found the same pattern as described above for total diaspore availability: the number of ant-attractive ripe diaspores found per transect did not differ between the two forest types ($F = 0.006$, $P = 0.94$), but sites differed within the type of forest ($F = 6.11$, $P < 0.002$) with a significant effect of sampling month ($F = 4.62$, $P < 0.0001$; Fig. 1B). Variation among months was higher in FF sites, where fruiting was notably concentrated in the wet season (from November to March). Nonetheless, the four continuous forest sites presented a richer assemblage of ripe and ant-attractive diaspore species than three of the fragments (the exception was FF3; see Table 2). Despite the absence of difference between forest types regarding diaspore abundance, there was a significant effect of the treatment on the number of ant-diaspore interactions recorded ($F = 6.47$, $P < 0.03$), without a nested effect of forest site ($F = 1.86$, $P = 0.15$). The quantity of interactions also varied significantly among months ($F = 2.87$, $P < 0.002$; Fig. 1C), with FF sites presenting more interactions during summer. The richness of interacting diaspore species was higher on CF than on FF sites, again with a consistent difference among sites within the same forest type (Table 2). However, with the exception of the ant communities

in two fragments (FF1 and FF3), the number of interacting ant species per site did not present marked divergences among the other six sites (Table 2).

A data-base containing 75 ant-attractive diaspore species (out of the 105 species recorded in interactions) was used for the species composition analysis (singletons were not included). MDS ordination of the eight sites clearly segregated continuous and fragmented forest sites (Fig. 2; stress value of 0.09). Furthermore, this analysis showed that difference in diaspore species composition is bigger within fragmented sites than within the continuous forests. Additionally, ANOSIM reinforced the idea that forest type has an important effect on the similarity of ant-attractive diaspore assemblages across forest sites ($R = 0.80$; $P < 0.03$).

Moreover, analyzing the rank-abundance curves for both diaspore and ant species reveals two distinctive patterns. The diaspore species that rated first with respect to number of interactions in each of the fragmented forests accounted for more than 38% of the observed interactions at these sites (see Table 1). The high frequency of these diaspore species in interactions with ants reflects their natural occurrence on the floor of forest fragments (Figure 3). In continuous forests, on the other hand, differences between the first- and second-ranked interacting diaspore species are not high and the first-ranked interacting species is not necessarily the most frequently found on the floor. Rank-abundance curves of interacting ant species, however, did not differ between fragmented and continuous sites. In all studied sites, the most common ant species interacting with diaspores accounted for 0.9 to 0.20 of overall interactions recorded (Table 1, Figure 4). Unfortunately, we have no data on the natural occurrence of ground-dwelling ants at these sites.

The best-fitted model to explain the variation on the number of interactions observed was composed by two explanatory variables: forest type and number of available diaspores on the forest ground (see Table 1). There were more interactions per month in the continuous forests than in the fragmented forests, and with increasing the number of diaspores available. As expected, the number of interacting diaspore species recorded monthly in each of the two forest types was satisfactorily explained only by the number of diaspore species available. Finally, the number of interacting ant species recorded monthly was explained by the same two variables that explained the number of interactions: forest type and number of available diaspores. The explanatory power of these three models was regarded as very satisfactory, accounting for 50% or more of the variation observed in the dependent variables tested. The two climatic variables included in the analyses (monthly precipitation and monthly mean temperature) were never selected as good explanatory variables during the analyses.

Discussion

The prominence of the interactions between ants and non-myrmecochorous diaspores in the Brazilian Atlantic forest is well documented (Pizo & Oliveira 2000; Passos & Oliveira 2003; Bottcher 2010; Costa et al. in press). However, this is the first study to investigate the interaction of ants and non-myrmecochorous diaspores at the community level in a fragmented landscape (but see Mitchell et al. 2002, on true myrmecochorous diaspores). Our survey registered 998 ant-diaspore interactions, unevenly distributed along months, transects, and sites. The overall availability of fleshy diaspores and also the abundance of ant-attractive diaspores on the forest ground did not differ between continuous and fragmented rainforest sites. Nevertheless, there were striking differences when analyzing species richness and composition of ant-attractive

diaspores. Most likely, these differences are the proximate explanation for the observed differences in ant-diaspore interactions. We discuss below the implications of our results for forest functioning.

Natural history of ant-diaspore interactions

Our list of interacting species for a lower montane forest in São Paulo State adds to the already wide spectrum of ants and diaspores known to interact in the Brazilian Atlantic rainforest. Previous studies on the same biome have focused in other vegetation types located under 500 m a.s.l., such as the lowland rainforest (Pizo & Oliveira 2000; Bottcher 2010; Costa et al. in press), and the restinga (a coastal sandy forest; Passos & Oliveira 2003; Bottcher 2010). The plant families most rich in species producing ant-attractive diaspores (Myrtaceae, Lauraceae, Annonaceae, Araceae and Rubiaceae) in our study sites are also among the most species-rich families of the Atlantic Forest biome (regional scale: Catharino et al. 2006; biome scale: Stehmann et al. 2009), and are well represented in other studies on ant-diaspore interactions performed in Southeast Brazil (Pizo & Oliveira 2000; Passos & Oliveira 2003; Bottcher 2010). Similarly, the most frequently registered ant genera (*Pheidole*, *Solenopsis* and *Wasmannia*) are common representatives of the ground-dwelling ant fauna of Neotropical rainforests (Ward 2000), and are frequently recorded interacting with fallen fleshy diaspores (Pizo & Oliveira 2000; Christianini & Oliveira 2011). The predominance of common species/genera (of both plants and ants) involved in this type of interaction reinforces the opportunistic and non-specialized character of this ubiquitous relationship (Pizo et al. 2005; Rico-Gray & Oliveira 2007).

Because the main focus of this study was to compare patterns of ant-diaspore interactions in two contrasting forest types, the sampling method consisted of searching for these interactions while monitoring the forest floor along transects. This method, however, resulted in a small number of observations of diaspore removal by ants. The witnessing of active transportation of diaspores by ants in our study was rather uncommon compared to other studies that combined sampling with the offering of especially attractive diaspores (Pizo & Oliveira 2000; Christianini et al. 2011), added by direct observation of ant nests (Leal & Oliveira 1998). Thus our chances of observing removal events were reduced. Moreover, our sampling protocol may also likely explain the rare observations of large ponerines. Since large ponerines attending fleshy diaspores are mostly solitary fast-moving foragers such as *Odontomachus* and *Pachycondyla* species (Pizo & Oliveira 2000; Passos & Oliveira 2003), these ants render undetectable by quickly hiding in the leaf-litter. In fact previous work in Neotropical savannas and rainforests highlight the role of ponerines and leaf-cutting ants (*Atta* and *Acromyrmex*) as the main removers of small and medium-sized fleshy diaspores on the ground (Horvitz & Beattie 1980; Pizo & Oliveira 1998, 2001; Passos & Oliveira 2002, 2004; Christianini & Oliveira 2009).

Contrasting patterns between CF and FF sites

In spite of the similarity in the total abundance of fruits between fragmented and continuous forests, ant-diaspore interactions were more frequently registered in the latter. We attribute these apparently contrasting results to the different quality of diaspores found in each forest type. The analyses of richness estimates, rank-abundance curves, and the MDS ordination of sites according to ant-attracting diaspore species, all point to the same direction: fragments and continuous forests in the same landscape do differ with respect to the diaspore species exploited

by ants. The four CF sites presented the highest values of diaspore richness and clearly formed a separate group in terms of species composition. Fragments, on the other hand, appeared more dispersed in the MDS ordination, suggesting that each site has a unique species-poor group of plants whose diaspores are attended by ants. Due to forest fragmentation, selective logging, and secondary regrowth, the actual community of plants bearing fleshy diaspores in the four studied fragments is formed by species that either survived the anthropogenic process, or colonized the fragments afterwards. Historical differences in the processes faced by each fragment may have lead to the observed differences among the floras in the fragments ('Landscape-divergence Hypothesis'; see Laurance et al. 2007). Although distant from each other, continuous forest sites pertain to the same well preserved forest block capable of maintaining high plant species diversity and a constant species exchange among areas. In such a species-rich scenario of continuous forests, ants should be able to select the most attractive diaspores (*e.g.*, lipid- or protein-rich fruits; Pizo & Oliveira 2000, 2001), and not simply exploit the most abundant ones as they do in forest fragments (see rank-abundance curves in Fig.3).

The observation that ants in the studied fragments were attracted to abundant, but apparently less attractive, diaspores raises an interesting question on the relevance of ants in the recruitment of non-myrmechochorous species in fragmented landscapes, where primary vertebrate dispersers may be locally rare or extinct (Silva & Tabarelli 2000; Cordeiro & Howe 2003). In this context, a recent work in small forest fragments of Madagascar, from which primary dispersers are absent, the ant *Aphaenogaster swammerdami* was able to perform seed removal and cleaning of the diaspores of *Strychnos madagascariensis* (Loganiaceae; Dausmann et al. 2008). Previous studies in the Atlantic forest (Pizo & Oliveira 1998; Passos & Oliveira 2002, 2004) and also in other biomes (Farji-Brener & Silva 1996; Dalling & Wirth 1998; Böhning-Gaese et al. 1999;

Christianini & Oliveira 2009, 2010) have highlighted the importance of ants in complementing the dispersal benefits of avian frugivores, by reorganizing the frugivore-generated seed shadow and carrying seeds to favorable micro-sites (i.e., ant nests). Even diaspores that are too large to be carried by ants (> 1g; Pizo & Oliveira 2001) may benefit from the interaction with these insects, since they remove its fleshy part on the spot and increase seed germination success (Oliveira et al. 1995).

Plant species which may benefit from attracting ants

Possible plant groups that may benefit from attracting ants are fragment-occurring species whose fruiting period is concentrated partially or entirely during winter. We expect that the few species that produce fruits during winter months will face a greater probability of attracting ants, since fragments present a low overall abundance of fallen diaspores in this period and preferred invertebrate prey are scarcer during winter (Levings & Windsor 1984). Seasonal scarcity of fleshy fruits in the Atlantic forest of Southeast Brazil seems to be related to the degradation process of this biome. Morellato et al. (2000) did not find any seasonality in four well-preserved sites when considering the fruiting phenology of trees, whereas Genini et al. (2009) reported a strong seasonality for fleshy fruits in a land-bridge island occupied mostly by secondary vegetation. In our study region, fragment-occurring species producing fruits in winter months are: *Cryptocaria mandioccana*, *Eugenia subavenia*, *Marcgravia polyantha* and *Prunus myrtifolia*.

In fragmented landscapes, fruits with lipid-rich appendages will certainly be the most putative ant-attractive diaspores, since ant preference for lipids have already been demonstrated (Hughes et al. 1994; Pizo & Oliveira 2001). However, given that these diaspores are also very

attractive to vertebrate dispersers (birds and mammals; Galetti et al. 2011), fruit availability of this specific group might even decrease in fragments, referred to as more food-scarce habitats (Genini et al. 2009; but see Ganzhorn 1995 for a discussion on fruit availability under low-level forest disturbance). Therefore, we strongly encourage future investigation on possible changes of the complementary roles played by primary (vertebrates) and secondary (ants) dispersers (Böhning-Gaese et al 1999; Christianini & Oliveira 2010) in the dispersal and recruitment of lipid-rich diaspores in anthropogenically fragmented landscapes. In our study region, some plant species that might deserve further investigation on this topic due to their occurrence in both forest types, and their lipid- or protein-rich diaspores (according to Galetti et al. 2011) are: *Alchornea triplinervia*, *Cabralea canjerana* (see also Pizo 1997 and Pizo & Oliveira 1998) and *Guapira opposita* (see also Passos & Oliveira 2004). Nonetheless, more detailed surveys will certainly detect many other species.

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Table 1: Among-site differences in relation to: ant-attractive diaspore species on the forest floor, diaspore species recorded in interactions and ant species recorded in interactions. The eight sites were surveyed for ant-diaspore interactions in a fragmented landscape (four continuous forest sites, CF, and four forest fragments, FF) of the Atlantic forest, Southeast Brazil. S_{obs} – observed number of species. Jackknife (95% CI) – mean estimated number of species per site and confidence limit (95%) based on the Jackknife-I procedure. Means followed by different letters indicate significant differences (at $\alpha=0.05$) among sites. Domin. – dominance refers to the percentage of the most abundant species in each forest site.

Forest sites	Ant-attractive diaspores			Diaspores in interactions			Ants in interactions		
	S_{obs}	Jackknife (95% CI)	Domin.	S_{obs}	Jackknife (95% CI)	Domin.	S_{obs}	Jackknife (95% CI)	Domin.
CF1	40	57.8 (49.32 - 66.28) ^a	27%	33	53.77 (44.91 - 62.63) ^a	27%	36	48.86 (41.71 - 56.01) ^a	9%
CF2	31	48.8 (40.79 - 56.81) ^{b, c}	23%	25	41.81 (33.48 - 50.14) ^b	36%	32	44.86 (37.17 - 52.55) ^a	15%
CF3	32	42.88 (36.12 - 49.64) ^{b, f}	15%	24	37.84 (31.04 - 44.64) ^b	22%	28	39.87 (30.11 - 49.63) ^{a, c}	15%
CF4	35	50.82 (43.65 - 57.99) ^{a, c}	26%	30	45.82 (37.18 - 54.46) ^{a, b}	13%	34	45.87 (38.92 - 52.82) ^a	15%
FF1	14	17.96 (13.19 - 22.73) ^d	54%	9	12.96 (9.11 - 16.81) ^c	52%	14	18.94 (13.81 - 24.07) ^b	16%
FF2	22	28.92 (23.89 - 33.95) ^e	52%	18	26.9 (21.28 - 32.52) ^d	46%	36	50.83 (42.80 - 58.86) ^a	12%
FF3	24	38.83 (31.84 - 45.82) ^f	52%	16	27.87 (20.38 - 35.36) ^d	38%	21	33.86 (25.69 - 42.03) ^c	20%
FF4	21	28.91 (22.89 - 34.93) ^e	34%	16	23.91 (15.58 - 29.14) ^d	43%	31	45.83 (36.05 - 55.61) ^a	18%

Table 2. Best-fit models selected through forward stepwise regression to explain the variation recorded in the ant-diaspore interactions sampled monthly during one year in two different forest types in a fragmented landscape (continuous and fragmented forests) of the Atlantic forest, Southeast Brazil. See methods for the list of all explanatory variables tested.

Dependent Variables	Best-Fit Model (Selected Explanatory Variables)
Number of ant-diaspore interactions	Overall $F = 13.14$; $P < 0.0005$; $R^2(\text{Adj.}) = 51.36\%$; AIC = 138.47 Forest type ($F = 7.82$; $P < 0.015$) Number of available diaspores ($F = 18.69$; $P < 0.0005$)
Number of interacting diaspore species	Overall $F = 45.13$; $P < 0.0001$; $R^2(\text{Adj.}) = 65.74\%$; AIC = 50.41 Number of diaspore species available ($F = 45.13$; $P < 0.0001$)
Number of interacting ant species	Overall $F = 12.20$; $P < 0.0005$; $R^2(\text{Adj.}) = 49.33\%$; AIC = 83.93 Forest type ($F = 6.19$; $P < 0.03$) Number of available diaspores ($F = 18.40$; $P < 0.0005$)

Legends to Figures

Figure 1. Yearly variation in the abundance of (A) ripe fleshy diaspores, (B) ripe and ant-attracting diaspores, and (C) ant-diaspore interactions in two contrasting forest types (four continuous forest sites – CFs; and four forest fragments – FFs) in the Atlantic forest, Southeast Brazil. Points represent mean value per transect each month, considering all sites within a forest type together. Whiskers indicate the standard error. CFs designated by black circles; FFs designated by unfilled triangles.

Figure 2. Non-metric multi-dimensional scaling (MDS) ordination of eight forest sites studied in a fragmented landscape of the Atlantic forest, Southeast Brazil, based on the Bray-Curtis similarity matrix of ant-attractive diaspore species. The four continuous forest sites (CF) are represented by black circles and the four fragmented forests (FFs) by unfilled triangles.

Figure 3. Rank-abundance curves of all ant-attractive diaspore species (unfilled circles) found on the ground, and of the diaspores found in interaction with ants (filled circles). Surveys were performed in eight studied sites in a fragmented landscape of the Atlantic forest, Southeast Brazil: four continuous forest sites (CF), and four forest fragments (FF). Names of the five most common species in interactions at each site are given in order of importance and the relative position of each of these species is identified in the curve for general abundance of diaspores on the ground.

Figure 4. Rank-abundance curves of the ant species interacting with fallen diaspores for each of eight studied sites in a fragmented landscape of the Atlantic forest, Southeast Brazil: four continuous forest sites (CF), and four forest fragments (FF). Names are given for the three most frequent interacting ants.

Figure 1

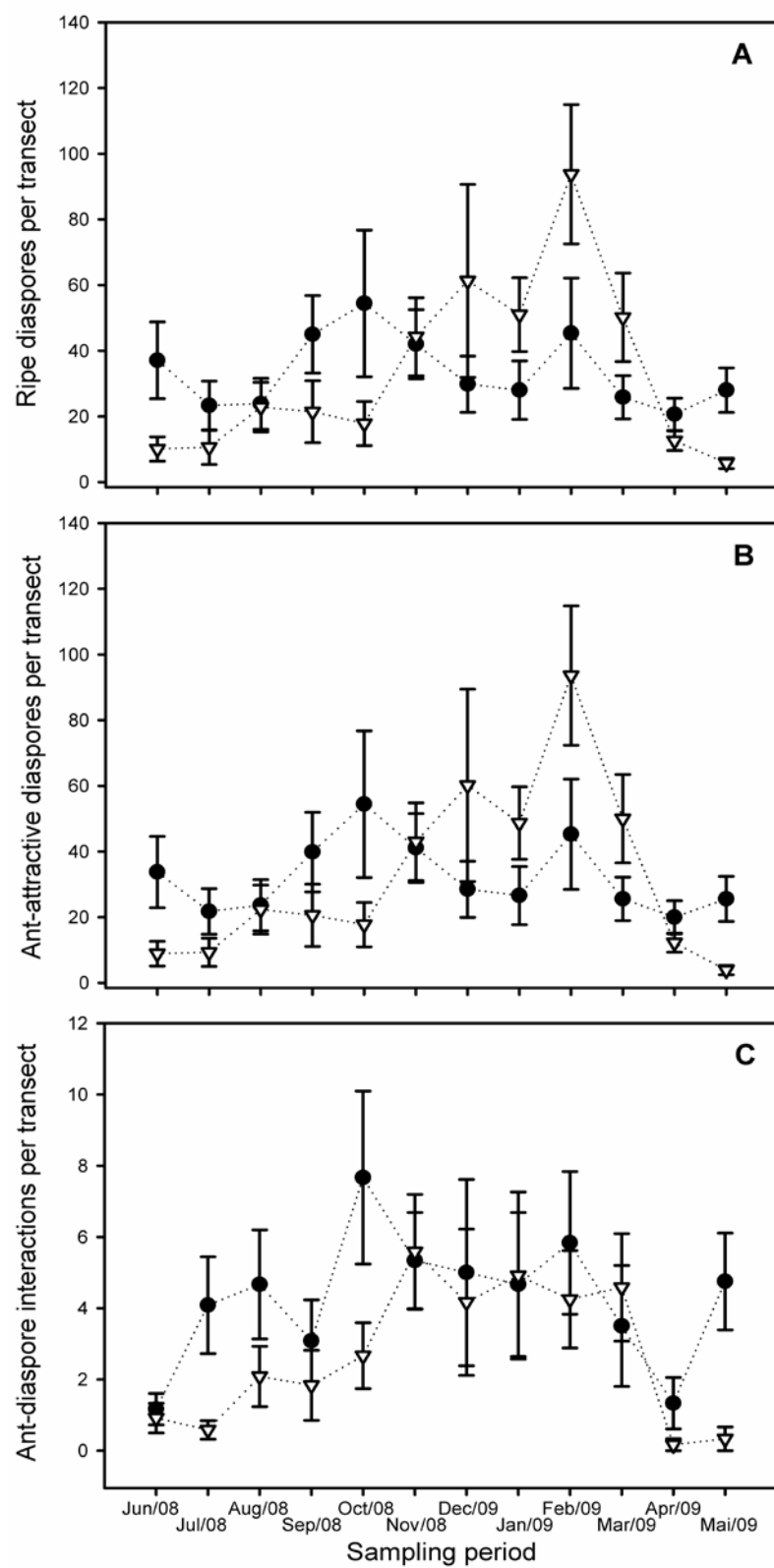


Figure 2.

