UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA

VALÉRIA FORNI MARTINS

"PADRÃO ESPACIAL DE TRÊS ESPÉCIES ARBÓREAS ORNITOCÓRICAS DA FLORESTA OMBRÓFILA DENSA DE TERRAS BAIXAS NO LITORAL NORTE DO ESTADO DE SÃO PAULO"

Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato (a)
Valéria Forni Martins
e aprovada pela Comissão Julgadora.

Tese apresentada ao Instituto de Biologia para obtenção do Título de Doutor em Ecologia.

Orientador: Prof. Dr. Flavio Antonio Maës dos Santos

Campinas, 2011

FICHA CATALOGRÁFICA ELABORADA PELA
BIBLIOTECA DO INSTITUTO DE BIOLOGIA – UNICAMP

M366p

Martins, Valéria Forni

Padrão espacial de três espécies arbóreas ornitocóricas da Floresta Ombrófila Densa de Terras Baixas no litoral norte do estado de São Paulo / Valéria Forni Martins. – Campinas, SP: [s.n.], 2011.

Orientador: Flavio Antonio Maës dos Santos.
Tese (doutorado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Núcleo Picinguaba (Ubatuba, SP). 2. Chuva de sementes. 3. Plantas - Ontogenia. 4. Floresta ombrófila densa de terras baixas. 5. Parque Estadual da Serra do Mar (SP). I. Santos, Flavio Antonio Maës dos. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Título em inglês: Spatial pattern of three ornitochorous tree species of a Lowland Atlantic Rainforest in Southeastern Brazil.
Palavras-chave em inglês: Núcleo Picinguaba (Ubatuba, SP); Seed rain; Plants - Ontogeny; Lowland atlantic rainforest; Parque Estadual da Serra do Mar (SP, Brazil).
Área de concentração: Ecologia.
Titulação: Doutor em Ecologia.
Banca examinadora: Flavio Antonio Maës dos Santos, Simone Aparecida Vieira, Gislene Ganade, Patrícia Morellato, Paulo Roberto Guimarães Junior.
Data da defesa: 29/06/2011.
Programa de Pós-Graduação: Ecologia.

Campinas, 29 de junho de 2011.

BANCA EXAMINADORA

Prof. Dr. Flavio Antonio Maës dos Santos (Orientador)

Assinatura

Profa. Dra. Simone Aparecida Vieira

Assinatura

Profa. Dra. Gislene Ganade

Assinatura

Profa. Dra. Patrícia Morellato

Assinatura

Prof. Dr. Paulo Roberto Guimarães Jr.

Assinatura

Prof. Dr. João Semir

Assinatura

Prof. Dr. Gustavo Quevedo Romero

Assinatura

Prof. Dr. Alexander Vicente Christianini

Assinatura

AGRADECIMENTOS

Agradeço a:

Prof. Dr. Carlos Joly, coordenador do Projeto Temático "Composição Florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar" (Biota/FAPESP), no qual este trabalho esteve inserido, por toda a ajuda logística e condições propiciadas, sem as quais não teria sido possível a relização deste trabalho;

Equipe do Projeto Temático, especialmente Prof. Jorge Tamashiro, Dra. Luciana Alves, Prof. Dr. Marco Assis e Profa. Dra. Simone Vieira, pela troca de informações e ideias, as quais contribuíram imensamente para a realização deste trabalho e para o meu maior entendimento sobre a Mata Atlântica;

Neusa Trevizan, secretária do Projeto Temático, pela ajuda com as diárias e notas;

Funcionários e ex-funcionários da Pousada Betânia em Ubatuba, especialmente Eliane, Mair, Dos Anjos, Edvaldo e Teresa, pela acolhida nos dias de campo;

Joselino Santos, Manoel Assunção e Edvaldo Pereira pela enorme ajuda na coleta de dados, pela instalação de parte dos coletores de sementes nas parcelas do Projeto Temático onde foi realizado este trabalho, pela coleta mensal do material dos coletores e pela manutenção das parcelas estudadas;

Amigos e colegas que estiveram comigo na Pousada Betânia ou no mato e fizeram meus dias de campo mais alegres: Adaises Silva, Aline Lima, Aloysio Teixeira, Ana Paula Moraes, André Rochelle, Andréa Tavares, Ataliba Gomes, Bete Canela, Bruno Aranha, Bruno Rosado, Carlos Eduardo Nunes, Carol Virillo, Chris Corrêa, Dalila Freitas, Edmar Miranda, Eduardo Prata, Eliana Gressler e seus ajudantes, equipe de Ecofisiologia, Flá Tirolo, Giseli Areias, Graham Wyatt, Gui Sanvido, Juliano van Melis, Lara Cazotto, Larissinha Veiga, Ligia Sims, Lori Fonseca, Lu Alves, Luís Bernacci, Mao Otárola, Marco Assis e seus alunos, Mardiori Tanara Pinheiro dos Santos, Mari Campos, Marlies e Ivan Sazima, Marcos A. Scaranello, Nivea Santos, Pedro Cavalin, Pedro Eisenlohr, Rafa Costa, Renato "Pezão", Rubem Ávila, Simey Fisch e seus alunos, Simone Vieira, Susian Martins, Su Alcantara, Vanessa Mancuso, Vinicius Brito, Vivi Oliveira e outros que por ventura eu tenha esquecido...

Amigos da UNICAMP, especialmente André Rochelle, Carol Virillo, Chris Corrêa, Pedro Eisenlohr e Rafa Costa, pelas dúvidas solucionadas, conversas produtivas e momentos de descontração;

Pedro Cavalin, que, durante sua estadia na Califórnia, pacientemente "escaneou" e me enviou, arquivo a arquivo, dois trabalhos científicos de grande interesse (Houle 1995 e Schupp & Fuentes 1995, ambos utilizados no capítulo 2);

Equipe do CENA-USP responsável pelos coletores de sementes instalados nas parcelas do Projeto Temático onde foi realizado este trabalho, em especial Prof. Dr. Luís Antônio Martinelli, Profa. Dra. Janaína Carmo, Dra. Susian Martins, Luís Fernando Martins, Edmar Miranda e a técnica Fabiana Fracassi, pela coleta, triagem e troca de parte do material;

Angélica Carvalho, Jéssica Harue, Carlos Eduardo Nunes e Luciano Tortellini pela triagem de parte do material dos coletores de sementes;

Dra. Christiane Corrêa e Rafael Costa pelas fotos hemisféricas de parte das parcelas do Projeto Temático onde foi realizado este trabalho;

Gisele Garcia pela análise das fotos hemisféricas das parcelas do Projeto Temático onde foi realizado este trabalho;

Prof. Dr. Thorsten Wiegand, que me recebeu em Leipzig, Alemanha, para me ensinar a *O-ring statistics* e a *pair correlation function* no Programita, e que continuou a me ajudar com as análises nos meses seguintes;

Prof. Dr. José Alexandre Diniz-Filho e Dr. Thiago Rangel, que me ensinaram as regressões espaciais durante um curso sobre o SAM; em especial, Dr. Thiago Rangel, que continuou a me ajudar com as análises dos meus dados mesmo após o curso;

Prof. Dr. Thomas Lewinsohn pelas sugestões feitas a este trabalho ainda na fase de projeto;

Profa. Dra. Gislene Ganade, Prof. Dr. Mauro Galetti e Profa. Dra. Simone Aparecida Vieira, membros da pré-banca, por suas importantes críticas e sugestões a este trabalho;

Profa. Dra. Gislene Ganade, Profa. Dra. Patrícia Morellato, Profa. Dra. Simone Aparecida Vieira e Prof. Dr. Paulo Roberto Guimarães Jr., membros da banca, por suas importantes críticas e sugestões a este trabalho;

Todos os professores, funcionários e amigos que, de alguma maneira, contribuíram para que este trabalho fosse desenvolvido;

Funcionários da Secretaria de Pós-Graduação do Instituto de Biologia da UNICAMP, especialmente a secretária da Ecologia Maria Célia Duarte Pio, por toda ajuda ao longo dos anos em que estive vinculada ao Programa de Pós-Graduação em Ecologia;

Minha família, especialmente meus pais, Fernando Roberto Martins e Eliana Regina Forni Martins, por sempre me apoiarem e me ajudarem incondicionalmente;

Guilherme Sanvido, meu namorado, por sua inestimável e infinita ajuda na coleta de dados e na confecção de figuras, e também por sua imensa paciência e carinho em todos os momentos;

Prof. Dr. Flavio Santos, meu orientador, pela paciência, conversas e estímulo ao longo dos anos em que estive sob sua orientação, os quais certamente me fizeram amadurecer muito profissional e também pessoalmente;

UNICAMP, por oferecer excelentes ensino e infra-estrutura;

CNPq pelo auxílio concedido em forma de bolsa (142295/2006-0), e FAPESP pelo auxílio concedido como parte do Projeto Temático (03/12595-7).

RESUMO

Muitas espécies arbóreas apresentam distribuição espacial agregada. As dióicas e que ocorrem em baixa densidade geralmente são mais agregadas e geram plântulas que são mais espacialmente associadas às fontes de semente do que as homóicas e as mais densas. Devido a eventos locais de dispersão de sementes, comumente há associação espacial entre adultos, sementes e plântulas. Isto ocorre especialmente entre adultos e sementes, mas nem sempre entre sementes e plântulas. Assim, os processos pós-dispersão também podem ter um efeito na estrutura espacial da população, com mecanismos dependentes de distância e densidade possivelmente reduzindo a agregação da mesma, enquanto a heterogeneidade ambiental geralmente aumenta a agregação. O objetivo deste estudo foi determinar como a densidade das fontes de semente, a dispersão e os processos pós-dispersão influenciam a estrutura espacial de três espécies arbóreas da Floresta Ombrófila Densa de Terras Baixas no litoral norte do estado de São Paulo.

Nós amostramos todos os indivíduos das três espécies em duas parcelas de 1 ha cada, identificamos seus estádios ontogenéticos e os mapeamos. Durante dois anos, coletamos mensalmente a chuva de sementes. Por último, avaliamos as plântulas previamente amostradas para determinar se elas haviam morrido, recrutado para estádios ontogenéticos subsequentes ou permanecido no mesmo estádio. Então, comparamos os padrões espaciais da sobrevivência, da taxa de mortalidade e da taxa de recrutamento a seis variáveis preditoras.

As sementes e os estádios ontogenéticos das três espécies apresentaram agregação, principalmente em pequenas classes de distância. Não houve um padrão claro da influência da densidade das fontes de semente na estrutura espacial das populações. Os adultos de todas as

espécies apresentaram associações espaciais com sementes e plântulas, mas estas estiveram associadas em apenas metade das comparações. A mortalidade das plântulas ocorreu aleatoriamente e não modificou o padrão espacial agregado das populações. Os sobreviventes se localizaram principalmente em áreas com alta densidade inicial de plântulas. As taxas de mortalidade não apresentaram relação com as variáveis preditoras e ocorreram aleatoriamente. O mesmo padrão foi encontrado para as taxas de recrutamento de uma das espécies estudadas, mas outra recrutou mais em áreas com maior área basal da população e maior porcentagem de abertura de dossel, e menos em áreas com maior diferença de altitude.

Nossos resultados estão de acordo com outros estudos que mostraram que espécies arbóreas tropicais são geralmente agregadas. No entanto, este padrão não pode ser atribuído à densidade das fontes de semente. Por outro lado, a agregação é explicada pela dispersão, uma vez que adultos ocorrem associados a sementes e plântulas. Os processos pós-dispersão não modificam o padrão espacial das populações após os eventos de mortalidade no estádio de plântula. A sobrevivência é maior em áreas com alta densidade de plântulas, como próximo aos adultos reprodutivos. Porém, não é possível prever onde a mortalidade e o recrutamento ocorrem em maiores taxas no ambiente. De forma geral, parece haver um maior recrutamento perto da planta parental devido à maior abundância de sementes neste local, apesar da baixa sobrevivência das mesmas, como proposto no modelo de recrutamento de Hubbell.

ABSTRACT

Many tree species present an aggregated spatial distribution. Dioecious, low-density species tend to be more aggregated and generate seedlings that are more spatially associated to seed sources than homoecious, high-density species. Due to local seed dispersal, adults, seeds and seedlings are generally spatially associated. This is commonly found for adults and seeds, but not always for seeds and seedlings. Therefore, post-dispersal processes can also affect the spatial structure of the population. Distance and density-dependent mechanisms usually decrease the aggregation of the population through ontogeny, while environmental heterogeneity tends to increase the aggregation through ontogeny. This study aimed at determining how density of seed sources, seed dispersal and post-dispersal processes influence the spatial structure of three tree species of a Lowland Atlantic Rainforest in Southeastern Brazil.

We sampled every individual of the three species studied within two 1-ha plots. We also identified its ontogenetic stage and mapped the plants. During two years, we monthly sampled the seed rain. Last, we checked the previously sampled seedlings in order to determine if they had died, recruited to further ontogenetic stages or remained at the same stage. Then, we compared the spatial structure of seedling survival, mortality rates and recruitment rates to six predictor variables.

The seeds and the ontogenetic stages of the three species studied were aggregated, especially at small distance classes. The influence of density of seed sources on the spatial structure of the populations was not clear. Adults of all species presented associations with seeds and seedlings, but seeds and seedlings were associated in only half of the comparisons. Seedling mortality occurred randomly and did not modify the aggregated spatial pattern of the populations.

Survivals were located especially in areas with higher initial seedling density. Mortality rates were not related to the predictor variables and occurred randomly. The same pattern was found for the recruitment rates of one species, but other recruited more in areas with greater population basal area and higher percentage of canopy opening, and less in areas with greater elevation range.

Our results agree with previous studies that showed that tropical tree species are generally aggregated. Nevertheless, this spatial pattern cannot be attributed to density of seed sources. On the other hand, the aggregation is explained by seed dispersal, since adults were always spatially associated to seeds and seedlings. Post-dispersal processes do not modify the spatial pattern of the populations after mortality events during the seedling stage. The chance of surviving is enhanced in areas with higher initial seedling density, such as near reproductive adults. However, it is not possible to predict where mortality and recruitment operate at higher rates in the forest due to idiosyncrasies of the species. Overall, recruitment seems to be higher close to the parent plant because of considerably greater seed abundance there, despite very low seed survival, as proposed in the Hubbell's recruitment model.

SUMÁRIO

Introdução……………………………………………………………………………Página 13

Objetivos e expectativas..………………………………………………………………Página 19

Área de estudo…………………………………………………………………………..Página 23

Espécies estudadas………………………………………………………………………Página 30

Literatura Citada………………………………………………………………………...Página 34

Capítulo 1: Densidade de fontes de semente, dispersão de sementes, processos pós-dispersão e a agregação de espécies arbóreas em uma floresta tropical.......................................Página 46

Capítulo 2: Relação espacial desacoplada entre sementes e plântulas não desacopla a distribuição de sementes e adultos em uma floresta tropical..Página 89

Capítulo 3: A sobrevivência de plântulas determina o padrão espacial de espécies arbóreas em uma floresta tropical..Página 138

Considerações finais..Página 176

Literatura Citada...Página 185

INTRODUÇÃO

A distribuição espacial de indivíduos de uma mesma espécie é um tema central na ecologia teórica (Dale 1999). A estrutura espacial de populações de espécies arbóreas tem sido investigado em muitos estudos, que mostram que a maioria das espécies arbóreas tropicais ocorre principalmente com forte agregação em escalas que variam de poucos metros até algumas centenas de metros (Hubbell 1979, Forman & Hahn 1980, Condit *et al.* 2000, Plotkin *et al.* 2000). No entanto, os estudos que examinam os possíveis fatores que determinam este padrão espacial são raros (*e.g.*, Hubbell 1979, Condit *et al.* 2000, Plotkin *et al.* 2000, Bleher *et al.* 2002, Seidler & Plotkin 2006) e as causas da agregação de coespecíficos ainda não foram bem compreendidas (Levine & Murrell 2003).

A estrutura espacial de espécies arbóreas é potencialmente influenciada por: (1) densidade das fontes de semente, (2) dispersão de sementes e (3) processos pós-dispersão. A densidade das fontes de semente, por sua vez, é determinada pela densidade de indivíduos potencialmente reprodutivos e pelo sistema reprodutivo da espécie (Bleher *et al.* 2002). Populações com baixa densidade de indivíduos potencialmente reprodutivos, como comumente ocorre na região tropical (Hubbell 1979, Pitman *et al.* 1999), tendem a ser mais agregadas e a produzir plântulas que são mais espacialmente associadas às fontes de semente do que populações mais densas (Hubbell 1979, He *et al.* 1987, Condit *et al.* 2000, Nanami *et al.* 1999, Plotkin *et al.* 2000, Bleher *et al.* 2002).

Muitas espécies arbóreas tropicais são dióicas (Bawa 1974, Bawa & Opler 1975, Nanami *et al.* 1999), apresentando uma densidade menor de fontes de semente (*i.e.*, indivíduos femininos) em relação às espécies homóicas (*sensu* Cruden & Lloyd 1995), nas quais todos os adultos produzem frutos e contribuem com a dispersão. Por se comportarem como populações de espécies homóicas com menor densidade de indivíduos, espécies dióicas tendem a ser mais agregadas e a produzir plântulas que são mais espacialmente associadas às fontes de semente do que as homóicas (Nanami *et al.* 1999, Bleher *et al.* 2002, mas veja Hubbell 1979).

A dispersão de sementes também pode influenciar a estrutura espacial de espécies arbóreas (Nathan & Muller-Landau 2000, Bleher *et al.* 2002). Isto ocorre porque a distribuição espacial das sementes no ambiente forma um molde para a regeneração e o recrutamento futuros de uma população ou comunidade vegetal, com sementes depositadas em locais propícios para a germinação e o estabelecimento da plântula gerando novos indivíduos (Loiselle *et al.* 1996, Levine & Murrell 2003). Desta forma, os fatores que operam na dispersão de sementes podem influenciar o padrão espacial do recrutamento (Houle 1998). No entanto, o período compreendido entre a liberação das sementes da planta parental e o estabelecimento das plântulas é potencialmente a transição mais variável e menos previsível na vida de plantas perenes (Clark *et al.* 1999), e algumas hipóteses foram propostas para conectar espacialmente estes estádios de recrutamento (*sensu* Hampe *et al.* 2008).

Janzen (1970) e Connell (1971) foram os primeiros a sugerir que, conforme a densidade de sementes diminui com a distância a partir da planta parental, a sua sobrevivência aumenta, resultando em um maior recrutamento a uma certa distância do adulto. Com isto, as populações devem apresentar uma redução na agregação ao longo da ontogenia, diferentemente do que ocorreria se os fatores de mortalidade operassem ao acaso. Além disto, a distribuição espacial de sementes e plântulas é desacoplada, o que pode resultar em uma relação espacial negativa, *i.e.* discordante, entre estes dois estádios nos casos em que a mortalidade é extremamente maior perto da planta parental e a sobrevivência é extremamente alta a uma certa distância do adulto. Já em 1980, Hubbell propôs que o recrutamento é maior perto da planta parental devido a uma abundância de sementes consideravelmente maior neste local, apesar da sobrevivência das mesmas ser muito baixa. Neste caso, os adultos são pelo menos tão agregados quanto as sementes, e a relação espacial entre sementes e plântulas é sempre positiva, *i.e.* concordante. Outras funções de sobrevivência de sementes sugeriram diferentes relações espaciais entre sementes e plântulas (concordante, discordante ou independente; *e.g.*, McCanny 1985, McCanny & Cavers 1987), e padrões de distribuição distintos para as mesmas (Houle 1995).

Apesar de muitos estudos terem demonstrado que os padrões de distribuição das sementes refletem eventos de dispersão local, com o depósito da maioria das sementes embaixo ou perto das plantas parentais (Janzen 1970, Connell 1971, Clark *et al.* 1999, Nathan & Muller-Landau 2000, Nathan *et al.* 2000), as relações espaciais entre sementes e plântulas não são tão previsíveis. Isto ocorre devido a processos pós-dispersão, que incluem heterogeneidade ambiental, herbivoria, competição e ataque de patógenos (Janzen 1970, Connell 1971). Muitos pesquisadores têm estudado tais relações, especialmente em espécies arbóreas que produzem frutos carnosos (*e.g.*, Clark & Clark 1984, Schupp 1988, Burkey 1994, Herrera *et al.* 1994, Jordano & Herrera 1995, Schupp 1995, Rey & Alcantara 2000, Calviño-Cancela 2002, García *et al.* 2005, Hampe 2004, Hampe *et al.* 2008). Alguns destes estudos têm demonstrado que a dispersão de sementes e os padrões de recrutamento de plântulas são espacialmente independentes (*e.g.*, Rey & Alcantara 2000, Calviño-Cancela 2002, Hampe 2004). Porém, outros encontraram relações espaciais concordantes entre estes dois estádios de recrutamento (*e.g.*, Jordano & Herrera 1995, García *et al.* 2005). Além destes resultados contrastantes, as relações espaciais também podem variar de acordo com a espécie e o tipo de sistema estudado (*e.g.*, Herrera *et al.* 1994), de forma que mais estudos são necessários para o entendimento da relação espacial entre sementes e plântulas.

As possíveis alterações nos padrões espaciais de sementes, plântulas e adultos, e nas relações espaciais entre os mesmos decorrem dos processos pós-dispersão. Tais processos afetam principalmente as plântulas, que ocorrem em alta densidade e apresentam altas taxas de mortalidade nas florestas. Isto ocorre porque as plântulas geralmente são mais suscetíveis a fatores de mortalidade do que as plantas bem estabelecidas (Fenner 1987, Kitajima & Fenner 2000). Assim, os processos que ocorrem durante o estádio de plântula podem ter um grande impacto nas populações vegetais, incluindo um efeito forte na sua estrutura espacial resultante (Janzen 1970, Connell 1971).

Sobrevivência, mortalidade e recrutamento das plântulas de muitas espécies arbóreas tropicais são simultaneamente governados por mecanismos positivamente dependentes de distância e negativamente dependentes de densidade. Isto ocorre devido à elevada mortalidade de sementes e plântulas perto das plantas parentais, onde também há uma alta densidade de coespecíficos (Augspurger & Kelly 1984, Harms *et al.* 2000, Packer & Clay 2000) devido aos eventos de dispersão local (Janzen 1970, Connell 1971). Tais mecanismos incluem competição intraespecífica, a qual geralmente não é um fator importante de mortalidade de plântulas em florestas tropicais, pelo menos nos estágios iniciais de crescimento (Wright 2002, Bell *et al.* 2006). No entanto, ela comumente leva à mortalidade dependente de densidade de indivíduos maiores (Hubbell 1979, Forman & Hahn 1980, Condit *et al.* 2000, Plotkin *et al.* 2000). Assim, ela retira da população os indivíduos que se localizam perto uns dos outros, o que é conhecido como auto-desbaste (Sterner *et al.* 1986, He & Duncan 2000, Getzin *et al.* 2006). Isto resulta em uma forte diminuição na agregação de espécies abundantes ao longo da ontogenia, enquanto espécies raras tendem a apresentar uma diminuição fraca ou até mesmo um aumento na agregação (Murrell 2009).

Além da competição intraespecífica, alelopatia, modificação do microambiente, como alteração dos minerais do solo, e inimigos naturais das plantas (Schupp 1988, Maetô & Fukuyama 1997, Wright 2002, Bell *et al.* 2006) também podem resultar em uma menor agregação da população após os eventos de mortalidade (Janzen 1970, Connell 1971, Condit *et al.* 2000, Harms *et al.* 2000, Wiegand *et al.* 2007). Porém, como proposto por Hubbell (1980), esta diminuição nem sempre ocorre, devido a um efeito numérico das sementes localizadas próximo à planta parental.

Existem outros fatores bióticos que também afetam o destino das plântulas: idade, já que a susceptibilidade dos indivíduos ao ataque de patógenos geralmente decresce conforme a planta se torna mais madura e suas defesas químicas e/ou físicas se desenvolvem (Hanley *et al.* 1995); tamanho, com plântulas maiores apresentando menores taxas de mortalidade (Pigot & Leather 2008), e competição interespecífica (Franklin *et al.* 1987, De Steven 1991). Estes fatores podem alterar a agregação da população ao longo da ontogenia de uma forma muito imprevisível, tanto porque eles podem apresentar estruturas espaciais distintas como também porque eles podem não ser espacialmente estruturados.

Fatores abióticos que influenciam o destino das plântulas incluem luz e suas variáveis microclimáticas relacionadas, como umidade e temperatura (Augspurger & Kelly 1984, Kobe *et al.* 1995); propriedades físicas e químicas do solo (Rey *et al.* 2006), e estresse hídrico (Franklin *et al.* 1987, Herrera *et al.* 1994). A heterogeneidade ambiental comumente encontrada em florestas tropicais pode resultar na mortalidade de plântulas localizadas em microhabitats que são menos favoráveis para a espécie. Assim, os indivíduos localizados em microhabitats específicos com maior favorabilidade tendem a sobreviver mais do que aqueles localizados em outros locais. Desta forma, os adultos geralmente apresentam uma maior agregação do que as plântulas (Hubbell 1979, Hutchings 1997, Itoh *et al.* 1997, Condit *et al.* 2000). Além da heterogeneidade ambiental, interações positivas, como associação com micorrizas e facilitação, também podem resultar em maior agregação da população ao longo da ontogenia. Isto ocorre porque somente os indivíduos próximos, que interagem entre si ou com outros organismos presentes no microhabitat, beneficiam-se das interações positivas, apresentando maior sobrevivência (Dickie *et al.* 2007).

Outros mecanismos que afetam o destino das plântulas são aqueles relacionados aos danos físicos, causados por queda de serapilheria, deslizamento de terra, inundação e pisoteio por vertebrados (Clark & Clark 1989, Mack 1998, Scariot 2000, Portela & Santos 2009). Assim como os fatores bióticos que não são dependentes de distância ou de densidade, os danos físicos também podem alterar a agregação da população ao longo da ontogenia de uma forma muito imprevisível.

A deposição de sementes e a demografia de plantas, especialmente a distribuição de plântulas, tendem a ser altamente variáveis no espaço (Boerner & Brinkman 1996, Gómez-Aparicio *et al*. 2005 e referências citadas, Hampe *et al.* 2008) e, portanto, inerentes à autocorrelação espacial. Por causa disto, são necessárias técnicas de análise espacial que controlem a autocorrelação espacial dos dados ecológicos, de forma que estimadores dos padrões da deposição de sementes e do destino de plântulas possam ser obtidos e comparados sem nenhum tipo de viés (Hampe *et al.* 2008).

OBJETIVOS E EXPECTATIVAS

O objetivo deste estudo foi determinar como a densidade das fontes de semente, a dispersão de sementes e os processos pós-dispersão influenciam a estrutura espacial de três espécies arbóreas da Floresta Ombrófila Densa de Terras Baixas no litoral norte do estado de São Paulo. *Faramea picinguabae* M. Gomes (Rubiaceae) é homóica e os indivíduos reprodutivos ocorrem em alta densidade (*observ. pes.*, Eliana Gressler *comun. pes.*); *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae) é dióica e os indivíduos femininos ocorrem em densidade intermediária (Joly & Martinelli 2006, Eliana Gressler *comun. pes.*); *Pourouma guianensis* Aubl. (Urticaceae) também é dióica (Lorenzi 1998, Backes & Irgang 2004), mas os indivíduos femininos ocorrem em densidade muito baixa (Joly & Martinelli 2006).

As três espécies são ornitocóricas, que é a síndrome de dispersão mais importante na área de estudo (Cazotto *et al. in prep.*). Elas apresentam diásporos carnosos com uma única semente relativamente grande e dura, a qual pode ser facilmente encontrada em coletores de sementes. *Faramea picinguabae*, *M. schottiana* e *P. guianensis* são as únicas espécies com estas características e que também apresentam uma alta abundância de indivíduos pequenos na área de estudo (*observ. pes.*). Apesar de existirem relatos de mamíferos, especialmente macacos, consumindo frutos de diferentes espécies de *Pourouma* (*e.g.*, Kelly 1995, Riba-Hernández *et al.* 2003, Catenacci *et al.* 2009), acreditamos que as aves são o principal agente dispersor de *P. guianensis* na área de estudo, onde mamíferos diurnos, como primatas, não são observados desde 1.990 (Pedroni 2001). No entanto, o padrão de deposição de sementes desta espécie pode ser menos agregado do que o de *F. picinguabae* e *M. schottiana*, já que as sementes de *P. guianensis* são maiores. Por isto, elas podem ser dispersas por aves maiores, que são capazes de carregá-las para distâncias mais longas a partir da planta parental (Wheelwright 1985, Seidler & Plotkin

2006). Além disto, indivíduos reprodutivos de *P. guianensis* são muito mais altos do que os das outras duas espécies, o que deve resultar em um maior espalhamento das sementes em torno da planta parental.

O primeiro capítulo desta tese teve como objetivo detectar a influência da densidade das fontes de semente, a dispersão de sementes e os processos pós-dispersão na estrutura espacial das três espécies estudadas. Considerando a densidade de adultos potencialmente reprodutivos e o sistema reprodutivo, esperamos encontrar que: (1) a agregação é maior para todos os estádios ontogenéticos de *P. guianensis* e menor para todos os estádios de *F. picinguabae*; (2) a associação espacial entre plântulas e fontes de semente é mais forte para *P. guianensis* e mais fraca para *F. picinguabae*, e (3) a agregação ao longo da ontogenia se mantém constante, diminui ou aumenta devido aos processos pós-dispersão; se ela diminuir devido ao auto-desbaste, *F. picinguabae* deve apresentar o maior decréscimo e *P. guianensis*, o menor. Como não há replicas para densidade de adultos potencialmente reprodutivos e sistema reprodutivo, não podemos desenvolver testes formais para determinarmos sua influência na estrutura espacial de espécies arbóreas tropicais. No entanto, se estes fatores afetarem fortemente a estrutura espacial das espécies estudadas, esperamos detector alguma influência na agregação, na associação espacial entre plântulas e fontes de semente, e na alteração da agregação ao longo da ontogenia de *F. picinguabae*, *M. schottiana* e *P. guianensis*. Por último, também esperamos que (4) as relações espaciais entre plântulas e jovens, e entre todos os estádios ontogenéticos subsequentes de uma única espécie sejam positivas se a mortalidade não desacoplar os padrões de recrutamento da dispersão local; se a mortalidade levar ao desacoplamento, as relações espaciais devem ser negativas, especialmente entre plântulas e jovens.