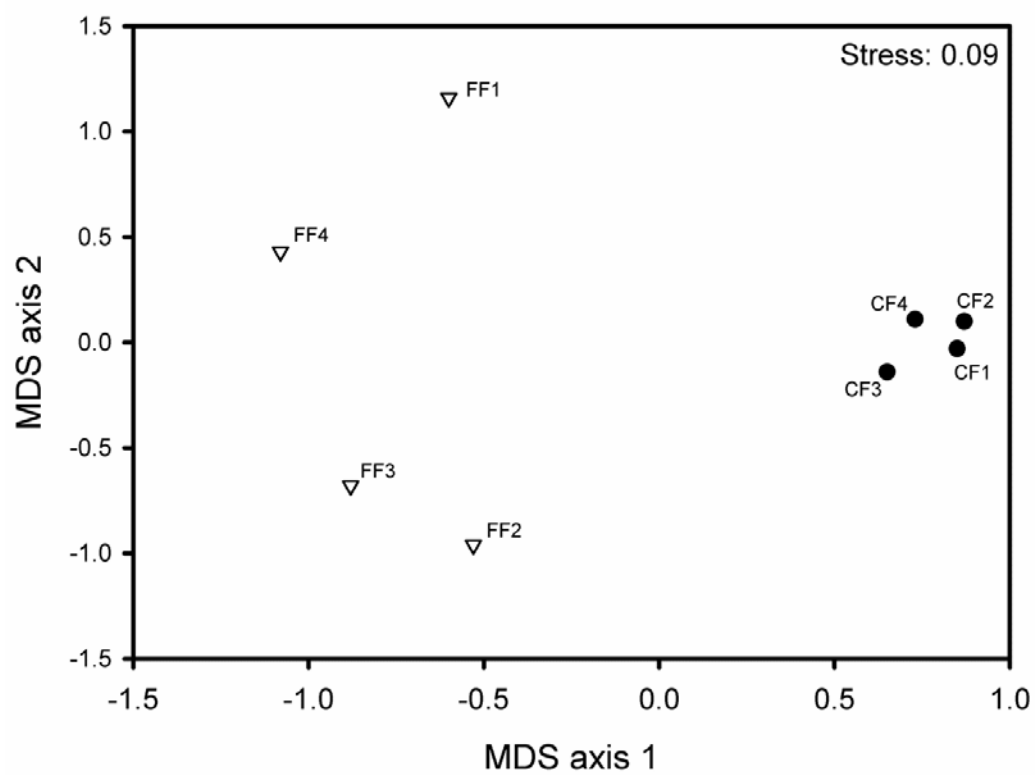


Figure 3.

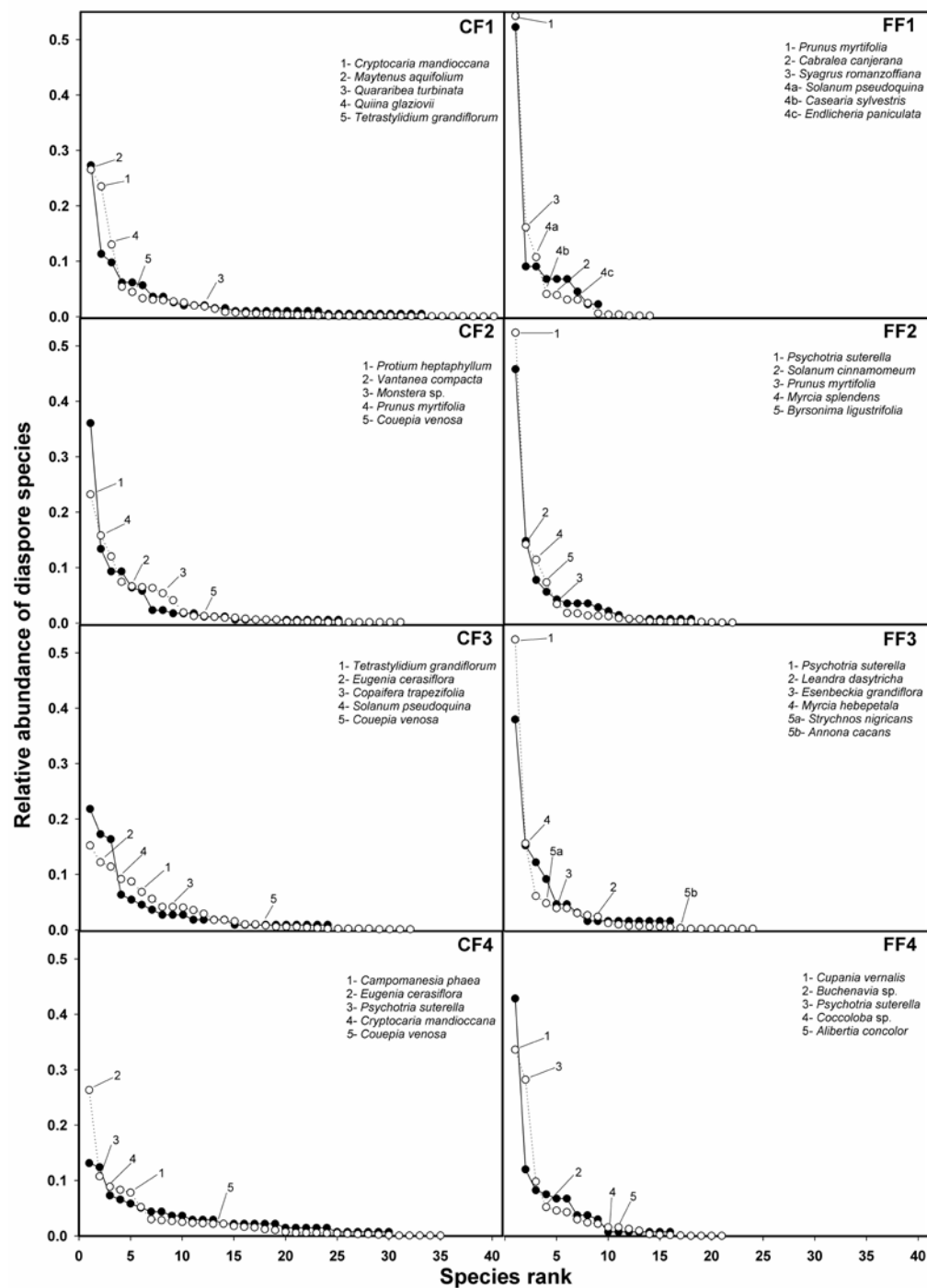
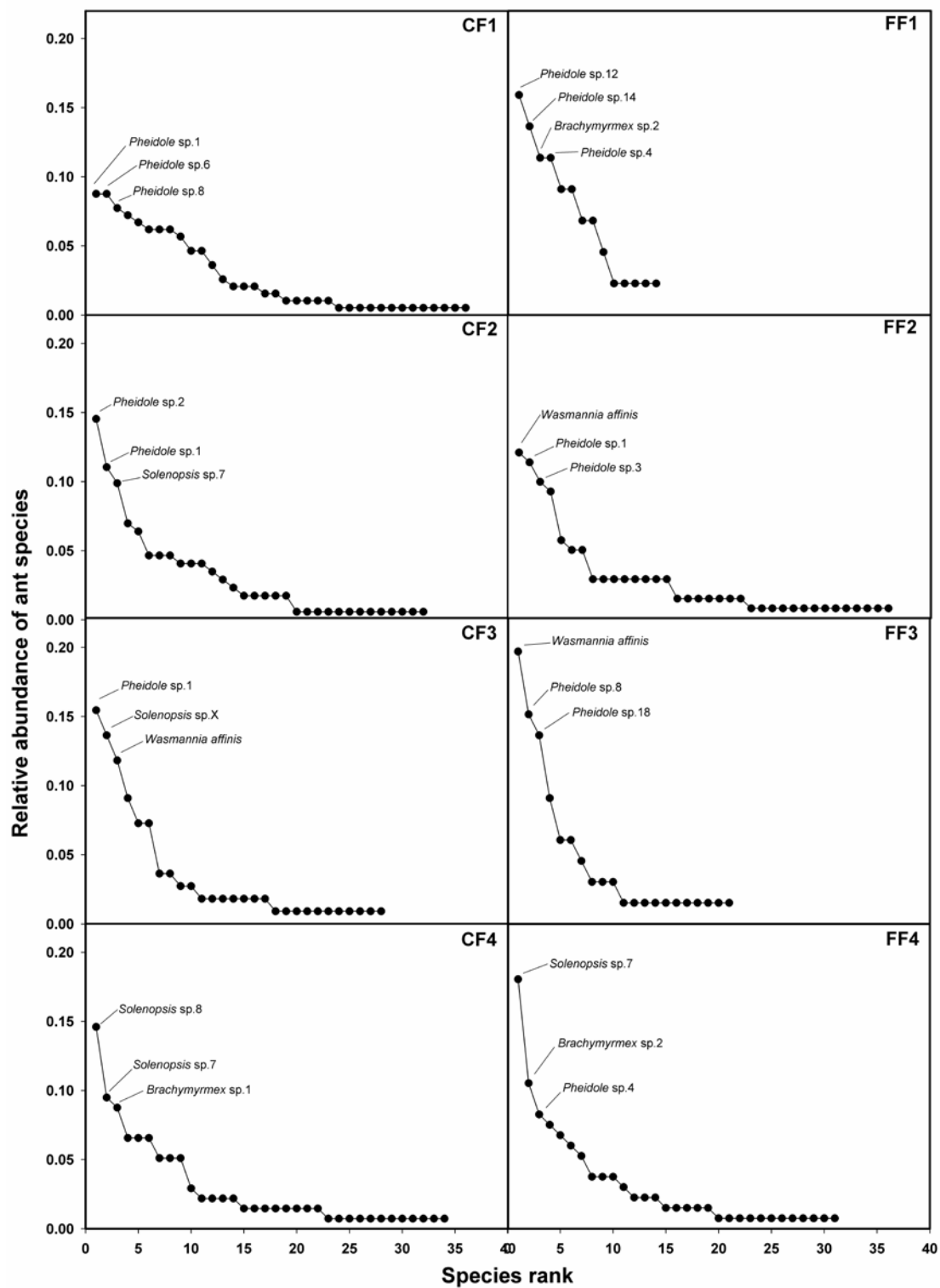


Figure 4.



Appendix 1: List of plant species whose diaspores attracted ants in the eight forests sites (four continuous forest sites, CFs, and four forest fragments, FFs) located within a fragmented landscape of the Atlantic Forest, São Paulo State, Southeast Brazil. Surveys were carried out monthly during one year, using three 300-m transects in each forest site (total sampling effort of 86.4 km). Ant species attending each diaspore species are indicated by numbers (see Appendix 2). The total number of interactions per species for both forest types and the fruiting period for each species are given. The five most important diaspore species (as expressed by the number of interactions) of each forest type are indicated by CF or FF superscripts. Species recorded only once are followed by an asterisk. Months followed by # indicate that the species was found in interactions with ants only when unripe.

Plant Family/ Species	Associated ant species	CF sites	FF sites	Fruiting period
Acanthaceae				
<i>Mendoncia velloziana</i> Mart.*	30	0	1	Mar-May
Annonaceae				
<i>Annona cacans</i> Warm.	20, 34, 63	0	3	Feb-Mar
<i>Annona neosericea</i> H.Rainer	33, 39, 63	4	0	Apr
<i>Duguetia lanceolata</i> A.St.-Hil.	30, 31, 39, 53	7	0	Nov
<i>Guatteria australis</i> A.St.-Hil	8, 59	0	2	Jan-Feb

<i>Guatteria nigrescens</i> Mart.	8, 35	0	2	Mar; Oct
Araceae				
<i>Anthurium scandens</i> (Aubl.) Engl. subsp. <i>scandens</i>	29, 30	2	0	Jan
<i>Anthurium sellowianum</i> Kunth*	55	1	0	Jan
<i>Monstera</i> sp.	14, 26, 29, 34, 35, 50, 52, 55, 56, 58	18	0	Nov-Mar
<i>Philodendron corcovadense</i> Kunth	30, 33, 40, 45, 60	5	0	Jan-Feb
<i>Philodendron</i> sp.	15, 30	2	0	Mar
Arecaceae				
<i>Lytocaryum hoehnei</i> (Burret) Toledo*	7	1	0	Nov-Feb
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	15, 24, 29, 54, 55	0	5	Jan-Feb
Burseraceae				
<i>Protium heptaphyllum</i> (Aubl.) March. ^{CF}	2, 4, 6, 11, 26, 28-32, 35, 42, 50, 51, 54- 58, 60, 63	64	0	Nov-Jan
Cactaceae				
<i>Lepismium warmingianum</i> (K.Schum.) Barthlott	28, 52, 57	3	0	Feb-Mar

Celastraceae

<i>Maytenus aquifolium</i> Mart.	24, 29, 30, 33, 35, 37, 51, 54, 55, 57	22	0	Sep-Dec
<i>Maytenus</i> sp. 2	17, 29, 54	11	0	Oct-Nov
<i>Salacia grandifolia</i> (Mart. ex Schult.) G.Don	30, 53	2	0	Dec
<i>Tontelea miersii</i> (Peyr.) A.C.Sm.	15, 30, 32	4	0	Nov-Jun

Chrysobalanaceae

<i>Couepia venosa</i> Prance ^{CF}	7, 16, 26, 29, 30, 32, 35, 39, 50, 54-57, 60, 63, 64	26	0	May
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Clusiaceae

<i>Garcinia gardneriana</i> (Planch., and Triana) Zappi	48, 56	2	0	Feb-Mar
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Combretaceae

<i>Buchenavia</i> sp. ^{FF}	5, 28, 32, 37, 39, 40, 46, 55	0	16	Feb-Mar
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Elaeocarpaceae

<i>Sloanea monosperma</i> Vell.	29, 36, 54, 57	0	5	Jun-Jul#
<i>Sloanea retusa</i> (Schum.) Uitt.	42, 58	2	0	Feb

Euphorbiaceae

<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	18, 29, 50, 55, 58, 63	8	1	Feb-May
undetermined 1	22, 38, 54, 57	0	4	Nov

Humiriaceae

<i>Vantanea compacta</i> (Schnizl.) Cuatrec.	26, 29, 31, 32, 34, 50, 55-57, 60, 63	25	0	Jan-Feb
<i>Humirastrum dentatum</i> (Casar.) Cuatrec.	30, 35	3	0	Dec

Lauraceae

<i>Cryptocaria mandioccana</i> Meisn. ^{CF}	9, 15, 24, 28-31, 33-35, 37, 38, 41, 50-52, 54-57, 60, 61, 63	64	1	Jun-Oct
<i>Endlicheria paniculata</i> (Spreng.) J. F. Macbr.	54, 55	0	3	Oct-Dec
<i>Ocotea catharinensis</i> Mez	30-32, 48, 50, 51, 55, 62, 63	13	0	Feb-May
<i>Ocotea</i> sp.	31, 32, 39, 55	0	4	Dec-Feb
<i>Persea wilddenovii</i> Kosterm.*	29	0	1	Jan-Feb
undetermined 2*	51	0	1	Jul-Nov
undetermined 3*	42	0	1	Aug-Nov
undetermined 4*	29	1	0	Nov

Fabaceae

<i>Copaifera trapezifolia</i> Hayne	29, 32, 35, 50, 55-57, 61, 63	18	0	Sep-Dec
<i>Inga sessilis</i> (Vell.) Mart.	15, 64	2	0	Dec-Feb
undetermined 5*	42	0	1	Sep

Loganiaceae

<i>Strychnos nigricans</i> Progel	24, 28-30, 33, 35, 39, 51, 54-57, 63	10	8	Jun-Mar
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Loranthaceae

<i>Psittacanthus robustus</i> (Mart.) Mart.	18, 34, 49, 57, 60	5	0	Mar-Jul
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Malpighiaceae

<i>Byrsonima ligustrifolia</i> A.Juss.	30, 34, 56, 63	0	6	Jan-Apr
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Malvaceae

<i>Quararibea turbinata</i> (Sw.) Poir.	29, 31, 33, 39, 40, 50, 51, 54, 55, 57	19	0	Jul-Sep
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Marcgraviaceae

<i>Marcgravia polyantha</i> Delpino	24, 26, 42, 50	4	1	Aug-Dec
<i>Schwartzia brasiliensis</i> (Choisy) Bedell ex Gir.-	29, 51	3	0	Jan-Mar

Cañas

Melastomataceae

<i>Leandra dasytricha</i> (A. Gray) Cogn.	28, 31, 42, 43, 55, 59	0	10	Mar-May
<i>Miconia cabucu</i> Hoehne	26, 30, 55, 57	5	0	Nov-Dec
undetermined 6*	57	1	0	Sep

Meliaceae

<i>Cabralea canjerana</i> (Vell.) Mart.	33, 35, 37, 39	2	4	Feb-May
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Moraceae

<i>Ficus</i> cf. <i>luschnathiana</i> (Miq.) Miq.	50, 52, 55	4	0	Apr-May
<i>Ficus</i> sp.2	10, 29, 30, 32, 35, 50	6	0	Nov; Feb- Mar; Jun

Myristicaceae

<i>Virola bicuhyba</i> (Schott ex Spreng.) Warb.*	28	1	0	Aug
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Myrsinaceae

<i>Ardisia martiana</i> Miq.*	30	1	0	Apr-May
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Myrtaceae

<i>Campomanesia phaea</i> (O.Berg) Landrum	7, 26, 30, 33, 50, 55, 56	19	0	Mar-Apr
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<i>Campomanesia xanthocarpa</i> (Mart.) O.Berg	14, 31, 47, 54, 55, 63	0	6	Jan-Mar
<i>Campomanesia</i> sp. 3	29	0	1	Jan-Feb
<i>Eugenia cerasiflora</i> Miq. ^{CF}	7, 29, 30-32, 38, 49, 50, 52, 54-57, 63	38	0	Aug-Nov
<i>Eugenia subavenia</i> O.Berg	6, 29, 30, 51, 56, 63	4	5	Jul-Oct
<i>Eugenia</i> sp. 3	29	1	0	May
<i>Eugenia</i> sp. 4	29, 42, 57	3	0	Jan
<i>Marlierea excoriata</i> Mart.	34, 55	2	0	Oct-Nov
<i>Myrcia</i> (sect. <i>Gomidesia</i>) <i>hebepetala</i> DC.	16, 55, 63	0	6	Jul-Sep
<i>Myrcia pubipetala</i> Miq.	29, 30, 33, 35, 50, 57, 63	10	0	Jun-Jul
<i>Myrcia spectabilis</i> DC.	50, 56	6	0	Oct
<i>Myrcia splendens</i> (Sw.) DC.	15, 27-30, 43, 63	0	8	Sep-Dec
<i>Myrcia</i> (sect. <i>Marlierea</i>) sp. 5*	50	1	0	Jun-Sep#
<i>Myrcia</i> sp. 6	21, 40, 55	1	2	Nov
<i>Myrcia</i> sp. 7	29, 30, 35, 50, 57	7	0	Mar
<i>Psidium guajava</i> L.*	30	1	0	Jan
<i>Psidium myrtoides</i> O.Berg	26, 30, 31, 35	5	0	May-Aug

<i>Syzigium</i> sp.*	57	0	1	Jun-Aug
Undetermined 7*	33	0	1	Oct
Nyctaginaceae				
<i>Guapira opposita</i> (Vell.) Reitz	8, 15, 26, 28, 29, 35, 43, 44, 55	4	8	Oct-Nov
Olacaceae				
<i>Tetrastylidium grandiflorum</i> (Baill.) Sleumer ^{CF}	8, 9, 13, 14, 20, 28-31, 38, 39, 50, 52, 54- 58, 60, 61, 63, 66	42	0	Aug-Dec
Polygonaceae				
<i>Coccoloba</i> sp.	17, 20	0	10	Feb
Quinaceae				
<i>Quiina glaziovii</i> Engl.	20, 25, 29, 30, 33, 42, 55, 57, 63	15	0	Feb
Rosaceae				
<i>Prunus myrtifolia</i> (L.) Urb. ^{FF}	6-8, 19, 23-26, 29-32, 37, 39, 40, 43, 51, 52, 54-57, 63	16	34	Jun-Nov
Rubiaceae				
<i>Cordia concolor</i> (Cham.) Kuntze	8, 24, 31, 55, 60, 63	0	9	Oct-Dec

<i>Hoffmania dusenii</i> Standl.*	54	1	0	Apr
<i>Posoqueria latifolia</i> (Rudge) Schult.*	63	0	1	Feb
<i>Psychotria suterella</i> Müll. Arg. ^{FF}	1, 6, 7, 14, 15, 20, 22, 23, 25, 29-36, 39, 42, 46, 54-57, 60, 63, 65	14	102	Nov-May
<i>Rudgea jasminoides</i> (Cham.) Müll. Arg.	7, 20, 29, 37, 63	3	3	Aug-Jan
Rutaceae				
<i>Esenbeckia grandiflora</i> Mart.	38, 42, 55, 63	0	8	Oct-Dec#
Sabiaceae				
<i>Meliosma sellowii</i> Urb.*	55	1	0	Jul
Salicaceae				
<i>Casearia decandra</i> Jacq.	1, 35	2	0	Dec-Jan
<i>Casearia sylvestris</i> Sw.	8, 31	0	12	Nov-Dec
Sapindaceae				
<i>Cupania oblongifolia</i> Mart.*	28	1	0	Nov
<i>Cupania vernalis</i> Cambess. ^{FF}	3, 8, 15, 17, 21, 23, 24, 29, 31-33, 35, 37- 40, 51, 54-58, 60, 63, 65	0	57	Oct-Dec

<i>Paullinia seminuda</i> Radlk.	7	2	0	Oct-Nov
<i>Paullinia trigonia</i> Vell.	35, 60	1	1	Jul-Sep
Sapotaceae				
<i>Diploon cuspidatum</i> (Hoehne) Cronquist	24, 33, 41, 55	4	0	Jan
<i>Pouteria gardneriana</i> (A.DC.) Radlk.	35, 51, 53, 55	4	0	Sep-Nov
Solanaceae				
<i>Solanum argenteum</i> Dunal*	31	1	0	Aug-Sep
<i>Solanum cinnamomeum</i> Sendtn. ^{FF}	5, 7, 8, 11, 26, 29, 30, 34, 35, 50, 54, 55, 63	4	21	Jul-Dec
<i>Solanum pseudoquina</i> A.St.-Hil.	15, 29, 30, 31, 33, 50, 55	8	3	Dec-May
Symplocaceae				
<i>Symplocos estrellensis</i> Casar.*	31	0	1	Aug-Nov
<i>Symplocos laxiflora</i> Benth.	12, 29, 40, 50, 51, 56, 60, 63	11	0	Apr-May
Unknown Families				
undetermined 8*	66	1	0	Sep
undetermined 9*	28	1	0	Nov

undetermined 10*	28	0	1	Dec
undetermined 11	42, 54, 56	0	3	Aug-Sep
undetermined 12	29, 31, 33, 57, 63	4	2	Nov-Mar
undetermined 13	35	2	0	Jan
undetermined 14	7, 56	3	0	Oct
undetermined 15	35, 50	2	0	May-Sep
Number of diaspore species per forest type		74	46	

Appendix 2: Ant species recorded exploiting non-myrmecochorous diaspores on the ground of eight forests sites (four continuous forest sites, CFs, and four forest fragments, FFs) located within a fragmented landscape of the Atlantic Forest, São Paulo, Southeast Brazil. Surveys were carried out monthly during one year, using three 300-m transects in each forest site (total sampling effort of 86.4 km). For each species, the following information is given: number of interactions at CF and FF sites (in parenthesis, the number of sites where it was encountered), its behavior during interactions, and the number of diaspore species explored. The five most important ant species (as expressed by the number of interactions) in each forest type are indicated by CF or FF superscripts. Species recorded only once are followed by an asterisk. Key to ant behavior: R = one or more individuals remove the diaspore (> 5 cm); C = clean the seed by continual removal of pulp/aril on spot; CP = clean the pulp partially (max. 25%) on spot, E = inspect or collect liquids, no removal; P = prey on the seed; CS = cover diaspore with soil particles.

Ant species	CF sites	FF sites	Behavior	Number of partners
Dolichoderinae				
1- <i>Linepithema pulex</i> Wild	1 (1)	1 (1)	E	2
2- <i>Tapinoma melanocephalum</i> Fabricius*	1 (1)	--	E	1
3- <i>Tapinoma</i> sp. 3*	--	1 (1)	?	1
Ectatomminae				
4- <i>Ectatomma edentatum</i> Roger*	1 (1)	--	CP	1

5- <i>Gnamptogenys lucaris</i> Kempf	--	2 (2)	E	2
6- <i>Gnamptogenys striatula</i> Mayr	2 (2)	2 (1)	CP, E	4
Formicinae				
7- <i>Brachymyrmex</i> sp. 1	15 (2)	4 (1)	CP, E	10
8- <i>Brachymyrmex</i> sp. 2 ^{FF}	1 (1)	20 (3)	CP, E	9
9- <i>Brachymyrmex</i> sp. 3	2 (1)	--	CP	2
10- <i>Brachymyrmex</i> sp. 4*	1 (1)	--	CP	1
11- <i>Brachymyrmex</i> sp. 7	1 (1)	1 (1)	CP, E	2
12- <i>Myrmelachista</i> sp. 1*	1 (1)	--	E	1
13- <i>Nylanderia</i> sp. 1*	1 (1)	--	CP	1
14- <i>Nylanderia</i> sp. 2	4 (3)	5 (2)	CP, E	4
Heteroponerinae				
15- <i>Heteroponera inermis</i> (Emery)	7 (2)	10 (3)	CP, E	10
Myrmicinae				
16- <i>Acromyrmex rugosus</i> (F. Smith)	1 (1)	4 (1)	C, R	2
17- <i>Acromyrmex</i> sp. 1	9 (1)	10 (1)	C, R	3

18- <i>Carebara</i> sp. 1	2 (2)	--	CP, E	2
19- <i>Cyphomyrmex</i> cf. <i>olitor</i> Forel*	1 (1)	--	CP	1
20- <i>Cyphomyrmex rimosus</i> (Spinola)	4 (3)	2 (2)	CP, E	6
21- <i>Megalomyrmex</i> sp. 1	--	2 (2)	E	2
22- <i>Megalomyrmex</i> sp. 2	--	3 (2)	CP, E	2
23- <i>Octostruma rugifera</i> (Mayr)	--	3 (2)	E	3
24- <i>Octostruma stenognatha</i> Brown, and Kempf	6 (3)	4 (2)	CP, E	9
25- <i>Oxyepoecus</i> cf. <i>rosai</i> Albuquerque, and Brandão	1 (1)	2 (1)	CP, E	3
26- <i>Pheidole borgmeieri</i> Kempf	30 (4)	--	CP, E, P	11
27- <i>Pheidole gertrudae</i> Forel*	--	1 (1)	CP	1
28- <i>Pheidole nesiota</i> Wilson	11 (4)	7 (3)	CP, E	13
29- <i>Pheidole</i> sp. 1 ^{CF,FF}	62 (4)	27 (4)	CP, C, E	37
30- <i>Pheidole</i> sp. 3 ^{CF}	41 (4)	17 (3)	CP, C, E	32
31- <i>Pheidole</i> sp. 4 ^{FF}	18 (4)	22 (4)	CP, C, P, E	21
32- <i>Pheidole</i> sp. 5	13 (4)	7 (3)	CP, E	13
33- <i>Pheidole</i> sp. 6	24 (2)	12 (3)	CP, C, E	16

34- <i>Pheidole</i> sp. 7	6 (3)	5 (2)	CP, E.	9
35- <i>Pheidole</i> sp. 8	27 (4)	18 (4)	CP, C, P, E	23
36- <i>Pheidole</i> sp. 11	--	2 (1)	CP, E	2
37- <i>Pheidole</i> sp. 12	3 (2)	9 (2)	CP, C	7
38- <i>Pheidole</i> sp. 13	4 (3)	3 (3)	E	6
39- <i>Pheidole</i> sp. 14	7 (3)	13 (4)	CP, C, E	12
40- <i>Pheidole</i> sp. 15	4 (3)	4 (2)	CP, E	7
41- <i>Pheidole</i> sp. 17	2 (1)	--	CP	2
42- <i>Pheidole</i> sp. 18	4 (3)	13 (2)	CP, E	11
43- <i>Pheidole</i> sp. 20	--	6 (2)	CP	4
44- <i>Pheidole</i> sp. 21*	1 (1)	--	CP	1
45- <i>Pheidole</i> sp. 23*	1 (1)	--	CP	1
46- <i>Pheidole</i> sp. 24	--	2 (2)	E	2
47- <i>Pheidole</i> sp. 25*	--	1 (1)	CP	1
48- <i>Pyramica denticulata</i> (Mayr)	2 (2)	--	E	2
49- <i>Pyramica</i> sp. 2	2 (2)	--	E	2

50- <i>Solenopsis</i> sp. 1 ^{CF}	39 (4)	1 (1)	CP, E	23
51- <i>Solenopsis</i> sp. 2	16 (2)	5 (2)	E	13
52- <i>Solenopsis</i> sp. 3	8 (3)	--	E	7
53- <i>Solenopsis</i> sp. 4	4 (1)	--	CP, CS	3
54- <i>Solenopsis</i> sp. 5	15 (3)	16 (3)	CP, E	20
55- <i>Solenopsis</i> sp. 7 ^{CF,FF}	57 (4)	42 (4)	CP, E, P	38
56- <i>Solenopsis</i> sp. 8 ^{CF}	45 (4)	6 (3)	CP, E, P	20
57- <i>Solenopsis</i> sp. 9	35 (4)	17 (3)	CP, E, P	25
58- <i>Solenopsis</i> sp. 11	9 (4)	1 (1)	CP, C	6
59- <i>Solenopsis</i> sp. 12	--	3 (2)	CP	2
60- <i>Solenopsis</i> sp. 13	16 (4)	12 (3)	CP, E	12
61- <i>Solenopsis</i> sp. 14	3 (2)	--	CP	3
62- <i>Strumigenys louisianae</i> Roger*	1 (1)	--	E	1
63- <i>Wasmannia affinis</i> Santschi ^{FF}	36 (4)	35 (3)	CP, E	29
Ponerinae				
64- <i>Hypoponera</i> sp. 1	3 (2)	--	E	2

65- <i>Hypoponera</i> sp. 2	--	2 (2)	E	2
66- <i>Pachycondyla striata</i> Fr. Smith	2 (2)	--	R, CP	2
Number of ant species per forest type	54	46		

Capítulo 3:

Forest structure influences the topology of ant-fruit interaction networks in a fragmented rainforest landscape

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Running head: Ant-fruit networks in a fragmented landscape

KEY-WORDS: Atlantic forest, mutualism, ant-plant interactions, nestedness, myrmecochory, H₂' index.

Abstract: Ant-fruit interactions on the ground of tropical forests/savannas are intrinsically opportunistic, although benefits to both partners have already been recognized (i.e., characterizing a facultative mutualism). As human-imposed changes to terrestrial ecosystems are likely to greatly change mutualistic interactions among species, our question here was whether forest disturbance influences the topology of ant-fruit interacting networks. We used a data set of a one-year survey of ant-diaspore interactions in eight distinct forests (four fragments and four continuous forest sites) located in a fragmented landscape of the Brazilian Atlantic Forest. The following network-level metrics (most of them quantitative) were calculated for each of the eight networks: connectance, linkage density, generality, vulnerability, interaction evenness, H_2' index and specialization asymmetry. Plant species number per network varied from nine to 31, while ant species ranged from 14 to 36 species. Networks on continuous forest sites presented a higher mean number of diaspore species than networks of the fragments. Networks of fragments also differed from those of more preserved sites in relation to three out of seven tested metrics: generality, interaction evenness, and H_2' index. Ant-fruit interactions were characterized by a high level of generalism and changes in the topology of networks are attributed to differences regarding plant species composition and richness between the two types of forest. As ant species number and composition did not present strong differences between the studied areas, the maintenance of the role played by ants as seed-cleaners and short-distance dispersers of fleshy diaspores may be guaranteed in moderately disturbed forest areas.

Introduction

Ant attraction to fallen fleshy plant diaspores (the unit of plant dispersal: fruit, seed or infructescence; *sensu* Van der Pijl 1972) is a widespread phenomenon on the ground of tropical forests and savannas (Leal & Oliveira 1998; Pizo & Oliveira 2000; Passos & Oliveira 2003; Bottcher 2010; Christianini et al. 2011). This essentially opportunistic interaction involves ants foraging on diaspores that arrive on the ground at an unpredictable manner, either after being handled/eaten by vertebrate frugivores or directly falling from the fruiting plant (Rico-Gray & Oliveira 2007). Unlike ant relation with true myrmecochoric diaspores (see Beattie 1985), fleshy diaspores do not present clear morphological adaptations for attracting or for being carried by ants (Rico-Gray & Oliveira 2007). Nonetheless, its mutualistic character is being revealed by several studies, mostly developed in the last twenty years (see review in Rico-Gray & Oliveira 2007).

A good example of the mutual benefit of ants and plants is the interaction of ground-dwelling ant species with the primarily ornithochoric diaspore of *Cabralea canjerana* (Meliaceae), in the Brazilian Atlantic forest (Pizo & Oliveira 1998; Bottcher 2010). Through field and greenhouse experiments, the authors stated that most of the attracted ant species were interested in consuming *C. canjerana* aril, whose removal significantly increases the seed's germination success (Pizo & Oliveira 1998). One of the main removers of these diaspores is the ant *Odontomachus chelifer*, which transports the arillate seeds (ca 1 g each) up to 180 cm away from the initial deposition site (Pizo & Oliveira 1998). Recently, a benefit to the ants was also demonstrated. Under lab controlled conditions, ant colonies of *O. chelifer* being fed with a synthetic diet for ants together with some arillate *C. canjerana* seeds produced heavier larvae

than colonies which received only the synthetic diet (Bottcher 2010). Although this remains the sole study to demonstrate a benefit to the ant partner in the interaction with non-myrmecochoric diaspores, there are many other studies showing benefits to primary vertebrate-dispersed plants belonging to different families (Anacardiaceae, Annonaceae, Clusiaceae, Fabaceae, Melastomataceae, Nyctaginaceae) in many ecosystems (Argentinian ‘algarrobal’, Brazilian Atlantic Forest and Cerrado, Venezuelan Llanos) (Farji-Brener & Silva 1996; Passos & Oliveira 2002, 2004; Milesi & Lopez de Casenave 2004; Christianini & Oliveira 2009, 2010).

Due to the natural variation in species abundances throughout their occurrence range, animal-plant interactions vary widely in space and time (Thompson 2005). Moreover, human-imposed changes to natural ecosystems are modifying even more the realized interactions by differentially altering landscapes and impacting species composition and abundance (Tylianakis et al. 2008; Morris 2010). In this sense, the worldwide destruction and fragmentation of rainforests, one of the most pervasive threats to global diversity (Turner & Corlett 1996; Wright 2005), present a still largely unexplored potential to modify species interactions (Morris 2010; Tylianakis et al. 2010). For example, Cramer et al. (2007) have shown that Amazonian forest fragmentation affects differentially the seed dispersal of two vertebrate-dispersed plants. While the large-seeded *Duckeodendron cestroides* (Moraceae), primarily dispersed by primates, showed a decrease in number of removed fruits and dispersal distance in small fragments; the bird-dispersed *Bocageopsis multiflora* (Annonaceae) was largely unaffected. Silva et al. (2002) compared the whole assemblage of bird frugivores and their consumed fruits occurring in two neighboring tracts of the Atlantic forest, with different conservation status. Although the plant species composition was very different, bird community did not differ that much, indicating that birds are able to switch their food items according to fruit availability (Silva et al. 2002).

Network analyses are a promising way of analyzing whole communities of interacting organisms, such as plants and their pollinators or seed dispersers (Bascompte et al. 2003), marine cleaning symbiosis (Guimarães et al. 2007b), insects hosts and parasitoids (Memmott et al. 1994) and plants and their herbivores (Prado & Lewinsohn 2004). Particularly, studies on animal-plant mutualistic networks, mostly pollination and seed dispersal interactions, have demonstrated that these interactions are based on weak or asymmetric dependences between interacting partners (Jordano 1987; Bascompte et al. 2006). When applied to the whole community, this asymmetry of dependences generates a nested network, where interactions between generalist partners form the core of the web and specialists interact preferentially with generalists, rather than with other specialists (Bascompte et al. 2003; Guimarães *et al.* 2006, 2007b). The nested structure of mutualistic networks is considered as a key factor for maintaining the stability of the interacting community in relation to human-generated disturbances (Bascompte et al. 2006; Montoya et al. 2006), minimizing the extinction of interacting partners (Memmott et al. 2004).

Until now, in spite of the ubiquity of ants on most terrestrial ecosystems (Hölldobler & Wilson 1990) and their enrolment in a variety of mutualisms with plants (Rico-Gray & Oliveira 2007), no study has yet investigated how ant-plant networks' topology is influenced by human disturbances to natural ecosystems (but see Díaz-Castelazo et al. 2010 for a temporal approach on network changes). We present here the first comparison on how ant-diaspore networks are organized in two differing forest types, sites with well-preserved old-growth vegetation within a large forest block (hereafter, referred as continuous forests) and secondary-growth forest fragments (hereafter, fragmented forests). For this, we used an interaction data set of our own (see Chapter 2), containing information of a one-year survey of ant-diaspore interactions in eight forest sites within a fragmented landscape of the Brazilian Atlantic Forest, São Paulo State.

Nowadays, this biome exhibits only 13% of its original extent, subdivided in multiple remnants which greatly differ in size and conservation status (Ribeiro et al. 2009). Our aim here was to investigate if forest fragmentation/disturbance alters the topology of ant-diaspore networks. Due to the largely opportunistic nature of ground-dwelling ants' interaction with fleshy diaspores, our initial prediction was that, in spite of the already known alteration in species composition (Chapter 2), overall network structure would not be influenced by forest disturbance level. The standardized sampling effort applied in all eight areas reinforces that the observed differences reflect genuine divergences in ant-diaspore network topology among sites.

Methods

Study site

Our study site encompasses two neighboring municipalities (Piedade and Tapiraí; S23°59'49" - 23°57'48", W47°22'52" - 47°28'47"), located within the Atlantic Plateau of São Paulo State, Brazil. Altitudinal variation in this area is from 700 to 1100 m above sea level, and the native vegetation in this area is classified as lower montane rainforest (*sensu* Veloso et al. 1991). Monthly mean temperatures vary from 15° to 22° and rainfall is *ca.* 1800 mm yr⁻¹ (<http://www.ciiagro.sp.gov.br/ciiagroonline/>). Nearly 65% of the annual precipitation is concentrated during the rainy season (October to March). Sampling was performed in four forest fragments (FFs) and four continuous forest (CFs) sites. Fragments varied from 91 to 146 ha in size, and were surrounded mainly by herbaceous cropland and by pastures (Banks-Leite et al. 2010; AGD Bieber pers. observation). Vegetation in the fragments is almost completely constituted by secondary regrowth forest in various successional stages, from 20 to more than 100 years (Banks-Leite et al. 2010). The continuous forest sites were located inside the *Parque*

Estadual de Jurupará (PEJU), whose total area is more than 26,000 ha, mainly composed by old-regrowth secondary forests, in a late successional stage (Banks-Leite et al. 2010). The continuous forest sites are situated at least 1.5 km apart from each other, for guaranteeing spatial independency.

Interaction sampling

Here, we analyzed the network structure of eight communities of interacting ants and plant diaspores, already published elsewhere (see Chapter 2). The entire dataset comprises 998 ant-diaspore interactions, involving diaspores of 105 plant species and 66 ant species. Each of the eight forest sites were sampled once in a month during one year (June 2008 to Mai 2009), by walking through three 300-m transects (1.5 m wide) and recording all interactions between ants and fleshy diaspores. Among several characteristics used for describing the interaction, the following are important for this study: ant and diaspore species, diaspore ontogenetic state (whether ripe or not), seed state (whether predated or not) and the exact location of each record (in relation to the transect length). Detailed information on the sampling protocol may be found in Chapter 2.

Network analyses

For constructing our interaction webs, we first eliminated all interactions where the seed was absent or predated, because the nonexistence of viable seeds already mischaracterizes the existence of any benefit to the plant (see Silva et al. 2002 for a similar approach with avian

frugivores). Prior to constructing our interaction matrices, we eliminated some interactions that may be regarded as pseudo-replication. If more than one interaction of diaspore species *i* with ant species *j* were found in the same place and in the same month or in consecutive months, we considered them as one sole interaction, since these diaspores come from the same parental plant and most probably ant individuals found on diaspores belong to the same colony (a similar approach was adopted by Dworschak & Blüthgen 2010 for a bee-flower network). Each of the eight ant-diaspore webs was arranged in a matrix, where diaspore species were represented in rows and ant species in columns. Cells were filled with zeros when no interaction of ant species *j* with diaspore species *i* was recorded or with integer numbers representing the number of interactions of one ant species *j* with one diaspore *i*, no matter how many ant individuals were seen, and excluding the above mentioned cases (absent/predated seeds and pseudo-replications).

For characterizing each of the eight interaction webs, seven network-level metrics were calculated in R 2.14.0 (R development Core Team 2011) using the R-package Bipartite (Dormann et al. 2008, 2009), based on analyses found in Blüthgen et al. (2007, 2008) and Tylanakis et al. (2007). Connectance is a qualitative index and indicates the proportion of possible links actually observed in a web (Dunne et al. 2002). The weighted linkage density indicates the mean number of interactions per species (considering both trophic levels together). Generality indicates the effective mean number of host/prey species (in our case, diaspores) per consumer species (ants) and vulnerability indicates the effective mean number of consumer per host/prey. Here, the weighted counterparts of these three indices (introduced by Bersier et al. 2002) were used, since Tylanakis et al. (2007) argue that these are more conservative than the respective qualitative indices. Interaction evenness measures the uniformity of energy flows along different pathways (Tylanakis et al. 2007). The standardized interaction diversity (H_2')

indicates how much the observed distribution of interactions deviates from a random web generated only based on the abundance distributions of all interacting species. The H_2' index ranges from 0 (generalism) to 1 (complete specialization). Specialization asymmetry is obtained by subtracting the mean d' -value for the lower trophic level from that of the higher level, positive values indicate a higher specialization of the higher trophic level. This index is based on d' (a species-level measure of specialization related to H_2'), which is insensitive to the dimensions of the web.

Statistical analyses

We tested for differences between the two forest types (continuous *versus* fragmented forests) in relation to each of the seven cited network metrics. Moreover, we also tested if these two diverging forest types differed in relation to the mean number of ant species and plant species present in each network. For this, we performed nine t tests (Sokal & Rohlf 1995). If the two forest types presented different variances (according to Levene's test), a test with separate variance estimates was used (Sokal & Rohlf 1995). Since all nine tests were performed for testing a unique hypothesis, about differences in the network topology of ant-diaspore interactions between two forest types (see Rice 1989), we adopted a Bonferroni corrected α of 0.0056. Statistical analyses were performed in the software STATISTICA 8.0 (StatSoft 2007).