O segundo capítulo teve como objetivo determinar o padrão espacial e as associações espaciais de sementes, plântulas e adultos das três espécies estudadas, utilizando-se uma técnica de análise espacial diferente da empregada no capítulo anterior. A agregação comumente observada em espécies arbóreas tropicais (*e.g.*, Hubbell 1979, Forman & Hahn 1980, Condit *et al.* 2000, Plotkin *et al.* 2000) parece estar altamente relacionada à dispersão de sementes (Condit *et al*. 2000, Svenning 2001, Svenning & Skov 2005), principalmente porque a maior parte delas é depositada embaixo ou perto das plantas parentais (Janzen 1970, Connell 1971, Clark *et al*. 1999, Nathan & Muller-Landau 2000, Nathan *et al*. 2000). Por isto, nós esperamos encontrar que sementes, plântulas e adultos das três espécies estudas são agregados e espacialmente associados, o que está de acordo com o modelo de recrutamento de Hubbell (Hubbell 1980).

O terceiro capítulo teve como objetivo determinar como a sobrevivência, a mortalidade e o recrutamento durante o estádio de plântula afetam o padrão espacial resultante das plântulas das três espécies estudadas. Especificamente, nós fizemos as seguintes perguntas: (1) os sobreviventes são mais ou menos agregados do que as plântulas antes dos eventos de mortalidade? (2) Quais características bióticas e abióticas resultam na ocorrência de mais sobreviventes em um dado microhabitat após os eventos de mortalidade? (3) Quais características resultam em maiores taxas de mortalidade em um dado microhabitat? (4) Quais características resultam em maiores taxas de recrutamento em um dado microhabitat?

Nós esperamos que os sobreviventes sejam menos agregados do que as plântulas antes dos eventos de mortalidade se os mecanismos positivamente dependentes de distância e negativamente dependentes de densidade atuarem como fatores importantes de mortalidade. Neste caso, tais fatores devem resultar na ocorrência de menos sobreviventes após os eventos de mortalidade, maiores taxas de mortalidade e menores taxas de recrutamento em áreas mais densas. Por outro lado, nós esperamos que os sobreviventes sejam mais agregados do que as plântulas antes dos eventos de mortalidade se a heterogeneidade ambiental atuar como um fator importante de mortalidade ou se as interações positivas beneficiarem a sobrevivência das plântulas. Neste caso, a ocorrência de mais sobreviventes após eventos de mortalidade, menores taxas de mortalidade e maiores taxas de recrutamento devem estar relacionados a características do microhabitat. Assim, nosso objetivo não é determinar como cada um dos fatores afeta o destino das plântulas. Ao invés disto, esperamos determinar microhabitats onde há um conjunto de características que permite a sobrevivência, resulta em mortalidade ou beneficia o recrutamento das plântulas.

ÁREA DE ESTUDO

A Mata Atlântica é considerada um dos *hotspots* mundiais para a conservação da biodiversidade (Myers *et al.* 2000), restando apenas cerca de 7% de sua cobertura original (Fundação SOS Mata Atlântica 2011). A maior porção contínua preservada no Brasil inclui a Serra do Mar, no estado de São Paulo, sudeste do Brasil, onde se localiza Parque Estadual da Serra do Mar (PESM; 23°34' - 23°17'S e 45°02' - 45°11'W; 0 – 1.200 m de altitude; Alves *et al.* 2010). Com quase 315 mil ha (SOS Mata Atlântica/INPE/ISA 1998), o PESM abrange uma extensão que vai desde a divisa dos estados de São Paulo e Rio de Janeiro até Itariri, no sul do estado de São Paulo. O PESM foi criado em 1977 por meio do Decreto Estadual n.º 10.251, de 30 de agosto de 1977, e posteriormente alterado pelo Decreto Estadual nº 13.313, de 6 de março de 1979. Devido à sua grande dimensão, o PESM é dividido em alguns núcleos administrativos, que são bases instaladas em áreas de domínio do estado de São Paulo (Joly & Martinelli 2004).

Em 2006-2007, a equipe do Projeto Temático “Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar” (Processo Biota/FAPESP 03/12595-7) instalou 14 parcelas permanentes (A-N) de 1 ha (100 m x 100 m) cada ao longo do gradiente altitudinal do PESM (Fig. 1). As parcelas são isoladas e estatisticamente consideradas como réplicas (Joly *et al.* 2008). Todas as parcelas foram demarcadas com um teodolito eletrônico (estação total) a cada 10 m devido às características topográficas em pequena escala, as quais incluem desde ondulações no terreno até encostas muito íngremes com deslizamento de terra. Portanto, todas as parcelas têm a mesma área quando projetadas em um plano horizontal (Alves *et al.* 2010). Cada parcela também foi dividida em 100 subparcelas de 10 m x 10 m, delimitadas com estacas permanentes de tubos de PVC de 1,2 m de altura e ¾" de diâmetro. Dentro das parcelas, a equipe do Projeto Temático marcou, mapeou, mediu o PAP (perímetro à altura do peito, medido à 1,3 m da superfície do solo), a altura total e a altura do fuste, e identificou todos os indivíduos arbóreos vivos (incluindo palmeiras) com PAP igual ou maior a 15,0 cm. O material testemunho está depositado nos herbários da UNICAMP (UEC), do Instituto Agronômico de Campinas (IAC) e da UNESP *campus* Rio Claro (HRCB; Joly *et al.* 2008).

Fig. 1: Distribuição das 14 parcelas instaladas na Mata Atlântica do gradiente altitudinal do Parque Estadual da Serra do Mar pela equipe do Projeto Temático "Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar" (Processo Biota/FAPESP 03/12595-7). Figura adaptada de Joly & Martinelli (2006).

Das 14 parcelas, 10 (A-J) foram instaladas no Núcleo Picinguaba (23°31' - 23°34'S e 45°02' - 45°05'W), município de Ubatuba, litoral norte do estado de São Paulo (Joly *et al.* 2008).

Este Núcleo compreende ca. 47,5 mil ha (SMA 1996), e é administrado pelo Instituto Florestal do Estado de São Paulo e pelo Ministério do Meio Ambiente (MMA). O relevo da região é dominado pela Planície Costeira, mas apresenta morros isolados e serras alongadas da Morraria Costeira, atingindo no seu limite interior as escarpas festonadas ou com espigões digitados da Serrania Costeira (Ponçano *et al.* 1981). No Núcleo Picinguaba, as temperaturas vão de 25,5º C em fevereiro a 18,4º C em julho. Não há uma estação seca marcada e a precipitação varia entre 376 mm em janeiro e 11 mm em julho (Sentelhas *et al.* 2003). A umidade relativa do ar permanece sempre acima de 80% (Morellato *et al.* 2000) e a insolação média diária anual varia entre 15,5 h em maio e 9,1 h em outubro. A direção predominante dos ventos é sudeste (ventos do litoral), com velocidade média anual de 0,9 m/s que varia pouco durante o ano (0,7 - 1,0 m/s; Alves 2000, CPTEC 2010).

O Núcleo Picinguaba é a única porção do PESM que atinge a orla marítima e, devido principalmente à sua grande variação de altitude, é composto por um mosaico vegetacional que inclui Formações Pioneiras com Influência Marinha (Dunas), Formações Pioneiras com Influência Fluvial (Caxetal), Formações Pioneiras com Influência Flúvio-Marinha (Mangue), Mata de Restinga, Floresta Ombrófila Densa de Terras Baixas, Floresta Ombrófila Densa Submontana e Floresta Ombrófila Densa Montana (Assis 1999). Os pesquisadores do Projeto Temático distribuíram uma parcela na Floresta de Restinga, cinco na Floresta Ombrófila Densa de Terras Baixas e quatro parcelas na Floresta Ombrófila Densa Submontana (Joly *et al.* 2008; Fig. 1).

No presente estudo, foram coletados dados em todas as subparcelas de 2 ha (ca. 23°22'S, 44°48'W) da Floresta Ombrófila Densa de Terras Baixas, chamados de parcela B e parcela E pela equipe do Projeto Temático (Fig. 2). Nos capítulos desta tese, a parcela B foi chamada de

Lowland 1 (L1) e a parcela E, de *Lowland* 2 (L2). Estas parcelas foram escolhidas porque foram onde os pesquisadores da área de Funcionamento do Ecossistema do Projeto Temático instalaram coletores de serapilheira, utilizados no presente estudo para obter sementes. A Floresta Ombrófila Densa de Terras Baixas recobre o sopé da Serra do Mar, em altitudes que variam de 50 m a 100 m acima do nível do mar, ocorre em cambisolos (solos recentemente formados pela sedimentação do produto da erosão montanhosa), e apresenta muitos matacões rochosos e leitos secos de riachos (Joly *et al.* 2008).

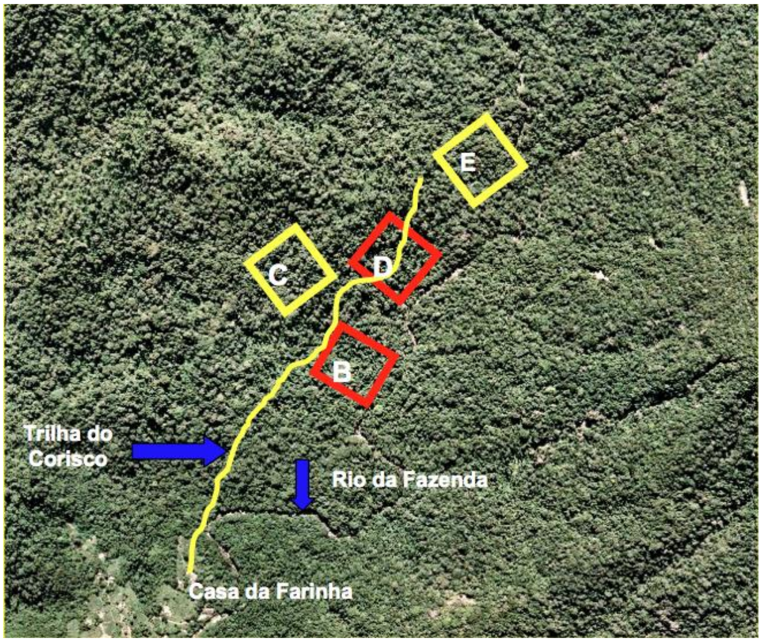


Fig. 2: Parcelas instaladas na Floresta Ombrófila Densa de Terras Baixas do Núcleo Picinguaba (B-E), Parque Estadual da Serra do Mar, pela equipe do Projeto Temático "Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar" (Processo Biota/FAPESP 03/12595-7). As parcelas localizam-se próximas à margem do Rio da Fazenda e da Trilha do Corisco, cerca de 1 km além da Casa da Farinha. Figura retirada de Joly & Martinelli (2006).

O ambiente físico de L1 e L2 apresenta algumas diferenças, como nas quantidades de fósforo (P), enxofre (S), acidez potencial (H+Al), soma de bases (SB, soma das quantidades de potássio, cálcio, magnésio e sódio), argila e silte no solo, nas porcentagens de nitrogênio e de argila mais silte no solo, na altitude (e seus fatores associados, como temperatura e incidência de ventos) e na amplitude de inclinação do terreno. Outros fatores, como pH e porcentagem de carbono no solo, e abertura de dossel não apresentam diferenças marcantes entre as duas parcelas (Tabela 1). Os dados de solo foram obtidos a partir de 32 tradagens na camada 0 – 5 cm do solo, distribuídas em forma de grade (Martins 2010); os dados de topografia foram obtidos a partir da medida da altitude do vértice de cada subparcela nos 2 ha (Joly & Martinelli 2006) e as variáveis aqui analisadas foram calculadas por André Rochelle; os dados de abertura de dossel foram obtidos a partir de fotos hemisféricas tiradas no centro de cada subparcela nos 2 ha e analisadas com o *software Data Gap Analyzer* 2.0 (Frazer *et al.* 1999; Joly & Martinelli 2010).

Tabela 1: Média ± desvio padrão dos valores de características do solo, abertura do dossel e características topográficas para duas parcelas de 1 ha cada (L1 e L2) da Floresta Ombrófila Densa de Terras Baixas no Núcleo Picinguaba do Parque Estadual da Serra do Mar. Para mais informações sobre os dados apresentados, favor ver texto.

	L1	L2
pH $CaCl_2$	3.67 ± 0.35	3.58 ± 0.25
P (mg x kg^{-1})	17.27 ± 7.21	122.50 ± 48.44
S (mg x kg^{-1})	30.19 ± 12.13	9.34 ± 6.40
H+Al (mmolc x kg^{-1})	128.50 ± 53.29	17.86 ± 9.31
SB (mmolc x kg^{-1})	13.59 ± 6.87	22.11 ± 12.85
C (%)	5.00 ± 1.19	4.03 ± 2.46
N (%)	0.38 ± 0.09	0.29 ± 0.17
Argila	40.90 ± 8.41	22.05 ± 7.72
Silte	10.62 ± 3.94	5.64 ± 2.15
Argila+silte (%)	51.52 ± 10.22	27.69 ± 9.34
Abertura do dossel (%)	7.50 ± 1.84	7.00 ± 2.09
Altitude (m)	45.49 ± 4.85	73.22 ± 4.90
Ampliture de inclinação (m)	3.42 ± 1.34	2.59 ± 1.24

Apesar das diferenças no ambiente físico, a composição florística e a estrutura da comunidade em L1 e L2 são muito similares: a altura das árvores varia entre ca. 1,6 m e 25 m, e o diâmetro do caule varia entre ca. 5 cm e 94 cm. Foram encontradas cerca de 1.200 árvores pertencentes a 145 espécies em cada parcela (Joly & Martinelli 2006). Além disto, estão presentes um sobosque denso, sub-dossel, dossel e árvores emergentes (Morellato & Haddad 2000), apesar de nem sempre ser possível distinguir claramente os estratos vegetacionais (Cazotto *et al.*, dados não publicados). Também é comum a presença de palmeiras, epífitas, samambaias e bromélias (Morellato & Haddad 2000). As espécies arbóreas mais abundantes pertencem aos gêneros *Bathysa* (Rubiaceae), *Chrysophyllum* (Sapotaceae), *Coussarea* (Rubiaceae), *Eugenia* (Myrtaceae), *Euterpe* (Arecaceae), *Garcinia* (Clusiaceae), *Guapira* (Nyctaginaceae), *Marlierea* (Myrtaceae), *Mollinedia* (Monimiaceae), *Myrcia* (Myrtaceae), *Rustia* (Rubiaceae), *Sloanea* (Elaeocarpaceae), *Syagrus* (Arecaceae) e *Virola* (Myristicaceae; Joly & Martinelli 2006).

ESPÉCIES ESTUDADAS

Nós selecionamos as espécies estudadas a partir de duas listas florísticas obtidas para o Núcleo Picinguaba anteriormente ao início do Projeto Temático. Uma das listas foi elaborada para espécies que ocorrem entre o nível do mar e 100 m de altitude (Pedroni 2001), e que também continha uma descrição morfológica dos frutos dos indivíduos amostrados, o que auxiliou na escolha das espécies aqui estudadas. A outra lista florística foi elaborada para espécies que ocorrem entre o nível do mar e 1.000 m de altitude (Lacerda 2001). Ambas amostragens incluíram as parcelas aqui estudadas. Com base na descrição morfológica dos frutos de Pedroni (2001), nós selecionamos espécies ornitocóricas, que é a síndrome de dispersão mais importante na área de estudo (Cazotto *et al. in prep.*). Dentro da ornitocoria, selecionamos espécies com diásporos carnosos com uma única semente relativamente grande e dura, a qual pode ser facilmente encontrada em coletores de sementes. Espécies com estas características e que também apresentam uma alta abundância de indivíduos pequenos na área de estudo são *Faramea picinguabae* M. Gomes (Rubiaceae), *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae) e *Pourouma guianensis* Aubl. (Urticaceae; Fig. 3-5).

Apesar de existirem relatos de mamíferos, especialmente macacos, consumindo frutos de diferentes espécies de *Pourouma* (*e.g.*, Kelly 1995, Riba-Hernández *et al.* 2003, Catenacci *et al.* 2009), acreditamos que as aves são o principal agente dispersor de *P. guianensis* na área de estudo, onde mamíferos diurnos, como primatas, não são observados desde 1.990 (Pedroni 2001). No entanto, o padrão de deposição de sementes desta espécie pode ser menos agregado do que o de *F. picinguabae* e *M. schottiana*, já que as sementes de *P. guianensis* são maiores. Por isto, elas podem ser dispersas por aves maiores, que são capazes de carregá-las para distâncias mais longas a partir da planta parental (Wheelwright 1985, Seidler & Plotkin 2006). Além disto, indivíduos reprodutivos de *P. guianensis* são muito mais altos do que os das outras duas espécies, o que deve resultar em um maior espalhamento das sementes em torno da planta parental.

Faramea picinguabae é uma arvoreta ou árvore geralmente com menos de 10 m de altura. A espécie parece ser tolerante à sombra e suas plântulas são capazes de se estabelecer em habitats que variam de clareiras ao sobosque escuro da floresta, assim como descrito para *F. occidentalis* (Schupp 1988). *Faramea picinguabae* é uma das espécies mais abundantes na Floresta Ombrófila Densa de Terras Baixas no Núcleo Picinguaba, apesar de ter sido pouco amostrada pela equipe do Projeto Temático por raramente atingir PAP maior ou igual a 15 cm (*observ. pes.*). A espécie é homóica e os adultos se reproduzem duas ou três vezes ao ano, todos os anos. Os indivíduos que produzem flores também produzem frutos (*observ. pes.*; Eliana Gressler, *comun. pes.*) e geralmente há três ou quatro frutos por infrutescência. Os frutos são drupóides, roxos a atropúrpuros quando maduros, com ca. 1,5 cm – 2 cm de diâmetro e remanescentes do cálice floral aderidos; há apenas uma semente ou, raramente, duas, que não excedem 1 cm de diâmetro (*observ. pes.*; Müller 1881-1888; Fig. 3).

Fig. 3: Frutos maduros de *Faramea picinguabae* M. Gomes (Rubiaceae).

Mollinedia schottiana é uma árvore geralmente com menos de 10 m de altura. A espécie é uma das mais abundantes na Floresta Ombrófila Densa de Terras Baixas no Núcleo Picinguaba (Joly & Martinelli 2006). *Mollinedia schottiana* é dióica e os adultos se reproduzem uma vez ao ano, todos os anos (*observ. pes.*; Eliana Gressler, *comun. pes.*). Os representantes da família Monimiaceae caracterizam-se por apresentarem ginoicia apocárpica e carpelos uniovulados (Endress & Ingersheim 1997), que se desenvolvem em um receptáculo floral mais ou menos plano ou côncavo (Endress 1980, Lorence 1985). Após a polinização, cada carpelo restante nas flores do gênero *Mollinedia* desenvolve-se em um frutículo séssil com uma semente, semelhante a uma drupa. Os frutículos provenientes da mesma inflorescência são apresentados no receptáculo floral, que se inverte e mostra uma cor clara, contrastante com a dos frutículos maduros (observação pessoal; Romanov *et al.* 2007). Os frutículos de *M. schottiana* têm ca. 1 cm de diâmetro e coloração atropúrpura quando maduros, e suas sementes são apenas um pouco menor do que cada frutículo (observação pessoal; Fig. 4).

Fig. 4: Frutos imaturos (esquerda) e maduros (direita) de *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae).

Pourouma guianensis é uma árvore heliófila (van der Meer *et al.* 1998, Kobe 1999, Rijkers *et al*. 2000 para outras espécies do gênero) e emergente, atingindo até 20 m de altura na área de estudo. Poucos indivíduos ocorrem em cada parcela (Joly & Martinelli 2006). A espécie é dióica e os adultos se reproduzem uma vez ao ano, todos os anos. Os indivíduos femininos produzem frutos em infrutescências. Cada fruto é uma drupa atropúrpura com ca. 1,5 cm de diâmetro e uma única semente, que é apenas um pouco menor do que o fruto (observação pessoal, Lorenzi 1998, Backes & Irgang 2004; Fig. 5).

Fig. 5: Frutos imaturos de *Pourouma guianensis* Aubl. (Urticaceae). Foto retirada de http://www6.ufrgs.br/fitoecologia/florars/open_sp.php?img=2129 em 17 de maio de 2011.

LITERATURA CITADA

Alves, L.F. 2000. Estrutura, dinâmica e alometria de quatro espécies arbóreas tropicais. Tese de doutorado, Universidade Estadual de Campinas, Campinas.

Alves, L.F.; Vieira, S.A.; Scaranello, M.A.; Camargo, P.B.; Santos, F.A.M.; Joly, C.A. & Martinelli, L.A. 2010. Forest structure and abovegroung biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). Forest Ecology and Management 260: 679-691.

Assis, M.A. 1999. Florística e caracterização das comunidades vegetais da Planície Costeira de Picinguaba, Ubatuba/SP. Tese de Doutorado, Universidade Estadual de Campinas, Campinas.

Augspurger, C.K. & Kelly, C.K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects for dispersal distance, seedling density, and light conditions. Oecologia 61: 211–217.

Backes, P. & Irgang, B. 2004. Mata Atlântica – As árvores e a paisagem. Ed. Paisagem do Sul, Porto Alegre.

Bawa, K.S. 1974. Breeding systems of tree species of a Lowland tropical community. Evolution 28: 85-92.

Bawa, K.S. & Opler, P.A. 1975. Dioecism in tropical forest trees. Evolution 29: 167-179.

Bell, T.; Freckleton, R.P. & Lewis, O.T. 2006. Plant pathogens drive density-dependent seedling mortality in a tropical tree. Ecology Letters 9: 569-574.

Bleher, B.; Oberrath, R. & Böhning-Gaese, K. 2002. Seed dispersal, breeding system, tree density and the spatial pattern of trees – a simulation approach. Basic and Applied

Ecology 3: 115-123.

Boerner, R.E.J. & Brinkman, J.Á. 1996. Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. Bulletin of the Torrey Botanical Club 123: 309-317.

Burkey, T.V. 1994. Tropical tree species diversity: a test of the Janzen-Connell model. Oecologia 97: 533–540.

Calviño-Cancela, M. 2002. Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empetraceae): the importance of unspecialized dispersers for regeneration. Journal of Ecology 90: 775–784.

Catenacci, L.S.; De Vleeschouwer, K.M. & Nogueira-Filho, S.L.G. 2009. Seed dispersal by golden-headed lion tamarins *Leontopithecus chrysomelas* in Southern Bahian Atlantic Forest, Brazil. Biotropica 41: 744-750.

Cazotto, L.P.D.; Martins, V.F. & Santos, F.A.M. *in prep.* Dispersal spectrum of four tree physiognomies along an altitudinal gradient of the Brazilian Atlantic Rainforest.

Clark, D.A. & Clark, D.B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell Model. American Naturalist 124: 769-788.

Clark, D.B. & Clark, D.A. 1989. The role of physical damage in the seedling mortality regime of a neotropical Rain Forest. Oikos 55: 225-230.

Clark, D.B.; Palmer, M.W. & Clark, D.A. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology 80: 2662–2675.

Condit, R.; Ashton, P.S.; Baker, P.; Bunyavejchewin, S.; Gunatilleke, S.; Gunatilleke, N.; Hubbell, S.P.; Foster, R.B.; Itoh, A.; LaFrankie, J.V.; Lee, H.S.; Losos, E.; Manakaran, N.; Sukumar, R. & Yamakura, T. 2000. Spatial patterns in the distribution of tropical tree species. Science 288: 1414–1418.

Connell, J.H. 1971. On the role of natural enemies in pre- venting competitive exclusion in some marine animals and in rain forest trees. *In* Den Boer, P.J. & Gradwell, G.R. (eds.) Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, pp 298–310.

CPTEC – Centro de Previsão de Tempo e Estudos Climáticos 2010. Dados metereológicos, hidrológicos e ambientais de Plataformas de Coletas de Dados no PESM Picinguaba. http://satelite.cptec.inpe.br/PCD/metadados.jsp?uf=25&id=30887&tipo=AGROMET. 08 de abril de 2010.

Cruden, R.W. & Lloyd, R.M. 1995. Embryphytes have equivalent sexual phenotypes and breeding systems: why not a common terminology to describe them? American Journal of Botany 82: 816-825.

Dale, M.R.T. 1999. Spatial patterns analysis in plant ecology. Cambridge University Press, Cambridge.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72: 1066–1075.

Dickie, I.A.; Schnizter, S.A.; Reich, P.B. & Hobbie, S.E. 2007. Is oak establishment in old fields and savanna openings context dependent? Journal of Ecology 95: 309–320.

Endress, P.K. 1980. Ontogeny, function and evolution of extreme floral construction in Monimiaceae. Plant Systematics and Evolution 134: 79-120.

Endress, P.K. & Ingersheim, A. 1997. Gynoecium diversity and systematic of the Laurales. Botanical Journal of the Linnean Society 125: 93-168.

Fenner, M. 1987. Seedlings. New Phytologist 106(suppl): 35–47.

Forman, R.T.T. & Hahn, D.C. 1980. Spatial patterns of trees in a Caribbean semievergreen forest. Ecology 61: 1267–1274.

Franklin, J.F.; Shugart, H.H. & Harmon, M.E. 1987. Tree death as an ecological process. Bioscience 37: 550–556.

Frazer, G.W.; Canham, C.D. & Lertzman, K.P. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs - Users manual and program documentation. Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.

Fundação SOS Mata Atlântica 2011. Mata Atlântica. www.sosmatatlantica.org.br. 23 de abril de 2011.

García, D.; Obeso, J.R. & Martínez, I. 2005. Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? Journal of Ecology 93: 693-704.

Getzin, S.; Dean, C.; He, F.; Trofymow, J.A.; Wiegang, K. & Wiegang, T. 2006. Spatial pattern and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. Ecography 29: 671-682.

Gómez-Aparicio, L.; Gómez, J.M. & Zamora, R. 2005. Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate. Journal of Ecology 93: 1194–1202.

Hampe, A. 2004. Extensive hydrochory uncouples spatial-temporal patterns of seedfall and seedling recruitment in a “bird-dispersed” riparian tree. Journal of Ecology 92: 979-807.

Hampe, A.; García-Castaño, J.L.; Schupp, E.W. & Jordano, P. 2008. Spatial-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. Journal of Ecology 96: 668-678.

Hanley, M.E.; Fenner, M. & Edwards, P.J. 1995. The effect of seedling age on the likelihood of herbivory by the slug *Deroceras reticulatum*. Functional Ecology 9: 754-759.

Harms, K.E.; Wright, S.J.; Calderon, O.; Hernandez, A. & Herre, E.A. 2000. Pervasive density-dependent recruitment enhances seedlings diversity in a tropical forest. Nature 404: 493-495.

He, F.; Legendre, P. & LaFrankie, J.V. (1987) Distribution patterns of tree species in a Malaysian tropical rain forest. Journal of Vegetation Science 8: 105-114.

He, F. & Duncan, R.P. 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. Journal of Ecology 88: 676-688.

Herrera, C.M.; Jordano, P.; López-Soria, L. & Amat, J.A. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs 64: 315–344.

Houle, G. 1995. Seed dispersal and seedling recruitment: the missing link (s). Écoscience 2: 238–244.

Houle, G. 1998. Seed dispersal and seedling recruitment of *Betula alleghanienesis*: spatial inconsistency in time. Ecology 79: 807-818.

Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299–1309.

Hubbell, S.P. 1980. Seed predation and coexistence of tree species in tropical forests. Oikos 35: 214-229.

Hutchings, M.J. 1997. The structure of plant populations. *In* Crawley, M.J. (ed.) Plant Ecology. Blackwell Science, Oxford, pp. 325–358.

Itoh, A.; Yamakura, T.; Ogino, K.; Lee, H.S. & Ashton, P.S. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia. Plant Ecology 132: 121-136.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501–528.

Joly, C.A. & Martinelli, L.A. (Coord.) 2004. Projeto "Composição Florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar". Projeto Temático Biota/FAPESP 03/12595-7.

Joly, C.A. & Martinelli, L.A. (Coord.) 2006. Primeiro relatório "Composição florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar". Projeto Temático Biota/FAPESP 03/12595-7.

Joly, C.A. & Martinelli, L.A. (Coord.) 2010. Quinto relatório "Composição florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar". Projeto Temático Biota/FAPESP 03/12595-7.

Joly, C.A.; Martinelli, L.A.; Alves, L.F.; Vieira, S.A.; Tamashiro, J.Y.; Aidar, M.P.M.; Camargo, P.B.; Assis, M.A. & Bernacci, L.C. 2008. As Parcelas Permanentes do Projeto Temático Biota Gradiente Funcional: Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do

Mar, Estado de São Paulo, Brasil. *In:* Sanquetta, C.R. (Ed.) Experiências de monitoramento no bioma Mata Atlântica com o uso de parcelas permanentes. RedeMAP: Rede de Parcelas Permanentes dos Biomas Mata Atlântica e Pampa & Funpar, Curitiba, Brasil, pp. 109-148.

Jordano, P. & Herrera, C.M. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. Écoscience 2: 230–237.

Kelly, C.K. 1995. Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. Oecologia 102: 377-388.

Kitajima, K. & Fenner, M. 2000. Ecology of seedling regeneration. *In* Fenner, M. (ed.) Seeds. Cabi publishing, Wallingford, pp. 331–359.