Results

Our entire dataset for the network analyses included 675 interactions, involving 98 plant species and 66 ant species. The number of plant species in each network varied from nine to 31 (Table 2). No plant species was registered in all forest sites. While the common treelet *Psychotria suterella*

(code P3) was registered in interaction with ants in five forest sites, most plant species were registered in a rather small number of forest sites (from one to three sites) (Figure 1; see also Appendix 1 for species names). The mean number of diaspore species per network at continuous forest sites was twice of that found at fragmented sites ($p < 0.004$; Table 1). Interacting ant species number ranged from 14 to 36 species. Contrary to the pattern observed for the lower trophic level, ant species composition varied less among sampling sites (Figure 1; see also Appendix 1 for species names). For example, the ant species *Pheidole* sp. 1 (code A29) was registered in all eight networks, being one of the most linked species in seven out of eight sites (exception is the fragment FF3). Overall, species of three ant genera, *Pheidole*, *Solenopsis* and *Wasmannia*, were ranked among the species with more plant partners. No significant difference regarding ant species number was found between the two forest types.

Moreover, fragments and continuous forest sites significantly differed from each other in relation to three out of seven calculated network metrics (Table 1). Observed generality values were significantly higher in the continuous forests than in the fragmented forests, indicating that the more disturbed sites present a decrease in the number of diaspore species used per ant species. Although observed interaction evenness values were very high for all sites (0.95 to 1), fragments presented a mean value significantly lower. Finally, the network index of specialization (H_2') ranged from 0.05 (in CF4) to 0.24 (in FF4), typical values for generalist networks. Analyzing the two forest types, fragmented forests presented more specialized networks than those of the more preserved forests.

Discussion

In this study, we adopted an approach based on quantitative network metrics for evaluating whether anthropogenic disturbances to forests influence ant-diaspore interactions. The number of interacting diaspore species and three (out of seven) network-level metrics significantly differed between the well-preserved continuous forest sites and the secondary-growth forest fragments: generality, interaction evenness, and H_2' . To the best of our knowledge, this is the second time that networks involving ants and fleshy diaspores were analyzed (see also Guimarães et al. 2007a) and the first time ever that ant-plant interaction networks were analyzed in the light of human-made disturbances.

Studies on ecological networks are likely to discuss the uncovered patterns as the result of a shared coevolutionary history among the interacting partners (e.g., Jordano et al. 2003; Rezende et al. 2007). In our case, this tendency is by no means accepted based on two main arguments. First of all, the type of interacting networks studied here is not formed by coevolved interacting species that depend on each other throughout their evolutionary history. The focused interaction is based on the opportunistically exploitation by ants of fallen fleshy diaspores that were somehow 'wasted' by their primary dispersers (i.e., birds and mammals; Rico-Gray & Oliveira 2007). However, in some cases, there are very strong arguments for the evolution of a diplochoric dispersal system (Vander Wall & Longland 2004) involving birds and ants (see Böhning-Gaese et al. 1999, Christianini & Oliveira 2010). Second, as our main aim was to compare networks in different sites applying the same sampling effort, our networks are far from complete, certainly missing links and species. Networks on which conclusions about the coevolutionary processes are made most commonly are based on datasets constructed throughout a rather long sampling period

(see Jordano 1987 and Bascompte et al. 2003). Recently, network analyses have been applied to analyze the community structure of human-disturbed areas (e.g., Albrecht et al. 2007; Tylianakis et al. 2007; Piazon et al. 2011). In these three cases and in the present work, sampling effort was strongly controlled for guaranteeing that metrics are ecologically meaningful (see Tylianakis et al. 2010).

In spite of the same sampling effort applied, ant-fruit networks in the more disturbed sites (see also Chapter 2) were constituted by a smaller number of diaspore species. Studies on other types of mutualisms (Silva et al. 2002; Díaz-Castelazo et al. 2010) as well as antagonistic interactions (Albrecht et al. 2007), which examined network changes in response to varying disturbances, have also identified a significant decrease in the number of species structuring the lower trophic level (i.e., plant species or insect host species) with increasing level of anthropogenic disturbances. In our case, differences in the lower trophic level species richness seem to be the main underlying factor behind the significant results found in the comparison of two network-level metrics (generality and H_2') between our two forest types (see also Albrecht et al. 2007; Díaz-Castelazo et al. 2010). On the other hand, the biological meaning of the third significant difference between fragments and continuous forests (regarding interaction evenness values) should be regarded with care. In spite of the observed statistical significance, all observed values for interaction evenness were extremely high (ranging from 0.95 to 1), thus the small difference between means may not have any biological significance. This contrasts, for example, with Tylianakis et al. (2007) results, where interaction evenness values of insect host-parasitoid networks strongly diverged between the two most distinct habitat types (rice plantations/pastures vs. forests).

All eight networks presented a high generalism (H_2' from 0.05 to 0.24), a feature shared by other animal-plant mutualistic interactions, such as networks involving flower visitors (Blüthgen et al. 2007; Dworschak & Blüthgen 2010), vertebrate frugivores (Blüthgen et al. 2007, Schleuning et al. 2011) and ants feeding on extra-floral nectar (Blüthgen et al. 2007). Notwithstanding the new approach used here, the generalist nature of ant interactions with fleshy diaspore was already recognized (Pizo et al. 2005; Rico-Gray & Oliveira 2007; see also Guimarães et al. 2007a, which adopt another network-level metric). Here, generalism was higher in the continuous forest areas. Since H_2' is not sensitive to network size (Blüthgen et al. 2007), this pattern may be attributed to changes in plant species composition and, thus, diaspore attractiveness. The relatively higher specialization of the four forest fragments may be identifiable by analyzing the interaction webs illustrated in Figure 1. In these areas, one plant species is highly linked to many ant species, with a considerable number of species being ‘specialized’ on it (just linked to it). In networks of fragments, these plant species should be regarded as a key-resource for fruit-feeding ants, but also as essential for maintaining the whole network structure. Furthermore, the observed decrease in network generality (*i.e.*, the effective mean number of diaspore species per species) observed in the fragments should be justified by a decrease in plant richness, together with the fact that ant species richness was not significantly affected. A shift in plant species composition, with fragmented forests presenting diaspores that are less attractive to ants (as suggested in the Chapter 2), may have intensified the observed decrease in generality scores.

As above discussed, changes in ant-fruit network metrics in response to forest fragmentation are attributed to the observed differences in plant species richness and composition among the studied sites (see Chapter 2). In spite of this, there was a high constancy in terms of

dominant ant genera in the eight studied webs. Apparently, in this type of facultative mutualistic network, large changes in the basal trophic level may not translate into changes at the higher trophic level, given that fruits are only a minor portion of the ants diet (Rico-Gray & Oliveira 2007). So, in moderately disturbed rainforests patches, such as those studied here, we may expect the maintenance of the role played by ants as seed-cleaners and short-distance dispersers (Passos & Oliveira 2002; Christianini & Oliveira 2009, 2010) of fleshy diaspores, even with profound changes in plant community composition. We strongly recommend future studies to evaluate how ant-diaspore networks behave along a stronger disturbance gradient (see for example Tylianakis et al. 2007). Moreover, the evaluation of the role of specific diaspore and ant species among distinct networks is also promising (see Schleuning et al. 2011 and Dormann 2011 for distinct approaches using species-level metrics).

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Table 1. Mean values and *t*-tests for seven network-level metrics, together with number of ant and plant species, calculated for eight ant-diaspore interaction networks. The study was conducted in two forest types, continuous forests (CFs, N=4) and fragmented forests (FFs, N=4) in a lower montane Atlantic forest landscape, São Paulo State, Brazil. Tests were considered significant (*p* followed by an asterisk) only if the associated *p* was less than our Bonferroni adjusted α of 0.0056.

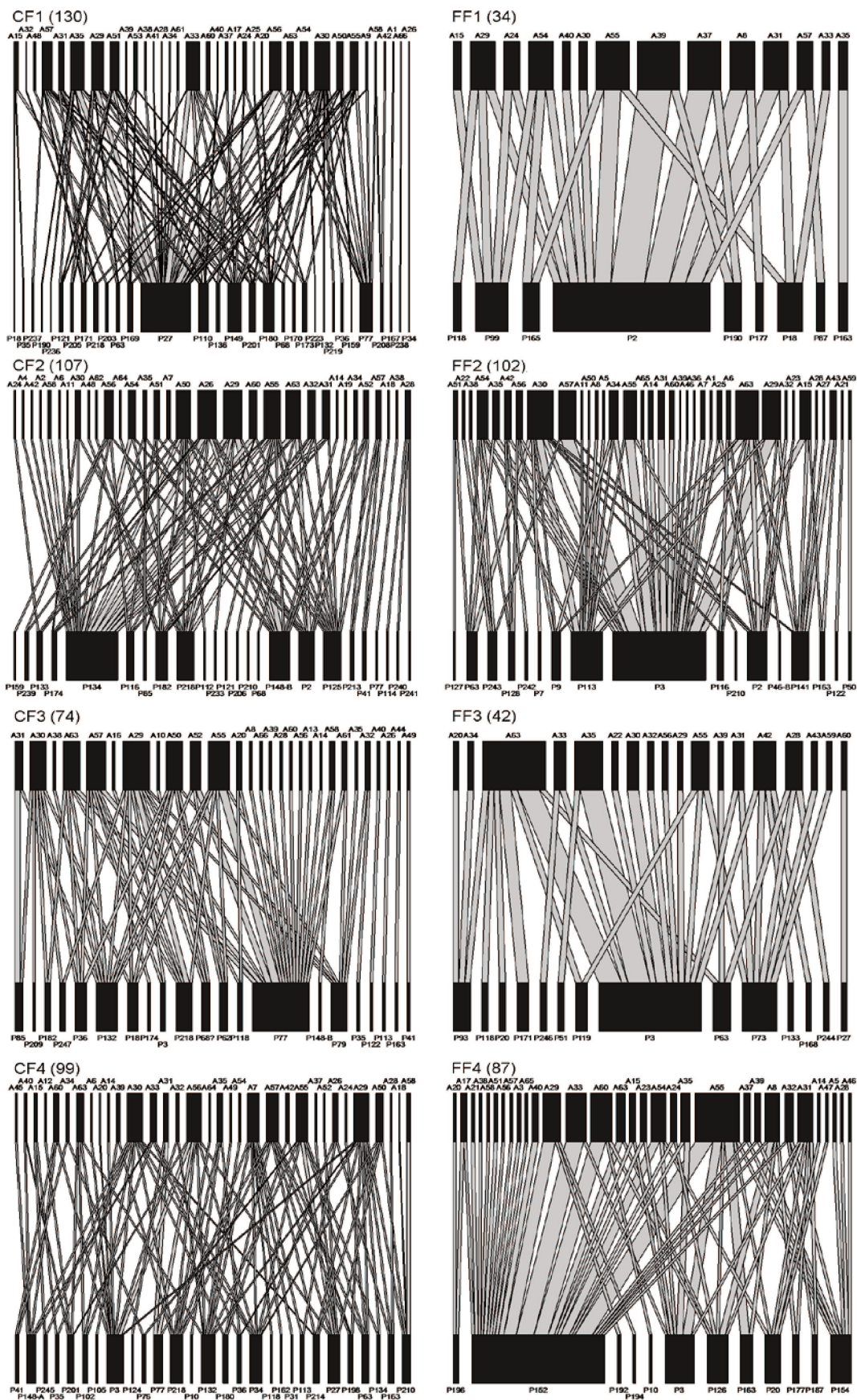
Network-level metrics	CFs (mean)	FFs (mean)	<i>t</i> -value	d.f.	<i>p</i>
Connectance	0.10676	0.15546	-2.4895	6	0.0472
Linkage density [§]	5.93119	5.60117	0.3627	4.8	0.7322
Generality	4.52403	2.70245	6.2595	6	0.0008*
Vulnerability	7.33836	8.49989	-0.6513	6	0.5390
Interaction evenness	0.98689	0.96098	4.5139	6	0.0040*
H2' index	0.09349	0.20773	-4.7925	6	0.0030*
Specialization asymmetry	-0.05049	-0.17753	2.3475	6	0.0573
Number of ant species [§]	32.00	24.75	1.3372	3.5	0.2620
Number of plant species	26.00	13.00	4.6950	6	0.0033*

[§]for these tests, a *t* test with separate variance estimates was used.

Legend to Figure

Figure 1. Graphic representation of eight ant-diaspore interaction webs surveyed in the Atlantic forest, Southeast Brazil. Networks for the continuous forest sites (CFs) are shown on the left, while fragmented forests networks (FFs) are on the right. Ant species are represented by the upper black bars and diaspore species are represented by the lower black bars. Bar width represents the relative importance (in terms of frequency) of each species in relation to the total number of interactions (which is given in parentheses after network code). The gray lines connect ant species with the diaspores on which they feed upon. Linkage width indicates the frequency of each interaction. Codes for interacting species can be found on the Appendices.

Figure 1.



Appendix 1: List of plant species present in the eight ant-diaspore networks studied in a fragmented Atlantic forest landscape, with their respective codes used in the graphic representation of interacting webs.

Family	Species	Plant codes
Acanthaceae	<i>Mendoncia velloziana</i> Mart.	P7
Annonaceae	<i>Annona cacans</i> Warm.	P93
Annonaceae	<i>Annona neosericea</i> H.Rainer	P102
Annonaceae	<i>Duguetia lanceolata</i> A.St.-Hil.	P169
Annonaceae	<i>Guatteria australis</i> A.St.-Hil	P50
Annonaceae	<i>Guatteria nigrescens</i> Mart.	P51
Araceae	<i>Anthurium scandens</i> (Aubl.) Engl. subsp. <i>scandens</i>	P247
Araceae	<i>Anthurium sellowianum</i> Kunth	P206
Araceae	<i>Monstera</i> sp.	P148-B
Araceae	<i>Philodendron corcovadense</i> Kunth	P148-A
Araceae	<i>Philodendron</i> sp.	P245
Burseraceae	<i>Protium heptaphyllum</i> (Aubl.) March.	P134
Cactaceae	<i>Lepismium warmingianum</i> (K.Schum.) Barthlott	P213
Celastraceae	<i>Maytenus aquifolium</i> Mart.	P149
Celastraceae	<i>Maytenus</i> sp.	P136
Celastraceae	<i>Salacia grandifolia</i> (Mart. ex Schult.) G.Don	P170
Celastraceae	<i>Tontelea miersii</i> (Peyr.) A.C.Sm.	P35
Chrysobalanaceae	<i>Couepia venosa</i> Prance	P218
Clusiaceae	<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	P203
Combretaceae	<i>Buchenavia</i> sp.	P154
Elaeocarpaceae	<i>Sloanea retusa</i> (Schum.) Uitt.	P208
Euphorbiaceae	<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	P210
Euphorbiaceae	undetermined 1	P243
Fabaceae	<i>Copaifera trapezifolia</i> Hayne	P79
Fabaceae	undetermined 5	P242
Humiriaceae	<i>Humiriastrum dentatum</i>	P105
Humiriaceae	<i>Vantanea compacta</i> (Schnizl.) Cuatrec.	P125
Lauraceae	<i>Cryptocaria mandioccana</i> Meisn.	P27
Lauraceae	<i>Endlicheria paniculata</i> (Spreng.) J. F. Macbr.	P165
Lauraceae	<i>Ocotea catharinensis</i> Mez	P182
Lauraceae	<i>Ocotea</i> sp.	P187
Lauraceae	<i>Persea willdenovii</i> Kosterm.	P192
Lauraceae	undetermined 2	P127
Lauraceae	undetermined 3	P168
Loganiaceae	<i>Strychnos nigricans</i> Progel	P63
Loranthaceae	<i>Psittacanthus robustus</i> (Mart.) Mart.	P41
Malpighiaceae	<i>Byrsonima ligustrifolia</i> A.Juss.	P9
Malvaceae	<i>Quararibea turbinata</i> (Sw.) Poir.	P110

Marcgraviaceae	<i>Marcgravia polyantha</i> Delpino	P133
Marcgraviaceae	<i>Schwartzia brasiliensis</i> (Choisy) Bedell ex Gir.-Cañas	P205
Melastomataceae	<i>Leandra dasytricha</i> (A. Gray) Cogn.	P73
Melastomataceae	<i>Miconia cabucu</i> Hoehne	P174
Melastomataceae	undetermined 6	P237
Meliaceae	<i>Cabrlea canjerana</i> (Vell.) Mart.	P190
Moraceae	<i>Ficus</i> cf. <i>luschnathiana</i> (Miq.) Miq.	P62
Moraceae	<i>Ficus</i> sp. 2	P68
Myristicaceae	<i>Virola bicuhyba</i> (Schott ex Spreng.) Warb.	P114
Myrsinaceae	<i>Ardisia martiana</i> Miq.	P219
Myrtaceae	<i>Campomanesia phaea</i> (O.Berg) Landrum	P34
Myrtaceae	<i>Campomanesia</i> sp.	P194
Myrtaceae	<i>Campomanesia xanthocarpa</i> (Mart.) O.Berg	P20
Myrtaceae	<i>Eugenia cerasiflora</i> Miq.	P132
Myrtaceae	<i>Eugenia</i> sp. 3	P233
Myrtaceae	<i>Eugenia</i> sp. 4	P198
Myrtaceae	<i>Eugenia subavenia</i> O.Berg	P116
Myrtaceae	<i>Marlierea excoriata</i> Mart.	P76
Myrtaceae	<i>Myrcia</i> (sect. <i>Gomidesia</i>) <i>hebeptala</i> DC.	P119
Myrtaceae	<i>Myrcia</i> (sect. <i>Marlierea</i>) sp. 5	P112
Myrtaceae	<i>Myrcia pubipetala</i> Miq.	P36
Myrtaceae	<i>Myrcia</i> sp. 6	P122
Myrtaceae	<i>Myrcia</i> sp. 7	P214
Myrtaceae	<i>Myrcia spectabilis</i> DC.	P159
Myrtaceae	<i>Myrcia splendens</i> (Sw.) DC.	P141
Myrtaceae	<i>Psidium guajava</i> L.	P209
Myrtaceae	<i>Psidium myrtoides</i> O.Berg	P85
Myrtaceae	<i>Syzigium</i> sp.	P87
Myrtaceae	undetermined 7	P246
Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	P163
Olacaceae	<i>Tetrastylidium grandiflorum</i> (Baill.) Sleumer	P77
Palmeae	<i>Lytocaryum hoehnei</i> (Burret) Toledo	P31
Palmeae	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	P99
Polygonaceae	<i>Coccoloba</i> sp.	P196
Quinaceae	<i>Quiina glaziovii</i> Engl.	P180
Rosaceae	<i>Prunus myrtifolia</i> (L.) Urb.	P2
Rubiaceae	<i>Cordia concolor</i> (Cham.) Kuntze	P126
Rubiaceae	<i>Hoffmania dusenii</i> Standl.	P223
Rubiaceae	<i>Posoqueria latifolia</i> (Rudge) Schult.	P46-B
Rubiaceae	<i>Psychotria suterella</i> Müll. Arg.	P3
Rubiaceae	<i>Rudgea jasminoides</i> (Cham.) Müll. Arg.	P118
Salicaceae	<i>Casearia decandra</i> Jacq.	P167
Salicaceae	<i>Casearia sylvestris</i> Sw.	P177
Sapindaceae	<i>Cupania oblongifolia</i> Mart.	P240
Sapindaceae	<i>Cupania vernalis</i> Cambess.	P152
Sapindaceae	<i>Paullinia seminuda</i> Radlk.	P162

Sapindaceae	<i>Paullinia trigonia</i> Vell.	P10
Sapotaceae	<i>Diploon cuspidatum</i> (Hoehne) Cronquist	P173
Sapotaceae	<i>Pouteria gardneriana</i> (A.DC.) Radlk.	P121
Solanaceae	<i>Solanum argenteum</i> Dunal	P124
Solanaceae	<i>Solanum cinnamomeum</i> Sendtn.	P113
Solanaceae	<i>Solanum pseudoquina</i> A.St.-Hil.	P18
Symplocaceae	<i>Symplocos laxiflora</i> Benth.	P201
Unknown Family	undetermined 10	P244
Unknown Family	undetermined 11	P128
Unknown Family	undetermined 12	P171
Unknown Family	undetermined 13	P236
Unknown Family	undetermined 14	P239
Unknown Family	undetermined 8	P238
Unknown Family	undetermined 9	P241

Appendix 2: List of ant species present in the eight ant-diaspore networks studied in a fragmented Atlantic forest landscape, with their respective codes used in the graphic representation of interacting webs.

Subfamily	Ant species	Ant code
Dolichoderinae	<i>Linepithema pulex</i> Wild	A1
Dolichoderinae	<i>Tapinoma melanocephalum</i> Fabricius	A2
Dolichoderinae	<i>Tapinoma</i> sp. 3	A3
Ectatomminae	<i>Ectatomma edentatum</i> Roger	A4
Ectatomminae	<i>Gnamptogenys striatula</i> Mayr	A6
Ectatomminae	<i>Gnamptogenys lucaris</i> Kempf	A5
Formicinae	<i>Brachymyrmex</i> sp. 1	A7
Formicinae	<i>Brachymyrmex</i> sp. 2	A8
Formicinae	<i>Brachymyrmex</i> sp. 3	A9
Formicinae	<i>Brachymyrmex</i> sp. 4	A10
Formicinae	<i>Brachymyrmex</i> sp. 7	A11
Formicinae	<i>Myrmelachista</i> sp. 1	A12
Formicinae	<i>Nylanderia</i> sp. 1	A13
Formicinae	<i>Nylanderia</i> sp. 2	A14
Heteroponerinae	<i>Heteroponera inermis</i> (Emery)	A15
Myrmicinae	<i>Acromyrmex</i> sp. 1	A17
Myrmicinae	<i>Acromyrmex rugosus</i> (F. Smith)	A16
Myrmicinae	<i>Carebara</i> sp. 1	A18
Myrmicinae	<i>Cyphomyrmex rimosus</i> (Spinola)	A20
Myrmicinae	<i>Cyphomyrmex</i> cf. <i>olitor</i> Forel	A19
Myrmicinae	<i>Megalomyrmex</i> sp. 1	A21
Myrmicinae	<i>Megalomyrmex</i> sp. 2	A22
Myrmicinae	<i>Octostruma rugifera</i> (Mayr)	A23
Myrmicinae	<i>Octostruma stenognatha</i> Brown & Kempf	A24
Myrmicinae	<i>Oxyepoecus</i> cf. <i>rosai</i> Albuquerque & Brandão	A25
Myrmicinae	<i>Pheidole</i> sp. 1	A29
Myrmicinae	<i>Pheidole</i> sp. 11	A36
Myrmicinae	<i>Pheidole</i> sp. 12	A37
Myrmicinae	<i>Pheidole</i> sp. 13	A38
Myrmicinae	<i>Pheidole</i> sp. 14	A39
Myrmicinae	<i>Pheidole</i> sp. 15	A40
Myrmicinae	<i>Pheidole</i> sp. 17	A41
Myrmicinae	<i>Pheidole</i> sp. 18	A42
Myrmicinae	<i>Pheidole nesiota</i> Wilson	A28
Myrmicinae	<i>Pheidole borgmeieri</i> Kempf	A26
Myrmicinae	<i>Pheidole</i> sp. 20	A43
Myrmicinae	<i>Pheidole</i> sp. 21	A44
Myrmicinae	<i>Pheidole gertrudae</i> Forel	A27
Myrmicinae	<i>Pheidole</i> sp. 23	A45
Myrmicinae	<i>Pheidole</i> sp. 24	A46
Myrmicinae	<i>Pheidole</i> sp. 25	A47

Myrmicinae	<i>Pheidole</i> sp. 3	A30
Myrmicinae	<i>Pheidole</i> sp. 4	A31
Myrmicinae	<i>Pheidole</i> sp. 5	A32
Myrmicinae	<i>Pheidole</i> sp. 6	A33
Myrmicinae	<i>Pheidole</i> sp. 7	A34
Myrmicinae	<i>Pheidole</i> sp. 8	A35
Myrmicinae	<i>Pyramica denticulata</i> (Mayr)	A48
Myrmicinae	<i>Pyramica</i> sp. 2	A49
Myrmicinae	<i>Solenopsis</i> sp. 4	A53
Myrmicinae	<i>Solenopsis</i> sp. 11	A58
Myrmicinae	<i>Solenopsis</i> sp. 12	A59
Myrmicinae	<i>Solenopsis</i> sp. 13	A60
Myrmicinae	<i>Solenopsis</i> sp. 14	A61
Myrmicinae	<i>Solenopsis</i> sp. 1	A50
Myrmicinae	<i>Solenopsis</i> sp. 2	A51
Myrmicinae	<i>Solenopsis</i> sp. 3	A52
Myrmicinae	<i>Solenopsis</i> sp. 5	A54
Myrmicinae	<i>Solenopsis</i> sp. 7	A55
Myrmicinae	<i>Solenopsis</i> sp. 8	A56
Myrmicinae	<i>Solenopsis</i> sp. 9	A57
Myrmicinae	<i>Strumigenys louisianae</i> Roger	A62
Myrmicinae	<i>Wasmannia affinis</i> Santschi	A63
Ponerinae	<i>Hypoponera</i> sp. 1	A64
Ponerinae	<i>Hypoponera</i> sp. 2	A65
Ponerinae	<i>Pachycondyla striata</i> Fr. Smith	A66

Capítulo 4:

Does forest fragmentation affect patterns of ant-fruit interaction? A study case in the Atlantic rainforest using synthetic fleshy fruits

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Running head: Ant-fruit interactions and forest fragmentation

Keywords: anthropogenic disturbances, ant-seed interaction, artificial fruits, dispersal distance, Formicidae, habitat fragmentation, myrmecochory, seed dispersal

Abstract: Ants frequently interact with non-myrmecochoric fleshy diaspores on the ground of tropical forests. While ants use the fleshy parts of the diaspores to complement their diets, diaspores can benefit from this interaction in two ways: ants often consume the fleshy part on the spot, enhancing the germination chances of cleaned seeds; and ants may carry the diaspore to the nest, offering a directed dispersal benefit. Given that forest fragmentation affects many attributes of the community such as species abundance, species composition, and interactions among species, we asked whether the Atlantic forest fragmentation affects the interaction between ants and fleshy diaspores. We controlled diaspore type and quantity by offering synthetic fruits (a plastic ‘seed’ covered by a lipid-rich ‘pulp’) in eight sites (four continuous forests and four fragments). We recorded the attracted ant species, ant behavior, and fruit removal distance. Fruits in continuous forest sites attracted a richer ant assemblage and a higher number of species per station than fragmented sites. The frequency of fruit-carrying ponerines (i.e., *Pachycondyla* and *Odontomachus*) was higher in the preserved sites, whereas large *Pheidole* spp. that were also able to remove fruits did not differ between forest types. Removal was higher in continuous forests than in fragments, whereas seed-cleaning behavior did not differ between the two habitats. Finally, fruit removal distance was greater in continuous than in fragmented forests. Our data suggest that fallen fruits interacting with ground-dwelling ants face different fates depending on whether the forest is continuous or fragmented. Our results expand the already pessimistic scenario faced by zoochoric fruits in fragments; potential ant-derived benefits to small diaspores may decrease in fragments, due to shifts in the composition of interacting ant species.

Introduction

Anthropogenic changes to natural ecosystems severely affect species richness, diversity, and composition of various taxonomic groups (Laurance & Bierregaard 1997; Mack et al. 2000; Hutchings & Reynolds 2004). Habitat fragmentation is frequently considered as one of the most pervasive man-induced disturbances (Wilcox & Murphy 1985; Laurance & Bierregaard 1997). Biodiversity loss through habitat fragmentation is directly caused by: loss of original habitat, reduction of the remaining area, increased isolation of the remnants and increased remnant area under edge effects (Turner 1996; Laurance & Bierregaard 1997; Fahrig 2003). Recently, Winfree et al. (2009) compared the effects of various anthropogenic disturbances on the richness and abundance of pollinating bees and concluded that habitat loss and fragmentation produced the most deleterious consequences to this economically important species group. Alterations in species diversity are frequently related to changes in ecologically important interactions such as pollination (Aizen & Feinsinger 1994), frugivory and seed dispersal (Cordeiro & Howe 2003), and seed predation (Donoso et al. 2003). For instance, in Chilean temperate forest large-seeded species are especially endangered due to the higher predation rates registered in small fragments and edge habitats compared to the interior of continuous forest (Donoso et al. 2003).

Losing mutualistic interactions involved in plant reproduction and recruitment may have drastic consequences for the ecosystem's functioning as a whole (Howe 1984; Terborgh et al. 2001). One such important interaction is seed dispersal by animals, mainly vertebrates, which is considered beneficial due to either one or more of the following consequences: escape of density-dependent mortality near the parent tree, colonization of new habitats, and directed dispersal to more suitable micro-habitats (see Janzen 1970; Howe & Smallwood 1982; Augspurger 1984). Due to habitat fragmentation, loss of forested areas and hunting, large vertebrate species

(including frugivores) have already disappeared from many small fragments in the tropical region (Redford 1992; Terborgh et al. 2001). On the long run, the continuing disappearance of vertebrate frugivores may lead to local extinction of large-seeded zoochoric species (Silva & Tabarelli 2000; Cordeiro & Howe 2003; Cramer et al. 2007). Although some studies argue that this impact may not be as deleterious as predicted (e.g., Chapman & Chapman 1995; Dausmann et al. 2008), case studies show that some plant species are negatively affected by the loss of specialist frugivore species (Cordeiro & Howe 2003; Cramer et al. 2007).

Although ca. 90% of the plants in Neotropical forests bear vertebrate-dispersed seeds (Frankie et al. 1974), interactions with some invertebrate groups may also benefit these diaspores (Andresen 2002; Rico-Gray & Oliveira 2007). In the last two decades several studies have documented that ground-dwelling ants can play a key role in the dispersal, germination and, to a lesser degree, establishment of non-myrmechochoric plant species (i.e., not adapted for dispersal by ants; see Oliveira et al. 1995; Leal & Oliveira 1998; Pizo & Oliveira 1998; Böhning-Gaese et al. 1999; Passos & Oliveira 2002, 2004; Dausmann et al. 2008). For instance, whereas seed cleaning by the attine ant *Mycocepurus goeldii* increases germination success in *Hymenaea courbaril* (Fabaceae) (Oliveira et al. 1995), directed seed dispersal by the ponerine ant *Odontomachus chelifer* to their nutrient-rich nests improves seedling establishment in *Guapira opposita* (Nyctaginaceae) (Passos & Oliveira 2004).

Compared to vertebrates, insect populations are considered less susceptible to the loss of forested area per se, due to their smaller body size, smaller home range, and lower trophic position (Didham et al. 1996; Gascon et al. 1999; see also Laurance & Bierregaard 1997). Moreover, while vertebrates are directly threatened by hunting (Redford 1992), the only direct threat imposed by humans to insects is pest control (e.g., leaf-cutter ants in cultivated areas;

Fowler et al. 1989). Thus, insects and their ecological interactions may be considered less threatened by habitat fragmentation. Indeed, Bruna et al. (2005) found no difference in species richness of myrmecophytes (plants with specialized organs that house ant colonies) and their associated ants between continuous forests and 25-year isolated fragments in the Brazilian Amazon. To date most studies investigating insect-plant interactions in tropical fragmented forests concern pollination systems (see Aizen & Feinsinger 1994; Lopes & Buzato 2007; Winfree et al. 2009). In one of the few studies dealing with forest fragmentation and ant-seed interactions, Guimarães and Cogni (2002) showed that non-myrmecochoric arillate seeds of *Cupania vernalis* (Sapindaceae) were more frequently attended by ants in the interior than at the border of a semi-deciduous forest in Brazil (see also Crist 2009 for a review on ant interactions' responses in a fragmented landscape).

In spite of the scarcity of studies on ant-fruit interactions in fragmented landscapes, there is evidence suggesting that ants may play a fundamental role in the dispersal of some plant species in human-modified environments due to an impoverishment of vertebrate assemblages (Rico-Gray & Oliveira 2007; Christianini & Oliveira 2009). The Brazilian Atlantic rainforest, a biodiversity hotspot, is considered one of the world's most threatened ecosystems (Mittermeier et al. 2005), and in the past few decades habitat loss and other human-associated disturbances have increased drastically (Morellato & Haddad 2000; Tabarelli et al. 2010). Currently, only 13% of the original forest remains interspersed in a highly fragmented landscape (Ribeiro et al. 2009). Here, we investigated how Atlantic forest fragmentation affects the interaction of ants with non-myrmecochoric fruits. More specifically, we asked if continuous forest sites and forest fragments differ in the following attributes: ant species richness; frequency of particular ant groups; frequency of fruit removal and of seed cleaning (i.e., pulp removal) by ants; and distance of fruit

removal by ants. We controlled diaspore type by offering synthetic fruits whose size and composition were compatible with many non-myrmechochoric species found in the study area (see chapter II).

Methods

Study sites

This study was carried out in the municipalities of Piedade and Tapiraí (23°50'S, 47°20'W) at São Paulo State, Southeast Brazil. Native vegetation is classified as lower montane rainforest (Veloso et al. 1991), with altitudes ranging from 680 to 1,030 m a.s.l. The climate is characterized by a warm rainy summer and by the absence of a true dry season during winter (April to September). Monthly mean temperatures vary from 15° to 22°C and rainfall is ca. 1,800 mm yr⁻¹ (<http://www.ciiagro.sp.gov.br/ciiagroonline/>). The rainy season is from October to March, accounting for nearly 65% of the annual rainfall (further details in Banks-Leite et al. 2010).

The landscape presents ca. 50% of remaining forest cover, divided in fragments of secondary forests of various sizes and at various succession stages, from 20 to more than 100 years old. We used four forest fragments (FF) ranging from 91 to 146 ha, which were mainly surrounded by herbaceous cropland, such as ginger and yam, and by pastures (Banks-Leite et al. 2010). Adjacent to this fragmented landscape, a continuous forest (CF) located at the Parque Estadual de Jurupará (PEJU) was selected as the control area. This continuous forest area consists of 26,000 ha of old-regrowth secondary forests in a late successional stage (Banks-Leite et al. 2010). Replications for the continuous forest were obtained by selecting four areas inside

PEJU at least 1.5 km apart from each other, which were considered as spatially independent (for a similar design see Banks-Leite et al. 2010).

Ant attraction to synthetic fruits

Synthetic fruits are commonly used to investigate how different fruit traits affect response patterns by frugivores (see Alves-Costa & Lopes 2001 and references therein). Given that ants show a high preference for lipid-rich fleshy fruit parts (Hughes et al. 1994; Pizo & Oliveira 2001), we used here a standardized synthetic lipid-rich fruit. The synthetic pulp was produced following the method developed by the Institute of Food Technology (*Instituto de Tecnologia de Alimentos* - ITAL, Campinas, Brazil), which consisted of cotton fat SC (75% of the entire weight), casein (7%), calcium carbonate (3%), fructose (4.8%), sucrose (0.5%), glucose (4.7%), and maltodextrin (5%) (see Raimundo et al. 2004). As “seeds” we used red plastic beads of ca. 0.06 g and ≈ 3 mm diameter. The synthetic fruit contained a single seed entirely covered by a whitish “pulp”, with a total weight of ca. 0.19 g and 8 mm diameter. Final size of synthetic fruits lied between the “small” to “medium” size categories (weight 0.05-0.90 g, diameter 5-13 mm) previously adopted by Pizo and Oliveira (2001) in experiments of fruit removal by ants in Atlantic forest.

Field work was carried out from 17 to 27 March 2010. Thirty sampling stations, 10 m apart from each other, were established along one transect in each of the eight sites (four fragmented and four continuous sites). In the continuous forest sites, transects were established at least 300 m from any forest edge to avoid confounding edge affects. In fragments, since edge effects normally come together with area reduction effects (Fahrig 2003), we kept a minimum

distance of only 50 m to the nearest edge. In each experimental station we deposited on the ground five synthetic fruits on a piece of white filter paper (4 x 4 cm) to facilitate visualization. Fruits were covered with a wire cage (1.5 cm mesh) to exclude vertebrate access (see Pizo & Oliveira 2001). The experiment was set at 10.00 h and ant attendance to fruits at sampling stations was checked at 11.00, 13.00 and 15.00 h. During each sampling, we recorded the attracted ant species and their behavior toward the fruits. Stations were re-checked the following day at 08.00 h to record the number of synthetic fruits cleaned (i.e., pulp removed) or removed by ants and, when applicable, the removal distance. Study sites were sampled on consecutive days, under similar weather conditions (sunny to partially cloudy days; no rainfall).

A synthetic fruit was considered removed if not found within a 30-cm radius of its original position (*sensu* Christianini & Oliveira 2009). Removal distances were measured only for fruits whose final locations were detected. Experimental fruits were considered cleaned when more than 75% of the synthetic pulp had been removed after 22 hours of exposure (from 10.00 h to 08.00 h of the next day).

Statistical Analyses

Our predictor variable for the following analyses was the type of forest (fragmented or continuous), but whenever appropriate we considered the eight studied areas as a random factor nested within forest type. Total ant species richness in the different forest sites was compared by estimating species richness using the Jackknife I procedure (see Krebs 1998) in the program EstimateS (Version 7.5, R. K. Colwell, <http://purl.oclc.org/estimates>). Based on the richness estimates and the standard errors, we calculated the corresponding 95% confidence intervals.

Nested analyses of variance (ANOVAs) were used to compare the number of ant species per sampling station, the number of fruits removed per station, and distances of fruit removal by ants. In cases we were unable to collect ant attendants (i.e., ants were too quick at removing the fruits), the sampling station was removed from the analysis of ant species richness per station (10 cases removed; $n=230$ stations). We applied a Chi-square test of independence (with Yates correction) to compare fragmented and continuous forest sites with respect to the frequency of stations with particular ant species groups, whose behavior to fruits could be classified as potentially beneficial (i.e., fruit dispersal or pulp cleaning). The same procedure was applied to compare the frequency of stations with removed and cleaned fruits. Statistical procedures follow Sokal and Rohlf (1995), and were performed using Statistica 7.1 (Statsoft 2005).

Results

The ant fauna attracted to fruits

A total of 51 ant species were attracted to the lipid-rich synthetic fruits (see Appendix 1). Although other invertebrates such as springtails, crickets, harvestmen, spiders and flies were also occasionally attracted to fruits, they neither discouraged approaching ants nor removed themselves any fruit. Ant richness ranged from 16 to 24 species per forest site (Appendix 1). Estimated species richness differed among the eight sampled areas; three continuous forest areas (CF1, CF2, CF3) and one fragment site (FF2) presented the highest estimated richness values, whereas fragment FF3 presented the lowest estimated number (Fig. 1).

The ant species most frequently recorded at sampling stations were *Pheidole* sp. 3 (in 51 out of 240 stations), *Solenopsis* sp. 7 (44 stations), *Pheidole* sp. 1 (39 stations), *Pachycondyla striata*

(36 stations), *Pheidole* sp. 8 (25 stations) and *Wasmannia affinis* (25 stations). *Pheidole* and *Solenopsis* presented the greatest number of species, although the frequency of particular species in these genera differed between fragmented and continuous forests (e.g., *Pheidole* sp. 3, *Solenopsis* sp. 1; see Appendix 1).

Patterns of ant attendance to fruits

The number of ant species per sampling station varied from none to six species. The mean number of species per station was higher in continuous than in fragmented forest sites ($F=4.89$, $p<0.03$; Fig. 2), with no nested effect of the site ($F=0.52$, $p=0.79$).

Ant species of two groups whose behaviors are considered to be potentially beneficial to seeds (i.e., fruit dispersal, or pulp cleaning) had contrasting occurrence patterns in the two forest types. The two large ponerines, *Odontomachus chelifer* and *Pachycondyla striata*, which act as seed dispersers, were more frequently recorded in continuous than in fragmented areas (29 vs. 12 stations; $\chi^2 = 4.5$, $df=1$, $p<0.04$). On the other hand, large species of *Pheidole* (≥ 3 mm length), capable of both cleaning and removing the fruits, were equally frequent in the two forest types (70 vs. 65 stations; $\chi^2 = 0.18$, $df=1$, $p=0.67$) (see Fig.3A; Appendix 1).

Ant behavior toward fruits

Patterns of fruit discovery and fruit use by ants also differed between the two forest types. Fruits were discovered faster in continuous than in fragmented sites – after one hour, a higher number of the stations had already been discovered by ants in continuous forest sites (29 to 30 attended

stations per site) compared to fragments (24 to 27 stations; $n=4$, $Z_{\text{adjusted}} = 2.37$; $p<0.02$). Continuous forest sites presented a higher proportion of stations with fruits removed by ants compared to fragmented sites ($\chi^2 = 64.29$, $p<0.0001$; Fig. 3B). Ant species frequently observed removing fruits were *P. striata*, *O. chelifer*, and a few large species of *Pheidole* (see Appendix 1). At the end of our experiment, the number of fruits removed by ants per sampling station was higher at continuous than at fragmented forest sites ($F=111.69$, $p<0.0001$), with a nested effect of the site ($F=7.96$, $p<0.0001$; Fig. 4A). Although the number of fruits removed varied among fragments, no difference was found within continuous forest sites (Fisher LSD post-hoc test; $p<0.05$; Fig. 4A).

Removal distances ranged from 0.1 to 165 cm ($N = 188$ synthetic fruits). Fruits were removed by ants to greater distances at the continuous forest sites (32.0 ± 4.0 cm; mean $\pm$ SE) than at fragmented sites (16.4 ± 4.0 cm; $F=18.53$, $p<0.0001$), with a significant nested effect of site ($F=3.21$, $p<0.006$; Fig. 4B). While removal distances were similar in continuous forest sites, they varied among fragments (Fisher LSD post-hoc test; $p<0.05$).