Kobe, R.K. 1999. Light gradient portioning among tropical tree species through differential seedling mortality and growth. Ecology 80: 187-201.

Kobe, R.K.; Pacala, S.W.; Silander, J.A. & Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5: 517-532.

Köppen, W. 1948. Climatologia. México: Fondo de Cultura Económica.

Lacerda, M.S. 2001. Composição florística e estrutura da comunidade arbórea num gradiente altitudinal da Mata Atlântica. Tese de doutorado, Universidade Estadual de Campinas, Campinas.

Levine, J.M. & Murrell, D.J. 2003. The community-level consequences of seed dispersal patterns. Annual Review of Ecology, Evolution and Systematics 34: 549-574.

Loiselle, B.A.; Ribbens, E. & Vargas, O. 1996. Spatial and temporal variation of seed rain in a Tropical Lowland Wet Forest. Biotropica 28: 82-95.

Lorence, D.H. 1985. A monograph of the Monimiaceae (Laurales) in the Malagasy region (SW Indian Ocean). Annals of the Missouri Botanical Garden 72: 142-210.

Lorenzi H. 1998. Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas do Brasil. Vol. 2, 2^a ed., Editora Plantarum, Nova Odessa.

Mack, A.L. 1998. The potential impact of small-scale physical disturbance on seedlings in a Papuan rainforest. Biotropica 30: 547-552.

Maetô, K. & Fukuyama, K. 1997. Mature tree effect of *Acer mono* on seedling mortality due to insect herbivory. Ecological Research 12: 337-343.

Martins, S.C. 2010. Caracterização dos solos e serapilheira ao longo do gradiente altitudinal da Mata Atlântica, estado de São Paulo. Tese apresentada ao Centro de Energia Nuclear na Agricultura na Universidade de São Paulo, para obtenção do título de Doutor em Ciências, área de concentração Química na Agricultura e no Ambiente. Piracicaba.

McCanny, S.J. 1985. Alternatives in parent-offspring relationships in plants. Oikos 45: 148–149.

McCanny, S.J. & Cavers, P.B. 1987. The escape hypothesis: a test involving a temperate, annual grass. Oikos 49: 67–76.

Morellato, L.P.C. & Haddad, C.F.B. 2000. Introduction: The Brazilian Atlantic Forest. Biotropica 32: 786–792.

Morellato, L.P.C.; Talora, D.C.; Takahasi, A.; Bencke, C.S.C.; Romera, E.C. & Ziparro, V. 2000. Phenology of Atlantic rain forest trees: a comparative study. Biotropica 32: 811-823.

Murrell, D.J. 2009. On the emergent spatial structure of size-structured populations: when does self-thinning lead to a reduction in clustering? Journal of Ecology 97: 256-266.

Müller, J. 1881-1888. Rubiaceae. *In* Martius, C.F.P. & Eichler, A.G. (eds.) Flora Brasiliensis. Vol. VI, Pars 5, Wheldon & Wesley Ltd, New York, pp. 208-209.

Myers, N.; Mittermeier, R.A; Mittermeier, C.G.; Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 852-858.

Nanami, S.; Kawaguchi, H. & Yamakura, T. 1999. Dioecy-induced spatial patterns of two codominant tree species, *Podocarpus nagi* and *Neolitsea aciculata*. Journal of Ecology 87: 678–687.

Nathan, R. & Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal: their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278–285.

Nathan, R.; Safriel, U.N.; Noi-Meir, I. & Schiller, G. 2000. Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. Ecology 81: 2156–2169.

Packer, A. & Clay, K. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404: 278-281.

Pedroni, F. 2001. Aspectos da estrutura e dinâmica da comunidade arbórea na Mata Atlântica de Planície e Encosta em Picinguaba, Ubatuba, SP. Doctoral thesis, Universidade Estadual de Campinas, Campinas.

Pigot, A.L. & Leather, S.R. 2008. Invertebrate predators drive distance-dependent patterns of seedling mortality in a temperate tree *Acer pseudoplatanus*. Oikos 117: 521-530.

Pitman, N.C.A.; Terborgh, J.; Silman, M.R. & Nuez, P. 1999. Tree species distributions in an upper Amazonian forest. Ecology 80: 2651–2661.

Plotkin, J.B.; Potts, M.D.; Leslie, N.; Manokaran, N.; LaFrankie, J. & Ashton, P.S. 2000. Species-area curves, spatial aggregation, and habitat specialization in tropical forests.

Journal of Theoretical Biology 207: 81–99.

Ponçano, W.L.; Carneiro, C.D.R.; Bistrichi, C.A.; Almeida, F.F.M. & Pradini, F.L. 1981. Mapa geomorfológico do estado de São Paulo. Vol. 1, Instituto de Pesquisas Tecnológicas do Estado de São Paulo, São Paulo.

Portela, R.C. & Santos, F.A.M. 2009. Mortality and mechanical damage of seedlings in different size fragments of the Brazilian Atlantic Forest. Tropical Ecology 50: 267-275.

Rey, P.J. & Alcantara, J.M. 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology* 88: 622–633.

Rey, P.J.; Ramírez, J.M.; Sánchez-Lafuente, A.M. & Alcántara, J.M. 2006. Seed- vs. microsite-limited recruitment in a myrmecochorous herb. Plant Ecology 184: 213-222.

Riba-Hernández, P.; Stoner, K.E. & Lucas, P.W. 2003. The sugar composition of fruits in the diet of spider monkeys (*Ateles geoffroyi*) in Tropical Humid Forest in Costa Rica. Journal of Tropical Ecology 19: 709-716.

Rijkers, T.; de Vries, P.J.; Pons, T.L. & Bongers, F. 2000. Photosynthetic induction in saplings of three shade-tolerant tree species: comparing understorey and gap habitats in a French Guiana rain forest. Oecologia 125: 331-340.

Romanov, M.S.; Endress, P.K.; Bobrov, A.V.F.C.H.; Melikian, A.P. & Bejerano, A.P. 2007. Fruit structure and systematics of Monimiaceae *s.s.* (Laurales). Botanical Journal of the Linnean Society 153: 265-285.

Scariot, A. 2000. Seedling mortality by litterfall in Amazonian forest fragments. Biotropica 32: 662-669.

Schupp, E.W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51: 71–78.

Schupp, E.W. 1995. Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82: 399–409.

Seidler, T.G. & Plotkin, J.B. 2006. Seed dispersal and spatial pattern in tropical trees. PLoS Biology 4: 2132-2137.

Sentelhas, P.C.; Marin, F.R.; Ferreria, A.S. & Sá, E.J.S. 2003. Banco de dados climáticos do Brasil. http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=&COD=492. 08 de abril de 2010.

SMA – Secretaria do Meio Ambiente. 1996. Atlas das unidades de conservação do estado de São Paulo. Parte 1 – Litoral, Secretaria do Meio Ambiente & CESP, São Paulo.

SOS Mata Atlântica/INPE/ISA. 1998. Atlas da evolução dos remanescentes florestais e ecossistemas associados ao domínio da Mata Atlântica no período 1990–95. SOS Mata Atlântica/INPE/ISA, São Paulo, SP.

Sterner, R.W.; Ribic, C.A. & Schatz, G.E. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. Journal of Ecology 74: 621-633.

Svenning, J.C. 2001. Environmental heterogeneity, recruitment limitation and the mesoscale distribution of palms in a tropical montane rainforest (Maquipucuna, Ecuador). Journal of Tropical Ecology 17: 97–113.

Svenning, J.C. & Skov, F. 2005. The relative roles of environment and history as controls of tree species composition and richness in Europe. Journal of Biogeography 32: 1019–1033.

van der Meer, P.J.; Sterck, F.J. & Bongers, F. 1998. Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French Guiana. Journal of Tropical Ecology 14: 119-137.

Wheelwright, N.T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66: 808-818.

Wiegand, T.; Gunatilleke, C.V.S.; Gunatilleke, I.A.U.N. & Okuda, T. 2007. Analyzing the spatial structure of a Sri Lankan tree species with multiple scales of clustering. Ecology 88: 3088-3102.

Wright, S.J. 2002. Plant diversity in tropical forests: a review of the mechanisms of species coexistence. Oecologia 130: 1-14.

CAPÍTULO 1

Densidade de fontes de semente, dispersão de sementes, processos pós-dispersão e a agregação de espécies arbóreas em uma floresta tropical

Valéria Forni Martins & Flavio Antonio Maës dos Santos

Resumo estendido

A estrutura espacial de espécies arbóreas é potencialmente influenciada por: (1) densidade das fontes de semente, (2) dispersão de sementes e (3) processos pós-dispersão. A densidade das fontes de semente, por sua vez, é determinada pela densidade de adultos potencialmente reprodutivos e pelo sistema reprodutivo da espécie. Populações de espécies dióicas e que ocorrem em baixa densidade tendem a ser mais agregadas e gerar plântulas que são mais espacialmente associadas às fontes de semente do que populações de espécies homóicas e que ocorrem em alta densidade. Espécies arbóreas tropicais são geralmente agregadas devido à dispersão local. Isto pode resultar em maior recrutamento perto das plantas parentais, de forma que a relação espacial entre estádios ontogenéticos é sempre positiva e os adultos são tão agregados quando as plântulas. No entanto, a mortalidade de sementes e plântulas pode ser tão alta perto das plantas parentais que as plântulas somente conseguem recrutar a alguma distância do adulto. Consequentemente, a relação espacial entre estádios é negativa e as populações apresentam uma redução na agregação ao longo da ontogenia.

A mortalidade em áreas com alta densidade de plantas, como próximo dos adultos, pode resultar da ação de inimigos naturais, modificação do microambiente e competição intraespecífica, também conhecida como auto-desbaste. Este é um fator importante para a mortalidade de plantas maiores em florestas tropicais e leva a uma forte diminuição na agregação ao longo da ontogenia de espécies que ocorrem em alta densidade, enquanto espécies menos densas tendem a apresentar uma diminuição fraca ou até mesmo um aumento na agregação. Outros processos pós-dispersão podem resultar em um aumento na agregação ao longo da ontogenia ao invés de um decréscimo. Por exemplo, a heterogeneidade ambiental comumente encontrada em florestas tropicais pode resultar na mortalidade de plântulas localizadas em microhabitats que são menos favoráveis para a espécie. Assim, os indivíduos tendem a sobreviver mais em microhabitats com maior favorabilidade, resultando em adultos que são mais agregados do que plântulas. Além disto, interações positivas, como associações com microrrizas e facilitação, podem resultar em um padrão similar à heterogeneidade ambiental, já que somente as plantas que ocorrem próximas de outros organismos interagem e se beneficiam pelas interações positivas.

O objetivo deste estudo foi detectar a influência da densidade das fontes de semente, a dispersão de sementes e os processos pós-dispersão na estrutura espacial de três espécies arbóreas da Floresta Ombrófila Densa de Terras Baixas no litoral norte do estado de São Paulo. *Faramea picinguabae* é homóica e os indivíduos reprodutivos ocorrem em alta densidade; *Mollinedia schottiana* é dióica e os indivíduos femininos ocorrem em densidade intermediária; *Pourouma guianensis* também é dióica, mas os indivíduos femininos ocorrem em densidade muito baixa.

Considerando a densidade de adultos potencialmente reprodutivos e o sistema reprodutivo, esperamos encontrar que: (1) a agregação é maior para todos os estádios ontogenéticos de *Pourouma* e menor para todos os estádios de *Faramea*; (2) a associação espacial entre plântulas e fontes de semente é mais forte para *Pourouma* e mais fraca para *Faramea*, e (3) a agregação ao longo da ontogenia se mantém constante, diminui ou aumenta devido aos processos pós-dispersão; se ela diminuir devido ao auto-desbaste, *Faramea* deve apresentar o maior decréscimo e *Pourouma*, o menor. Como não há replicas para densidade de adultos potencialmente reprodutivos e sistema reprodutivo, não podemos desenvolver testes formais para determinarmos sua influência na estrutura espacial de espécies arbóreas tropicais. No entanto, se estes fatores afetarem fortemente a estrutura espacial das espécies estudadas, esperamos detector alguma influência na agregação, na associação espacial entre plântulas e fontes de semente, e na alteração da agregação ao longo da ontogenia de *Faramea*, *Mollinedia* e *Pourouma*. Por último, também esperamos que (4) as relações espaciais entre plântulas e jovens, e entre todos os estádios ontogenéticos subsequentes de uma única espécie sejam positivas se a mortalidade não desacoplar os padrões de recrutamento da dispersão local; no entanto, o auto-desbaste deve desacoplar a distribuição de estádios mais avançados.

Nós procuramos sistematicamente e marcamos todos os indivíduos das três espécies estudadas em duas parcelas de 1 ha cada. Então, nós observamos as características morfológicas dos indivíduos para identificar os estádios ontogenéticos de cada uma das espécies. Por último, também mapeamos todos os indivíduos amostrados e calculamos sua posição dentro das parcelas. Para determinar o padrão espacial de cada estádio das três espécies nas parcelas, utilizamos a função K de Ripley. Também usamos a função K bivariada para determinar se havia associações entre os estádios ontogenéticos subsequentes da mesma espécie dentro de cada parcela.

Todos os estádios ontogenéticos das três espécies foram agregados, especialmente em pequenas classes de distância. *Pourouma* apresentou a maior agregação dos estádios e

Mollinedia, a menor. A associação espacial mais forte entre fontes de semente e plântulas foi encontrada para *Faramea* e *Pourouma*, e a mais fraca, para *Mollinedia*. A agregação diminuiu ao longo da ontogenia de *Mollinedia* e *Pourouma*, sendo o menor decréscimo observado para *Pourouma*. Por outro lado, a agregação se manteve constante ou aumentou ao longo da ontogenia de *Faramea*. Fontes de semente estiveram sempre associadas espacialmente às plântulas, que estiveram associadas aos jovens. Porém, estádios mais avançados apresentaram independência espacial em alguns casos.

Densidade de adultos potencialmente reprodutivos e sistema reprodutivo não afetaram fortemente a estrutura espacial das três espécies estudadas. Isto deve ocorrer porque a dispersão e os processos pós-dispersão provavelmente amenizam seus efeitos na estrutura espacial das populações. Por outro lado, a dispersão gera agregação, que pode aumentar ou diminuir ao longo da ontogenia de acordo com as respostas de cada espécie ao ambiente abiótico e biótico. Para indivíduos em estádios ontogenéticos mais avançados, o auto-desbaste resulta na falta de associação espacial entre estádios.

ORIGINAL ARTICLE

Density of seed sources, seed dispersal, post-dispersal processes and the aggregation of tree species in a tropical forest[a]

Valéria F. Martins[1,*] and Flavio A. M. dos Santos[2]

[1]*Programa de Pós-Graduação em Ecologia, Institute of Biology, CP 6109, University of Campinas - UNICAMP, 13083-970, Campinas, SP, Brazil,* [2]*Department of Plant Biology, Institute of Biology, CP 6109, University of Campinas - UNICAMP, 13083-970, Campinas, SP, Brazil.*

Aggregation of tree species in a tropical forest

[*]For correspondence. Email valeriafm@gmail.com

---

[a] Format and style: Annals of Botany

- *Background and Aims* The spatial structure of trees is potentially influenced by density of seed sources, seed dispersal and post-dispersal processes. The aim of this study was to detect the influence of each of these factors on the spatial structure of three ornithochorous tree species of a Lowland Atlantic Rainforest in Southeastern Brazil. *Faramea picinguabae* is homoecious and reproductive individuals occur at high density, *Mollinedia schottiana* is dioecious and feminine individuals occur at intermediate density, and *Pourouma guianensis* is also dioecious, but feminine individuals occur at very low density.

Methods We carried out a systematic survey of all individuals of the three species within two 1-ha plots. We identified their ontogenetic stages, mapped every individual and calculated its position within the plots. We used Ripley's *K*-function to determine the spatial pattern of the individuals in each ontogenetic stage and the bivariate *K*-function to check for spatial associations between consecutive stages.

- *Key Results* All stages of the three species were aggregated, especially in small distance classes. *Pourouma* presented the highest aggregation of the stages and *Mollinedia*, the lowest. The strongest spatial association between seed sources and seedlings was found for *Faramea* and *Pourouma*, and the weakest, for *Mollinedia*. The aggregation decreased through ontogeny for *Mollinedia* and *Pourouma*, being the lowest decrease observed for the latter. On the other hand, the aggregation was held constant or increased through ontogeny for *Faramea*. Seed sources were always spatially associated to seedlings, which were associated to juveniles. Nonetheless, more developed stages were sometimes spatially independent.
- *Conclusions* Density of seed sources does not strongly affect the spatial structure of the three species. On the other hand, seed dispersal generates aggregation, which can increase or decrease through ontogeny accordingly to each species' responses to the biotic and abiotic

environment. For individuals of more advanced ontogenetic stages, self-thinning results in the lack of spatial association between stages.

Key words: *Faramea picinguabae*, Lowland Atlantic Rainforest, *Mollinedia schottiana*, Núcleo Picinguaba, Parque Estadual da Serra do Mar, *Pourouma guianensis*, Ripley's *K*-function, spatial structure.

INTRODUCTION

The spatial structure of trees is potentially influenced by density of seed sources, seed dispersal and post-dispersal processes. The density of possible seed sources might be determined by breeding system and tree density (Bleher *et al.*, 2002). Both dioecious and low-density populations tend to be more aggregated and generate seedlings that are more spatially associated to seed sources than those of homoecious (*sensu* Cruden and Lloyd, 1995) and high-density populations. This is because few parents produce seeds in the former, whereas many parents fruit in the latter (Nanami *et al.*, 1999; Condit *et al.*, 2000; Bleher *et al.*, 2002; but see Hubbell, 1979).

For tropical forest tree species, aggregation is commonly observed (e.g., Hubbell, 1979; Boll *et al.*, 2005; Klimas *et al.*, 2007) and seems to be highly linked with seed dispersal (Condit *et al.*, 2000; Svenning, 2001), especially because most seeds fall beneath or near fruiting plants (Janzen 1970; Connell 1971; Clark *et al.*, 1999; Nathan *et al.*, 2000). This can lead to higher recruitment there, so that the spatial relationship between ontogenetic stages is always positive and adults are at least as aggregated as seedlings (Hubbell, 1980). However, seed and seedling mortality may be so high near the parent plant that seedlings can only recruit at some distance from it. As a consequence, the spatial relationship between ontogenetic stages is negative and populations show a reduction in aggregation through ontogeny (Janzen, 1970; Connell, 1971).

Mortality in areas with high plant density such as near the parent can be the outcome of plant natural enemies, microenvironmental modification such as soil mineral alteration and intraspecific competition (Schupp, 1988; Wright, 2002). The latter removes individuals that are close to one another in space, which is known as self-thinning (Sterner *et al.*, 1986; Getzin *et al.*, 2006). Although it is unlikely to be a major factor contributing to seedling mortality in tropical forests, self-thinning is an important process for larger plants such as juveniles and immatures (Hubbell, 1979; Sterner *et al.*, 1986; Condit *et al.*, 2000; Getzin *et al.*, 2006), resulting in a strong decrease in aggregation through ontogeny of high-density populations whereas low-density populations are more likely to show a weak decrease or even an increase in aggregation (Murrell, 2009).

Other post-dispersal processes can lead to an increase in aggregation through ontogeny rather than a decrease. For example, the patchiness common to tropical forests can result in mortality at microhabitats that are less favourable to the species. Therefore, individuals tend to survive more at microhabitats with greater favourability, resulting in adults that are more aggregated than seedlings (Condit *et al.*, 2000). Also, positive interactions such as association with mycorrhiza and facilitation can result in a similar pattern to patchiness, because only the plants that occur close to other organisms interact and benefit from the positive interactions (Dickie *et al.*, 2007).

The aim of this study was to detect the influence of density of seed sources, seed dispersal and post-dispersal processes on the spatial structure of three tree species of a Lowland Atlantic Rainforest (*sensu* Oliveira-Filho and Fontes, 2000) in Southeastern Brazil. *Faramea picinguabae* M. Gomes (Rubiaceae) is homoecious and reproductive individuals occur at high density ("pers. obs."; E. Gressler, Universidade Estadual Paulista "Júlio de Mesquita Filho" - UNESP, Brazil, "pers. comm."); *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae) is dioecious and feminine individuals occur at intermediate density (Joly and Martinelli, 2006; E. Gressler, Universidade Estadual Paulista "Júlio de Mesquita Filho" - UNESP, Brazil, "pers. comm.");

Pourouma guianensis Aubl. (Urticaceae) is also dioecious (Lorenzi, 1998; Backes and Irgang, 2004), but feminine individuals occur at very low density (Joly and Martinelli, 2006).

The three species are ornithochorous, which is the most important dispersal syndrome in the study site (Cazotto *et al.*, “in prep.”). They present fleshy diaspores with only one relatively large, hard seed, which can be easily found in seed traps in future studies. *Faramea picinguabae*, *M. schottiana* and *P. guianensis* were the only species presenting these features and also a great abundance of small individuals in the study site (“pers. obs.”). Although there have been reports of mammals, especially monkeys, consuming fruits of different species of *Pourouma* (e.g., Kelly, 1995; Riba-Hernández *et al.*, 2003; Catenacci *et al.*, 2009), we believe birds are the main dispersal agents of *P. guianensis* in the study site, where diurnal mammals such as primates have not been observed since 1990 (Pedroni, 2001). However, seed deposition patterns of this species may be less aggregated than *F. picinguabae* and *M. schottiana* because its seeds are larger and thus likely to be dispersed by larger birds, which are able to carry them for greater distances from the parent plant (Wheelwright, 1985; Seidler and Plotkin, 2006). Also, reproductive individuals of *P. guianensis* are much taller, which should aid the scattering of seeds.

Considering tree density and breeding system, we expect to find that: (1) the aggregation is the highest for all ontogenetic stages of *P. guianensis* and the lowest for all stages of *F. piginguabae*; (2) the spatial association between seedlings and seed sources is the strongest for *P. guianensis* and the weakest for *F. piginguabae*, and (3) aggregation through ontogeny is held constant, decreases or increases due to post-dispersal processes; if it decreases due to self-thinning, *F. picinguabae* is expected to present the greatest decrease and *P. guianensis*, the lowest decrease. Because there is no replicate for tree density and breeding system, we cannot make formal tests to determine their influence on the spatial structure of tree species. However, if they strongly affect the spatial structure of the species studied, we expect to detect some influence on the aggregation, spatial association between seedlings and seed sources, and alteration of aggregation through ontogeny of *F. picinguabae*, *M. schottiana* and *P. guianensis*. Last, we also expect that (4) the spatial relationships between seedlings and juveniles, and between all further ontogenetic stages of a single species are positive if mortality does not uncouple recruitment patterns from local dispersal; however, self-thinning is likely to uncouple the distribution of more advanced ontogenetic stages.

MATERIALS AND METHODS

Study site

The Brazilian Atlantic Forest is considered one of the world's hotspots for biodiversity conservation (Myers *et al.*, 2000), with only about 7% of its original cover remaining (Fundação SOS Mata Atlântica, 2011). The largest continuous stretch of this vegetation includes the Parque Estadual da Serra do Mar (PESM), SE Brazil. The PESM is a state park that comprises ca. 315,000 ha (SOS Mata Atlântica/INPE/ISA, 1998) and is divided into several administration nucleuses, one of which is Núcleo Picinguaba (23°31' - 23°34'S, 45°02' - 45°05'W). It is located at the mountain range of Serra do Mar, municipality of Ubatuba, northern coast of the state of São Paulo, and comprises ca. 47,500 ha (SMA, 1996). The region has mountainous relief, with altitudes varying between 0 m and 1,200 m (Alves *et al.*, 2010). At Núcleo Picinguaba, temperatures range from 25.5^{o} C in February to 18.4^{o} C in July. There is no marked dry season and rainfall ranges from 376 mm in January to 11 mm in July (Sentelhas *et al.*, 2003). Air relative humidity is always above 80% (Morellato *et al.*, 2000), daylength varies from 15.5 h in May to 9.1 h in October, and winds normally come from ocean and blow southeast at 0.7 m/s – 1.0 m/s (Alves, 2000; CPTEC, 2010).

The Núcleo Picinguaba is the only portion of PESM to reach the coast and, due especially to its great range of altitude, is composed of a mosaic of vegetation physiognomies. We collected data in two 1-ha plots of the Lowland Atlantic Rainforest (ca. 44°48'W, 23°22'S), namely Lowland 1 (L1 hereafter) and Lowland 2 (L2 hereafter). This phytophysiognomy covers mountain slopes from 50 m to 100 m above sea level and occurs in cambisols, which are soils formed recently from the sedimentation of mountain erosion. Many rocky formations and dry stream paths are also observed. Each study plot was divided in 100 sub-plots of 10 m x 10 m, where every living tree whose trunk perimeter at 1.3 m in height was equal to or larger than 15 cm was sampled and identified (Joly *et al.*, 2008).

L1 and L2 present differences in their abiotic environment, such as in the quantity of phosphorous (P), sulphur (S), potential acidity (H+Al), sum of bases (SB, the sum of potassium, calcium, magnesium and sodium quantities), clay and silt in the soil, percentages of nitrogen and clay plus silt in the soil, altitude (and associated factors, such as temperature and wind incidence) and elevation range. Other factors, such as pH and percentage of carbon in the soil, and canopy opening do not present striking differences between the study plots (Table 1). Soil data were obtained from 32 boreholes in the 0 – 5 cm soil layer, regularly distributed in L1 and L2 (Martins, 2010); topographic data were obtained from altitude measurement at each corner of every sub-plot at the two study plots (Joly and Martinelli, 2006); canopy opening data were obtained from hemispheric photographs taken at the centre of each sub-plot in L1 and L2 and analysed with the software Data Gap Analyzer 2.0 (Frazer *et al.*, 1999; Joly and Martinelli, 2010).

Despite differences in the abiotic environment, L1 and L2 present very similar species composition and community structure: tree height ranged from ca. 1.6 m to 25 m, and tree trunk diameter varied between ca. 5 cm (inclusion criteria) and 94 cm. About 1,200 trees of 145 species were sampled in each plot (Joly and Martinelli, 2006). A dense understorey, sub-canopy, canopy and emergent trees are present (Morellato and Haddad, 2000), but sometimes it is not possible to distinguish clearly between the sub-canopy and the understorey, and between the sub-canopy and the canopy (Lara Cazotto, Valéria Martins and Flavio Santos, "unpubl. data"). Lianas, palm trees, epiphytes, ferns, and bromeliads are common (Morellato and Haddad, 2000). Common tree species belong to the genera *Bathysa* (Rubiaceae), *Chrysophyllum* (Sapotaceae), *Coussarea* (Rubiaceae), *Eugenia* (Myrtaceae), *Euterpe* (Arecaceae), *Garcinia* (Clusiaceae), *Guapira* (Nyctaginaceae), *Marlierea* (Myrtaceae), *Mollinedia* (Monimiaceae), *Myrcia* (Myrtaceae), *Rustia* (Rubiaceae), *Sloanea* (Elaeocarpaceae), *Syagrus* (Arecaceae) and *Virola* (Myristicaceae; Joly and Martinelli, 2006).

Species studied

The species studied were selected from two species composition lists for Núcleo Picinguaba. One list contained species that occur between sea level and 100 m of altitude (Pedroni, 2001) as well as a morphological description of the diaspores of the individuals sampled, which aided the selection of the species studied here. The other species composition list contained species that occur between sea level and 1,000 m of altitude (Lacerda, 2001). Both sampling encompassed the two plots of Lowland Atlantic Rainforest studied here.

Faramea picinguabae (*Faramea* hereafter) is a treelet or tree generally less than 10 m in height. It seems to be shade-tolerant and its seedlings are able to establish in habitat ranging from treefall gaps to the dark forest understorey, as do *F. occidentalis* (Schupp, 1988). *Faramea* is one of the most abundant species in the Lowland Atlantic Rainforest of Núcleo Picinguaba, although poorly sampled in previous inventories due to its thin trunk ("pers. obs."). Adults reproduce two to three times a year, every year, and plants that produce flowers also produce fruits ("pers. obs."; E. Gressler, Universidade Estadual Paulista "Júlio de Mesquita Filho" - UNESP, Brazil, "pers. comm."). There are generally three or four fruits per infructescence. Each fruit is a round, ca. 1.5 cm – 2 cm of diameter, purple to dark red when mature drupoid with calyx remains; there is only one seed per fruit, rarely two, which do not exceed 1 cm in diameter ("pers. obs."; Müller, 1881-1888).

Mollinedia schottiana is a tree generally less than 10 m in height. The species is one of the most abundant in the Lowland Atlantic Rainforest of Núcleo Picinguaba (Joly and Martinelli, 2006). Adults reproduce once a year, every year ("pers. obs."; E. Gressler, Universidade Estadual Paulista "Júlio de Mesquita Filho" - UNESP, Brazil, "pers. comm."). The representatives of Monimiaceae are characterized by apocarpous gynoecia with uniovulate carpels (Endress and Ingersheim, 1997), which are borne in a more or less flat or concave floral cup (Endress, 1980; Lorence, 1985). After pollination, *Mollinedia*'s carpels develop into sessile drupelets with only one seed and are presented on the reversed light cream floral cup ("pers. obs."; Romanov *et al.*, 2007). *Mollinedia schottiana* (*Mollinedia* hereafter) produces obovate, ca. 1 cm of diameter, dark red when mature fruitlets, whose seeds are just a little smaller that the fruitlet ("pers. obs.").

Pourouma guianensis (*Pourouma* hereafter) is a light-demanding (van der Meer *et al.*, 1998; Kobe, 1999; Rijkers *et al*., 2000 for other species of the genera), emergent tree that reaches up to 20 m in height in the study site. Few individuals occur in each plot (Joly and Martinelli, 2006). Adults reproduce once a year, every year, and feminine plants produce fruits in infructescences. Each fruit is an obovate, ca. 1.5 cm of diameter, dark red when mature drupe, whose seed is just a little smaller than the fruit ("pers. obs."; Lorenzi, 1998; Backes and Irgang, 2004).

Ontogenetic stage structure

We carried out a systematic survey of all individuals of the three species studied within the two plots. L1 was sampled between Dec. 2007 and Jul. 2008, and L2 was sampled between Apr. and Oct. 2007, periods that together included two fruiting periods ("pers. obs."). All plants found were individually tagged with a number. We considered every ramet as one individual.

To identify the ontogenetic stages of each species, we observed the morphology of leaves and stems, and the presence or absence of embryonic and reproductive structures of all individuals sampled (Gatsuk *et al.*, 1980). We did not sample any plant with embryonic structures only, as it is not possible to undoubtedly identify its species. We could not identify the ontogenetic stage of some individuals of the three studied species due to breakages, cuts and sprouts. We considered the ontogenetic stage of these plants as undetermined.

During the sampling period, we observed flowers and fruits in some individuals of *Faramea* as small as 0.64 m and in some individuals of *Mollinedia* as small as 2.5 m. Because we could not distinguish immatures and adults of both species based on their morphology, we monitored monthly between Nov. 2008 and Oct. 2009 every plant of equal or greater height than the smaller reproductive individual of each species in order to determine whether they were reproductive or not. We also monitored individuals of *Pourouma* greater than 5 m, since we could not distinguish large immatures and adults based on their morphology. The individuals of the three studied species that did not reproduce during the year of observation were considered immatures, while individuals that reproduced were considered adults. During the monthly observations, we also determined if reproductive plants of *Mollinedia* and *Pourouma* were feminine or masculine, based on flower morphology or presence of fruits. We removed from observations the plants that had flowered or fruited in the previous months, as they had already been identified as feminine or masculine adults.

Spatial structure

We mapped every individual sampled using a measuring tape (accurate to ± 1 cm). To do that, we measured the distance from the plant to two laterals of the sub-plot, each of which we had previously determined as the x-axis or the y-axis of a grid. Therefore, we could calculate the position of each individual within L1 and L2, considering its position inside the sub-plots and the position of the sub-plots inside the plots.

Data analyses

To determine the ontogenetic stage structure of the three populations in the plots, we used frequency distributions of the individuals in the ontogenetic stages. We used Kolmogorov-Smirnov tests (Zar, 1999) to compare the ontogenetic stage distributions of each species between L1 and L2. We also compared the ontogenetic stage distributions of pairs of species within the same plot, using Kolgomorov-Smirnov tests with Bonferroni correction for sequential tests (Rice, 1989). For comparisons involving *Faramea* (three ontogenetic stages identified), we created one class with the first two ontogenetic stages of *Mollinedia* and *Pourouma* (four ontogenetic stages identified), so that the two species in the analysis would have the same number of classes. We did not include individuals of undetermined ontogenetic stages in the analyses. We used SYSTAT 11.0 to perform the analyses.

We used Ripley's *K*-function to determine the spatial pattern of the individuals in each ontogenetic stage for the three species studied in L1 and L2 (Moeur, 1993). The $K(t)$ function estimates spatial dependence between points of the same type (e.g., same ontogenetic stage) at a range of spatial scales. The function produces a cumulative distribution function that represents the expected number of neighbours in a circle of radius t centred on an arbitrary plant in the point pattern. This circle begins at a specified radius and is increased until it encompasses the entire study region (Fortin *et al.*, 2002; Klimas *et al.*, 2007). The $K(t)$ function is also weighted to correct for edge effects (Ripley, 1981). Since the number of plants should increase with an increasing circle radius, the linearized function $L(t)$ transforms $K(t)$ in its square root, stabilizing its variance. The model can be used to test point data for departure from a spatially random pattern, as described by a Poisson process. We computed 95% confidence envelopes on a Monte

Carlo simulated Poisson process using 99 simulations (Coomes *et al.*, 1999; Fortin *et al.*, 2002). Observed patterns differ from random at $p = 0.05$ where the plot of $L(t)$ falls outside the simulated confidence envelope. Aggregation is indicated by an $L(t)$ above the envelope, and regular plant spacing occurs where $L(t)$ falls below the envelope (Fortin *et al.*, 2002).

For each species in the same plot, we used bivariate *K*-function, Ripley's $K_{12}(t)$, to check for spatial associations between seed sources and seedlings (or juveniles of *Faramea*), seedlings and juveniles, juveniles and immatures, and immatures and adults (Diggle, 1983). This function calculates the expected mean number of individuals of one type (e.g., seedlings) within a given distance of an arbitrary individual of another type (e.g., seed sources). As for $K(t)$, $K_{12}(t)$ is linearized in $L_{12}(t)$. The null hypothesis of spatial independence between the two groups is refuted when values of $L_{12}(t)$ fall above or below a 95% confidence envelope, indicating a positive (attraction) or negative (repulsion) spatial relationship between the two groups. A 95% confidence envelope is calculated using random toroidal shifts of one pattern relative to the other during each of 99 Monte Carlo iterations (Coomes *et al.*, 1999).

We did not perform any analysis for individuals with undetermined ontogenetic stage. $L(t)$ and $L_{12}(t)$ were calculated for lag distances up to 50 m (half the distance of the plot axis). Other parameters for all analyses were: minimum circle radius = 0 m; intervals at which circle radius was analysed = 0.1 m for *Faramea*, 5.0 m for adults of *Mollinedia* and 1.0 m for all other ontogenetic stages of this species, 15.0 m for adults of *Pourouma*, 3.0 m for immatures and juveniles, and 5.0 m for seedlings of this species. We used SPPA 2.0 to perform the analyses (Haase, 2002).

RESULTS

Ontogenetic stage structure

We identified three ontogenetic stages of *Faramea*: the first is the juvenile stage, as we could not identify embryonic structures that differentiate them from seedlings (Gatsuk *et al.*, 1980). Juveniles present only one axis with decussate leaves. The second ontogenetic stage we identified is the immature, which presents branching and opposite, distichous leaves. Adults are similar to immatures but the fact that they flowered or fruited during the year they were monitored (Fig. 1a).

We identified four ontogenetic stages of *Mollinedia*: seedlings present only one axis with one to three pairs of leaves that are decussate and present serrulate margins in the apical third; below the lowest pair of leaves, there is a pair of first leaves, which are decussate to the lowest pair of leaves; the distances between each pair of leaves, and between the first leaves and the lowest pair of leaves are very short, which make the leaves look like whorled. Juveniles are similar to seedlings but the fact that the first leaves are no longer present and that there are more pairs of leaves. Immatures present branching and opposite, distichous leaves that are separated by a greater distance. Adults are similar to immatures but the fact that they flowered or fruited during the year they were monitored (Fig. 1b).

We also identified four ontogenetic stages of *Pourouma*: seedlings present only one axis with one pair of alternate, crenate leaves; below the leaves, there is a pair of first leaves, which are alternate and crossed to the pair of leaves. Juveniles are similar to seedlings but the fact that the first leaves are no longer present and that there are more pairs of leaves. Immatures differ from juveniles as to the presence of an incised leaf; large immatures present branching and only incised leaves. Adults are similar to large immatures but the fact that they flowered or fruited during the year they were monitored (Fig. 1c).

At L1, we found 934 individuals of *Faramea*, 3506 individuals of *Mollinedia* and 411 individuals of *Pourouma*. At L2, we found 696 individuals of *Faramea* (about 26% less than in L1), 960 individuals of *Mollinedia* (about 73% less than in L1) and 99 individuals of *Pourouma* (about 76% less than in L1; Fig. 2). The sex ratio of *Mollinedia* and *Pourouma* differed between the plots. At L1, there was 1 female to 1.64 male of *Mollinedia* and an equal sex proportion of individuals of *Pourouma*. However, there were many more males of both species at L2: there was 1 female to 2.36 males of *Mollinedia* and only males of *Pourouma*.

All species had the same ontogenetic stage structure in both plots ($p > 0.05$). They presented more individuals in the seedling stage and, especially, in the juvenile stage, and the number of plants in subsequent ontogenetic stages decreased. There were more seedlings, juveniles and immatures of the three species in L1 than in L2. We observed a decrease in the differences of the number of individuals in more advanced ontogenetic stages (*i.e.* immatures and adults) between the two plots. In fact, there was a slight increase in the number of adults of *Faramea* and *Mollinedia* in L2 (Fig. 2). Nevertheless, there were no differences in the ontogenetic stage structure among the three species within L1 nor L2 ($p > 0.05$).

Spatial structure

All ontogenetic stages of *Faramea* were aggregated at virtually all scales in L1 and L2. The ontogenetic stages of *Mollinedia* were also aggregated in the two plots, especially in small distance classes, with the exception of adults in L2 that were aggregated beyond 42 m only. Most ontogenetic stages of *Pourouma* were aggregated at virtually all scales in the plots, with the exception of adults that were randomly distributed in L1 and regularly spaced in L2 (Table 2).

When considering small distance classes, *Pourouma* presented the highest aggregation (highest value of univariate *L*(*t*)) of seedlings in L1 (only plot where seedlings were found), juveniles in the two plots and immatures in L2. However, *Faramea* presented the highest aggregation of immatures and adults in L1, and of adults in L2. The lowest aggregation (lowest value of univariate *L*(*t*)) was observed for seedlings, juveniles and immatures of *Mollinedia* in the two plots (in L2, only *Mollinedia* presented seedlings), and for adults of this species in L1. Adults of *Mollinedia* in L2 and of *Pourouma* in the two plots were not aggregated (Table 2).

The strongest spatial association (highest values of bivariate *L*(*t*)) between seedlings and seed sources was observed for *Faramea* in L2, followed by *Pourouma* in L1 and then by *Faramea* in L1. In both plots, the weakest spatial association (lowest values of bivariate *L*(*t*)) between seedlings and seed sources was observed for *Mollinedia* (Table 2).

The aggregation decreased through ontogeny for *Mollinedia* and *Pourouma*, being the lowest decrease observed for the latter. Adults of *Pourouma* were not aggregated in the plots whatsoever. On the other hand, the aggregation was held constant or increased through ontogeny for *Faramea* (Table 2).

In small distance classes, spatial associations between ontogenetic stages of *Faramea* were positive in the two plots, with the exception of spatial independency between immatures and adults in the interval 5 m - 43 m in L1. For *Mollinedia*, spatial associations were also positive in L1 and L2. The exceptions were juveniles and immatures that were spatially independent up to 5 m in L1, and immatures and adults that were spatially independent at virtually all scales in the two plots. Last, *Pourouma* presented positive spatial associations between ontogenetic stages, with the exception of spatial independency between juveniles and immatures at virtually all scales in L1, and between immatures and adults at virtually all scales in the two plots (Table 2).

DISCUSSION

Observations during fieldwork allowed the identification of the main ontogenetic stages of each of the species studied. The lack of seedlings of *Faramea* in both plots is due to subtle morphological differences between them and juveniles, which do not allow their easy identification in the field. Because we surveyed the individuals in the study site for a period superior to a year, we would have found any recently emerged seedlings if they were significantly different from juveniles.

On the other hand, seedlings and juveniles of *Pourouma* could be easily distinguished and the lack of seedlings in L2 is due to low seed arrival in the plot. As there were no female adults of *Pourouma* in L2, seed input is likely to be scarce and sporadic arrival that resulted in seedling emergence might have been represented by the juveniles found during the sampling period. We do not believe that seedling emergence can be attributed to seed banks, because those of tropical forests are mostly made up of seeds of pioneer species; seed banks of late-successional species stay viable and dormant for only short time periods after reaching the soil (Hopkins and Graham, 1987). The regeneration of such species relies much more on vegetative sprout (which is not the case for any of the three species studied) and on recent input of seeds from seed rain (e.g., Uhl *et al.*, 1981; Álvarez-Buylla and Martínez-Rámos, 1990). Therefore, the identification of female and male adults of dioecious species provides crucial information to the understanding of population structure and is only possible by monitoring every potential adult during an entire reproductive cycle.

The three species studied presented a reverse J-distribution of the ontogenetic stages in both L1 and L2, displaying a greater number of individuals in the first ontogenetic stages than adults. The greater number of juveniles than seedlings of *Mollinedia* and *Pourouma* indicates that the seedling stage of these species is very ephemerous, with nearly arrivals to the population quickly recruiting to juveniles. The reverse J-distribution of ontogenetic stages is a type of structure commonly found in tree populations (e.g., Manabe *et al.*, 2000; Klimas *et al.*, 2007) and indicates that adults produce new descendents regularly and/or that the species forms seedling or juvenile banks. Field observations have not provided any evidence of the latter for the three species studied. On the other hand, they reproduce every year and thus produce new descendents regularly. Although regular and high seedling input is often correlated with dynamic populations (*i.e.* populations with relatively high turnover of individual plants, high numbers of seedlings and juveniles, and low numbers of adults; e.g., Oostermeijer *et al*., 1994; Manabe *et al.*, 2000), no inferences about dynamics should be made from snapshot, structural patterns (Watkinson and Powell, 1997).

When considering all ontogenetic stages, we found a much smaller number of individuals of the three species in L2 than in L1. It was caused by an up to fourfold difference in seedling and juvenile densities between the plots. This can be explained by the male-biased sex ratio of *Mollinedia* and *Pourouma* in L2, which results in low seed and seedling input in the plot. However, there were also much less juveniles of the homoecious *Faramea* in L2, indicating that other factors might be contributing for the lower plant density in the plot. These factors are likely to be related to lack of suitable environmental conditions for seedling and juvenile growth and survival, probably conditioned by soil and topographic characteristics that differ between L1 and

L2 (Table 1). Also, antagonistic interactions may be held accountable for the low density of the initial ontogenetic stages of the three species studied in L2 (Clark and Clark, 2000).

The male-biased sex ratio of *Mollinedia* and *Pourouma* is frequently exhibited by populations of dioecious plant species (e.g., Garcia and Antor, 1995; Nicotra, 1998). Sex ratio biases may result from sex-based differences in life history traits (Meagher and Antonovics, 1982) and, less frequently, from spatial segregation of the sexes (SSS), the non-random distribution of the sexes with regard to physical space and availability of a limiting resource (Bierzychudek and Eckhart, 1988; Nicotra, 1998). We carried out exploratory $K_{12}(t)$ to check for SSS of *Mollinedia* in L1 and L2, and of *Pourouma* in L1, and found complete spatial independence of female and male of both species. Therefore, their male-biased sex ratio does not result from SSS. One possible explanation for this bias is precocial reproduction of males, which is most pronounced in the youngest or smallest size classes (Garcia and Antor, 1995). Another possibility is the common higher mortality rates of females of larger or older size classes due to higher costs of reproduction (e.g., Meagher and Antonovics, 1982; Bierzychudek and Eckhart, 1988; Garcia and Antor, 1995). Further studies should evaluate differential reproduction and mortality of sexes in order to elucidate which sex-related differences in life history traits are most likely to cause biased sex ratios.

The aggregation observed for the ontogenetic stages indicates that local dispersal has great influence on the spatial structure of the populations studied (Condit *et al.*, 2000; Svenning, 2001), especially because aggregation occurs in small distance classes where the effects of dispersal are more intense (Augspurger, 1984; Murrell, 2009). However, adults of *Mollinedia* in L2 and of *Pourouma* in the two plots were not aggregated. For the former, the decrease in aggregation through ontogeny is likely to be the result of extremely high mortality in denser areas

(Janzen, 1970; Connell, 1971) in L2, where mortality factors may operate with more intensity than in L1 probably due to soil and topographic characteristics of the plot. On the other hand, the lack of aggregation of adults of *Pourouma* is highly likely to be an artefact of the analysis, as it was performed for only six individuals in L1 and three individuals in L2.

In general, *Pourouma* presented the highest aggregation of the ontogenetic stages, as expected for a dioecious, low-density species whose seedlings concentrate beneath a few parents and recruit there (Nanami *et al.*, 1999; Condit *et al.*, 2000; Bleher *et al.*, 2002). Indeed, this species presented a strong spatial association between seedlings and seed sources. Nevertheless, we also found a strong association between these stages for *Faramea*, which is contrary to the expected for a homoecious, high-density species. This suggests that seed deposition of *Faramea* is higher close to the parent plant than seed deposition of *Pourouma*, thus counteracting the effects of tree density and breeding system on the spatial structure of populations. A less aggregated deposition pattern of seeds of *Pourouma* agrees with the prediction that larger birds disperse them and that taller parent plants may aid the scattering of seeds.

Moreover, *Faramea* presented the highest aggregation of immatures in L1, probably because post-dispersal processes also counteract the influence of tree density and breeding system on the spatial structure of populations. Hence, post-dispersal processes can increase the aggregation through ontogeny at such a high proportion that species with seedlings and juveniles with low aggregation become more aggregated as they develop to further stages than other species whose seedlings and juveniles presented high aggregation.

Contrary to our expectation, we found the lowest aggregation of the ontogenetic stages for *Mollinedia*, which presented the weakest spatial association between seedlings and seed sources. Probably, seed dispersal is also counteracting the effects of tree density and breeding system on the spatial structure of this species. It is likely to present a more scattered seed rain than *Faramea* and *Pourouma*, mediated by diaspore characteristics such as nutritional value that differ among the three species. These differences could result in distinct avian dispersers and, hence, dissimilar patterns of seed deposition among the species.

The aggregation through ontogeny of *Faramea* was held constant or increased, which has been found for some other tropical species (e.g., Hubbell, 1979). Therefore, *Faramea*'s recruitment patterns are probably more related to patchiness and positive interactions (Condit *et al.*, 2000; Dickie *et al.*, 2007) than to mortality in high-density areas, such as near the parent plant (Janzen, 1970; Connell, 1971). On the other hand, *Mollinedia* and *Pourouma* suffer high mortality in denser areas. This is indicated by the decrease in aggregation through ontogeny of both species, which has also been related in studies of many tropical tree species (e.g., Condit *et al.*, 2000; Klimas *et al.*, 2007). The lowest decrease was found for *Pourouma*, as expected for a low-density species subject to self-thinning (Murrell, 2009).

Mortality did not uncouple recruitment patterns from local dispersal, since seed sources were always spatially associated to the first ontogenetic stage, which, in turn, was associated to further ontogenetic stages. Although *Pourouma* is described as a light-demanding species (van der Meer *et al.*, 1998; Kobe, 1999; Rijkers *et al.*, 2000 for other species of the genera), the positive association between seed sources and seedlings, and between seedlings and juveniles indicate that germination, establishment and recruitment of this species are not dependent of canopy openings. This was also observed by Rijkers *et al.* (2000) to *P. bicolour* sp *digitata*, but is contrary to results for other light-demanding species (e.g., Forget *et al.*, 1999). Nonetheless, more developed ontogenetic stages of *Pourouma* and also of *Mollinedia* were sometimes spatially independent at larger spatial scales. Because self-thinning is an important process for larger plants (Hubbell, 1979; Sterner *et al.*, 1986; Condit *et al.*, 2000; Getzin *et al.*, 2006), this result indicates that mortality caused by intraspecific competition has great influence in the alteration of the associations between individuals of more advanced stages of *Mollinedia* and *Pourouma*. This is reinforced by the highest decrease in the aggregation through ontogeny of *Mollinedia*, as expected for a high-density species subject to self-thinning, and by the lowest decrease in the aggregation through ontogeny of *Pourouma*, which is in accordance with a low-density species subject to self-thinning (Murrell 2009).

CONCLUSIONS

Understanding the relative importance of factors that influence the spatial structure of trees remains an important challenge to ecologists (Murrell, 2009). In this study, we show that tree density and breeding system do not strongly affect the spatial structure of the three species studied, as also found by Hubbell (1979). This is because seed dispersal and post-dispersal processes can counteract their effect on the spatial structure of populations. On the other hand, seed dispersal generates aggregation, which can increase or decrease through ontogeny accordingly to each species' responses to the biotic and abiotic environment. For individuals of more advanced ontogenetic stages, self-thinning results in the lack of spatial association between stages.

FUNDING

This work was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico [142295/2006-0 to V.F.M. and 207132/2004-8 to F.A.M.S.] and the Fundação de Amparo à Pesquisa do Estado de São Paulo as part of the Thematic Project "Composição

Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar - Functional Gradient" [03/12595-7].

ACKNOWLEDGMENTS

We thank Guilherme Sanvido, Flávia Tirolo, Joselino Vieira dos Santos and Manuel Vieira de Assunção for help during fieldwork; Guilherme Sanvido also prepared ontogenetic stage schemes. We also thank André Rochelle for the calculation of the topographic variables in Table 1. This research has been authorized by COTEC/IF 44.924/2006 and IBAMA 12170-1 permits.

LITERATURE CITED

Alves LF 2000. *Estrutura, dinâmica e alometria de quatro espécies arbóreas tropicais.* PhD Thesis, Universidade Estadual de Campinas, Brazil.

Alves LF, Vieira SA, Scaranello MA, Camargo PB, Santos FAM, Joly CA, Martinelli LA 2010. Forest structure and abovegroung biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecology and Management* **260**: 679-691.

Álvarez-Buylla ER, Martínez-Rámos M. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* **84**: 314-325.

Augspurger CK. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology* **65**: 1705–1712.

Backes P, Irgang B. 2004. *As árvores de A a Z. Mata Atlântica – As árvores e a paisagem.* Porto Alegre: Paisagem do Sul.

Bierzychudek P, Eckhart V. 1988. Spatial segregation of the sexes of dioecious plants. *American Naturalist* **132**: 34-43.

Bleher B, Oberrath R, Böhning-Gaese K. 2002. Seed dispersal, breeding system, tree density and the spatial pattern of trees – a simulation approach. *Basic and Applied Ecology* **3**: 115-123.

Boll T, Svenning JC, Vormisto J, Normand S, Grández C, Balslev H. 2005. Spatial distribution and environmental preferences of the piassaba palm *Aphandra natalia* (Arecaceae) along the Pastaza and Urituyacu rivers in Peru. *Forest Ecology and Management* **213**: 175–183.

Catenacci, LS; De Vleeschouwer KM; Nogueira-Filho SLG. 2009. Seed dispersal by golden-headed lion tamarins *Leontopithecus chrysomelas* in Southern Bahian Atlantic Forest, Brazil. *Biotropica* **41**: 744-750.

Cazotto LPD, Martins VF, Santos FAM. "in prep." Dispersal spectrum of four tree physiognomies along an altitudinal gradient of the Brazilian Atlantic Rainforest.

Clark DB, Palmer MW, Clark DA. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* **80**: 2662–2675.

Condit R, Ashton PS, Baker P, *et al.* 2000. Spatial patterns in the distribution of tropical tree species. *Science* **288**: 1414–1418.

Connell JH. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Den Boer PJ, Gradwell GR, eds. *Dynamics of populations*. Wageningen: Centre for Agricultural Publishing and Documentation, 298–310.

Coomes DA, Rees M, Turnbull L. 1999. Identifying aggregation and association in fully mapped spatial data. *Ecology* **80**: 554-565.

CPTEC – Centro de Previsão de Tempo e Estudos Climáticos 2010. *Dados metereológicos, hidrológicos e ambientais de Plataformas de Coletas de Dados no PESM Picinguaba.* http://satelite.cptec.inpe.br/PCD/metadados.jsp?uf=25&id=30887&tipo=AGROMET. 08 Apr. 2010.

Cruden RW, Lloyd RM. 1995. Embryphytes have equivalent sexual phenotypes and breeding systems: why not a common terminology to describe them? *American Journal of Botany* **82**: 816-825.

Dickie IA, Schnizter SA, Reich PB, Hobbie SE. 2007. Is oak establishment in old fields and savanna openings context dependent? *Journal of Ecology* **95**: 309–320.

Diggle PJ. 1983. *Statistical analysis of spatial point patterns*. New York: Academic Press.

Endress PK. 1980. Ontogeny, function and evolution of extreme floral construction in *Monimiaceae*. *Plant Systematics and Evolution* **134**: 79-120.

Endress PK, Ingersheim A. 1997. Gynoecium diversity and systematic of the Laurales. *Botanical Journal of the Linnean Society* **125**: 93-168.

Forget P-M, Mercier F, Collinete F. 1999. Spatial patterns of two rodent-dispersed rain forest trees *Carapa procera* (Meliaceae) and *Vouacapoua Americana* (Caesalpinaceae) at Paracou, French Guiana. *Journal of Tropical Ecology* **15**: 301-313.

Fortin M-J, Dale MRT, ver Hoef J. 2002. Spatial analysis in Ecology. In: El-Shaarawi AH, Piegorsch WW, eds. *Encyclopedia of environmetrics*, Vol. 4. Chichester: John Wiley & Sons Ltd, 2051-2057.

Frazer GW, Canham CD, Lertzman KP 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs - Users manual and program documentation. Millbrook: Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies.

Fundação SOS Mata Atlântica 2011. *Mata Atlântica*. www.sosmatatlantica.org.br. 23 Apr. 2011.

Garcia M, Antor R. 1995. Sex ratio and sexual dimorphism in the dioecious *Borderea pyrenaica* (Dioscoreaceae). *Oecologia* **101**:59-67.

Gatsuk LE, Smirnova OV, Vorontzova LI, Zaugolnova LB, Zhukova LA. 1980. Age stages of plants of various growth forms: a review. *Journal of Ecology* **68**: 675-696.

Getzin S, Dean C, He F, Trofymow JA, Wiegang K, Wiegang T. 2006. Spatial pattern and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography* **29**: 671-682.

Haase P. 2002. *SPPA EXE Statistical Program*. http://haasep.homepage.t-online.de/. 02 Aug. 2011.

Hopkins MS, Graham AW. 1987. The viability of seeds of rainforest species after experimental soil burials under tropical wet lowland forest in north-eastern Australia. *Australian Journal of Ecology* **12**: 97-108.

Hubbell SP. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**: 1299–1309.

Hubbell SP. 1980. Seed predation and coexistance of tree species in tropical forests. *Oikos* **35**: 214-229.

Janzen DH. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**: 501–528.

Joly CA, Martinelli LA. 2006. *Composição Florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar.* Projeto Temático Biota/FAPESP 03/12595-7.

Joly CA, Martinelli LA. 2010. *Composição Florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar.* Projeto Temático Biota/FAPESP 03/12595-7.

Joly CA, Martinelli LA, Alves LF, Vieira SA, Tamashiro JY, Aidar MPM, Camargo PB, Assis MA, Bernacci LC 2008. As Parcelas Permanentes do Projeto Temático Biota Gradiente Funcional: Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar, Estado de São Paulo, Brasil. In: Sanquetta CR, eds. *Experiências de monitoramento no bioma Mata Atlântica com o uso de parcelas permanentes*. Curitiba: RedeMAP: Rede de Parcelas Permanentes dos Biomas Mata Atlântica e Pampa & Funpar 109-148.

Kelly CK. 1995. Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. *Oecologia* **102**: 377-388.

Klimas CA, Kainer KA, Wadt LHO. 2007. Population structure of *Carapa guianensis* in two forest types in the southwestern Brazilian Amazon. *Forest Ecology and Management* **50**: 256-265.

Kobe RK. 1999. Light gradient portioning among tropical tree species through differential seedling mortality and growth. *Ecology* **80**: 187-201.

Lacerda MS. 2001. *Composição florística e estrutura da comunidade arbórea num gradiente altitudinal da Mata Atlântica.* PhD Thesis, Universidade Estadual de Campinas, Brazil.

Lorence DH. 1985. A monograph of the Monimiaceae (Laurales) in the Malagasy region (SW Indian Ocean). *Annals of the Missouri Botanical Garden* **72**: 142-210.

Lorenzi H. 1998. Pourouma guianensis. *Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas do Brasil*, Vol. 2, 2nd edn. Nova Odessa: Editora Plantarum.

Manabe T, Nishimura N, Miura M, Yamamoto S. 2000. Population structure and spatial patterns of trees in a temperate old-growth evergreen broad-leaved forest in Japan. *Plant Ecology* **151**: 181-197.

Martins SC. 2010. *Caracterização dos solos e serapilheira ao longo do gradiente altitudinal da Mata Atlântica, estado de São Paulo*. PhD Thesis, Centro de Energia Nuclear na Agricultura na Universidade de São Paulo, Brazil.

Meagher TR, Antonovics J. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: life history studies. *Ecology* **63**: 1690-1700.

Moeur M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *Forest Science* **39**: 756–775.

Morellato LPC, Haddad CFB 2000. Introduction: The Brazilian Atlantic Forest. *Biotropica* **32**: 786–792.

Morellato LPC, Talora DC, Takahasi A, Bencke CSC, Romera EC, Ziparro V. 2000. Phenology of Atlantic rain forest trees: a comparative study. *Biotropica* **32**:811-823.

Müller J. 1881-1888. Rubiaceae. In: Martius CFP, Eichler AG eds. *Flora Brasiliensis,* Vol. VI, Pars 5. New York: Wheldon & Wesley Ltd, 208-209.

Murrell DJ. 2009. On the emergent spatial structure of size-structured populations: when does self-thinning lead to a reduction in clustering? *Journal of Ecology* **97**: 256-266.

Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 852-858.

Nanami S, Kawaguchi H, Yamakura T. 1999. Dioecy-induced spatial patterns of two codominant tree species, *Podocarpus nagi* and *Neolitsea aciculata*. *Journal of Ecology* **87**: 678–687.

Nathan R, Safriel UN, Noi-Meir I, Schiller G. 2000. Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology* **81**: 2156–2169.

Nicotra AB. 1998. Sex ratio variation and spatial distribution of *Siparuna glandiflora*, a tropical dioecious shrub. *Oecologia* **115**: 102-113.

Oliveira-Filho AT, Fontes MAL. 2000. Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. *Biotropica* **32**: 793-810.

Oostermeijer JGB, Van't Veer R, Den Nijs JCM. 1994. Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in The Netherlands. *Journal of Applied Ecology* **31**: 428-438.

Pedroni F. 2001. Aspectos da estrutura e dinâmica da comunidade arbórea na Mata Atlântica de Planície e Encosta em Picinguaba, Ubatuba, SP. PhD Thesis, Universidade Estadual de Campinas, Brazil.