The proportion of sampling stations with seeds entirely cleaned did not differ between continuous and fragmented forests (31.37% in CFs vs. 22.45% in FFs; χ^2 (Yates correction)=0.98; $p=0.32$; Fig.3B). The ant species most commonly seen removing pulp from synthetic fruits were *Megalomyrmex iheringi*, *Solenopsis* sp. B. and a few *Pheidole* species. Most ant species, especially the small ones, were neither capable of displacing fruits nor of cleaning them entirely from the synthetic pulp (see Appendix 1).

Discussion

Our experiment using lipid-rich synthetic fruits revealed that habitat fragmentation has a strong impact on patterns of ant-fruit interaction in the Atlantic rainforest. Overall, continuous forest sites hosted a richer assemblage of ant species interacting with synthetic fruits than forest fragments. Additionally, undisturbed sites had higher numbers of ant species per sampling station, higher rates of fruit removal by ants, and greater distances of removal compared to fragmented sites. These results indicate that fallen fleshy fruits in forest fragments will face a lower probability of interacting with potentially beneficial seed-cleaning ants (Oliveira et al. 1995; Ohkawara & Akino 2005) and/or with fine-tuned ant dispersers (Böhning-Gaese et al. 1999; Passos & Oliveira 2002, 2004; Christianini & Oliveira 2010).

General patterns of ant attendance

Values of ant species richness at synthetic fruits (16 to 24 species per site) are quite similar to published results of ants attending fleshy diaspores in the Atlantic rainforest: 26 and 16 ant species were recorded at the lipid-rich arillate seeds of *Cabralea canjerana* (Meliaceae; Pizo & Oliveira 1998), and *Clusia criuva* (Clusiaceae; Passos & Oliveira 2002), respectively, and 11 species attended the protein-rich fruits of *Guapira opposita* (Nyctaginaceae; Passos & Oliveira 2004). Moreover, the spectrum of ant genera recorded at synthetic fruits is analogous to other Neotropical studies on the ant fauna interacting with fleshy diaspores of local floras (Pizo & Oliveira 2000; Passos & Oliveira 2003; Christianini et al. 2011), as well as to more general studies on ground-dwelling ant communities (Kaspari 1996; Vasconcelos et al. 2000; Ward 2000). For instance, the genera *Pheidole* and *Solenopsis*, which are frequently recorded

interacting with fleshy fruits (e.g., Pizo & Oliveira 2000; Passos & Oliveira 2003), are also among the most abundant and species-rich genera of tropical litter-dwelling ant communities (Wilson 1976; Kaspari 1996; Ward 2000). Indeed, the correspondence of the ant fauna consuming fleshy fruits with the overall ground-dwelling ant fauna confirms the generalized character of the interactions between ants and fallen fleshy diaspores (Rico-Gray & Oliveira 2007; see chapter 2).

The estimated species richness of ants at synthetic fruits was in general higher in continuous than in fragmented forest sites. This pattern is not surprising given that many studies in tropical and non-tropical ecosystems report lower species richness in the ground-dwelling ant fauna of anthropogenically disturbed areas than in control sites (Suarez et al. 1998; Carvalho & Vasconcelos 1999; Vasconcelos 1999; Gotelli & Arnett 2000; Brühl et al. 2003). In addition, because sampling stations with synthetic fruits were discovered faster and by a higher number of ant species in continuous forest sites than in fragments, we may predict that naturally fallen fruits in undisturbed forests will have increased chances of interacting with any ant species capable of providing beneficial services such as seed-cleaning (e.g., Oliveira et al. 1995; Leal & Oliveira 1998) and/or directed dispersal to a soil-enriched nest microsite (e.g., Böhning-Gaese et al. 1999, Passos & Oliveira 2004). A higher number of ant species per sampling point in less disturbed areas was previously recorded by other studies (Majer et al. 1997; Marinho et al. 2002; Brühl et al. 2003; Silva et al. 2011; but see also Vasconcelos 1999).

Frequency and behavior of particular ant groups

The detected differences between continuous and fragmented forests in the frequencies of particular ant groups may have direct consequences for fruit removal. A higher frequency of large ponerines (*Pachycondyla* and *Odontomachus*) in continuous forest likely explains the higher scores of fruit removal rates and removal distances at these habitat types. Large ponerines are especially important from a plant's standpoint because an individual forager is capable of transporting small- to medium-sized diaspores (weight < 1 g, sensu Pizo & Oliveira 2001) to relatively large distances (≈ 10 m) and thus act as effective seed dispersers (Horvitz & Beattie 1980; Pizo & Oliveira 1998; Passos & Oliveira 2002, 2004; Christianini & Oliveira 2010). The removal distances of synthetic fruits are similar to those reported for *Pachycondyla striata* and *Odontomachus chelifer* toward fleshy diaspores in Atlantic forest (Pizo & Oliveira 1998; Passos & Oliveira 2002, 2004). In fact dispersal values may be even higher since distances are frequently underestimated due to rapid disappearance of seed-carrying ponerines in the leaf litter (Horvitz & Beattie 1980; Pizo & Oliveira 1998; Passos & Oliveira 2002, 2004). However, the frequency of large-sized *Pheidole* species, which also removed fruits to considerable distances (see also Milesi & Lopez De Casenave 2004; Christianini & Oliveira 2010), did not differ between forest types. In fact, considering the prevalence of this genus in terms of abundance and species richness in most tropical litter-dwelling ant faunas (Wilson 1976), together with its omnivorous diet (Carroll & Janzen 1973), *Pheidole* spp. are not expected to be severely affected by forest fragmentation.

Conclusions and implications for conservation

Most ant species were too small to transport the synthetic fruits or even to entirely remove the pulp (Appendix 1), as also noted in other studies of ant-fruit interactions (e.g., Pizo & Oliveira 1998; Milesi & Lopez De Casenave 2004; Christianini & Oliveira 2010). Thus ant-derived benefits to seeds and/or seedlings may largely depend on the identity of the interacting ant species (Leal & Oliveira 1998; Passos & Oliveira 2002, 2004; Christianini & Oliveira 2010; see also Andersen & Morrison 1998 and Cuautle *et al.* 2005 for true myrmecochores). Because the frequencies of particularly beneficial ant groups such as seed-dispersing ponerines decreases from continuous to fragmented forests, we expect that potential benefits to plants (i.e., directed dispersal to nutrient-rich microsites) will also decrease with habitat disturbance levels. Indeed, Guimarães and Cogni (2002) showed that edge effects negatively affect the interaction between ants and arillate seeds of *Cupania vernalis* in a tropical semi-deciduous forest. Similarly, in Northern Australia, Andersen & Morrison (1998) also reported changes in ant behavior toward the true myrmecochore *Acacia holosericea* among savanna sites with different disturbance regimes. Although seed cleaning was higher in disturbed sites, mean dispersal distance in the two most disturbed areas was much smaller (Andersen & Morrison 1998).

Overall, our results on ants attending lipid-rich synthetic fruits parallel in many aspects the patterns previously described for ant-fruit interactions in the Atlantic forest (Pizo & Oliveira 2000; Passos & Oliveira 2003). The data indicate that forest fragmentation may affect the potentially mutualistic interaction between ground-dwelling ants and small-seeded fleshy fruits. Compared to continuous forest sites, fragmented areas exhibited a decrease in most of the investigated parameters (number of ant species per sampling station, dispersal distance and frequency of fruit removal), all of which may negatively influence ant-derived benefits to plants.

The potential decrease in the benefits resulting from this opportunistic ant-fruit interaction adds up to the already pessimistic scenario faced by vertebrate-dispersed plants (Pizo 1997; Silva & Tabarelli 2000; Cordeiro & Howe 2003), since large vertebrate frugivores are among the first to disappear from human-disturbed forests (Redford 1992; Estrada & Coates-Estrada 1996; Terborgh et al. 2001). We hope that our conclusions can be useful at predicting some of the ecological consequences of the ongoing fragmentation of the Brazilian Atlantic rainforest landscape.

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Legends to Figures

Figure 1. Mean estimated ant species richness based on the Jackknife I procedure ($\pm$ 95% confidence intervals) for each of eight studied sites in a fragmented landscape of the Atlantic forest, southeast Brazil, where lipid-rich synthetic fruits were exposed to ant visitation in 30 sampling stations per site. Ant samplings were carried out in four continuous forest sites (CF) and in four forest fragments (FF).

Figure 2. Number of ant species per sampling station baited with synthetic fruits in continuous and fragmented sites (N=30 stations per site) in the Atlantic forest, southeast Brazil. Central lines and borders in each box-plot indicate the mean value and the mean $\pm$ its standard error; whiskers delimit the range of the 95% confidence interval.

Figure 3. (A) Frequency of occurrence at synthetic fruits of particular ant groups (i.e., large ponerines and large *Pheidole* spp.) whose behavior is considered as potentially beneficial to seeds, and (B) frequency of sampling stations whose synthetic fruits were either removed or cleaned (i.e., pulp removed) by ants during a 22-hour experiment in continuous (white bars) and fragmented forest sites (gray bars) in the Atlantic forest, southeast Brazil. Asterisks indicate significant differences ($p < 0.05$) between forest types.

Figure 4. (A) Number of synthetic fruits removed per sampling station and (B) mean distance of fruit removal in continuous (CF; four sites) and fragmented sites (FF; four sites), in a fragmented landscape of the Atlantic forest, southeast Brazil. Central lines and borders in each box-plot indicate the mean value and the mean $\pm$ its standard error; whiskers delimit the range of the 95% confidence interval. Different letters above boxes indicate statistically significant differences

(Fisher LSD post-hoc test; $p < 0.05$) among forest sites. As in each site, a different number of fruits were removed by ants, the number of fruits is given below each box.

Figure 1

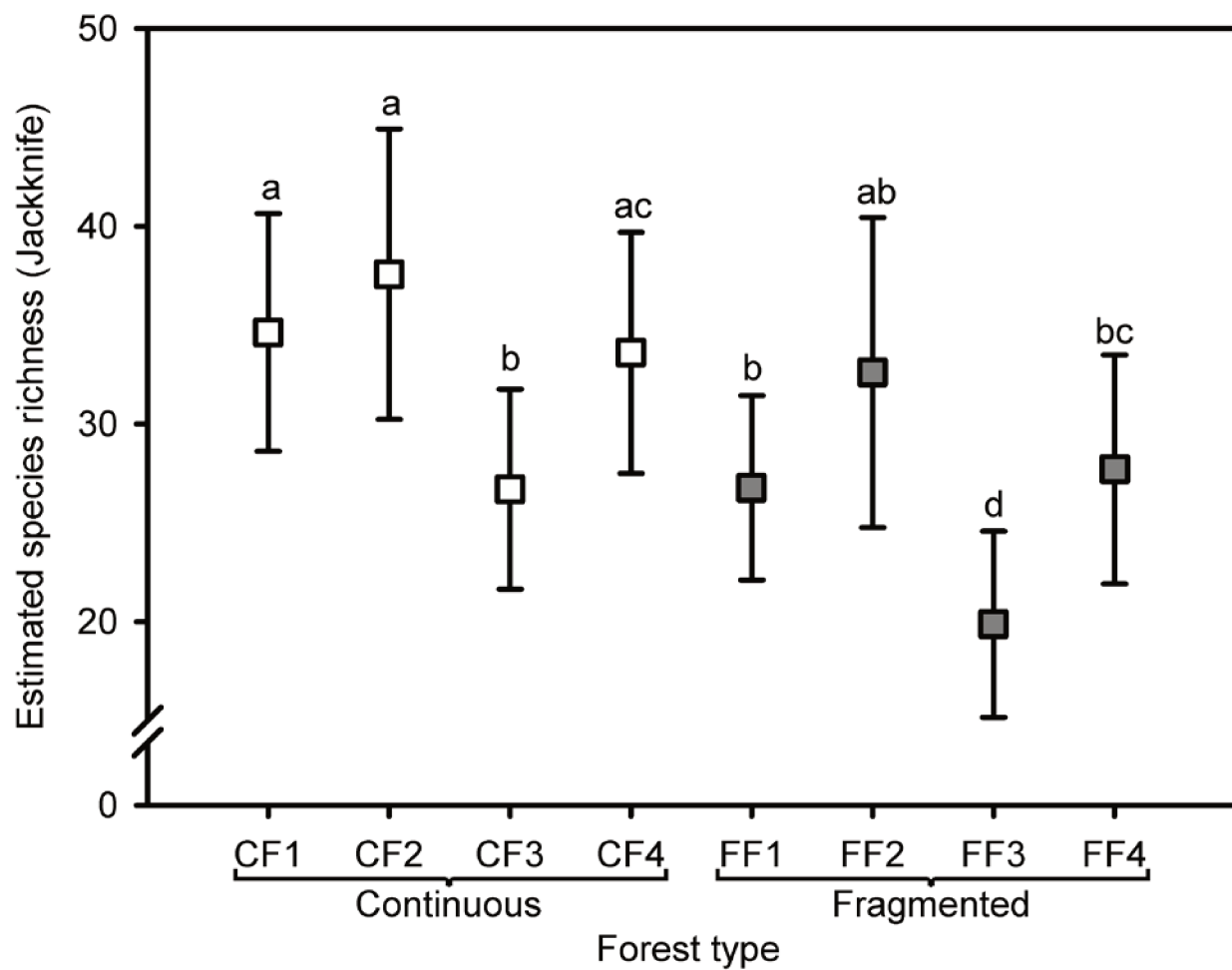


Figure 2

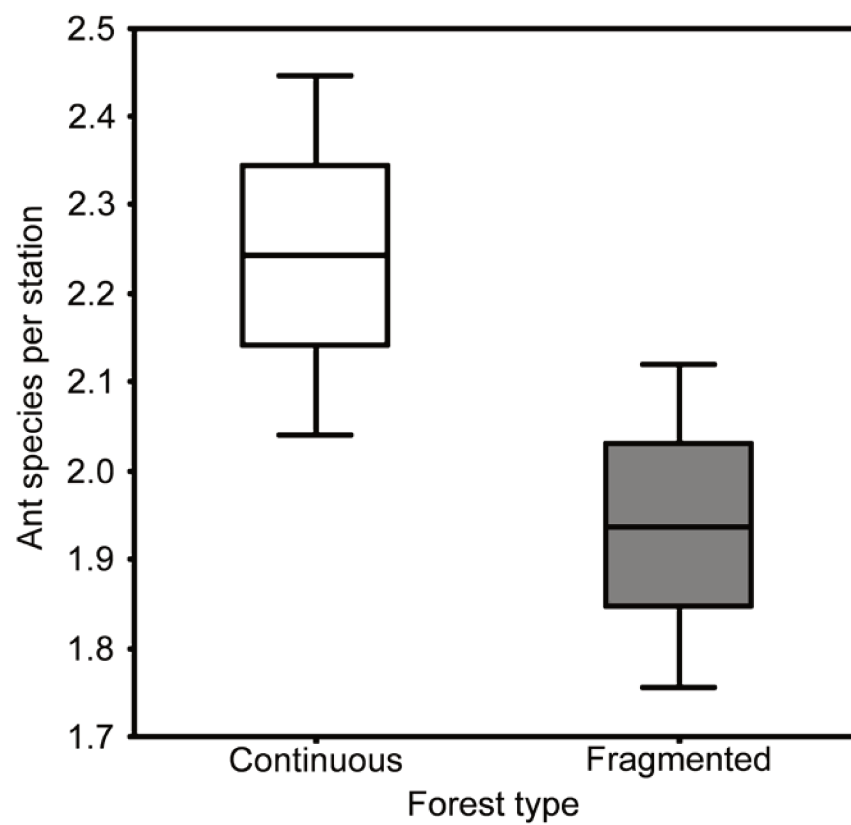


Figure 3

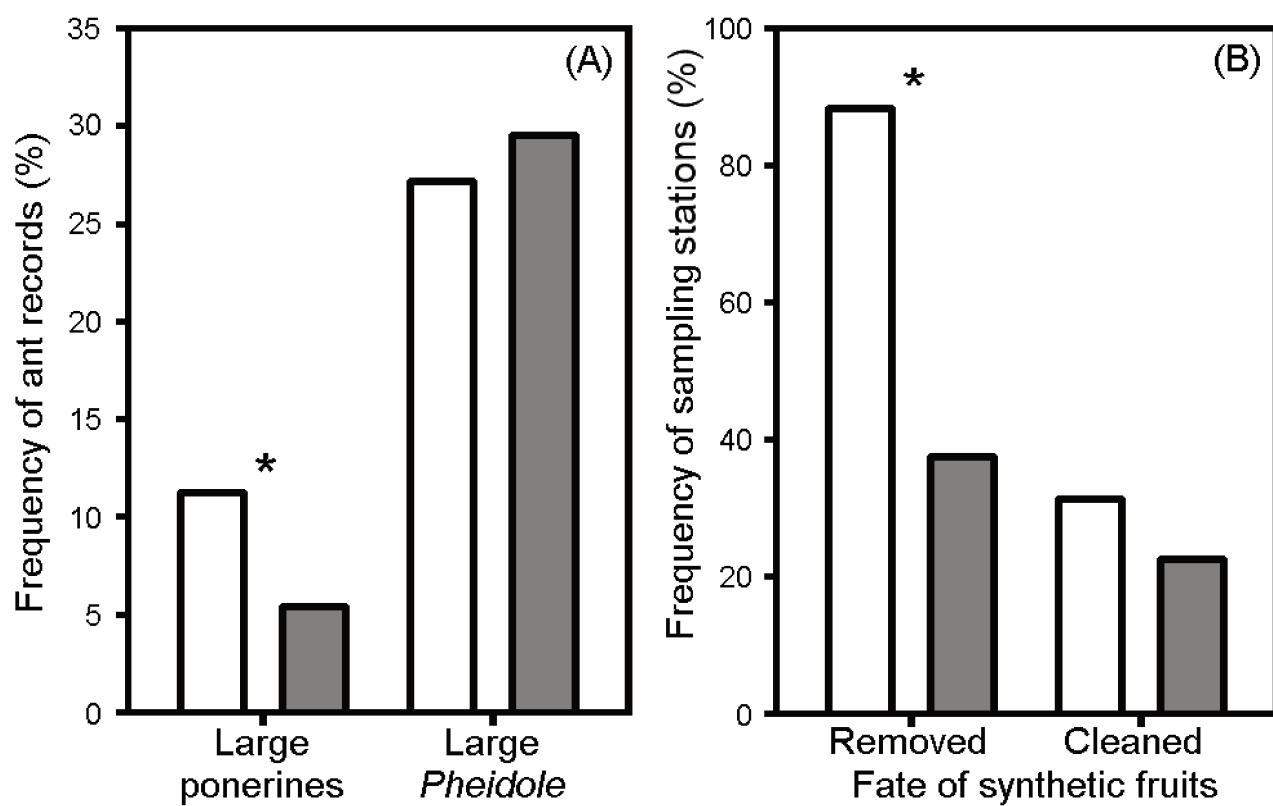
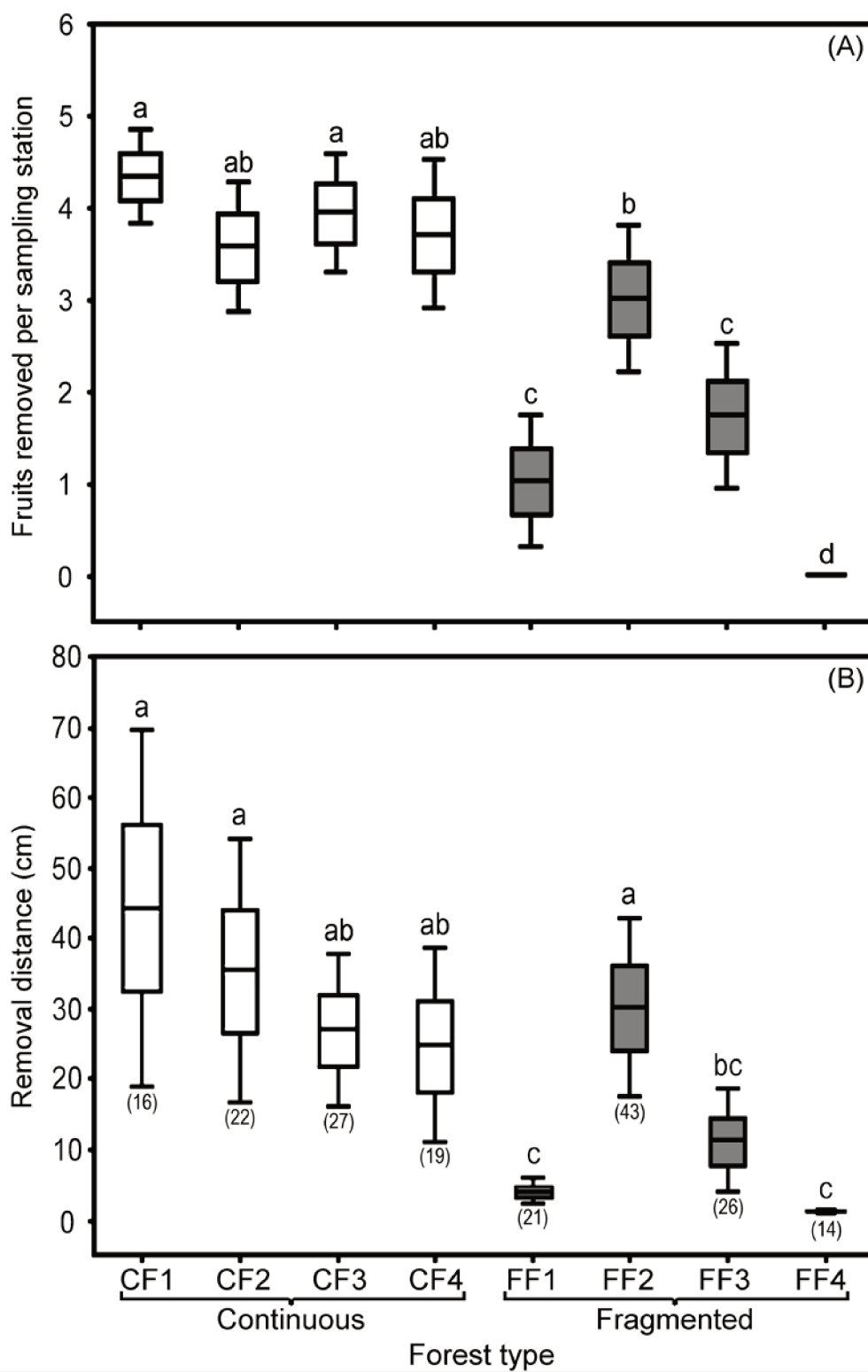


Figure 4



Appendix 1. Ant species attending lipid-rich synthetic fruits in four sites within a continuous forest area (CFs) and in four forest fragments (FFs) in the Atlantic Forest, São Paulo State, southeast Brazil. Values indicate the number of stations per site where each ant species was captured (N = 30 stations in each of the eight sites).