Riba-Hernández P, Stoner KE, Lucas PW. 2003. The sugar composition of fruits in the diet of spider monkeys (*Ateles geoffroyi*) in Tropical Humid Forest in Costa Rica. *Journal of Tropical Ecology* **19**: 709-716.

Rice WR. 1989. Analyzing tables of statistical tests. *Evolution* **43**: 223-225.

Rijkers T, de Vries PJ, Pons TL, Bongers F. 2000. Photosynthetic induction in saplings of three shade-tolerant tree species: comparing understorey and gap habitats in a French Guiana rain forest. *Oecologia* **125**: 331-340.

Ripley BD. 1981. *Spatial Statistics*. New York: John Wiley and Sons.

Romanov MS, Endress PK, Bobrov AVFCH, Melikian AP, Bejerano AP. 2007. Fruit structure and systematics of Monimiaceae *s.s.* (Laurales). *Botanical Journal of the Linnean Society* **153**: 265-285.

Schupp EW. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* **51**: 71-78.

Seidler TG, Plotkin JB. 2006. Seed dispersal and spatial pattern in tropical trees. *PLoS Biology* **4**: 2132-2137.

Sentelhas PC, Marin FR, Ferreria AS, Sá EJS. 2003. *Banco de dados climáticos do Brasil*. http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=&COD=492. (08 Apr. 2010).

SMA – Secretaria do Meio Ambiente. 1996. *Atlas das unidades de conservação do estado de São Paulo. Parte 1 – Litoral.* São Paulo: Secretaria do Meio Ambiente & CESP.

SOS Mata Atlântica/INPE/ISA. 1998. *Atlas da evolução dos remanescentes florestais e ecossistemas associados ao domínio da Mata Atlântica no período 1990–95.* São Paulo: SOS Mata Atlântica/INPE/ISA.

Sterner RW, Ribic CA, Schatz GE. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. *Journal of Ecology* **74**: 621-633.

Svenning JC. 2001. Environmental heterogeneity, recruitment limitation and the mesoscale distribution of palms in a tropical montane rainforest (Maquipucuna, Ecuador). *Journal of Tropical Ecology* **17**: 97–113.

Uhl C, Clark K, Clark H, Murphy P. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. *Journal of Ecology* **69**: 631-649.

van der Meer PJ, Sterck FJ, Bongers F. 1998. Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French Guiana. *Journal of Tropical Ecology* **14**: 119-137.

Watkinson AR, Powell JC. 1997. The life history and population structure of *Cycas armstrongii* in monsoonal Northern Australia. *Oecologia* **111**: 341-349.

Wheelwright NT. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* **66**: 808-818.

Wright SJ. 2002. Plant diversity in tropical forests: a review of the mechanisms of species coexistence. *Oecologia* **130**: 1-14.

Zar JH. 1999. *Biostatistical analysis*. New Jersey: Prentice-Hall.

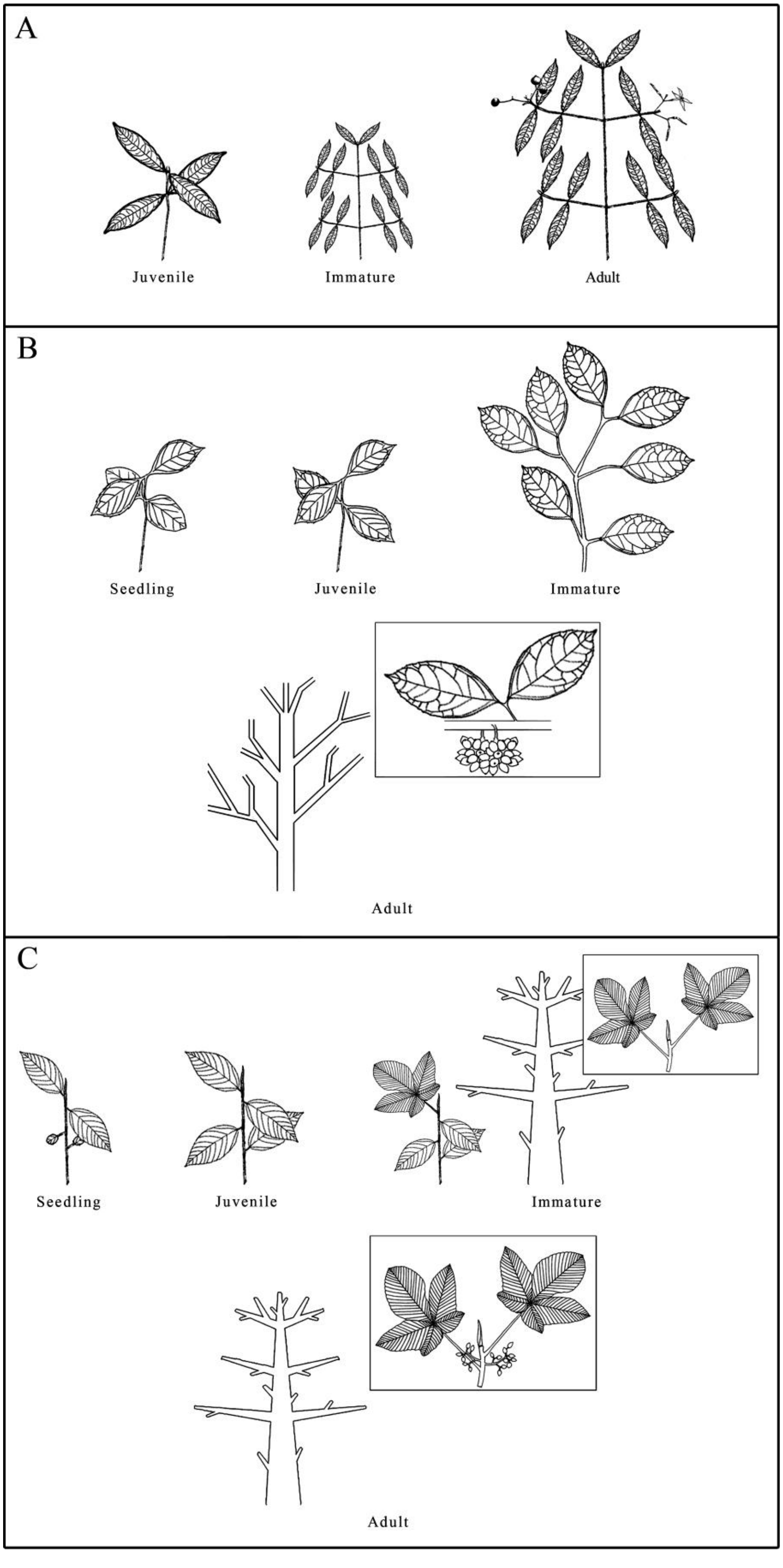
LIST OF CAPTIONS TO FIGURES AND TABLES

FIG. 1 Ontogenetic stages of *Faramea picinguabae* (A), *Mollinedia schottiana* (B) and *Pourouma guianensis* (C). Adults of *Mollinedia* and *Pourouma* are represented by a feminine, fruiting individual. For descriptions of each stage, please refer to the text.

FIG. 2 Number of individuals of *Faramea picinguabae* (A), *Mollinedia schottiana* (B) and *Pourouma guianensis* (C) in different ontogenetic stages at two 1 ha-plots (L1 and L2) of Lowland Atlantic Rainforest. Full bars represent individuals sampled at L1 and empty bars represent individuals sampled at L2.

TABLE 1. *Mean ± standard deviation of values of soil characteristics, canopy opening and topographic characteristics for two 1 ha-plots (L1 and L2) of Lowland Atlantic Rainforest. For further explanation on data, please refer to the text*

TABLE 2. *Results of univariate and bivariate K-functions for different ontogenetic stages and associations between ontogenetic stages of* Faramea picinguabae*,* Mollinedia schottiana *and* Pourouma guianensis *at two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. The unit for all distances is the metre. CSR means completely spatial randomness*


A
Juvenile
Immature
Adult
B
Seedling
Juvenile
Immature
Adult
C
Seedling
Juvenile
Immature
Adult

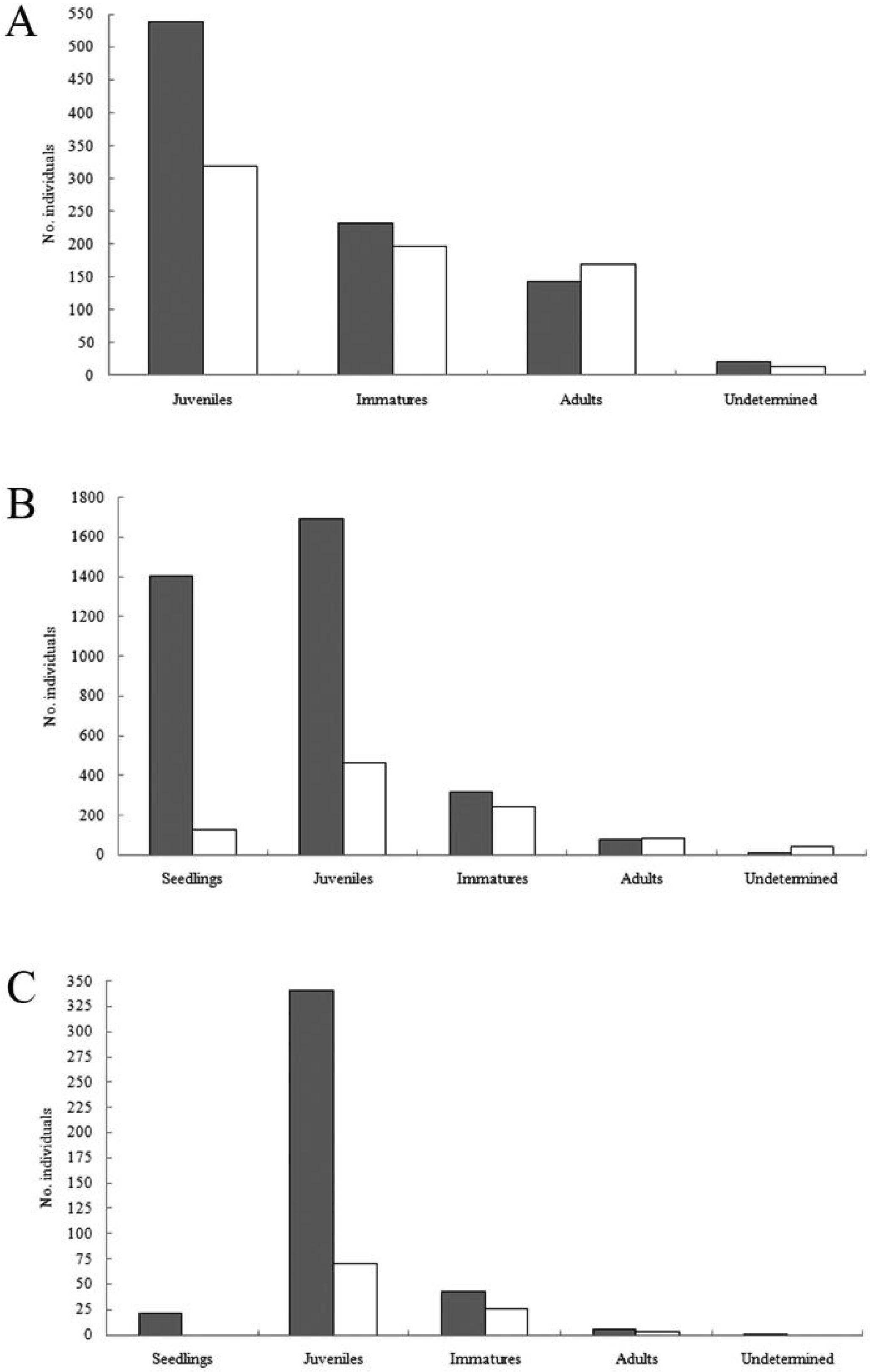

A
550
500
450
400
350
300
250
200
150
100
50
0
No. individuals
Juveniles
Immatures
Adults
Undetermined
B
1800
1600
1400
1200
1000
800
600
400
200
0
No. individuals
Seedlings
Juveniles
Immatures
Adults
Undetermined
C
350
325
300
275
250
225
200
175
150
125
100
75
50
25
0
No. individuals
Seedlings
Juveniles
Immatures
Adults
Undetermined

Table 1: Mean ± standard deviation of values of soil characteristics, canopy opening and topographic characteristics for two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. For further explanation on data, please refer to the text.

	L1	L2
pH $CaCl_2$	3.67 ± 0.35	3.58 ± 0.25
P (mg x kg^{-1})	17.27 ± 7.21	122.50 ± 48.44
S (mg x kg^{-1})	30.19 ± 12.13	9.34 ± 6.40
H+Al (mmolc x kg^{-1})	128.50 ± 53.29	17.86 ± 9.31
SB (mmolc x kg^{-1})	13.59 ± 6.87	22.11 ± 12.85
C (%)	5.00 ± 1.19	4.03 ± 2.46
N (%)	0.38 ± 0.09	0.29 ± 0.17
Clay	40.90 ± 8.41	22.05 ± 7.72
Silt	10.62 ± 3.94	5.64 ± 2.15
Clay+silt (%)	51.52 ± 10.22	27.69 ± 9.34
Canopy opening (%)	7.50 ± 1.84	7.00 ± 2.09
Altitude (m)	45.49 ± 4.85	73.22 ± 4.90
Elevation range (m)	3.42 ± 1.34	2.59 ± 1.24

Table 2: Results of univariate and bivariate *K*-functions for different ontogenetic stages and associations between ontogenetic stages of *Faramea picinguabae*, *Mollinedia schottiana* and *Pourouma guianensis* at two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. The unit for all distances is the metre. CSR means completely spatial randomness.

Species	Ontogenetic stage	Plot	*K*-function type	Interval of aggregation	Distance class of maximum aggregation	*L*(*t*) at maximum aggregation	Interval of repulsion	Distance class of maximum repulsion	*L*(*t*) at maximum repulsion	Interval of CSR
Faramea	Juveniles	L1	Univariate	0 - 48	20	7				48 - 50
	Immatures			0 - 50	20	11				
	Adults			0 - 50	20 - 30	10				
	Adults vs. juveniles		Bivariate	0 - 40	15 - 25	5	43 - 50	43 - 50	-3.5	40 - 43
	Juveniles vs. immatures			0 - 50	20 - 30	9				
	Immatures vs. adults			0 - 5	5	1	43 - 50	43 - 50	-6	5 - 43
	Juveniles	L2	Univariate	0 - 50	40	9				
	Immatures			0 - 50	45 - 50	7				
	Adults			0 - 50	40	9				
	Adults vs. juveniles		Bivariate	0 - 50	35 - 45	10				
	Juveniles vs. immatures			0 - 50	30 - 50	6				
	Immatures vs. adults			0 - 50	45 - 50	9				

Table 2 (cont.).

Species	Ontogenetic stage	Plot	*K*-function type	Interval of aggregation	Size of maximum aggregation	$L(t)$ at maximum aggregation	Interval of repulsion	Size of maximum repulsion	$L(t)$ at maximum repulsion	Interval of CSR
Mollinedia	Seedlings	L1	Univariate	0 - 50	4 - 12	4.2				
	Juveniles			0 - 23	6 - 9	3.2				24 - 50
	Immatures			0 - 44	2 - 8	0.9				44 - 50
	Adults			0 - 9	5	1				9 - 50
	Adults vs. seedlings		Bivariate	0 - 17; 35 - 50	5 - 12; 45 - 50	1.3	18 - 32	25	-1	17 - 18; 32 - 35
	Seedlings vs. juveniles			0 - 23	4 - 14	3				23 - 50
	Juveniles vs. immatures			5 - 26; 34 - 45	5 - 26; 34 - 45	0.6				0 - 5; 26 - 34; 45 - 50
	Immatures vs. adults									0 - 50
	Seedlings	L2	Univariate	0 - 36	6 - 9	11				36 - 50
	Juveniles			0 - 50	6 - 11	5				
	Immatures			0 - 50	46 - 50	1.5				
	Adults			42 - 50	50	1.5				0 - 42
	Adults vs. seedlings		Bivariate	0 - 17	7	2	31 - 41	34	-1.5	17 - 31; 41 - 50
	Seedlings vs. juveniles			0 - 35	6 - 12	7				35 - 50
	Juveniles vs. immatures			0 - 50	4 - 24; 46 - 50	1.8				
	Immatures vs. adults									0 - 50

Table 2 (cont.).

Species	Ontogenetic stage	Plot	*K*-function type	Interval of aggregation	Size of maximum aggregation	$L(t)$ at maximum aggregation	Interval of repulsion	Size of maximum repulsion	$L(t)$ at maximum repulsion	Interval of CSR
Pourouma	Seedlings	L1	Univariate	0 - 50	11 - 17	12				
	Juveniles			0 - 50	27 - 42	9				
	Immatures			0 - 28	7	4				28 - 50
	Adults									0 - 50
	Adults vs. seedlings		Bivariate	0 - 28	16	7				28 - 50
	Seedlings vs. juveniles			0 - 50	37 - 45	10.5				
	Juveniles vs. immatures									0 - 50
	Immatures vs. adults									0 - 50
	Juveniles	L2	Univariate	0 - 50	7 - 12	23				
	Immatures			0 - 50	6 - 16	15				
	Adults						0 - 50	50	-23	
	Juveniles vs. immatures		Bivariate	0 - 50	7 - 15	20				
	Immatures vs. adults									0 - 50

CAPÍTULO 2

Relação espacial desacoplada entre sementes e plântulas não desacopla a distribuição de sementes e adultos em uma floresta tropical

Valéria Forni Martins & Flavio Antonio Maës dos Santos

Resumo estendido

A dispersão de sementes pode influenciar o padrão espacial de espécies arbóreas, já que a distribuição espacial das sementes no ambiente forma um molde para a regeneração e o recrutamento futuros de uma população ou comunidade vegetal. A distribuição de sementes reflete eventos de dispersão local, mas a relação espacial entre sementes e plântulas não é tão previsível. O modelo de Janzen-Connell sugere que ela é desacoplada devido a uma diminuição na densidade de sementes e a um aumento na sobrevivência das mesmas em função da distância a partir da planta parental, o que resulta em um maior recrutamento a uma certa distância do adulto. No entanto, Hubbell sugeriu uma relação espacial concordante entre sementes e plântulas devido a um maior recrutamento perto da planta parental, apesar da baixa sobrevivência das sementes neste local.

O objetivo deste estudo foi determinar o padrão espacial e as associações espaciais de sementes, plântulas e adultos de três espécies arbóreas da Floresta Ombrófila Densa de Terras Baixas no litoral norte do estado de São Paulo, sudeste do Brasil. Espécies arbóreas tropicais comumente apresentam distribuição agregada, que parece estar altamente relacionada à dispersão

de sementes, principalmente porque a maior parte delas é depositada embaixo ou perto das plantas parentais. Por isto, nós esperamos encontrar que sementes, plântulas e adultos das três espécies estudas são agregados e espacialmente associados, o que está de acordo com o modelo de recrutamento de Hubbell.

Durante dois anos, nós coletamos mensalmente a chuva de semente em duas parcelas de 1 ha cada. No primeiro ano, utilizamos 30 coletores aleatoriamente distribuídos em cada parcela; no segundo ano, adicionamos mais 20 coletores em cada uma delas. Dados sobre a localização e o estádio ontogenético de cada indivíduo das três espécies já estavam disponíveis. Nós usamos duas abordagens para analisar o padrão espacial das sementes: na primeira, utilizamos os dados obtidos nos 30 coletores durante dois anos; com isto, obtivemos informações detalhadas sobre cada coletor ao longo do tempo. A segunda abordagem consistiu em realizar uma técnica de interpolação para 100 pontos com os dados obtidos nos 50 coletores durante o segundo ano de amostragem; com isto, obtivemos um detalhamento espacial maior da chuva de semente. Então, nós utilizamos *Spatial Analysis by Distance Indices* (SADIE) para determinar o padrão espacial e as associações de sementes em 30 e 100 pontos, plântulas e adultos das três espécies estudadas em cada parcela.

As sementes apresentaram padrão espacial aleatório em 30 pontos, mas tiveram distribuição agregada em 100 pontos. Plântulas e adultos apresentaram um padrão espacial agregado ou aleatório, dependendo da espécie e da parcela. As três espécies não apresentaram associações espaciais entre adultos e sementes quando foram considerados apenas 30 pontos de amostragem da chuva de semente. Porém, estes estádios ontogenéticos estiveram associados quando foram considerados os 100 pontos. Sementes e plântulas apresentaram mais associações ao se aumentar o número de pontos com informação sobre a chuva de semente. Porém, mesmo com 100 pontos, apenas em metade das comparações as sementes e plântulas estiveram associadas. Ainda assim, plântulas e adultos estiveram associados na maior parte das vezes.

Therefore, the use of a greater number of seed traps per area is recommended because a better understanding of spatial patterns can be achieved when accounting for great spatial information rather than more details details about each sampling unit.

A agregação encontrada para as sementes em 100 pontos e as associações entre elas e adultos e entre elas e plântulas indicam que o uso de um maior número de coletores é recomendado para um melhor entendimento dos padrões espaciais. Nossos resultados apoiam os estudos que mostraram que a dispersão ocorre localmente, mas estão de acordo apenas parcialmente com outros trabalhos que mostraram que espécies arbóreas tropicais são agregadas. Associações espaciais entre plântulas e adultos indicam que a distribuição dos adultos é relacionada à distribuição de plântulas, a qual se assemelha aos padrões espaciais das sementes em metade dos casos devido aos processos propostos no modelo Janzen-Connell. No entanto, a mortalidade não desacopla espacialmente a distribuição de sementes e adultos e, portanto, o padrão espacial das espécies estudadas pode ser explicado pelo modelo de Hubbell.

Diferentes autores têm relatado a influência da dispersão na distribuição espacial de espécies arbóreas tropicais. Este estudo também mostra que, apesar da relação espacial entre sementes e plântulas ser desacoplada em alguns casos, os adultos ainda refletem a distribuição das sementes.

Uncoupled seed-seedling spatial relationship does not uncouple seed and adult distributions in a tropical forest[a]

Valéria F. Martins[1*] and Flavio A. M. dos Santos[2]

[1]Programa de Pós-Graduação em Ecologia, Institute of Biology, CP 6109, University of Campinas - UNICAMP, 13083-970, Campinas, SP, Brazil; [2]Department of Plant Biology, Institute of Biology, CP 6109, University of Campinas - UNICAMP, 13083-970, Campinas, SP, Brazil

[*]Correspondence author. E-mail: valeriafm@gmail.com

Seed-seedling-adult spatial relationships

---

[a] Format and style: Journal of Ecology

Summary

1. Seed distribution reflects local dispersal, but seed-seedling spatial relationship is not so predictable. The Janzen-Connell model suggests it is uncoupled because of a decrease in seed density and an increase in seed survival with distance from the parent plant, which results in a higher recruitment at some distance from the plant. However, Hubbell suggested concordant seed-seedling spatial relationship due to high recruitment close to the parent plant despite low seed survival.

2. We determine the spatial pattern and associations of seeds, seedlings and adults of three tree species of a Lowland Atlantic Rainforest in Southeastern Brazil. Because tropical populations are aggregated due to seed dispersal, we expected to find evidence supporting Hubbell's model.

3. During two years, we monthly sampled the seed rain in two 1-ha plots. Data on the location and ontogenetic stage of every individual of the three species were already available.

4. Seeds were aggregated, while seedlings and adults were aggregated or randomly distributed. All species presented associations between adults and seeds, while seeds and seedlings were associated in only half of the comparisons. Nevertheless, seedlings and adults were spatially associated in most cases.

5. Our results support previous studies that showed that dispersal is local, but partially agree with those that showed that tropical tree species are aggregated. Spatial associations between seedlings and adults indicate that adult distribution is linked to seedling distribution, which is related to seed spatial patterns in only half of the cases due to the processes proposed in the Janzen-Connell model. However, mortality does not spatially uncouple seed-adult distribution and thus the spatial pattern of the species studied can be explained by Hubbell’s model.

6. *Synthesis.* Different authors have related the influence of seed dispersal on the spatial distribution of tropical tree species. This study also shows that although seed-seedling spatial relationship is uncoupled in some cases, adults still reflect seed distribution.

Key-words: Dispersal, *Faramea picinguabae*, Lowland Atlantic Rainforest, *Mollinedia schottiana*, Núcleo Picinguaba, Parque Estadual da Serra do Mar, *Pourouma guianensis*, SADIE, seed rain, spatial pattern

Introduction

Seed dispersal can influence the spatial pattern of trees (Bleher, Oberrath & Böhning-Gaese 2002), since the spatial dispersion of seeds in a given area forms the template for later regeneration and recruitment patterns of a plant population or community, with seeds deposited in favourable sites for germination and seedling establishment originating new plants (Loiselle, Ribbens & Vargas 1996). Therefore, factors that operate on dispersal may ultimately influence the spatial patterns of recruitment (Houle 1998). However, the period spanning seed release and seedling establishment is potentially the most variable and least predictable transition in the life of long-lived plants (Clark *et al*. 1999) and some hypotheses as to spatially link these early recruitment stages (*sensu* Hampe *et al.* 2008) have been proposed.

Janzen (1970) and Connell (1971) first suggested that as seed density decreases with distance from the parent plant, seed survival increases and leads to higher recruitment at some distance from the plant. As a consequence, populations are expected to show a reduction in aggregation through ontogeny than if mortality factors operated randomly. Also, the spatial relationship between seeds and seedlings is uncoupled and may result in a negative, *i.e.* discordant, spatial relationship in cases when mortality is extremely high near the parent plant and survival is extremely high at some distance from the plant. Later, Hubbell (1980) proposed that recruitment is higher close to the parent plant because of considerably greater seed abundance there, despite very low seed survival. In this case, adults are at least as aggregated as seedlings and the spatial relationship between seeds and seedlings is always positive, *i.e.* concordant. Other possible seed survival functions suggested different spatial relationships between seeds and seedlings (concordance, discordance or independence; e.g., McCanny 1985; McCanny & Cavers 1987) and dissimilar seed and seedling dispersion patterns (Houle 1995).

Although seed distribution patterns have been consistently shown to reflect local dispersal with most seed arrival falling beneath or near parent plants (Janzen 1970; Connell 1971; Clark *et al*. 1999; Nathan *et al*. 2000), spatial relationships between seeds and seedlings are not so predictable. This is due to mortality caused by post-dispersal processes, which include environmental heterogeneity, herbivory, competition and pathogen attack (Janzen 1970; Connell 1971). Several researchers have studied such relationships, especially in fleshy-fruited trees (e.g., Schupp 1988; Herrera *et al.* 1994; Jordano & Herrera 1995; Rey & Alcantara 2000; Calviño-Cancela 2002; García, Obeso & Martínez 2005; Hampe *et al.* 2008), and some have shown seed dispersal and seedling recruitment patterns to be spatially independent (e.g., Rey & Alcantara 2000; Calviño-Cancela 2002) while others have found concordant spatial relationships between both recruitment stages (e.g., Jordano & Herrera 1995; García, Obeso & Martínez 2005). Adding to these contrasting results, spatial relationships may vary in relation to the species and the type of system studied (e.g., Herrera *et al*. 1994). Therefore, more studies are clearly needed in order to achieve a better understanding of seed-seedling spatial relationships.

Nevertheless, the realistic interpretation of ecological data linking seed release and seedling establishment has been hindered by two major limitations: (i) the idiosyncratic character of each particular study area and sampling design, which has so far precluded attempts to compare different studies and thereby inhibited a search for general relationships between the spatial (and the temporal) heterogeneity of initial recruitment, as well as (ii) the lack of analytical approaches that work over multiple spatial scales while controlling for spatial autocorrelation of data. In particular, seedfall and seedling distributions are often strongly contagious and thereby inherently subject to spatial autocorrelation (Hampe *et al.* 2008), but only one study on bird-dispersed species (e.g., Hampe *et al.* 2008) and two other on wind-dispersed species (e.g., Houle 1998; Nathan *et al*. 2000) have ever explored this aspect.

Here we assess adult-seed-seedling spatial relationships by using spatial analysis techniques. Such new approach is clearly needed to achieve both unbiased and mutually comparable estimates of recruitment patterns (Hampe *et al.* 2008). We used Spatial Analysis by Distance Indices (SADIE) techniques (Perry *et al*. 1999; Winder *et al*. 2001) in order to determine the spatial pattern and spatial relationships of seeds, seedlings and adults of three tree species of a Lowland Atlantic Rainforest (*sensu* Oliveira-Filho & Fontes 2000) in Southeastern Brazil. Aggregation is commonly observed in plant populations of tropical forests (e.g., Hubbell 1979; Klimas, Kainer & Wadt 2007) and seems to be highly linked with seed dispersal (Condit *et al*. 2000; Svenning 2001), especially because most seeds fall beneath or near parent plants (Janzen 1970; Connell 1971; Clark *et al*. 1999; Nathan *et al*. 2000). Therefore, we expect to find evidence supporting the Hubbell's recruitment model (Hubbell 1980) and thus find seeds, seedlings and adults of the three species studied to be aggregated and spatially associated.

Materials and methods

STUDY SITE

The Brazilian Atlantic Forest is considered one of the world's hotspots for biodiversity conservation (Myers *et al.* 2000), with only about 7% of its original cover remaining (Fundação SOS Mata Atlântica 2011). The largest continuous stretch of this vegetation includes the Parque Estadual da Serra do Mar (PESM), SE Brazil. The PESM is a state park that comprises ca. 315,000 ha (SOS Mata Atlântica/INPE/ISA 1998) and is divided into several administration nucleuses, one of which is Núcleo Picinguaba (23°31' - 23°34'S, 45°02' - 45°05'W). It is located at the mountain range of Serra do Mar, municipality of Ubatuba, northern coast of the state of São Paulo, and comprises ca. 47,500 ha (SMA 1996). The region has mountainous relief, with altitudes varying between 0 m and 1,200 m (Alves *et al.* 2010). At Núcleo Picinguaba, temperatures range from 25.5° C in February to 18.4° C in July. There is no marked dry season and rainfall ranges from 376 mm in January to 11 mm in July (Sentelhas *et al.* 2003). Air relative humidity is always above 80% (Morellato *et al.* 2000), daylength varies from 15.5 h in May to 9.1 h in October, and winds normally come from ocean and blow southeast at 0.7 m/s – 1.0 m/s (Alves 2000; CPTEC 2010).

The Núcleo Picinguaba is the only portion of PESM to reach the coast and, due especially to its great range of altitude, is composed of a mosaic of vegetation physiognomies. We collected data in two 1-ha plots of the Lowland Atlantic Rainforest (ca. 44°48'W, 23°22'S), namely Lowland 1 (L1 hereafter) and Lowland 2 (L2 hereafter). This phytophysiognomy covers mountain slopes from 50 m to 100 m above sea level and occurs in cambisols, which are soils formed recently from the sedimentation of mountain erosion. Many rocky formations and dry stream paths are also observed. Each study plot was divided in 100 sub-plots of 10 m x 10 m, where every living tree whose trunk perimeter at 1.3 m in height was equal to or larger than 15 cm was sampled and identified (Joly *et al.* 2008).

L1 and L2 present very similar species composition and community structure: tree height ranged from ca. 1.6 m to 25 m, and tree trunk diameter varied between ca. 5 (inclusion criteria) cm and 94 cm. About 1,200 trees of 145 species were sampled in each plot (Joly & Martinelli 2006). A dense understorey, sub-canopy, canopy and emergent trees are present (Morellato & Haddad 2000), but sometimes it is not possible to distinguish clearly between the sub-canopy and the understorey, and between the sub-canopy and the canopy (unpublished data, L.P.D. Cazotto, V.F. Martins, F.A.M. Santos). Lianas, palm trees, epiphytes, ferns, and bromeliads are common (Morellato & Haddad 2000). Common tree species belong to the genera *Bathysa* (Rubiaceae), *Chrysophyllum* (Sapotaceae), *Coussarea* (Rubiaceae), *Eugenia* (Myrtaceae), *Euterpe* (Arecaceae), *Garcinia* (Clusiaceae), *Guapira* (Nyctaginaceae), *Marlierea* (Myrtaceae), *Mollinedia* (Monimiaceae), *Myrcia* (Myrtaceae), *Rustia* (Rubiaceae), *Sloanea* (Elaeocarpaceae), *Syagrus* (Arecaceae) and *Virola* (Myristicaceae; Joly & Martinelli 2006).

SPECIES STUDIED

The species studied were selected from two species composition lists for Núcleo Picinguaba. One list contained species that occur between sea level and 100 m of altitude (Pedroni 2001) as well as a morphological description of the diaspores of the individuals sampled, which aided the selection of the species studied here. The other species composition list contained species that occur between sea level and 1,000 m of altitude (Lacerda 2001). Both sampling encompassed the two plots of Lowland Atlantic Rainforest studied here. Based on the morphological description of the diaspores by Pedroni (2001), we selected species belonging to ornithochory, which is the most important dispersal syndrome in the study site (Cazotto *et al. in prep.*). Within this syndrome, we chose the species with fleshy diaspores with only one relatively large, hard seed, which can be easily found in seed traps. Species with these features and also with great abundance of small individuals in the study site are *Faramea picinguabae* M. Gomes (Rubiaceae), *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae) and *Pourouma guianensis* Aubl. (Urticaceae).

Although there have been reports of mammals, especially monkeys, consuming fruits of different species of *Pourouma* (e.g., Kelly 1995; Riba-Hernández, Stoner & Lucas 2003; Catenacci, De Vleeschouwer & Nogueira-Filho 2009), we believe birds are the main dispersal agents of *P. guianensis* in the study site, where diurnal mammals such as primates have not been observed since 1990 (Pedroni 2001). However, seed deposition patterns of this species may be less aggregated than *F. picinguabae* and *M. schottiana* because its seeds are larger and thus likely to be dispersed by larger birds, which are able to carry them for greater distances from the parent plant (Wheelwright 1985; Seidler & Plotkin 2006). Also, reproductive individuals of *P. guianensis* are much taller, which should aid the scattering of seeds.

Faramea picinguabae (*Faramea* hereafter) is a treelet or tree generally less than 10 m in height. It seems to be shade-tolerant and its seedlings are able to establish in habitat ranging from treefall gaps to the dark forest understorey, as do *F. occidentalis* (Schupp 1988). *Faramea* in one of the most abundant species in the Lowland Atlantic Rainforest of Núcleo Picinguaba, although poorly sampled in previous inventories due to its thin trunk (unpublished data, V.F. Martins). It is homoecious (*sensu* Cruden & Lloyd 1995) and adult individuals reproduce two to three times a year, every year. Plants that produce flowers also produce fruits (unpublished data, V.F. Martins,

E. Gressler) and there are generally three or four fruits per infructescence. Each fruit is a round, ca. 1.5 cm - 2 cm of diameter, purple to dark red when mature drupoid with calyx remains; there is only one seed per fruit, rarely two, which do not exceed 1 cm in diameter (unpublished data, V.F. Martins; Müller 1881-1888).

Mollinedia schottiana is a tree generally less than 10 m in height. The species is one of the most abundant in the Lowland Atlantic Rainforest of Núcleo Picinguaba (Joly & Martinelli 2006). *Mollinedia schottiana* is dioecious and adult individuals reproduce once a year, every year (unpublished data, V.F. Martins, E. Gressler). The representatives of Monimiaceae are characterized by apocarpous gynoecia with uniovulate carpels (Endress & Ingersheim 1997), which are borne in a more or less flat or concave floral cup (Endress 1980; Lorence 1985). After pollination, *Mollinedia*'s carpels develop into sessile drupelets with only one seed and are presented on the reversed light cream floral cup (unpublished data, V.F. Martins; Romanov *et al.* 2007). *Mollinedia schottiana* (*Mollinedia* hereafter) produces obovate, ca. 1 cm of diameter, dark red when mature fruitlets, whose seeds are just a little smaller that the fruitlet (unpublished data, V.F. Martins).

Pourouma guianensis (*Pourouma* hereafter) is a light-demanding (van der Meer *et al.* 1998; Kobe 1999; Rijkers *et al*. 2000 for other species of the genera), emergent tree that reaches up to 20 m in height in the study site. Few individuals occur in each plot (Joly & Martinelli 2006). The species is dioecious and adult individuals reproduce once a year, every year. Feminine plants produce fruits in infructescences. Each fruit is an obovate, ca. 1.5 cm of diameter, dark red when mature drupe, whose seed is just a little smaller than the fruit (unpublished data, V.F. Martins; Lorenzi 1998; Backes & Irgang 2004).

SEED DISTRIBUTION

In order to assess the net input of seed of the three species studied to the forest floor, we took advantage of 30 seed traps distributed in April 15th 2007 by other researchers in both L1 and L2. They randomly chose by simple sampling without reposition the sub-plots where the traps were installed as near as possible to its centre. In April 15th 2008, we distributed 20 more traps in each plot. They were also randomly distributed in order to follow the same experimental design previously established by the researchers (Fig. 1). The use of seed traps is a direct way to assess seed rain patterns (Hoppes 1988), *i.e.* the distribution of seeds within the habitat occupied by a population (Debussche & Issenmann 1994). Each trap had an area of 0.29 m^2 and was made of a 1 mm nylon mesh suspended in a plastic round frame approximately 50 cm above the ground.

Although we took advantage of an experimental design that was not elaborated for the collection of seed rain, we believe that randomly distributed seed traps fairly cover the two plots studied here. Also, the size of each sampling unit (sub-plots of 10 m x 10 m) is adequate to assess adult-seed-seedling spatial relationships: because seed dispersal is local (Janzen 1970; Connell 1971; Clark *et al.* 1999; Nathan *et al.* 2000), interactions involving seedlings are more intense near adults, where plants are more abundant (Janzen 1970; Connell 1971). Therefore, the effects of dispersal and interactions occur mostly between 10 m and 20 m around adults (Augspurger 1984; Uriarte *et al.* 2004), a scale that encompasses one or two sampling units.

The content of the seed traps was collected around the 15th of each month until April 2009 and dried inside paper bags in a 58° C cabinet for 48 h. Then, we sorted every diaspore of the three species studied in a laboratory. We did not separate them as fruits fallen directly from the parent plant (intact fruits or fruitlets) and dispersed diaspores (beaked fruits or fruitlets, or clean seeds) for comparisons between seed (as a general term for each type of diaspore) and seedling distributions, as well as between adults and seed distributions. The reason for this is that both fruits fallen directly from the parent plant and dispersed diaspores can potentially germinate and originate seedlings. On the other hand, immature fruits were considered as aborted and, together with damaged seeds, were not included in the count since they would not be effective as diaspores as well as in increasing the population size (Stephenson 1981).

SEEDLING AND ADULT DISTRIBUTIONS

Every individual of the three species studied within L1 and L2 had already been censused and mapped, as well as had had its ontogenetic stage identified. For the dioecious *Mollinedia* and *Pourouma*, each adult had also been classified as feminine or masculine (Martins & Santos *in prep.*). Because seedlings of *Faramea* could not be differentiated from juveniles due to the absence of conspicuous embryonic structures that characterize the former (Gatsuk *et al.* 1980), the spatial distributions of both seeds and adults of this species were here compared to the distribution of juveniles (first ontogenetic stage of *Faramea*). We could not make any comparison for *Pourouma* in L2, as neither seedlings nor feminine adults of this species had been previously found in this plot (Martins & Santos *in prep.*; Table 1). We transformed the mapped position of each individual of the three species studied into density counts of juveniles and adults of *Faramea*, as well as of seedlings and feminine adults of *Mollinedia* and *Pourouma* in each of the sub-plots of L1 and L2.

DATA ANALYSES

In order to analyse the spatial pattern of seeds, we used two approaches: the first one consisted of pooling seed rain data at each of the same 30 traps used in the two sampling years; this was done in both L1 and L2 for the three species across all collection dates within the two years (Takahashi & Kamitani 2004). By doing this, we obtained detailed information about each seed trap along time, since seed counts per trap are usually low. The second approach consisted of pooling seed rain data at each of the 50 traps used in the second sampling year; as previously, this was done in both L1 and L2 for the three species studied across all collection dates within the year (Takahashi & Kamitani 2004). Then we used kriging, an interpolation technique, in order to obtain seed counts for the centre of every sub-plot of both L1 and L2. Kriging estimates the value of an attribute at unsampled points by using the semivariogram (function of spatial dependency among points) as the source of information about the shape and size of the area from which known points are used for calculating the attribute (Jongman, ter Braak & van Tongeren 1995). Kriging was conducted with the software Surfer 8.02 (Golden Software, Inc. 2002). Rather than obtaining great detail in each of the seed traps, this approach enabled us to gather much more detailed spatial information of seedfall.

Before performing spatial analyses with seed rain data of the 30 traps along two sampling years and kriging of seed rain data in 50 traps in the second sampling year, we made an area correction of the seed traps to the sub-plots. This was done to enable comparisons of seed counts to seedling and adult counts in the whole sub-plot (rather than in the 0.29 m^2 trap area). We first added 1 to each value found in the traps; this was done because a value of zero in a trap means that either not a single seed arrived at the sub-plot or that less than one seed arrived at each 0.29 m^2 of the sub-plot during the sampling period. By adding 1 to each value, we assume that any value between zero and less than one seed per 0.29 m^2 can be actually found in sub-plots where we have not obtained any seed in the trap. On the other hand, this extrapolation does not interfere with the distribution of seeds in the sub-plots without a trap. Last, we multiplied all the extrapolated values by 345 (100 m^2 of each sub-plot divided by 0.29 m^2 of each seed trap) as an area correction; we used an integer value as to obtain an integer count of seeds.

We used SADIE to determine the spatial pattern of (i) seeds in 30 traps along two sampling years, (ii) seeds in 100 sub-plots (obtained by kriging) in the second sampling year, (iii) individuals of the first ontogenetic stage and (iv) fruiting adults of each of the three species studied in both L1 and L2. SADIE is a powerful technique to study spatial patterns and associations as it overcomes the idiosyncratic character of each particular study area and sampling design, as well as the lack of analytical approaches that work over multiple spatial scales while controlling for spatial autocorrelation of data. Instead, it compares the spatial distributions of ecological data in the form of spatially referenced integer counts and produces standardized measures of their similarity that allow a direct comparison of different studies (Perry *et al.* 1999; Hampe *et al.* 2008). Although we had fully mapped data of all individuals of the three species studied, we chose to use SADIE because it has proved to be as or more powerful than point-pattern analysis techniques (Dungan *et al.* 2002; Perry *et al.* 2002). Also, SADIE is more appropriate to analyse counts of individuals of a particular animal or plant species than other geostatistical techniques because such counts are not continuous, but discrete; are often distributed exceedingly patchily, frequently comprising a majority of zero values; are highly dynamic and often characterized by isolated clusters, which may be acting as metapopulations with varying degrees of inter-cluster dispersal (Perry 1998).

SADIE seeks to identify clusters with relatively large counts close to one another in two-dimensional space (*i.e.* a patch) or with relatively small counts (*i.e.* a gap). The method works through equating the degree of spatial pattern in an observed arrangement of counts to the minimum effort that the individuals in the population would need to expend to move to a completely regular arrangement in which abundance was equal in each sample unit; in practice, this effort is equated with the minimum distance, D, required to move to complete regularity. The spatial pattern is quantified by permuting the observed set of counts amongst the sample units, which provides data for the null-hypothesis that the counts are arranged randomly with respect to one another, while maintaining precisely the numeric properties of the data. In particular, division of the observed value of D by the mean value from several hundred such randomizations gives an index of aggregation, I_a; values of $I_a = 1$ indicate randomly arranged counts, while $I_a > 1$ indicates aggregation of observed counts into clusters (Perry *et al.* 1999). Furthermore, comparison of the observed value of D with the tails of the distribution of corresponding values from these permutations leads to the usual formal randomization test (Besag & Diggle 1977) of the null hypothesis that the observed counts are arranged randomly (Perry *et al.* 1999).

However, I_a does not encompass all the facets of spatial pattern in an arrangement and so there are two other indices as to quantify the degree to which the count for each sample unit contributes towards the overall degree of clustering, either as part of a patch or as a gap: v_i is a standardized and dimensionless index of clustering that measures the degree to which the unit contributes to clustering, as a member of a group of donor units that constitute a patch. On the other hand, v_j is the correspondent index for units that are member of a group of receivers that constitute a gap; by convention, it is negative in sign. As a general rule, large values of v_i, *i.e.* greater than *c.*1.5, indicate patchiness; large negative values of v_j, *i.e.* < *c.* -1.5, indicate membership of a gap; values close to unity indicate a random placement of that unit in relation to others nearby (Perry *et al.* 1999). The interpolation of v_i and v_j may be presented as a map of density isolines, which is a great advantage over other autocorrelation techniques such as Moran's I that do not allow identification of clusters and gaps in space (Hampe *et al.* 2008).

We also used SADIE to check for associations between (i) fruiting adults and seeds in 30 traps along two sampling years, (ii) fruiting adults and seeds in 100 sub-plots (obtained by kriging) in the second sampling year, (iii) seeds in 30 traps along two sampling years and individuals of the first ontogenetic stage, (iv) seeds in 100 sub-plots (obtained by kriging) in the second sampling year and individuals of the first ontogenetic stage and, lastly, (v) fruiting adults and individuals of the first ontogenetic stage of each of the three species studied in both L1 and L2. Although spatial associations between seeds and seedlings (juveniles of *Faramea*) were not made using individuals of the same cohort, we believe they reflect an overall pattern of recruitment, especially because seed production by parent plants is relatively constant through time.

SADIE techniques for association tests differ from traditional techniques that assess similarity on the basis of correlation between the densities of the two populations in the form of logarithmically transformed counts. By contrast, SADIE assesses similarity on the basis of the similarity between the clustering indices of two data sets. This intrinsically allows for the spatial pattern in each component population and does not result in positive or negative associations due to numeric effects. SADIE deliberately downweights those isolated large and small density values with small cluster indices that are locally spatially random, so X, the measure of local association, is not greatly affected by noise of this form. Because of that, this technique has greater power to detect significant association when it is present (Winder *et al*. 2001).

The association index X ranges between +1 (complete spatial association) and –1 (complete spatial dissociation), with 0 indicating spatial independence. The extent of association can be tested statistically by a permutation procedure (Winder *et al*. 2001). Because the index itself and its test rely exclusively on the referenced count data without assuming any underlying distribution, outcomes are comparable across populations and sample designs of very different spatial structure (Hampe *et al.* 2008). Significance levels of X were Bonferroni corrected to account for multiple testing (Winder *et al.* 2001). All SADIE analyses were conducted with the software SadieShell v1.22 (Conrad 2001). Parameters for all analyses were *iseed* = 1000 (random number to generate randomizations) and *k5psim* = 150 (number of how many blocks of 39 randomizations are performed).

Results

SEED DISTRIBUTION

There were more diaspores of *Faramea* and *Mollinedia* in the seed traps in the first sampling year; most of them had been dispersed. On the other hand, *Pourouma* presented more diaspores in the second sampling year and most of them had fallen directly from the parent plant. In L1, there were more diaspores of *Faramea* and *Pourouma*, while in L2 there were more diaspores of *Mollinedia*. We found more diaspores of *Faramea* between April and September, but there were smaller peaks in January and February. Diaspores of *Mollinedia* were more abundant between February and August, while those of *Pourouma* were more abundant between January and June (Fig. 2).

The spatial pattern of seeds in 30 traps along two sampling years was random for the three species in both L1 and L2. No more than nine traps presented seeds and the maximum number of seeds per trap was 10. When increasing the spatial information of seedfall (seeds in 100 sub-plots obtained by kriging for the second sampling year), seeds were aggregated for the three species in the plots, with the exception of *Mollinedia* in L2, whose seeds were randomly distributed. No more than six traps presented seeds and the maximum number of seeds per trap was six (Figs. 3 and 4, Table 2).

SEEDLING AND ADULT DISTRIBUTIONS

Juveniles and adults of *Faramea* were aggregated in both L1 and L2, with adults presenting higher indexes of aggregation than juveniles. On the other hand, seedlings and feminine adults of *Mollinedia* were randomly distributed in the two plots. Seedlings of *Pourouma* were aggregated in L1, while feminine adults of this species were randomly distributed in the same plot (Fig. 3, Table 3).

SPATIAL ASSOCIATIONS OF SEEDS, SEEDLINGS AND ADULTS

Fruiting adults and seeds of the three species collected in 30 traps along two years were neither associated nor dissociated in the plots, with the exception of *Pourouma* in L1, whose individuals of both ontogenetic stages were associated. When increasing the spatial information of seedfall, the three species presented associations between fruiting adults and seeds in the plots, with the exception of *Mollinedia* in L2, whose ontogenetic stages were neither associated nor dissociated (Fig. 3, Table 4).

Seeds collected in 30 traps along two years and seedlings were only associated for *Mollinedia* in L2 and *Pourouma* in L1. Seedfall data from kriging also presented spatial association with seedlings of *Faramea* in L2, while seeds and seedlings of this species and of *Mollinedia* in L1 were neither associated nor dissociated. Seedlings and fruiting adults of the three species were spatially associated in the plots, with the exception of *Mollinedia* in L2, whose individuals of both ontogenetic stages were neither associated nor dissociated (Fig. 3, Table 4).

Discussion

Species of tropical forests commomly present inter-annual fluctuations in phenophase intensity (Engel 2001; Zipparro 2004). This can be held accountable for the presence of more diaspores of *Faramea* and *Mollinedia* in the seed traps in the first sampling year than in the second. Diaspores of these species seem to be very attractive to frugivores, as most of them were found as beaked fruits or fruitlets, or clean seeds at the traps. On the other hand, the presence of more diaspores of *Pourouma* in the seed traps in the second sampling year is simply a result of a greater number of traps per plot in this period. This is because most of the diaspores were found in two seed traps in L1 (10 out of 13 diaspores at the plot) and in one trap in L2 (1 out of 1 diaspore at the plot) that were installed in 2008. In L1, the traps were located very close to two of the three fruiting adults and thus, also explain why the diaspores found had fallen directly from the parent plant. The presence of only few dispersed diaspores in the traps was unexpected, since *Pourouma* is likely to be dispersed by larger birds that are able to carry seeds for greater distances from the parent plant (Wheelwright 1985; Seidler & Plotkin 2006). Nevertheless, the only fallen diaspore found in L2 might represent sporadic long-distance dispersal, as there is no fruiting adult of *Pourouma* in the plot.

The greater number of diaspores of *Faramea* in L1 and of *Mollinedia* in L2 was not related to the greater abundance of fruiting adults of the former in L2 and of the latter in L1 (Table 1). This indicates that factors other than the number of parent plants affect the abundance of diaspores found at a site. These factors include individual characteristics that result in lower or higher fruit production, and activity of mutualistic partners such as pollinators and dispersers. On the other hand, it was expected that the number of diaspores of *Pourouma* would be higher at L1, which is the only plot where fruiting adults of this species are present (Table 1).

In the Brazilian Atlantic Rainforest, diaspores are mature and available to dispersers especially in the colder and drier period (Morellato *et al.* 2000; Staggemeier *et al.* 2010), which extends from April to September at Núcleo Picinguaba (Sentelhas *et al.* 2003). Plants that fruit during this period benefit from seed germination and seedling establishment in the subsequent wetter period (Bendix *et al.* 2006; Selwyn & Pathasarathy 2007). The three species studied fruited during the colder and drier period at Núcleo Picinguaba and thus are likely to benefit from higher humidity. However, *Faramea* also presented smaller fruiting peaks at the wetter period, which should occur to a species that fruit two to three times a year. Although there are two climatic periods at the study site (Sentelhas *et al.* 2003), little seasonality is observed, enabling pollinators and dispersers to be found during the whole year. Therefore, there is no restriction to fruit development and maturing, and reproduction may occur several times throughout the year (Morellato *et al.* 2000; Bollen & Donati 2005).

When considering the diaspores collected in 30 seed traps along two sampling years, the randomly distributed seeds were contrary to the expectation that they would be aggregated because most of them fall beneath or near parent plants (Janzen 1970; Connell 1971; Clark *et al*. 1999; Nathan *et al*. 2000). However, this randomness is likely to be an artefact of few sampling units (only 30 seed traps in 100 sub-plots), since increasing the spatial information of seedfall (*i.e.* kriging of 50 seed traps in the second sampling year) resulted in an aggregated spatial pattern of seeds. The only exception was *Mollinedia* in L2, whose seeds were randomly distributed, indicating that dispersal occurs differently in the plots. One reason for this is that the relative importance of each disperser species is different within the study site, thus resulting in distinct seedfall patterns in close areas.

Our results partially agreed with other studies that showed that tropical tree species are generally aggregated (e.g., Hubbell 1979; Klimas, Kainer & Wadt 2007): juveniles and adults of *Faramea* presented this spatial pattern in the two plots, so did seedlings of *Pourouma* in L1. The aggregation of adults in relation to juveniles of *Faramea* was not reduced, indicating that processes proposed by Hubbell (1980) operate for this species. On the other hand, the reduction in the aggregation of adults in relation to seedlings of *Pourouma*, with adults actually being randomly distributed, is hardly a consequence of the mortality processes proposed by the Janzen-Connell model; instead, it is probably a consequence of very few individuals in the plot (only three). Seedlings and feminine adults of *Mollinedia* were randomly distributed in the two plots: in L1, the aggregated seeds generate randomly distributed seedlings due to the mortality processes proposed by the Janzen-Connell model; the spatial randomness of seedlings is maintained through further ontogenetic stages. However, seedlings and feminine adults of this species are randomly distributed in L2, which is explained by the random seedfall pattern in the plot.

Spatial associations between fruiting adults and seeds, as well as between seeds and seedlings (juveniles for *Faramea*) became more frequent when using seedfall data for 100 sub-plots (*i.e.* kriging) instead of only 30 along two sampling years. Therefore, the use of a greater number of seed traps per area is recommended because a better understanding of spatial patterns can be achieved when accounting for great spatial information rather than more details details about each sampling unit. Associations between fruiting adults and seeds are in accordance with the expectation that seed distribution patterns reflect local dispersal and reinforces the aggregated spatial pattern of seeds due to their great deposition beneath or near parent plants (Janzen 1970; Connell 1971; Clark *et al*. 1999; Nathan *et al*. 2000). The only exception was *Mollinedia* in L2, whose seeds and fruiting adults were neither associated nor dissociated. This may be an outcome of the differences in dispersal that occurs between L1 and L2, resulting in seeds that are aggregated near randomly distributed fruiting adults in the former and seeds that are scattered in L2 disregarded of the location of the randomly distributed parent plants.

When analysing the relief surface maps for seedfall and point maps for fruiting adults (Fig. 3), it is possible to notice seedfall peaks in areas without parent plants of *Faramea* and *Mollinedia*. This can be an outcome of bird's habitat preferences, which results in seed deposition at different densities in the environment (Debussche & Isenmann 1994; Takahashi & Kamitani 2004; Jordano *et al.* 2007). Factors influencing the density of seeds is the distance to fruiting adults, vegetation height and forest gaps (Hoppes 1988; Debussche & Isenmann 1994, but see also Loiselle, Ribbens & Vargas 1996, Jordano *et al.* 2007 and Martini & Santos 2007). *Pourouma* is the only species that presented all seedfall peaks overlapping with fruiting adults, which is also unexpected due its probable dispersal by larger birds. Thus, this species presents dispersal limitation in the study site, especially because monkeys are not found in the area (Pedroni 2001).

Seeds and seedlings (juveniles for *Faramea*) were associated in only about half of the comparisons involving the three species studied, as also found by Hampe *et al.* (2008) for other three species. Although it seems contradictory to support both Janzen-Connell and Hubbell's (1980) models, different recruitment patterns may be found in nature, as clarified by McCanny (1985). The fitting of data into one or other model depends only on the average distances of dispersal or predation: the Janzen-Connell model requires the mean dispersal distance to be higher than the mean predation distance (Nathan & Casagrandi 2004), which occurs when predators are strongly attracted to the proximity of fruiting adults and plants respond by dispersing seeds further away to escape predation (Janzen 1970; Connell 1971). Strongly distance-dependent predators are usually invertebrates, which are often highly host-specific and less mobile (Hammond & Brown 1998); long-distance dispersal can be achieved when plants present low fecundity, which generates (few) widely dispersed seeds that are therefore able to escape predators attracted to fruiting adults. On the other hand, Hubbell's model (1980) requires comparable magnitudes of dispersal and predation mean distances, so that there is an ideal free distribution in which each predator has access to the same density of seeds (Nathan & Casagrandi 2004). This occurs when vertebrates, often highly mobile and rarely host-specific, are the main seed predators (Hammond & Brown 1998) and plants present high fecundity (Nathan & Casagrandi 2004). Therefore, the relative importance of invertebrates and vertebrates that act as seed predators at a site, and each individual plant's fecundity can result in the patterns proposed in the Janzen-Connell model or in Hubbell's model (1980; Nathan & Casagrandi 2004). Further studies should aim at determining the contribution of these factors for the recruitment pattern around each fruiting adult in order to understand the joint pattern of the population studied.

Spatial associations between seedlings and fruiting adults show that adult distribution (either aggregated or random) is linked to seedling distribution, which is related to seed spatial patterns in only half of the cases due to the processes proposed in the Janzen-Connell model. However, mortality does not spatially uncouple seed-adult distribution and thus the spatial pattern of the species studied can be explained by Hubbell's model (Hubbell 1980). Only seedlings and fruitings adults of *Mollinedia* in L2 were neither associated nor dissociated, a spatial relationship also shown by adults and seeds, and by seeds and seedlings of this species in the plot.

Different authors have related the influence of seed dispersal on the spatial distribution of tropical tree species (e.g., Peart 1989; Condit *et al*. 2000; Svenning 2001). This study also shows that although seed-seedling spatial relationship is uncoupled in some cases, adults still reflect seed distribution. A better understanding of the spatial pattern and seed-seedling-adult spatial relationships of tropical tree species should be achieved through the investigation of the factors that determine the average distances of dispersal and predation.

Acknowledgements

V.F.M. held a scholarship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) while carrying out this study (Process Number 142295/2006-0) and F.A.M.S. was supported by a grant from the CNPq (Process Number 207132/2004-8). The research was supported by the State of São Paulo Research Foundation (FAPESP) as part of the Thematic Project "Composição Florística, Estrutura e Funcionamento da Flroesta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar - Functional Gradient" (Process Number 03/12595-7), within the BIOTA/FAPESP Program, The Biodiversity Virtual Institute (http://www.biota.org.br). This research has been authorized by COTEC/IF 44.924/2006 and IBAMA 12170-1 permits. The authors wish to thank Edvaldo Ramos Pereira, Joselino Vieira dos Santos and Manuel Vieira de Assunção for help during fieldwork. We also thank the researchers and technical staff of the Isotopic Ecology Laboratory from Centro de Energia Nuclear na Agricultura of the University of São Paulo for installing the seed traps in the study site and helping with the collection and processing of the seed rain material; Angélica Carvalho, Jéssica Harue, Carlos Eduardo Nunes and Luciano Tortellini for the trial of collected material; André Rochelle for help with kriging and surface maps, and Guilherme Sanvido for help with figure preparation.

References

Alves, L.F. (2000) Estrutura, dinâmica e alometria de quatro espécies arbóreas tropicais. PhD thesis, Universidade Estadual de Campinas, Campinas.

Alves, L.F.; Vieira, S.A.; Scaranello, M.A.; Camargo, P.B.; Santos, F.A.M.; Joly, C.A. & Martinelli, L.A. (2010). Forest structure and abovegroung biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecol. Manag.*, **260**, 679-691.