Species	Ant Behavior [#]	CF1	CF2	CF3	CF4	CFs total	FF1	FF2	FF3	FF4	FFs total	Total Sum
Dolichoderinae												
<i>Linepithema leucomelas</i>	RPC	0	0	0	0	0	2	0	0	0	2	2
<i>Linepithema pulex</i>	RPC	0	0	0	0	0	0	0	11	0	11	11
<i>Linepithema</i> sp. 4	RPC	0	0	0	0	0	1	0	0	0	1	1
Ectatomminae												
<i>Ectatomma edentatum</i>	RC, TR	0	1	0	0	1	0	0	0	0	0	1
<i>Gnamptogenys striatula</i>	RPC, TR	1	2	1	0	4	0	0	4	0	4	8
Formicinae												
<i>Brachymyrmex</i> sp. 1	RR, RC	0	1	0	1	2	0	0	0	0	0	2
<i>Brachymyrmex</i> sp. 2	RPC	0	1	0	0	1	1	0	0	0	1	2
<i>Brachymyrmex</i> sp. 3	RPC	0	0	0	0	0	1	0	0	0	1	1
<i>Brachymyrmex</i> sp. 4	RPC, TR	0	0	0	1	1	0	0	0	1	1	2

<i>Nylanderia</i> sp. C	RPC	1	0	0	0	1	3	1	0	2	6	7
Heteroponerinae												
<i>Heteroponera inermis</i>	RR	0	0	0	0	0	0	1	0	0	1	1
Myrmicinae												
<i>Acromyrmex rugosus</i>	R	1	0	0	0	1	0	0	0	0	0	1
<i>Apterostigma</i> sp. 1	RPC?	0	1	0	0	1	0	0	0	0	0	1
<i>Megalomyrmex iheringi</i>	RR, RC	0	0	0	0	0	2	4	0	7	13	13
<i>Oxyepoecus punctifrons</i>	RPC?	0	1	0	0	1	0	0	0	0	0	1
<i>Pheidole</i> sp. 1	RPC	3	9	11	7	30	1	3	0	5	9	39
<i>Pheidole</i> sp. 2	RC, TR	2	1	0	1	4	0	0	0	0	0	4
<i>Pheidole</i> sp. 3*	RPC, TR	9	8	11	13	41	0	6	4	0	10	51
<i>Pheidole</i> sp. 4	RPC	1	3	0	0	4	7	0	0	9	16	20
<i>Pheidole</i> sp. 5	RPC, TR	0	3	4	1	8	0	1	1	2	4	12
<i>Pheidole</i> sp. 6	RPC, TR	6	0	0	4	10	0	0	0	2	2	12
<i>Pheidole</i> sp. 7*	RC, RR	1	1	1	2	5	0	0	0	0	0	5
<i>Pheidole</i> sp. 8*	RC, RR	5	4	4	3	16	0	1	7	1	9	25
<i>Pheidole</i> sp. 11	RPC	0	0	0	0	0	0	1	0	0	1	1

<i>Pheidole</i> sp. 12*	RPC	0	0	1	0	1	6	0	2	8	16	17
<i>Pheidole</i> sp. 14	RPC	1	1	2	0	4	4	2	1	1	8	12
<i>Pheidole</i> sp. 15	RPC	0	0	0	0	0	0	0	0	1	1	1
<i>Pheidole</i> sp. 18*	RC, TR	2	0	0	0	2	1	1	8	1	11	13
<i>Pheidole</i> sp. 19*	RC, RR	2	0	1	1	4	1	0	2	4	7	11
<i>Pheidole</i> sp. 20*	RR	0	0	0	1	1	0	3	3	0	6	7
<i>Pheidole</i> sp. 24*	RPC	0	0	0	0	0	4	0	0	1	5	5
<i>Pheidole</i> sp. 27*	RR	1	1	0	1	3	0	1	0	0	1	4
<i>Pheidole</i> sp. 28	RPC	0	0	0	0	0	2	0	0	0	2	2
<i>Pheidole</i> sp. 29	RPC	1	0	0	0	1	0	0	0	0	0	1
<i>Solenopsis</i> sp. 1	RPC	5	7	1	1	14	0	0	0	0	0	14
<i>Solenopsis</i> sp. 2	RPC	4	0	0	1	5	0	0	0	0	0	5
<i>Solenopsis</i> sp. 3	RPC	0	2	0	0	2	0	0	0	1	1	3
<i>Solenopsis</i> sp. 5	RPC	0	0	1	4	5	7	2	2	0	11	16
<i>Solenopsis</i> sp. 7	RPC	6	5	4	3	18	5	1	8	12	26	44
<i>Solenopsis</i> sp. 8	RPC	1	1	1	4	7	1	2	0	1	4	11
<i>Solenopsis</i> sp. 9	RPC	1	2	0	1	4	2	1	1	0	4	8

<i>Solenopsis</i> sp. 10	RPC?	0	0	0	1	1	0	0	0	0	0	1
<i>Solenopsis</i> sp. 11	RC, RR	1	0	2	1	4	0	0	0	0	0	4
<i>Solenopsis</i> sp. 12	RPC	0	0	1	0	1	0	0	0	0	0	1
<i>Solenopsis</i> sp. 13	RPC	0	1	0	0	1	2	1	1	3	7	8
<i>Wasmannia affinis</i>	RPC	2	6	6	4	18	0	3	3	1	7	25
Ponerinae												
<i>Hypoponera</i> sp. 1	RPC	0	0	1	0	1	0	1	0	0	1	2
<i>Hypoponera</i> sp. 3	RPC	0	1	0	0	1	0	0	0	0	0	1
<i>Hypoponera</i> sp. 4	RPC	0	0	0	0	0	0	1	0	0	1	1
<i>Odontomachus chelifer</i>	R	3	2	0	0	5	0	0	0	0	0	5
<i>Pachycondyla striata</i>	R	6	3	5	10	24	2	8	2	0	12	36
Species richness		24	24	18	22	40	20	21	16	19	36	51

**Pheidole* spp. considered as large (worker length ≥ 3 mm).

#Key to ant behavior: R – individual worker remove fruit (> 5 cm); RR – recruited workers (> 5 ants) remove fruit (> 5cm); TR – try to remove fruit (< 5 cm); RC – recruited workers (> 5 ants) clean the seed by continual removal of pulp on spot; RPC – recruited workers remove the pulp partially (max. 25%) on spot, normally subordinate species.

Capítulo 5:

Attractiveness of Fallen Fleshy Fruits to Ants Increases with Previous Handling by Frugivores

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Running title: Ant-fruit interactions depend on frugivores

Key words: ant-fruit interactions, Atlantic forest, forest fragmentation, frugivory, *Psychotria suterella*, Rubiaceae, seed cleaning, seed dispersal, vertebrate loss.

Abstract: Ant-fruit interactions are prominent on the ground of tropical forests. These interactions are considered beneficial to seeds if ants clean the seed (which may prevent fungal contamination and/or increase germination success), or act as secondary fine-tuned dispersers (depositing the seed in nearby nutrient-enriched nest sites). Benefits to seeds, however, may be constrained by ant access to fruits. Here, we experimentally tested whether ant access to fallen fleshy fruits of *Psychotria suterella* (Rubiaceae) can be affected by previous handling (including ingestion) by birds. We found that mandibulated and feces-embedded fruits are more prone to interact with ants compared to entirely intact fruits, attracting a richer ant assemblage. Ongoing vertebrate loss may affect this highly opportunistic and potentially mutualistic interaction.

Introduction

Generally, when talking about ants interacting with fruits, we think on seeds with a lipid-rich appendage known as elaiosome. In fact, this is the typical syndrome for the ant-dispersed seeds of true myrmecochores (Beattie 1985). Nonetheless ants are commonly recorded interacting with non-myrmecochoric seeds/fruits (hereafter diaspores), which do not present adaptations to dispersal by ants (Vander Wall & Longland 2004; Rico-Gray & Oliveira 2007). In such cases ants usually act as secondary dispersers of vertebrate-dispersed diaspores (Böhning-Gaese *et al.* 1999; Christianini & Oliveira 2010). In fact many ant species are known to interact with a broad assemblage of fleshy diaspores found on the ground of tropical rainforests and savannas (Leal & Oliveira 1998; Pizo & Oliveira 2000; Passos & Oliveira 2003; Christianini *et al.* 2007). Upon reaching the ground such plant diaspores are found by the ants in either one of three different conditions: completely intact, mandibulated/manipulated by vertebrates, or embedded within vertebrate feces (Vander Wall & Longland 2004; Rico-Gray & Oliveira 2007).

In a two-year survey of ant-fruit interactions in the Brazilian Atlantic forest, Pizo and Oliveira (2000) found that some diaspore species were exploited by ants only if previously crushed by vertebrates, thus making the fleshy part accessible [*e.g.*, *Astrocaryum aculeatissimum* (Arecaceae), *Garcinia gardneriana* (Clusiaceae), *Abuta selloana* (Menispermaceae), *Posoqueria latifolia* (Rubiaceae)]. However, not only hard-coated fruits may render impenetrable to invertebrates. For instance, some studies have shown that previous handling by vertebrates of relatively soft-coated fruits may facilitate oviposition by invertebrate seed predators such as fruit flies and bruchid beetles (see Sallabanks & Courtney 1992; Silvius & Fragoso 2002; and included references). Contrary to fruit flies and bruchids, ants in tropical forests are commonly regarded as seed mutualists by acting as secondary fine-tuned dispersers (*i.e.*, seeds benefit by deposition in

nearby nutrient-enriched nest sites; Böhning-Gaese *et al.* 1999; Passos & Oliveira 2002), or by cleaning the seed and, thus, preventing fungal contamination (Oliveira *et al.* 1995; Leal & Oliveira 1998; but, for seed predation by ants in tropical rainforests, see Levey & Byrne 1993 and Rico-Gray & Oliveira 2007). Attraction of ants to fallen fleshy diaspores is known to vary with attributes of both ant and diaspore species (Pizo & Oliveira 2000, 2001). Given that fleshy diaspores reach the ground through different modes (see above), such variation may also likely affect their attractiveness to ants as well as possible benefits resulting from this interaction.

Here, we experimentally examine whether ant access to fleshy diaspores can be affected by previous handling (including ingestion) by frugivores. We hypothesized that ant attendance to fleshy fruits will differ in accordance with their state on the forest floor. Specifically, fruits previously mandibulated by vertebrate frugivores or within their feces should be more prone to interact with ants compared to entirely intact fruits. To test this hypothesis we used fruits of the primarily bird-dispersed species *Psychotria suterella* Müll. Arg. (Rubiaceae). We discuss our findings in the context of habitat fragmentation and current loss of vertebrate frugivores.

Methods

Study site

Field work was carried out in an Atlantic Forest remnant at Tapiraí (23°54'44''S; 47°28'47''W), São Paulo State, SE Brazil. The native vegetation in the region is classified as lower montane rainforest (Veloso *et al.* 1991), and the study site comprises 91 ha of second-growth forest. Monthly mean temperatures vary from 15 to 22°C (mean annual temperature of 19°C) and annual rainfall is near 1800 mm (Banks-Leite *et al.* 2010).

Diaspore species

Diaspores of *Psychotria* spp. are commonly dispersed by birds in tropical habitats (Snow 1981), including the Atlantic rainforest (Galetti *et al.* 2000), and ground-dwelling ants frequently exploit fallen fruits of *Psychotria* in tropical savannas and forests (Leal & Oliveira 1998; Pizo & Oliveira 2000; Passos & Oliveira 2003). Additionally, pulp removal by attine ants has been shown to improve seed germination of *P. stachyoides* in the Brazilian Cerrado savanna (Leal & Oliveira 1998). The species *P. suterella* is a common understory treelet in the study area and its fruits are frequently exploited by ants on the forest floor (A. G. D. Bieber, unpubl. data). Fruits are medium-sized purple drupes (length = 11 mm, width = 13 mm, weight = 0.8 g) containing two seeds (4 mm, 3 mm, < 0.1 g; Galetti *et al.* 2011).

Experimental design

Intact fruits of *P. suterella* were collected on the ground or directly from trees. These fruits were randomly submitted to distinct procedures in order to simulate the three most common conditions in which fruits are encountered on the forest ground: intact, opened by vertebrates (manipulated or mandibulated), or embedded in vertebrate feces. “Intact” fruits presented no marks or holes of any kind, and received no additional treatment. “Mandibulated” fruits were produced by making an opening with a forceps to simulate the mark left by the beak of a bird. We mimicked fruit passage through bird guts (“feces-embedded” fruits) by smashing an intact fruit and mixing it with fresh feces of curassows (*Crax* spp. and *Mitu* spp.; Cracidae), large birds known as mainly fruit- and seed-eaters, and which also include many Rubiaceae species in their diet (Muñoz & Kattan 2007). Bird feces were obtained from captive individuals fed with a fruit-based diet (mainly banana, apple, and papaya; no seeds) at a local private Zoo.

Experimental fruits were placed on the leaf litter at stations 5 m apart along one transect in the forest. The distance of 5 m is considered adequate to assure the independence of sampling units on the Atlantic forest floor (Pizo & Oliveira 2000). At each station, three fruits submitted each to one of the above treatments were placed separately on pieces of filter paper (4 x 4 cm), about 1 m from one another. The relative location of experimental fruits was switched across stations to avoid any visitation bias due to transect proximity. The proximity of stations to fruiting trees was not avoided, given that *P. suterella* is very abundant in the understory. Fallen fruits found near the stations, however, were removed before the experiment. After setting the fruits, the attracted ants and their behavior were recorded in four scan samples taken at 1-hour intervals from 1000 to 1300 h. Samplings were performed in two consecutive days under similar weather conditions (February 2009); 20 stations were established each day. On the second day, to avoid spatial pseudo-replication, the stations were established in a different part of the transect. Ant voucher specimens are deposited in the Museu de Zoologia "Adão José Cardoso" at the Universidade de Estadual de Campinas.

Data from scan samplings of ant visitation to stations were pooled to evaluate differential attractiveness among fruit treatments. The number of stations with ant attendants at each treatment was compared with a *G* test of independence, applying Williams' correction (Sokal & Rohlf 1995). Ant species per station (i.e, species density) in each fruit treatment was compared through an one-way ANOVA, followed by Tukey post-hoc tests (Sokal & Rohlf 1995). Stations in which none of the three fruits were discovered by ants (four out of 40 cases) were removed from the analyses. Statistical tests were performed with the software Statistica 7.1 (Statsoft 2005). Total ant species richness attracted to the different treatments was compared by estimating the species richness using the Jackknife I procedure (see Krebs 1998) in the program EstimateS

(Version 7.5, R. K. Colwell, <http://purl.oclc.org/estimates>). Based on the richness estimates and the standard errors given, we calculated the corresponding 95% confidence intervals. Checking if the confidence intervals of any two means do not overlap is one of the graphical procedures suggested to infer significant differences (Andrews et al. 1980).

Results

Overall, 23 ant species were attracted to the fruits of *Psychotria suterella* (Appendix 1). The myrmicine species *Pheidole* sp. 3 and *Wasmannia affinis* were the most frequently registered visiting the fruit stations. Eleven species were seen just once. Most ant species exploited the fruits on spot. The only ant species seen removing seeds from feces was the leaf-cutter *Acromyrmex* sp. 1, which also removed fecal parts. Ants exploiting “mandibulated” fruits collected mostly liquids from the already exposed fruit part (63% of the 38 records).

As predicted, there is a significant difference among fruit treatments in the number of stations with ant attendants. “Feces-embedded” and “mandibulated” fruits presented increased frequencies of ant visitation (26 and 23 stations, respectively) compared to “intact” fruits (12 stations) ($G_{adj} = 10.93$, $df=2$, $P < 0.005$; see Appendix 1). In addition, species density at “intact” fruits was significantly lower than in the other two fruit treatments ($F=8.32$, $df=2$; $p < 0.0005$; Fig. 1). Moreover, “feces-embedded” fruits attracted a richer assemblage of ant species compared to the other experimental fruit categories (Fig. 2).

Discussion

To our knowledge this is the first study using comparative data to show that previous handling (including ingestion) by vertebrate frugivores increases visitation by a potentially beneficial invertebrate group, *i.e.* ground-dwelling ants. Previous work on attraction of ants to fruits have never simultaneously compared ant visitation to the three fruit conditions considered here. Instead, these studies either used fruits in only one condition (*e.g.*, feces-embedded seeds in Levey & Byrne 1993, Pizo & Oliveira 1999; intact fruits in Leal & Oliveira 1998, Pizo & Oliveira 2001), or compared fruit attractiveness between two conditions (cleaned seeds *vs.* feces-embedded seeds in Roberts & Heithaus 1986, Martínez-Mota et al. 2004; fruit fragments *vs.* feces-embedded seeds in Roberts & Heithaus 1986).

Somewhat different results were reported by Roberts & Heithaus (1986) and Martínez-Mota et al. (2004). In their studies, feces-embedded seeds of two Neotropical *Ficus* species were less removed by ants compared to either cleaned seeds, or vertebrate-discarded fruit portions. The lower preference of feces-embedded seeds found by both previous studies may be attributed to the fact that *Ficus* seeds were mixed with feces only (Roberts & Heithaus 1986; Martínez-Mota et al. 2004), whereas we used a mixture of fresh pulp and feces. Moreover, while we used bird feces, Martínez-Mota et al. (2004) used howler monkey feces and Roberts & Heithaus (1986) used feces from many vertebrate species (including birds, peccaries, monkeys, and coatis). Indeed, there is evidence that feces type may affect seed removal by ants (Pizo et al. 2005).

The higher number of ant species recorded in “mandibulated” and “feces-embedded” fruits of *P. suterella* may be attributed to the fact that these conditions offer more variable possibilities of exploitation by ants. In “intact” fruits, only ants capable of tearing the coat were able to exploit the pulp. The exposed pulp and liquids of “mandibulated” fruits, on the other hand, were easily

accessible by many ant species. Finally, in the “feces-embedded” treatment, ants had full access not only to the fruit reward *per se* (*i.e.*, coat, pulp, and seeds), but to the feces constituents as well. Indeed some ant species may be even more attracted to bird feces than to the fruit itself, while others are much more interested in the pulp rewards (see Kaspari 1993; Levey & Byrne 1993; Pizo & Oliveira 1999, 2000). Together this might have yielded a higher estimate of ant species richness at feces-embedded *P. suterella* fruits. From the point of view of the seed, a wider variety of ant attendants may translate into a higher chance of interacting with a species providing an important benefit such as seed cleaning and/or dispersal (*e.g.*, Passos & Oliveira 2002, 2003). Nonetheless, the fact that more ants were attracted to these treatments does not necessarily imply an increased seed removal rate. For instance, feces-embedded *Ficus perforata* seeds are less removed by ants because howler monkey feces harden and trap the seeds (Martínez-Mota et al. 2004).

Although many studies have registered ants interacting with a wide variety of diaspore species on the ground of tropical habitats (see review by Rico-Gray & Oliveira 2007, and included references), our experiment suggests that fruit attractiveness to ants may depend on previous handling by frugivores to facilitate access to fruit rewards. Of course such dependence will vary with the toughness of the fruit coat. For instance while the hard-coated fruits of *Posoqueria latifolia* are only accessible to ants when crushed by vertebrates (Pizo & Oliveira 2000), our data on *Psychotria suterella* fruits indicate that ants are capable of exploiting them when intact. It is also possible that previous handling by frugivores increases emission of fruit volatiles, which in turn improve the attractiveness of fallen fruits to ground-dwelling ants. Based on our results, we suggest that future studies on interactions of ants with non-myrmechochoric fruits, especially those using diaspore removal experiments (*i.e.*, controlled conditions), should

also consider previous fruit condition (*i.e.*, intact, opened by vertebrates or embedded in vertebrate feces) .