Augspurger, C.K. (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light gaps, and pathogens. *Ecology*, **65**, 1705-1712.

Backes, P. & Irgang, B. (2004) Mata Atlântica – As árvores e a paisagem. Paisagem do Sul, Porto Alegre.

Bendix, J.; Homeier, E.; Ortiz, E.C. & Emck, P. (2006) Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *Int. J. Biometeorol.*, **50**, 370-384.

Besag, J. & Diggle, P.J. (1977) Simple Monte Carlo tests for spatial pattern. *Appl. Stat.*, **26**, 327-333.

Bleher, B.; Oberrath, R. & Böhning-Gaese, K. (2002) Seed dispersal, breeding system, tree density and the spatial pattern of trees – a simulation approach. *Basic Appl. Ecol.*, **3**, 115-123.

Bollen, A. & Donati, G. (2005) Phenology of the litoral forest of Sainte Luce, southeastern Madagascar. *Biotropica*, **37**, 32-43.

Calviño-Cancela, M. (2002) Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empetraceae): the importance of unspecialized dispersers for regeneration. *J. Ecol.*, **90**, 775–784.

Catenacci, L.S.; De Vleeschouwer, K.M. & Nogueira-Filho, S.L.G. (2009) Seed dispersal by golden-headed lion tamarins *Leontopithecus chrysomelas* in Southern Bahian Atlantic Forest, Brazil. *Biotropica*, **41**, 744-750.

Cazotto, L.P.D.; Martins, V.F. & Santos, F.A.M. *in prep.* Dispersal spectrum of four tree physiognomies along an altitudinal gradient of the Brazilian Atlantic Rainforest.

Clark, J.S.; Silman, M.; Kern, R.; Macklin, E. & HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.

Condit, R.; Ashton, P.S.; Baker, P.; Bunyavejchewin, S.; Gunatilleke, S.; Gunatilleke, N.; Hubbell, S.P.; Foster, R.B.; Itoh, A.; LaFrankie, J.V.; Lee, H.S.; Losos, E.; Manakaran, N.; Sukumar, R. & Yamakura, T. (2000) Spatial patterns in the distribution of tropical tree species. *Science*, **288**, 1414–1418.

Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine mammals and in rain forest trees. Dynamics of populations (eds. P.J. Boer & G. Gradwell), pp. 298-312. PUDOC, Wageningen.

Conrad, K.F. (2001) SADIEShell Version 1.22. http://www.rothamsted.ac.uk/pie/sadie/SADIE_downloads_software_sshell_page_5_2_1_a.php. 10th May 2010.

CPTEC – Centro de Previsão de Tempo e Estudos Climáticos (2010) Dados metereológicos, hidrológicos e ambientais de Plataformas de Coletas de Dados no PESM Picinguaba.

http://satelite.cptec.inpe.br/PCD/metadados.jsp?uf=25&id=30887&tipo=AGROMET. 08th Apr. 2010.

Cruden, R.W. & Lloyd, R.M. (1995) Embryphytes have equivalent sexual phenotypes and breeding systems: why not a common terminology to describe them? *Am. J. Bot.*, **82**, 816-825.

Debussche, M. & Isenmann, P. (1994) Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos*, **69**, 414-426.

Dungan, J.L.; Perry, J.N.; Dale, M.R.T.; Legendre, P.; Citron-Pousty, S.; Fortin, M.-J.; Jakomulska, A.; Miriti, M. & Rosenberg, M. S. (2002) A Balanced View of Scale in Spatial Statistical Analysis. *Ecography*, **25**, 626-640.

Endress, P.K. (1980) Ontogeny, function and evolution of extreme floral construction in *Monimiaceae*. *Plant Syst. Evol.*, **134**, 79-120.

Endress, P.K. & Ingersheim, A. (1997) Gynoecium diversity and systematic of the Laurales. *Bot. J. Linn. Soc.*, **125**, 93-168.

Engel, V.L. (2001) Estudo fenológico de espécies arbóreas de uma floresta tropical em Linhares, ES. PhD thesis, Universidade Estadual de Campinas, Campinas.

Fundação SOS Mata Atlântica (2011) Mata Atlântica. www.sosmatatlantica.org.br. 23rd Apr. 2011.

García, D.; Obeso, J.R. & Martínez, I. (2005) Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? *J. Ecol.*, **93**, 693-704.

Gatsuk, L.E.; Smirnova, O.V.; Vorontzova, L.I.; Zaugolnova, L.B. & Zhukova, L.A. (1980) Age stages of plants of various growth forms: a review. *J. Ecol.*, **68**, 675-696.

Golden Software, Inc. (2002) Surfer Version 8.02 – Surface Mapping System. Golden, Colorado.

Hammond, D.S. & Brown, V.K. (1998) Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. Dynamics of Tropical Communities (eds D.M. Newbery, H.H.T. Prins & N.D. Brown), pp. 51-78. Blackwell, Oxford.

Hampe, A.; García-Castaño, J.L.; Schupp, E.W. & Jordano, P. (2008) Spatial-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. *J. Ecol.*, **96**, 668-678.

Herrera, C.M.; Jordano, P.; López-Soria, L. & Amat, J.A. (1994) Recruitment of a mast-fruiting, bird dispersed tree: bridging frugivore activity and seedling establishment. *Ecol. Monogr.*, **64**, 315-344.

Hoppes, W.G. (1988) Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology*, **69**, 320-329.

Houle, G. (1995) Seed dispersal and seedling recruitment: the missing link (s). *Écoscience*, **2**, 238–244.

Houle, G. (1998) Seed dispersal and seedling recruitment of *Betula alleghanienesis*: spatial inconsistency in time. *Ecology*, **79**, 807-818.

Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.

Hubbell, S.P. (1980) Seed predation and coexistence of tree species in tropical forests. *Oikos*, **35**, 214-229.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.*, **104**, 501–528.

Joly, C.A. & Martinelli, L.A. (2006) Composição Florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar. Thematic Project Biota/FAPESP 03/12595-7.

Joly, C.A.; Martinelli, L.A.; Alves, L.F.; Vieira, S.A.; Tamashiro, J.Y.; Aidar, M.P.M.; Camargo, P.B.; Assis, M.A. & Bernacci, L.C. (2008). As Parcelas Permanentes do Projeto Temático Biota Gradiente Funcional: Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar, Estado de São Paulo, Brasil. Experiências de monitoramento no bioma Mata Atlântica com o uso de parcelas permanentes. (ed. C.R. Sanquetta), pp. 109-148. RedeMAP: Rede de Parcelas Permanentes dos Biomas Mata Atlântica e Pampa & Funpar, Curitiba.

Jongman, R.H.G.; ter Braak, C.J.F. & van Tongeren, O.F.R. (1995) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Jordano, P. & Herrera, C.M. (1995) Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Écoscience*, **2**, 230-237.

Jordano, P.; Garcia, C.; Godoy, J.A. & Garcia-Castaño, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *P. Natl. Acad. Sci. USA*, **104**, 3278-3282.

Kelly, C.K. (1995) Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. *Oecologia*, **102**, 377-388.

Klimas, C.A.; Kainer, K.A. & Wadt, L.H.O. (2007) Population structure of *Carapa guianensis* in two forest types in the southwestern Brazilian Amazon. *Forest Ecol. Manag.*, **50**, 256-265.

Kobe, R.K. (1999) Light gradient portioning among tropical tree species through differential seedling mortality and growth. *Ecology*, **80**, 187-201.

Lacerda, M.S. (2001) Composição florística e estrutura da comunidade arbórea num gradiente altitudinal da Mata Atlântica. PhD thesis, Universidade Estadual de Campinas, Campinas.

Loiselle, B.A.; Ribbens, E. & Vargas, O. (1996) Spatial and temporal variation of seed rain in a Tropical Lowland Wet Forest. *Biotropica*, **28**, 82-95.

Lorence, D.H. (1985) A monograph of the Monimiaceae (Laurales) in the Malagasy region (SW Indian Ocean). *Ann. Mo. Bot. Gard.*, **72**, 142-210.

Lorenzi, H. (1998) Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas do Brasil. Vol. 2, 2nd ed., Plantarum, Nova Odessa.

Martini, A.M.Z. & Santos, F.A.M. (2007) Effects of dystinct types of disturbance on seed rain in the Atlantic forest of NE Brazil. *Plant Ecol.* **190**, 81-95.

Martins, V.F. & Santos, F.A.M.S. *in prep.* Density of seed sources, seed dispersal, post-dispersal processes and the aggregation of tree species in a tropical forest.

McCanny, S.J. (1985) Alternatives in parent-offspring relationships in plants. *Oikos*, **45**, 148–149.

McCanny, S.J. & Cavers, P.B. (1987) The escape hypothesis: a test involving a temperate, annual grass. *Oikos*, **49**, 67–76.

Morellato, L.P.C. & Haddad, C.F.B. (2000) Introduction: The Brazilian Atlantic Forest. *Biotropica*, **32**, 786–792.

Morellato, L.P.C.; Talora, D.C.; Takahasi, A.; Bencke, C.S.C.; Romera, E.C. & Ziparro, V. (2000) Phenology of Atlantic rain forest trees: a comparative study. *Biotropica*, **32**, 811-823.

Müller, J. (1881-1888) Rubiaceae. Flora Brasiliensis (orgs. C.F.P. Martius & A.G. Eichler), pp. 208-209. Vol. VI, Pars 5, Wheldon & Wesley Ltd., New York.

Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 852-858.

Nathan, R. & Casagrandi, R. (2004) A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. *J. Ecol.*, **92**, 733-746.

Nathan, R.; Safriel, U.N.; Noi-Meir, I. & Schiller, G. (2000) Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. *Ecology*, **81**, 2156–2169.

Oliveira-Filho, A.T. & Fontes, M.A.L. (2000) Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. Biotropica 32: 793-810.

Peart, D.R. (1989) Species interactions in a successional grassland. I. Seed rain and seedling recruitment. *J. Ecol.*, **77**, 236-251.

Pedroni, F. (2001) Aspectos da estrutura e dinâmica da comunidade arbórea na Mata Atlântica de Planície e Encosta em Picinguaba, Ubatuba, SP. PhD thesis, Universidade Estadual de Campinas, Campinas.

Perry, J.N. (1998) Population and community ecology for insect management and conservation. Proceedings of the Ecology and Population Dynamics Section of the 20th International Congress of Entomology (eds. J. Baumgärtner; P. Brandmayr & B.F.J. Manly), pp. 21-33. Balkema, Rotterdam.

Perry, J.N.; Liebhold, A.M.; Rosenberg, M.S.; Dungan, J.; Miriti, M.; Jakomulska, A. & Citron-Pousty, S. (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography*, **25**, 578-600.

Perry, J.N.; Winder, L.; Holland, J.M. & Alston, R.D. (1999) Red-blue plots for detecting clusters in count data. *Ecol. Lett.*, **2**, 106-113.

Rey, P.J. & Alcantara, J.M. (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *J. Ecol.*, **88**, 622–633.

Riba-Hernández, P.; Stoner, K.E. & Lucas, P.W. (2003) The sugar composition of fruits in the diet of spider monkeys (*Ateles geoffroyi*) in Tropical Humid Forest in Costa Rica. *J. Trop. Ecol.*, **19**, 709-716.

Rijkers, T.; de Vries, P.J.; Pons, T.L. & Bongers, F. (2000) Photosynthetic induction in saplings of three shade-tolerant tree species: comparing understorey and gap habitats in a French Guiana rain forest. *Oecologia*, **125**, 331-340.

Romanov, M.S.; Endress, P.K.; Bobrov, A.V.F.CH.; Melikian, A.P. & Bejerano, A.P. (2007) Fruit structure and systematics of Monimiaceae *s.s.* (Laurales). *Bot. J. Linn. Soc.*, **153**, 265-285.

Schupp, E.W. (1988) Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos*, **51**, 71–78.

Seidler, T.G. & Plotkin, J.B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biol.*, **4**, 2132-2137.

Selwyn, M.A. & Parthasarathy, N. (2007) Fruiting phenology in a tropical dry evergreen forest on the Coromandel coast of India in relation to plant life-forms, physiognomic groups, dispersal modes, and climatic constraints. *Flora*, **202**, 371-382.

Sentelhas, P.C.; Marin, F.R.; Ferreria, A.S. & Sá, E.J.S. (2003) Banco de dados climáticos do Brasil. http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=&COD=492. 08th Apr. 2010.

SMA – Secretaria do Meio Ambiente. (1996) Atlas das unidades de conservação do estado de São Paulo. Parte 1 – Litoral, Secretaria do Meio Ambiente & CESP, São Paulo.

SOS Mata Atlântica/INPE/ISA. (1998) Atlas da evolução dos remanescentes florestais e ecossistemas associados ao domínio da Mata Atlântica no período 1990–95. SOS Mata Atlântica/INPE/ISA, São Paulo.

Staggemeier, V.G.; Diniz-Filho, J.A.F. & Morellato, L.P.C. (2010) The shared influence of phylogeny and ecology on the reproductive patterns of Myrteae (Myrtaceae). *J. Ecol.*, **98**, 1409-1421.

Stephenson, A.G. (1981) Flower and fruit abortion: proximate causes and ultimate functions. *Annu. Rev. Ecol. Evol. S.*, **12**, 253–279.

Svenning JC. (2001) Environmental heterogeneity, recruitment limitation and the mesoscale distribution of palms in a tropical montane rainforest (Maquipucuna, Ecuador). *J. Trop. Ecol.,* **17**, 97–113.

Takahashi, K. & Kamitani, T. (2004) Factors affecting seed rain beneath fleshy-fruited plants. *Plant Ecol.*, **174**, 247-256.

Uriarte, M.; Condit, R.; Canham, C.D. & Hubbell, S.P. (2004) A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *J. Ecol.*, **92**, 348-360.

van der Meer, P.J.; Sterck, F.J. & Bongers, F. (1998) Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French Guiana. *J. Trop. Ecol.*, **14**, 119-137.

Wheelwright, N.T. (1985) Fruit size, gape width, and the diets of fruit-eating birds. *Ecology*, **66**, 808-818.

Winder, L.; Alexander, C.J.; Holland, J.M.; Woolley, C. & Perry, J.N. (2001) Modelling the dynamic spatial-temporal response of predators to transient prey patches in the field. *Ecol. Lett.*, **4**, 568-576.

Zipparro, V.B. (2004) Fenologia reprodutiva da comunidade arbórea em floresta atlântica no Parque Estadual Intervales, SP. PhD thesis, Universidade Estadual Paulista, Rio Claro.

Table 1. Number of seedlings and fruiting adults of *Faramea picinguabae*, *Mollinedia schottiana* and *Pourouma guianensis* at two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. Here, seedling refers to the first ontogenetic stage, which is the juvenile for *Faramea* (please refer to the text for further explanation). Extracted from Martins & Santos (*in prep.*)

Species	Seedlings		Adults	
	L1	L2	L1	L2
Faramea	539	319	143	168
Mollinedia	1403	127	31	25
Pourouma	21	0	3	0

Table 2. Results of SADIE analyses for seeds of *Faramea picinguabae*, *Mollinedia schottiana* and *Pourouma guianensis* collected at two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. Seeds were collected in 30 seed traps along two years and in 50 seed traps in only one year; we performed kriging with data from the 50 traps to obtain seed counts across the plots. I_a is the index of aggregation, v_j is the index of clustering of a patch and v_j is the index of clustering of a gap; * indicates values with $p < 0.05$

	Faramea				*Mollinedia*				*Pourouma*	
	L1		L2		L1		L2		L1	
	30 traps	Kriging	30 traps	Kriging	30 traps	Kriging	30 traps	Kriging	30 traps	Kriging
I_a	1.055	1.680 *	0.816	1.306 *	1.008	1.736 *	1.013	0.929	1.111	1.630 *
v_j	-1.026	-1.734 *	-0.817	-1.292	-0.999	-1.778 *	-0.994	-0.926	-1.100	-1.651 *
v_i	1.070	1.753 *	0.799	1.349 *	1.028	1.940 *	1.194	0.845	1.477 *	1.647 *

Table 3. Results of SADIE analyses for the first ontogenetic stage and fruiting adults of *Faramea picinguabae*, *Mollinedia schottiana* and *Pourouma guianensis* at two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. I_a is the index of aggregation, v_j is the index of clustering of a patch and v_j is the index of clustering of a gap; * indicates values with $p < 0.05$

	Faramea				*Mollinedia*				*Pourouma*	
	L1		L2		L1		L2		L1	
	Juveniles	Adults	Juveniles	Adults	Seedlings	Adults	Seedlings	Adults	Seedlings	Adults
I_a	1.641 *	2.193 *	1.839 *	2.193 *	1.144	0.859	0.855	1.044	1.567 *	1.182
v_j	-1.592 *	-2.190 *	-1.714 *	-2.190 *	-1.121	-0.859	-0.845	-1.050	-1.567 *	-1.192
v_i	1.667 *	2.006 *	1.884 *	2.006 *	1.307 *	0.836	1.079	1.131	1.466 *	1.216

Table 4. Results of SADIE analyses for associations of seeds, first ontogenetic stage and fruiting adults of *Faramea picinguabae*, *Mollinedia schottiana* and *Pourouma guianensis* at two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. Seeds were collected in 30 seed traps along two years and in 50 seed traps in only one year; we performed kriging with data from the 50 traps to obtain seed counts across the plots. *X* is the measure of local association; * indicates values with $p < 0.025$ (two-tail test; the probability level should be less than 0.025 for significant association or greater than 0.975 for significant dissociation)

Species	Site	Association	*X*
Faramea	L1	Adults and seeds (30 traps)	0.283
		Adults and seeds (kriging)	0.326 *
		Seeds (30 traps) and juveniles	0.227
		Seeds (kriging) and juveniles	0.099
		Juveniles and adults	0.472 *
	L2	Adults and seeds (30 traps)	0.262
		Adults and seeds (kriging)	0.284 *
		Seeds (30 traps) and juveniles	0.087
		Seeds (kriging) and juveniles	0.215 *
		Juveniles and adults	0.883 *
Mollinedia	L1	Adults and seeds (30 traps)	0.252
		Adults and seeds (kriging)	0.276 *
		Seeds (30 traps) and seedlings	0.04
		Seeds (kriging) and seedlings	-0.124
		Seedlings and adults	0.266 *
	L2	Adults and seeds (30 traps)	-0.062
		Adults and seeds (kriging)	0.061
		Seeds (30 traps) and seedlings	0.630 *
		Seeds (kriging) and seedlings	0.446 *
		Seedlings and adults	0.009

Table 4. Cont

Species	Site	Association	*X*
Pourouma	L1	Adults and seeds (30 traps)	0.713 *
		Adults and seeds (kriging)	0.807 *
		Seeds (30 traps) and seedlings	0.735 *
		Seeds (kriging) and seedlings	0.711 *
		Seedlings and adults	0.821 *

List of figures

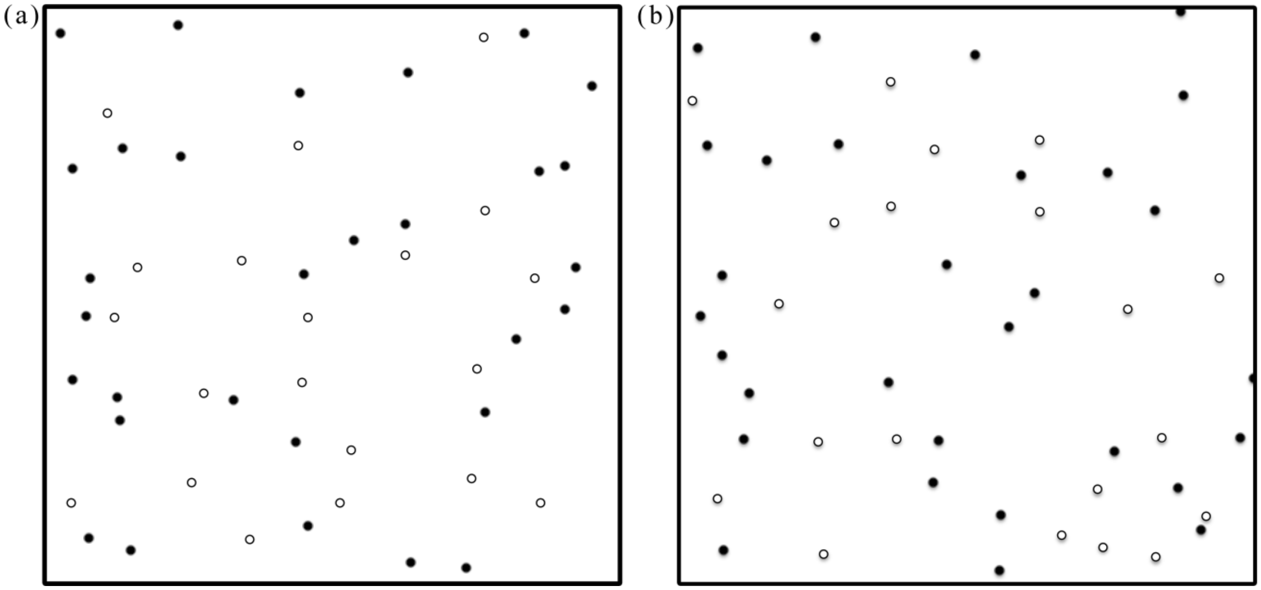
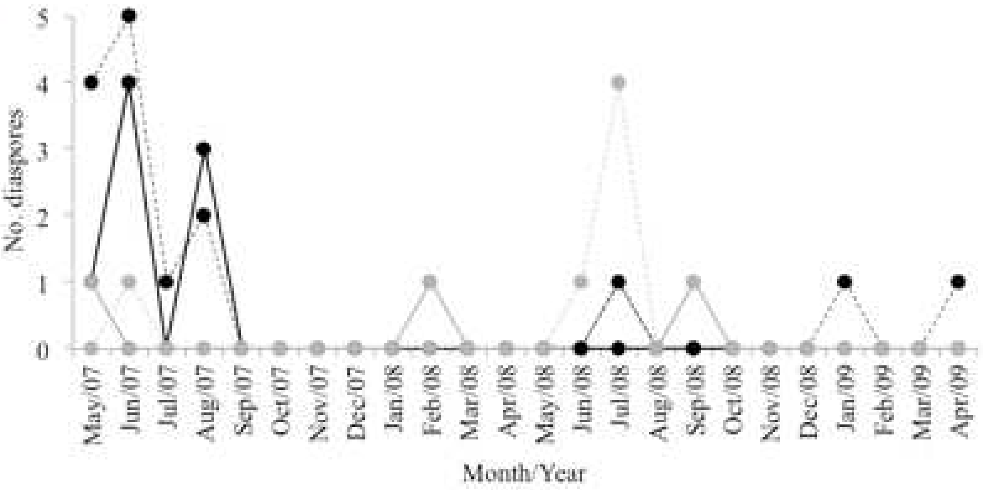
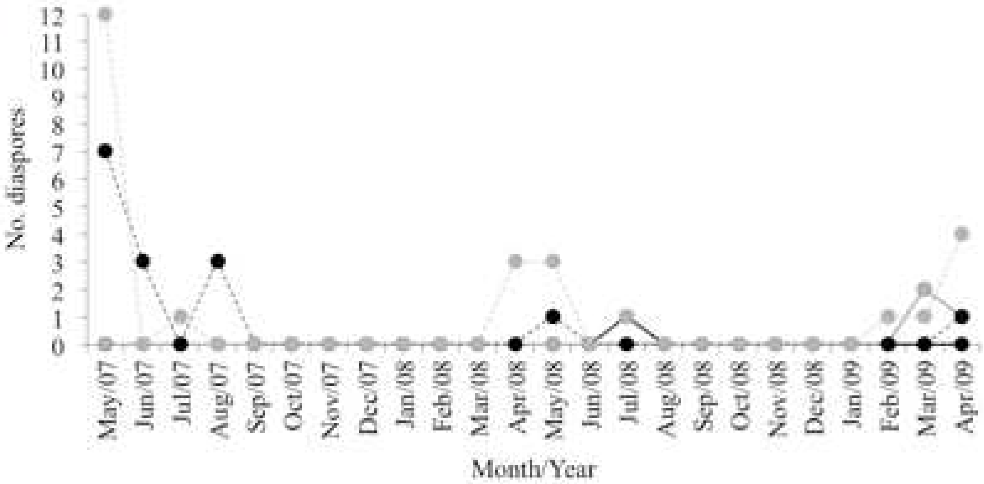


Fig. 1. Seed trap distribution in L1 (a) and L2 (b), two 1-ha plots of Lowland Atlantic Rainforest. Black-filled circles represent traps installed in 2007 and white-filled circles represent traps installed in 2008 in addition to those of 2007.

(a)


No. diaspores
0
1
2
3
4
5
May/07
Jun/07
Jul/07
Aug/07
Sep/07
Oct/07
Nov/07
Dec/07
Jan/08
Feb/08
Mar/08
Apr/08
May/08
Jun/08
Jul/08
Aug/08
Sep/08
Oct/08
Nov/08
Dec/08
Jan/09
Feb/09
Mar/09
Apr/09
Month/Year

(b)


No. diaspores
0
1
2
3
4
5
6
7
8
9
10
11
12
May/07
Jun/07
Jul/07
Aug/07
Sep/07
Oct/07
Nov/07
Dec/07
Jan/08
Feb/08
Mar/08
Apr/08
May/08
Jun/08
Jul/08
Aug/08
Sep/08
Oct/08
Nov/08
Dec/08
Jan/09
Feb/09
Mar/09
Apr/09
Month/Year

(c)

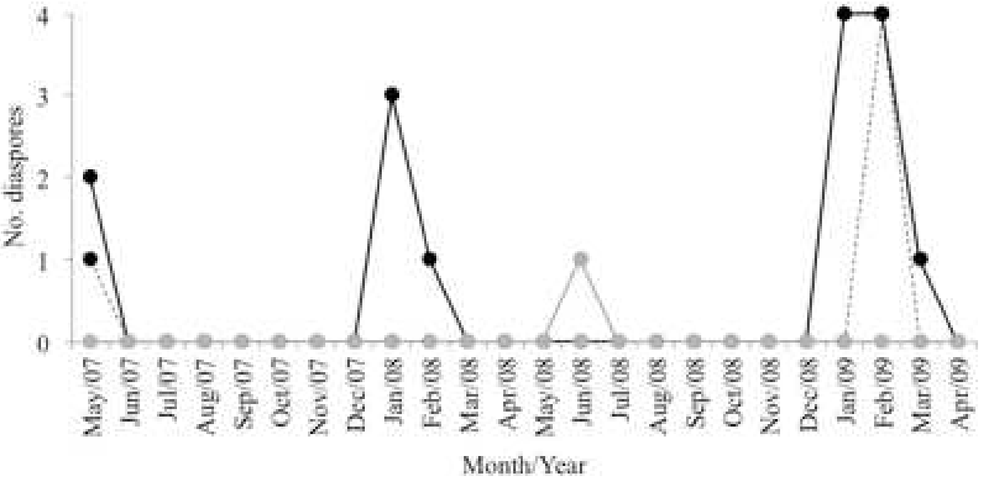

No. diaspores
0
1
2
3
4
May/07
Jun/07
Jul/07
Aug/07
Sep/07
Oct/07
Nov/07
Dec/07
Jan/08
Feb/08
Mar/08
Apr/08
May/08
Jun/08
Jul/08
Aug/08
Sep/08
Oct/08
Nov/08
Dec/08
Jan/09
Feb/09
Mar/09
Apr/09
Month/Year

Fig. 2. Fallen (continuous line) and dispersed (dashed line) diaspores of *Faramea picinguabae* (a), *Mollinedia schottiana* (b) and *Pourouma guianensis* (c) found at seed traps installed in two 1-ha plots (black represents L1 and gray represents L2) of Lowland Atlantic Rainforest. In the first sampling year, there were 30 traps/plot; in the second sampling year, there were 50 traps/plot.