Our results suggest that ongoing changes in the structure of vertebrate communities (*e.g.*, lower abundance, alteration in species composition, loss of specialist species) due to habitat fragmentation and hunting (Silva & Tabarelli 2000; Terborgh *et al.* 2001; Cordeiro & Howe 2003), will most likely produce negative indirect effects on the ant-diaspore interactions in tropical forests. Vertebrate-impoverished forest fragments will probably present lower frequencies of previously-manipulated fallen fruits, thus reducing the chances of ant-diaspore interactions. Many diaspore species falling still intact would render completely inaccessible to a number of ground-dwelling ant species. Together with the insidious consequences associated with the loss of specialist frugivores (Silva & Tabarelli 2000; Cordeiro & Howe 2003), vertebrate-dispersed species would likely be affected by the decreased attractiveness of their diaspores to potentially beneficial seed-cleaning and/or fine-tuned ant dispersers (Böhning-Gaese *et al.* 1999; Passos & Oliveira 2002).

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Legends to Figures

Figure 1. Species density of ants attracted to *Psychotria suterella* fruits submitted to three different treatments (intact, mandibulated, and feces-embedded) in an Atlantic forest remnant in SE Brazil (N = 36 sampling stations). Central lines and borders in each box plot indicate the mean $\pm$ 1SE, respectively. Whiskers indicate the range of the 95% confidence interval. Different letters denote significant differences.

Figure 2. Jackknife-I estimate of ant species number ($\pm$ 95% confidence interval) attracted to *Psychotria suterella* (Rubiaceae) fruits submitted to three different treatments (intact, mandibulated, and feces-embedded) in an Atlantic forest remnant in SE Brazil. Different letters indicate significant differences.

Figure 1

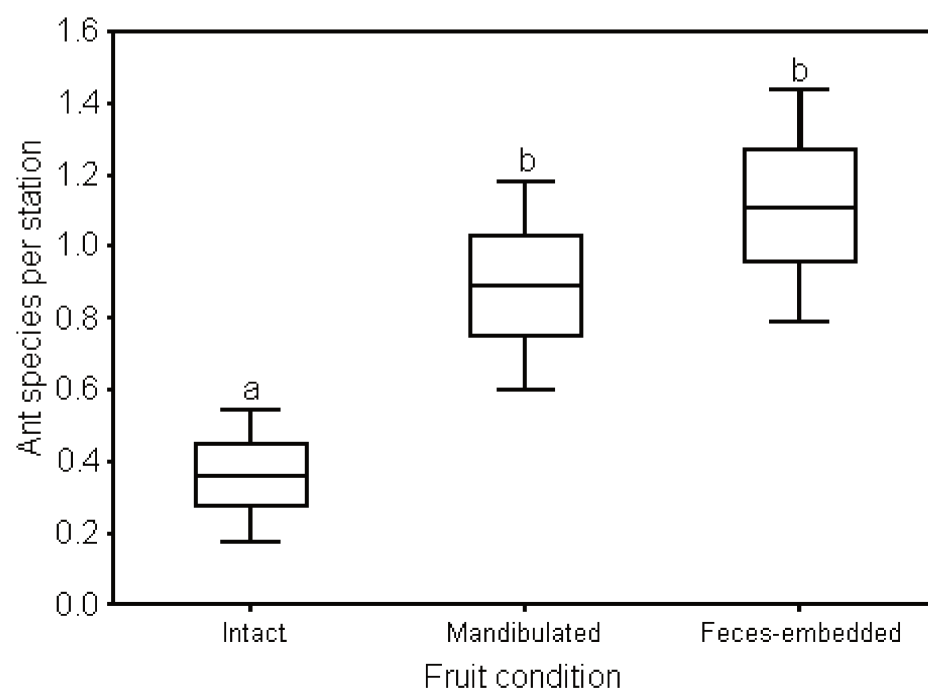
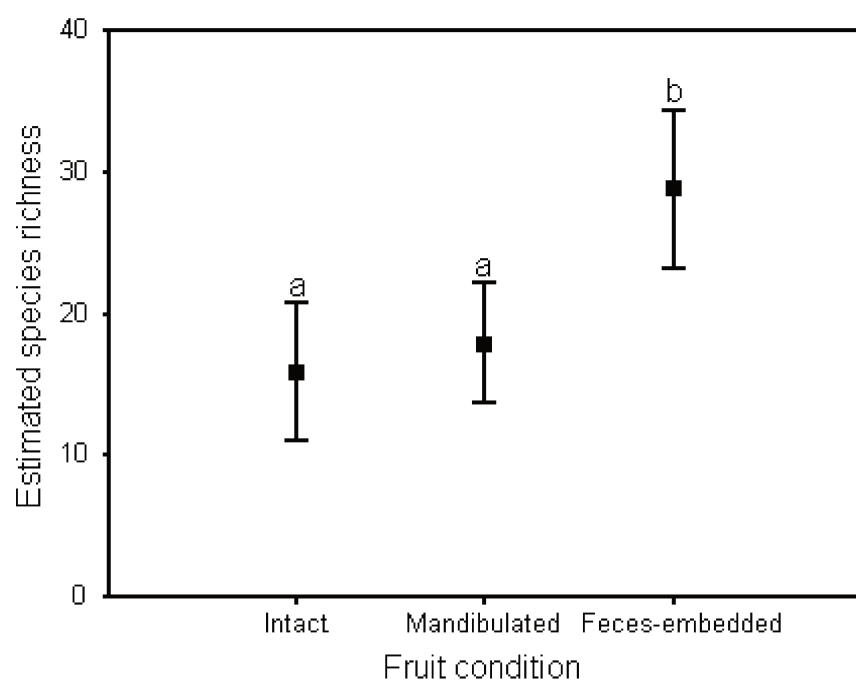


Figure 2



Appendix 1. Ant species attending fruits of *Psychotria suterella* (Rubiaceae) submitted to three different treatments (intact, mandibulated, and feces-embedded) in an Atlantic forest remnant in SE Brazil. Records refer to ant attendance to fruits at 40 sampling stations (40 fruits per category). Species are in alphabetical order within subfamilies.

Ant species	Records at experimental fruits			
	Feces-			Total
	Intact	Mandibulated	embedded	
Formicinae				
<i>Brachymyrmex</i> sp. 4	1	0	0	1
Heteroponerinae				
<i>Heteroponera inermis</i> (Emery)	0	2	1	3
Myrmicinae				
<i>Acromyrmex</i> sp. 1	0	2	1	3
<i>Basiceros disciger</i> (Mayr)	0	0	1	1
<i>Cyphomyrmex rimosus</i> (Spinola)	0	1	2	3
<i>Megalomyrmex iheringi</i> Forel	1	0	0	1
<i>Pheidole</i> sp. 1	1	2	5	8
<i>Pheidole</i> sp. 3	2	5	8	15
<i>Pheidole</i> sp. 4	1	2	0	3
<i>Pheidole</i> sp. 5	1	2	1	4
<i>Pheidole</i> sp. 7	0	0	1	1
<i>Pheidole</i> sp. 8	1	1	2	4
<i>Pheidole</i> sp. 14	0	1	0	1

<i>Pheidole</i> sp. 18	0	0	2	2
<i>Pheidole</i> sp. 19	0	0	1	1
<i>Pheidole</i> sp. 20	0	0	1	1
<i>Pheidole</i> sp. 21	0	0	1	1
<i>Pheidole</i> sp. 25	0	0	1	1
<i>Solenopsis</i> sp. 3	0	1	0	1
<i>Solenopsis</i> sp. 7	0	3	3	6
<i>Solenopsis</i> sp. 9	1	1	1	3
<i>Wasmannia affinis</i> Santschi	3	7	6	16
Ponerinae				
<i>Pachycondyla striata</i> Smith	0	0	1	1
Number of ant records	12	30	39	81
Number of ant species	9	13	18	23
Number of stations with ants	12	23	26	61

Capítulo 6. Considerações Finais

A discussão acerca dos efeitos negativos da fragmentação florestal sobre as espécies e o funcionamento dos ecossistemas tem sido um assunto freqüente das pesquisas ecológicas realizadas nas últimas três décadas (e.g., Bierregaard et al. 1992, Laurance & Bierregaard 1997, Cordeiro & Howe 2001, Metzger et al. 2009). Nesta tese, objetivando aumentar o conhecimento científico quanto aos efeitos da fragmentação florestal em relação a um tópico ainda pouco explorado, dois tipos de floresta (fragmentada e não-fragmentada) foram comparados quanto aos padrões de interação entre formigas e diásporos carnosos.

A interação formiga-diásporo carnoso é vista como oportunista (Rico-Gray & Oliveira 2007), uma vez que este tipo de diásporo é, em geral, especialmente atrativo para vertebrados frugívoros (como aves e mamíferos), sendo sua dispersão atrelada à ação dos mesmos (Howe & Smallwood 1982). Por outro lado, as formigas habitantes do folhiço são um grupo bastante diverso e abundante (Fittkau & Klinge 1973, Kaspari 2000, Ward 2000), cujos hábitos alimentares são em grande parte generalistas (Carrol & Janzen 1973), inclusive consumindo frutos e sementes (Pizo & Oliveira 2000, Bottcher 2010). Embora oportunista, sabe-se que, em muitos casos, esta interação traz benefícios para ambas as partes envolvidas: plantas (Oliveira et al. 1995; Farji-Brener & Silva 1996; Leal & Oliveira 1998; Pizo & Oliveira 1998; Böhning-Gaese et al. 1999; Guimarães & Cogni 2002; Passos & Oliveira 2002, 2004; Leal et al. 2007; Christianini & Oliveira 2009, 2010) e formigas (Bottcher 2010; ver também Morales & Heithaus 1998, Gammans et al. 2005, para diásporos verdadeiramente mirmecocóricos). Ao ser capaz de afetar diretamente a dispersão de sementes e o estabelecimento de plântulas (Rico-Gray & Oliveira 2007), etapas essenciais na manutenção das populações vegetais (Howe & Smallwood

1982), o estudo deste mutualismo facultativo em florestas fragmentadas mostra-se um tópico relevante, visto que a perturbação e destruição de florestas tropicais tende a aumentar cada vez mais (Aide & Grau 2004, Wright 2005).

Principais resultados

A comunidade de formigas e diásporos que foram encontrados durante nosso estudo foi extremamente alta (105 espécies de plantas e 66 espécies de formigas; Capítulo 2), reiterando a ubiquidade desta relação em ecossistemas brasileiros (Leal & Oliveira 1998, Pizo & Oliveira 2000, Passos & Oliveira 2003, Bottcher 2010, Christianini et al. 2011, Costa et al. no prelo). Além disso, os resultados do primeiro estudo desta tese apontam para o fato de que as mudanças observadas na interação formiga-diásporo devem-se principalmente a diferenças entre fragmentos e floresta contínua quanto à composição dos diásporos disponíveis no chão da floresta. De fato, sabe-se que os frutos zoocóricos da Floresta Atlântica variam bastante em sua composição química (Galetti et al. 2011) e que este atributo tem efeitos diretos sobre a atratividade dos frutos em relação às formigas (Pizo & Oliveira 2000, 2001). De certa forma, nossos resultados vão na mesma direção do estudo de Mitchell e colaboradores (2002), que investigaram a resposta da comunidade de plantas mirmecocóricas e de formigas dispersoras à fragmentação de uma floresta temperada nos EUA. Como a assembléia de formigas atraídas às iscas não apresentou diferenças marcantes entre as florestas estudadas, os pesquisadores sugerem que outro(s) fator(es) esteja(m) determinando a baixa abundância/diversidade de plantas mirmecocóricas apresentada pelos fragmentos menores e com alto grau de perturbação (Mitchell et al. 2002). No nosso contexto, a diferença entre fragmentos e floresta contínua na composição de plantas com diásporos carnosos

é certamente determinada por fatores associados à fragmentação/ secundarização da floresta, talvez até devido à ausência de dispersores primários (i.e., vertebrados frugívoros; Silva & Tabarelli 2000, Cordeiro & Howe 2003). No entanto, a constatação de que formigas em fragmentos também são atraídas pelos frutos disponíveis no solo sugere que este tipo de interação deve persistir em florestas alteradas (Capítulo 2), assim como seu efeito potencialmente benéfico sobre a dispersão/germinação de sementes e o estabelecimento de plântulas (Rico-Gray & Oliveira 2007).

Para as análises do capítulo seguinte (capítulo 3) utilizamos o mesmo conjunto de dados acima descrito com o intuito de comparar a estrutura das redes de interação formiga-fruto entre os dois tipos de floresta estudados. Fragmentos e florestas contínuas divergiram quanto a três das sete métricas quantitativas calculadas. Por exemplo, a generalidade (definida como o número efetivo médio de espécies de diásporos por espécie de formiga; Bersier et al. 2002) foi significativamente menor em fragmentos florestais. Acreditamos que as diferenças encontradas entre redes estão relacionadas principalmente ao menor número de espécies vegetais presentes nas redes dos fragmentos. No entanto, o fato do número de espécies de formigas nas redes ter permanecido relativamente constante (com exceção das redes FF1 e FF3) e das espécies mais freqüentes nas oito redes pertencerem, em sua maioria, aos gêneros *Pheidole* e *Solenopsis* (ver capítulo 2) sugere que, mesmo em florestas com maior grau de perturbação como os fragmentos aqui estudados, as formigas ainda seriam um agente relevante na interação com diásporos carnosos para a comunidade depauperada de plantas encontradas naqueles ambientes.

No capítulo 4 buscamos responder o que acontece com a interação entre formigas e frutos carnosos em fragmentos de floresta, caso a abundância dos diásporos permaneça inalterada. Sendo assim, controlamos a oferta e a qualidade dos frutos disponíveis ao oferecer frutos

sintéticos em estações experimentais dispostas nos dois tipos de floresta, verificando quais espécies de formigas eram atraídas, e seu comportamento. Ao contrário da expectativa gerada pelos resultados do Capítulo 2, detectamos diferenças marcantes entre a floresta contínua e os fragmentos florestais quanto ao padrão de visitação/remoção de frutos sintéticos por formigas. Foi possível identificar que um grupo extremamente importante na remoção de diásporos em ecossistemas neotropicais (i.e., o das grandes poneríneas; Horvitz & Beattie 1980; Pizo & Oliveira 1998; Passos & Oliveira 2002, 2004; Bottcher 2010; Christianini & Oliveira 2010) foi mais freqüente nas estações experimentais situadas na floresta melhor preservada. Assim, verificamos que, em média, frutos sintéticos são mais freqüentemente removidos (especialmente pela ponerínea *Pachycondyla striata*), e a maiores distâncias, nas florestas contínuas do que nas fragmentadas. Além do efeito particular de *P. striata*, as florestas contínuas apresentaram um maior número de espécies por estação experimental e, em geral, uma maior riqueza total de espécies de formigas. A maior densidade/diversidade de formigas interagindo com frutos pode ser vista como uma espécie de ‘garantia da realização do serviço’, embora espécies de formigas possam diferir quanto aos seus efeitos na interação com diásporos, sejam eles mirmecocóricos (Andersen & Morrison 1998, Cuautle et al. 2005, Gove et al. 2007) ou não-mirmecocóricos (Leal & Oliveira 1998; Passos & Oliveira 2002, 2004; Christianini & Oliveira 2010).

Finalmente, no Capítulo 5, realizamos um experimento com diásporos do arbusto *Psychotria suterella*, simulando a disponibilidade dos mesmos sob três condições distintas: intactos, em meio a fezes de aves e mandibulados por aves. De acordo com nossa hipótese inicial, vimos que o modo como o fruto se encontra no chão da floresta afeta a sua acessibilidade/atração a formigas. Assim, frutos que já tiveram contato com vertebrados (dispersores primários) apresentam uma maior chance de interagir com formigas (dispersores secundários). Nossas

observações durante o campo, assim como observações de Pizo e Oliveira (2000) e Milesi e Lopez de Casenave (2004), indicam que a importância da manipulação por vertebrados na atração posterior de formigas não acontece unicamente em *P. suterella*, nossa espécie modelo. Como grandes vertebrados, incluindo frugívoros especialistas, estão entre os principais grupos a desaparecerem de pequenos fragmentos florestais e de florestas extremamente antropizadas (Redford 1992, Chiarello 1999, Terborgh et al. 2001), a dispersão de diásporos carnosos será afetada de dois modos. Primeiramente, há o efeito direto da ausência de seus principais dispersores, diminuindo a quantidade de frutos removidos da copa de árvores parentais, juntamente com a diminuição na distância de remoção (Pizo 1997, Silva & Tabarelli 2000, Cordeiro & Howe 2003, Cramer et al. 2007). Ao lado disso, diásporos que não interagiram com vertebrados terão uma menor chance de atraírem formigas (Capítulo 5), cujo papel na retirada da polpa/arilo, o qual acarreta numa maior taxa de germinação das sementes, já é bem conhecido (Oliveira et al. 1995, Leal & Oliveira 1998, Ohkawara & Akino 2005, Christianini et al. 2007). Em casos extremos, a não-remoção da parte carnosa que envolve a semente resultou na completa ausência de germinação sob condições controladas em casa de vegetação (e.g., *Cupania vernalis* – Guimarães & Cogni 2002; *Erythroxylum pelleterianum* – Christianini et al. 2007). De modo geral, os resultados desta tese mostram que a fragmentação florestal afeta interações sutis como as que envolvem formigas e diásporos não-mirmecocóricos caídos ao solo, com potencial efeito negativo sobre o estabelecimento e regeneração de plantas.

Perspectivas

Certamente, mais do que responder às nossas questões iniciais, o desenvolvimento desta tese traz novas questões a serem respondidas por futuros estudos. Abaixo, ressaltamos algumas das questões que nos parecem mais pertinentes.

A fragmentação florestal, além de afetar a abundância e composição de diásporos disponíveis no chão da floresta como vimos no Capítulo 2, deve afetar também a disponibilidade de outros recursos presentes na dieta das formigas (como, por exemplo, a abundância de outros artrópodes; Didham 1997). Sabe-se que a inclusão de itens com diferentes composições químicas (especialmente no que se refere a nutrientes essenciais) é, muitas vezes, necessária para a sobrevivência e o crescimento das colônias (Gammans et al. 2005). Por exemplo, trabalhos envolvendo a adição de elaiossomos, ou de arilos ricos em lipídios, à dieta de colônias mantidas em laboratório mostraram um aumento significativo na produção de rainhas virgens (i.e., maior investimento reprodutivo; Morales & Heithaus 1998) e no peso de larvas (i.e., melhor desempenho; Gammans et al. 2005, Bottcher 2010). Em vista disso, será que colônias de uma mesma espécie, localizadas em ambientes com níveis de perturbação diferentes, apresentarão mudanças em suas dietas em resposta à disponibilidade local dos itens? No caso de haver de fato uma diferença na composição da dieta de colônias em diferentes ambientes, será que esta diferença afeta o desempenho das colônias?

O enfoque utilizado em dois capítulos desta tese representa uma abordagem no nível de comunidade, priorizando a detecção de padrões mais gerais em detrimento de interações focais formiga-diásporo (ver por exemplo Böhning-Gaese et al. 1999 e Christianini & Oliveira 2009, 2010). Este tipo de abordagem é essencial para um levantamento das interações existentes na

paisagem de estudo, bem como para o reconhecimento daquelas que podem ser mais profícuas. A partir deste estudo, futuros trabalhos abordando efeitos de perturbações antrópicas na Floresta Atlântica (incluindo a fragmentação) sobre interações formiga-diásporo podem concentrar-se em espécies focais de plantas e/ou formigas. A partir dos resultados do Capítulo 4, acreditamos que dois grupos de formigas cuja interação com frutos mereça ser especialmente estudada são as grandes poneríneas (ver acima), e espécies do gênero *Pheidole*, muitas das quais se mostraram boas removedoras dos frutos sintéticos (ver também Levey & Byrne 1993, Pizo 2008, Christianini & Oliveira 2010).

Quanto às plantas, acreditamos que estudos com enfoque em uma única espécie de planta, que abordem tanto a dispersão primária por vertebrados como a secundária por formigas (e.g. Christianini & Oliveira 2009, 2010) ajudariam a compreender se a fragmentação florestal afeta também a importância relativa destes dois grupos de dispersores para a planta em questão. Como formigas removem preferencialmente diásporos < 1g (Pizo & Oliveira 2001), é possível que elas sejam mais importantes para frutos dispersos por aves, cujo tamanho é em geral menor do que frutos dispersos por mamíferos (Jordano 1995). Em florestas fragmentadas, formigas devem ser especialmente importantes para dois grupos de plantas. Espécies com diásporos cujo apêndice carnoso é rico em lipídios têm se mostrado especialmente atrativas para formigas de folhço, especialmente poneríneas (Pizo & Oliveira 2000, 2001; Passos & Oliveira 2003; Christianini et al. 2007). Por outro lado, espécies de plantas cujos diásporos sejam produzidos durante a estação seca e fria, podem se tornar um recurso concorrido para formigas, visto que a disponibilidade de frutos em fragmentos diminui nesta época (ver Capítulo 2 e Genini et al. 2009). Além disto, na estação seca e fria a disponibilidade de presas animais (invertebrados) no folhço também é

menor (Levings & Windsor 1984), aumentando a importância relativa de diásporos carnosos para a dieta das formigas de solo.

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