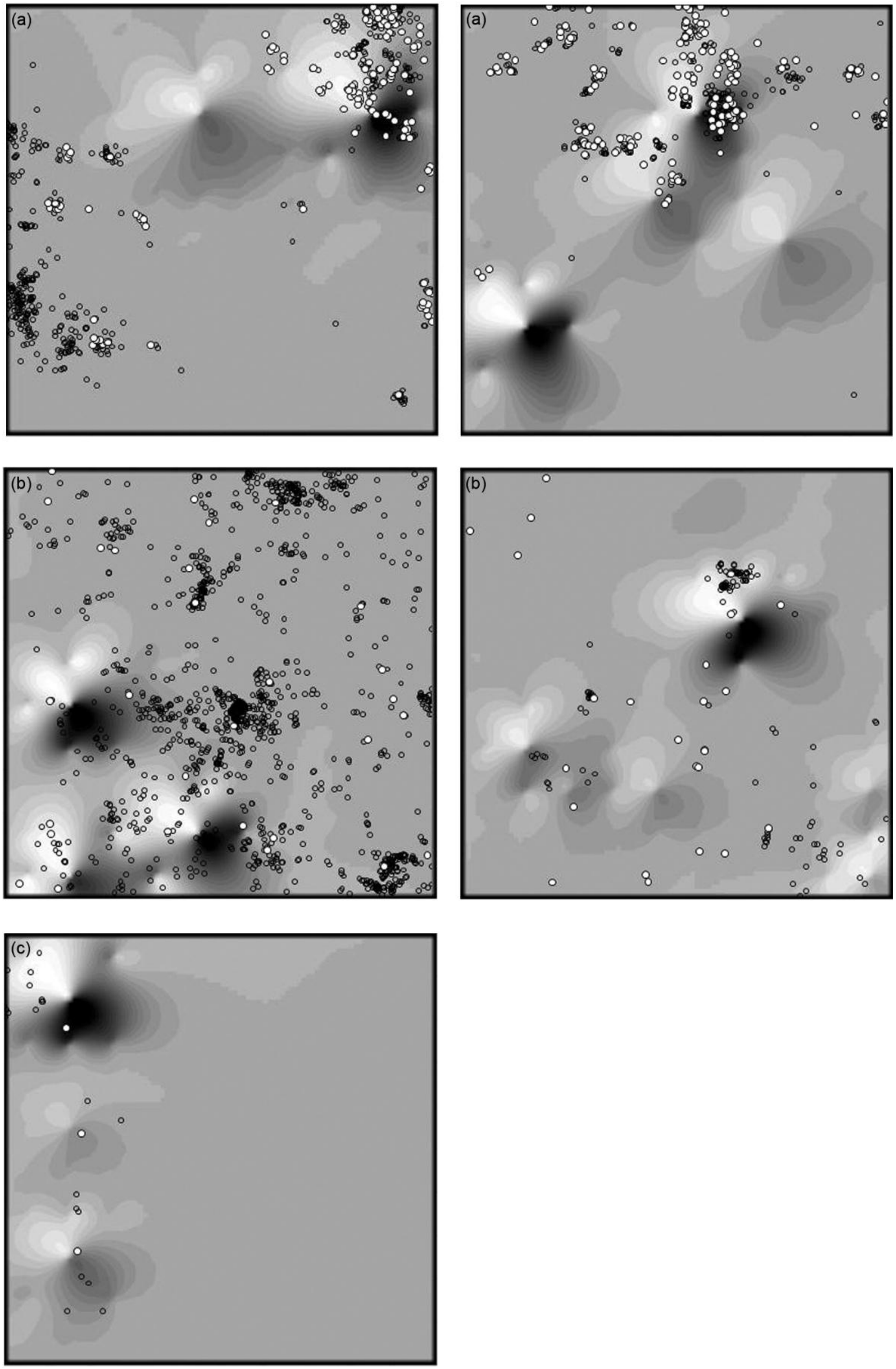
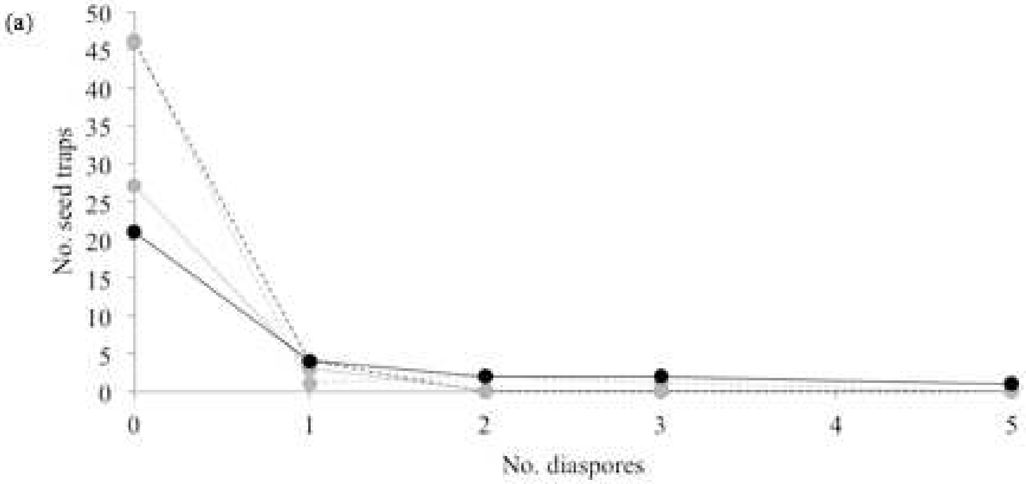
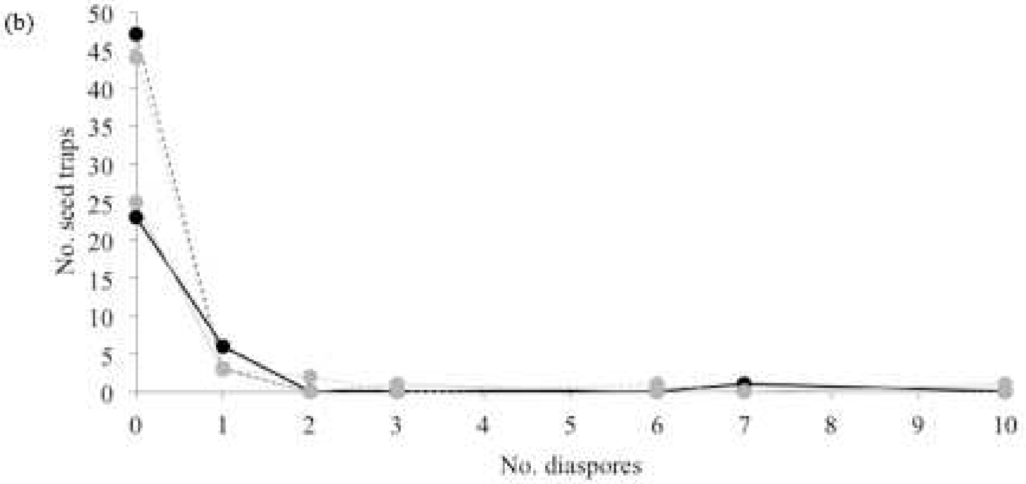

(a)
(a)
(b)
(b)
(c)

Fig. 3. Relief surface maps for seedfall and point maps for seedlings (empty circles) and fruiting adults (white-filled circles) of *Faramea picinguabae* (a), *Mollinedia schottiana* (b) and *Pourouma guianensis* (c) at two 1-ha plots (L1 at the left collum and L2 at the right collum) of Lowland Atlantic Rainforest. Here, seedling refers to the first ontogenetic stage, which is the juvenile for *Faramea* (please refer to the text for further explanation).


(a)
No. seed traps
50
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
No. diaspores


(b)
No. seed traps
50
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
5
6
7
8
9
10
No. diaspores

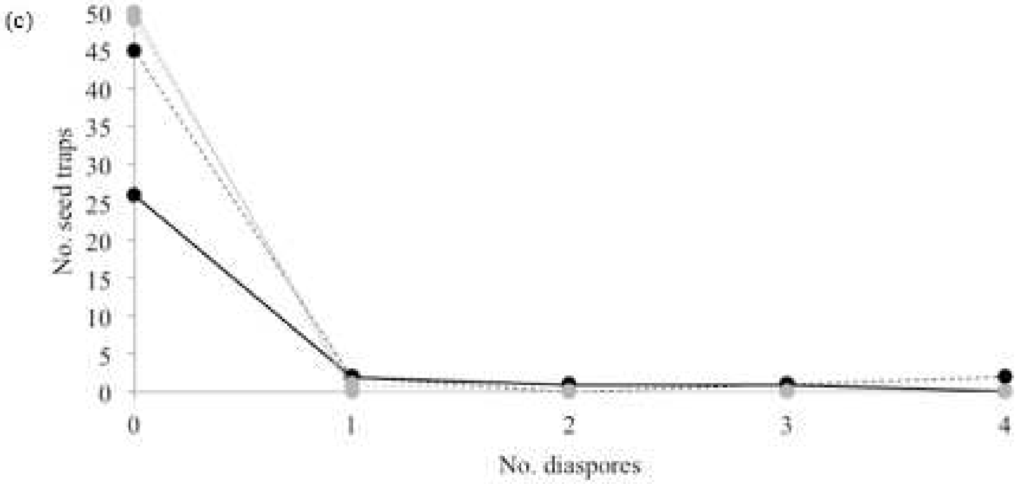

(c)
No. seed traps
50
45
40
35
30
25
20
15
10
5
0
0
1
2
3
4
No. diaspores

Fig. 4. Rank order distribution for diaspores of *Faramea picinguabae* (a), *Mollinedia schottiana* (b) and *Pourouma guianensis* (c) at two 1-ha plots (black represents L1 and gray represents L2) of Lowland Atlantic Rainforest. Seed rain was collected during two years: in the first, there were 30 traps/plot (continuous line); in the second sampling year, there were 50 traps/plot (dashed line).

CAPÍTULO 3

A sobrevivência de plântulas determina o padrão espacial de espécies arbóreas em uma floresta tropical

Valéria Forni Martins, André Luís Casarin Rochelle, Pedro Vasconcellos Eisenlohr & Flavio Antonio Maës dos Santos

Resumo estendido

Plântulas ocorrem em alta densidade e apresentam altas taxas de mortalidade nas florestas. Assim, os processos que ocorrem durante o estádio de plântula podem ter um grande impacto nas populações vegetais, incluindo um efeito forte na sua estrutura espacial resultante. Mecanismos dependentes de distância e densidade tendem a reduzir a agregação da população, enquanto heterogeneidade ambiental tende a aumentar a agregação.

O objetivo deste estudo foi determinar como a sobrevivência, a mortalidade e o recrutamento durante o estádio de plântula afetam o padrão espacial resultante das plântulas de *Faramea picinguabae* e *Pourouma guianensis* na Floresta Ombrófila Densa de Terras Baixas no litoral norte do estado de São Paulo, sudeste do Brasil. Especificamente, nós fizemos as seguintes perguntas: (1) os sobreviventes são mais ou menos agregados do que as plântulas antes dos eventos de mortalidade? (2) Quais características bióticas e abióticas resultam na ocorrência de mais sobreviventes em um dado microhabitat após os eventos de mortalidade? (3) Quais características resultam em maiores taxas de mortalidade em um dado microhabitat? (4) Quais características resultam em maiores taxas de recrutamento em um dado microhabitat? Nós

esperamos que os sobreviventes sejam menos agregados do que as plântulas antes dos eventos de mortalidade se os mecanismos positivamente dependentes de distância e negativamente dependentes de densidade atuarem como fatores importantes de mortalidade. Neste caso, tais fatores devem resultar na ocorrência de menos sobreviventes após os eventos de mortalidade, maiores taxas de mortalidade e menores taxas de recrutamento em áreas mais densas. Por outro lado, nós esperamos que os sobreviventes sejam mais agregados do que as plântulas antes dos eventos de mortalidade se a heterogeneidade ambiental atuar como um fator importante de mortalidade ou se as interações positivas beneficiarem a sobrevivência das plântulas. Neste caso, a ocorrência de mais sobreviventes após eventos de mortalidade, menores taxas de mortalidade e maiores taxas de recrutamento devem estar relacionados a características do microhabitat.

Entre oito e 19 meses após as plântulas das duas espécies estudadas terem sido amostradas e mapeadas em duas parcelas de 1 ha cada, nós as avaliamos para determinar se elas haviam morrido, recrutado para estádios ontogenéticos subsequentes ou permanecido no estádio de plântula. Para determinar se a mortalidade havia alterado o padrão espacial dos sobreviventes em relação às plântulas previamente amostradas, nós utilizamos a *bivariate O-ring statistics* e a *pair-correlation function* com o modelo nulo de *random labelling*. Nós também utilizamos regressões OLS e *Spatial Eigenvector Mapping* (SEVM) para comparar os padrões espaciais da sobrevivência, da taxa de mortalidade e da taxa de recrutamento a seis variáveis preditoras: densidade inicial de plântulas, área basal da população, área basal da comunidade, porcentagem de abertura de dossel, altitude e amplitude de elevação.

A mortalidade das plântulas ocorreu aleatoriamente e não modificou o padrão espacial das populações das duas espécies. Os sobreviventes se localizaram principalmente em áreas com alta densidade inicial de plântulas. As taxas de mortalidade não apresentaram relação com as variáveis preditoras ou com os filtros espaciais e ocorreram aleatoriamente. O mesmo padrão foi encontrado para as taxas de recrutamento de uma de *Faramea*, mas *Mollinedia* recrutou mais em áreas com maior área basal da população e maior porcentagem de abertura de dossel, e menos em áreas com maior amplitude de elevação.

Conhecer quais microhabitats são mais importantes para o destino das plântulas permite melhores desenhos experimentais para se determinar os fatores que resultam em sua sobrevivência, causam sua mortalidade ou beneficiam seu recrutamento. Neste estudo, encontramos que a mortalidade aleatória das plântulas não alterou o padrão espacial agregado das populações, o qual deve ser mantido ao longo da ontogenia. Nós pudemos prever onde mais sobreviventes podem ser encontrados na floresta: eles localizam-se principalmente em áreas com maior densidade de plântulas. No entanto, não foi possível indicar onde a mortalidade opera em maiores taxas, já que ela foi aleatória. Nós também não pudemos determinar onde o recrutamento ocorre em maiores taxas devido a características idiossincráticas das espécies: enquanto uma delas apresentou taxas de recrutamento distribuídas aleatoriamente no ambiente, as taxas de outra espécie estudada apresentaram relação com três das variáveis preditoras. Portanto, características que não são espacialmente estruturadas parecem ser de grande importância, principalmente para as taxas de mortalidade das espécies estudadas. Alternativamente, fatores que operam em uma escala espacial diferente da utilizada neste estudo podem ser mais importantes para a mortalidade e o recrutamento das espécies.

Seedling survival determines the spatial pattern of tree species in a tropical forest

Valéria Forni Martins[1], André Luís Casarin Rochelle[2], Pedro Vasconcellos Eisenlohr[3] & Flavio Antonio Maës dos Santos[4]

[1]Programa de Pós-Graduação em Ecologia, Institute of Biology, CP 6109, University of Campinas - UNICAMP, 13083-970, Campinas, SP, Brazil. E-mail: valeriafm@gmail.com.

[2]Programa de Pós-Graduação em Biologia Vegetal, Institute of Biology, CP 6109, University of Campinas - UNICAMP, 13083-970, Campinas, SP, Brazil.

[3]Programa de Pós-Graduação em Biologia Vegetal, Institute of Biology, CP 6109, University of Campinas - UNICAMP, 13083-970, Campinas, SP, Brazil & FAVALE/University of the State of Minas Gerais - UEMG, 36800-000, Carangola, MG, Brazil.

[4]Department of Plant Biology, Institute of Biology, CP 6109, University of Campinas - UNICAMP, 13083-970, Campinas, SP, Brazil.

ABSTRACT – Processes occurring during the seedling stage can have a strong effect on the population spatial structure. Distance and density-dependent mechanisms reduce the aggregation of the population, whereas environmental heterogeneity increases the aggregation. Our main goal was to determine how survival, mortality and recruitment during the seedling stage affect the resulting spatial pattern of seedlings of two tree species of a Lowland Atlantic Rainforest in Southeastern Brazil. We checked previously censused and mapped seedling of the species studied in order to determine if they had died, recruited to further ontogenetic stages or remained at the same stage. Then, we determined whether mortality changed the spatial pattern of survivals in relation to seedlings previously censused and compared the spatial patterns of seedling survival, mortality rate and recruitment rate to six predictor variables. Mortality occurred randomly and did not modify the aggregated spatial pattern of seedlings. We can predict where more survivals are found in the forest: they are located especially in areas with higher seedling density. However, mortality rates were related neither to predictor variables nor to spatial filters and occurred randomly. The same pattern was found for the recruitment rate of one species, but the other recruited more in areas with greater population basal area and higher percentage of canopy opening, and less in areas with greater elevation range. This shows each species' idiosyncrasies and indicates that characteristics that are not spatially structured or that operate on a different spatial scale than the one used in this study may have a great importance especially to mortality rates.

Keywords: *Faramea picinguabae*, *Mollinedia schottiana*, Núcleo Picinguaba, O-ring statistics, pair-correlation function, Parque Estadual da Serra do Mar, spatial eigenvector mapping.

INTRODUCTION

Seedlings in naturally regenerated forest stands occur as large numbers and present high mortality rates, since they are often more susceptible to mortality factors than well-established plants (Fenner 1987, Kitajima & Fenner 2000). Therefore, processes occurring during the seedling stage can have a major impact on plant populations, including a strong effect on their resulting spatial structure (Janzen 1970, Connell 1971, Kitajima & Fenner 2000).

Survival, mortality and recruitment of seedlings of many tropical tree species are simultaneously governed by positive distance and negative density-dependent mechanisms (Howe & Smallwood 1982, Willson 1993). This is because mortality of seeds and seedlings is elevated close to the parent tree, where there is also a high conspecific crowding (Augspurger & Kelly 1984, Packer & Clay 2000) due to local dispersal (Janzen 1970, Connell 1971). Such mechanisms include intraspecific competition, which is unlikely to be a major factor contributing to seedling mortality in tropical forests, at least in the initial stages of growth; allelopathy; microenvironmental modification such as soil mineral alteration, and plant natural enemies (Schupp 1988, Wright 2002, Bell *et al*. 2006). These mechanisms result in seedling mortality in areas with high plant density and are likely to reduce the aggregation of the population through ontogeny (Janzen 1970, Connell 1971, Condit *et al.* 2000).

There are other biotic factors that also affect seedling fate: age, as the susceptibility of seedlings to attack by herbivores generally declines as the plant mature and its chemical and/or physical defences develop (Hanley *et al.* 1995); size, with larger seedlings presenting lower mortality rates (Pigot & Leather 2008); interspecific competition (De Steven 1991), and seed dispersal (Russo & Augspurger 2004). These factors may change the aggregation of the population through ontogeny in a very unpredictable fashion, either because they present different spatial structure or because they are not spatially structured at all.

Influential abiotic factors to seedling fate include light and covariate microclimatic variables such as humidity and temperature (Augspurger & Kelly 1984); soil physical and chemical properties (Rey *et al*. 2006), and water stress (Herrera *et al*. 1994). The patchiness common to tropical forests can result in the mortality of seedlings located at microhabitats that are less favourable to the species. Therefore, individuals tend to survive more at microhabitats with greater favourability, which is likely to lead to a more aggregated spatial pattern of the population through ontogeny (Condit *et al.* 2000). Besides environmental heterogeneity, positive interactions such as association with mycorrhiza and facilitation can also result in a stronger aggregation of the population through ontogeny, because only the seedlings that occur close to other organisms interact and benefit from the positive interactions (Dickie *et al.* 2007).

Other mechanisms affecting seedling fate are those related to physical damage, caused by litterfall, landslides, floods and trampling by understory vertebrates (Clark & Clark 1989, Mack 1998, Portela & Santos 2009). As well as biotic factors that are neither distance nor density-dependent, physical damage may also change the aggregation of the population though ontogeny in a very unpredictable fashion.

The demographics of seedlings, specially their distribution, may be highly variable in space (Gómez-Aparicio *et al*. 2005 and references therein) and thereby inherently subject to spatial autocorrelation. Because of that, spatial analysis techniques that control for spatial autocorrelation of data are clearly needed to achieve both unbiased and mutually comparable estimates of seedling fate patterns (Hampe *et al.* 2008). We used O-ring statistics (Wiegand & Moloney 2004), pair-correlation function (Stoyan & Stoyan 1994) and spatial regressions (Bini *et al*. 2009, Rangel *et al.* 2010) in order to determine how survival, mortality and recruitment during the seedling stage affect the resulting spatial pattern of seedlings of two tree species of a Lowland Atlantic Rainforest (*sensu* Oliveira-Filho & Fontes 2000) in Southeastern Brazil. Although the final pattern of plants ingressing the population depends on seedling survival, mortality and recruitment, these three processes may not be spatially correlated, as there can be sites whose characteristics enable seedling survival, cause seedling mortality or benefit seedling recruitment. Therefore, by untangling the effects of each of theses processes on the resulting spatial pattern of seedlings, we are also able to determine which characteristics are more important for seedling survival, mortality and recruitment.

Specifically, we ask: (1) are surviving individuals more or less aggregated than seedlings before mortality events? (2) Which biotic and abiotic characteristics result in the occurrence of more survivals in a given microhabitat after mortality events? (3) Which characteristics result in higher mortality rates in a given microhabitat? (4) Which characteristics result in higher recruitment rates in a given microhabitat? We expect survivals to be less aggregated than seedlings before mortality events if positive distance and negative density-dependent mechanisms act as important mortality factors. In this case, these mortality factors should result in the occurrence of fewer survivals after mortality events, higher mortality rates and lower recruitment rates at denser sites. Alternatively, we expect survivals to be more aggregated if environmental heterogeneity acts as an important mortality factor or if positive interactions benefit seedling survival. In this case, the occurrence of more survivals after mortality events, lower mortality rates and higher recruitment rates should be related to microhabitat characteristics.

MATERIAL AND METHODS

Study site

The Brazilian Atlantic Forest is considered one of the world's hotspots for biodiversity conservation (Myers *et al.* 2000), with only about 7% of its original cover remaining (Fundação SOS Mata Atlântica 2011). The largest continuous stretch of this vegetation includes the Parque Estadual da Serra do Mar (PESM), SE Brazil. The PESM is a state park that comprises ca. 315,000 ha (SOS Mata Atlântica/INPE/ISA 1998) and is divided into several administration nucleuses, one of which is Núcleo Picinguaba (23°31' - 23°34'S, 45°02' - 45°05'W). It is located at the mountain range of Serra do Mar, municipality of Ubatuba, northern coast of the state of São Paulo, and comprises ca. 47,500 ha (SMA 1996). The region has mountainous relief, with altitudes varying between 0 m and 1,200 m (Alves *et al.* 2010). At Núcleo Picinguaba, temperatures range from 25.5^o C in February to 18.4^o C in July. There is no marked dry season and rainfall ranges from 376 mm in January to 11 mm in July (Sentelhas *et al.* 2003). Air relative humidity is always above 80% (Morellato *et al.* 2000), daylength varies from 15.5 h in May to 9.1 h in October, and winds normally come from ocean and blow southeast at 0.7 m/s – 1.0 m/s (Alves 2000, CPTEC 2010).

The Núcleo Picinguaba is the only portion of PESM to reach the coast and, due especially to its great range of altitude, is composed of a mosaic of vegetation physiognomies. We collected data in two 1-ha plots of the Lowland Atlantic Rainforest (ca. 44°48'W, 23°22'S), namely Lowland 1 (L1 hereafter) and Lowland 2 (L2 hereafter). This phytophysiognomy covers mountain slopes from 50 m to 100 m above sea level and occurs in cambisols, which are soils formed recently from the sedimentation of mountain erosion. Many rocky formations and dry stream paths are also observed. Each study plot was divided in 100 sub-plots of 10 m x 10 m, where every living tree whose trunk perimeter at 1.3 m in height was equal to or larger than 15 cm was sampled and identified (Joly *et al.* 2008).

L1 and L2 present differences in their abiotic environment, such as in the quantity of phosphorous (P), sulphur (S), potential acidity (H+Al), sum of bases (SB, the sum of potassium, calcium, magnesium and sodium quantities), clay and silt in the soil, percentages of nitrogen and clay plus silt in the soil, altitude (and associated factors, such as temperature and wind incidence) and elevation range. Other factors, such as pH and percentage of carbon in the soil, and canopy opening do not present striking differences between the study plots (Table 1). Soil data were obtained from 32 boreholes in the 0 – 5 cm soil layer, regularly distributed in L1 and L2 (Martins 2010); topographic data were obtained from altitude measurement at each corner of every sub-plot at the two study plots (Joly & Martinelli 2006); canopy opening data were obtained from hemispheric photographs taken at the centre of each sub-plot in L1 and L2 and analysed with the software Data Gap Analyzer 2.0 (Frazer *et al.* 1999, Joly & Martinelli 2010).

Despite differences in the abiotic environment, L1 and L2 present very similar species composition and community structure: tree height ranged from ca. 1.6 m to 25 m, and tree trunk diameter varied between ca. 5 (inclusion criteria) cm and 94 cm. About 1,200 trees of 145 species were sampled in each plot (Joly & Martinelli 2006). A dense understorey, sub-canopy, canopy and emergent trees are present (Morellato & Haddad 2000), but sometimes it is not possible to distinguish clearly between the sub-canopy and the understorey, and between the sub-canopy and the canopy (Cazotto, Martins & Santos, *unpubl. data*). Lianas, palm trees, epiphytes, ferns, and bromeliads are common (Morellato & Haddad 2000). Common tree species belong to the genera *Bathysa* (Rubiaceae), *Chrysophyllum* (Sapotaceae), *Coussarea* (Rubiaceae), *Eugenia* (Myrtaceae), *Euterpe* (Arecaceae), *Garcinia* (Clusiaceae), *Guapira* (Nyctaginaceae), *Marlierea* (Myrtaceae), *Mollinedia* (Monimiaceae), *Myrcia* (Myrtaceae), *Rustia* (Rubiaceae), *Sloanea* (Elaeocarpaceae), *Syagrus* (Arecaceae) and *Virola* (Myristicaceae; Joly & Martinelli 2006).

Species studied

The species studied were selected from two species composition lists for Núcleo Picinguaba. One list contained species that occur between sea level and 100 m of altitude (Pedroni 2001) as well as a morphological description of the diaspores of the individuals sampled, which aided the selection of the species studied here. The other species composition list contained species that occur between sea level and 1,000 m of altitude (Lacerda 2001). Both sampling encompassed the two plots of Lowland Atlantic Rainforest studied here. Based on the morphological description of the diaspores by Pedroni (2001), we selected species belonging to ornithochory, which is the most important dispersal syndrome in the study site (Cazotto *et al. in prep.*). Within this syndrome, we chose the species with fleshy diaspores with only one relatively large, hard seed, which can be easily found in seed traps in studies of seed rain and population spatial patterns that have also been conducted by us. Species with these features and also with great abundance of small individuals in the study site are *Faramea picinguabae* M. Gomes (Rubiaceae) and *Mollinedia schottiana* (Spreng.) Perkins (Monimiaceae).

Faramea picinguabae (*Faramea* hereafter) is a treelet or tree generally less than 10 m in height. It seems to be shade-tolerant and its seedlings are able to establish in habitat ranging from treefall gaps to the dark forest understorey, as do *F. occidentalis* (Schupp 1988). *Faramea* in one of the most abundant species in the Lowland Atlantic Rainforest of Núcleo Picinguaba, although poorly sampled in previous inventories due to its thin trunk (*pers. observ.*). *Mollinedia schottiana* (*Mollinedia* hereafter) is a tree generally less than 10 m in height. The species is one of the most abundant in the Lowland Atlantic Rainforest of Núcleo Picinguaba (Joly & Martinelli 2006). The seedlings of the two species studied occur in clumps in both L1 and L2 (Martins & Santos *in prep.* a, b), which is characteristic of plant populations in tropical forests (*e.g.*, Condit *et al.* 2000, Klimas *et al.* 2007). None of the species present evidence of releasing allelopathic compounds in the soil (*person. observ.*).

Seedling survival, mortality and recruitment

Martins & Santos (*in prep.* a) previously censused, marked with a numbered tag, measured the trunk diameter at soil height (DSH), mapped and identified the ontogenetic stage of every individual of the two species studied within L1 and L2 (Table 2); the time plants were censused is hereafter referred to as ‘time 1’. After a period of eight to 19 months after time 1, we checked every seedling of *Mollinedia* and every juvenile of *Faramea* in order to determine if they had died, recruited to further ontogenetic stages or remained at the same stage (‘time 2’ hereafter). We checked juveniles of *Faramea* because Martins & Santos (*in prep.* a) could not differentiate its seedlings from juveniles due to the absence of conspicuous embryonic structures that characterize the former (Gatsuk *et al.* 1980). In this study, we use seedling as a generic term for the first ontogenetic stage of each species.

In order to find the plants, we used the maps previously elaborated by Martins & Santos (*in prep.* a). The plants we did not find were considered as dead. To minimize the chances we did not find an individual because of minor errors in its mapped location, we searched for it in an area that encompassed a circle with 1 m radius centred at the point at which the plant should be. We also searched the litter in order to check if the individual was buried; at many times we found its numbered tag, which was an indication that the plant had died. If a seedling in time 1 was in a more advanced ontogenetic stage (such as juvenile or immature) in time 2, the individual was considered recruited, as it survived the stage when mortality is more pronounced and is likely to remain in the population (Fenner 1987, Kitajima & Fenner 2000). Seedlings and recruited individuals together are called ‘survivals’ hereafter.

Predictor variables

The spatial patterns of seedling survival, mortality and recruitment were compared to the spatial pattern of the following six variables. Their values were obtained for each of the 100 sub-plots in both L1 and L2.

(1) Density of seedlings of the two species at time 1, obtained from Martins & Santos (*in prep.* a). We transformed the mapped position of each individual of the species to density counts in each of the sub-plots of L1 and L2. Population response as a function of initial seedling density is an indicative of intraspecific competition among individuals of the same ontogenetic stage, allelopathy, microenvironmental modification and action of plant natural enemies. Because none of the species presented evidence of releasing allelopathic compounds in the soil (*person. observ.*), population response as a function of initial seedling density is not expected to indicate allelopathy.

(2) Sum of the basal area (πr^2) of every individual of the same species present at L1 and L2 at time 1. The radius r of each individual was obtained from its diameter at soil height measured by Martins & Santos (*in prep.* a). If tree diameter is correlated with root system size, then larger trees will represent stronger competition to conspecific seedlings. Moreover, tree size is often related to tree age (Packer & Clay 2000). With negative feedback, individuals ‘culture’ (*sensu lato*; Bever 1994) their soil communities leading to a positive correlation between pathogen accumulation and time that a site has been occupied by a species. Seedlings beneath larger trees would therefore experience greater distance and/or density-dependent mortality (Packer & Clay 2000).

(3) Sum of the basal area of every individual with perimeter at breast height (PBH) equal to or larger than 15 cm present at the plots. The radius of each individual was obtained from its PBH measured in previous inventories (Joly & Martinelli 2007). Community basal area is a

proxy for tree biomass (Norghauer *et al.* 2006), so that population response as a function of it is an indicative of interspecific competition with large plants.

(4) Percentage of canopy opening, obtained from hemispheric photographs. They were previously taken at the centre of each sub-plot in both L1 and L2. Two digital cameras were used, a Nikon Coolpix 950 and a Nikon Coolpix 5000, both with a fisheye lens Nikon FC E8. The two cameras were adjusted to the same settings and fixed at a tripod with the lens facing upwards, at 1.3 m from the soil surface and parallel to it. All photographs were taken from 8 a.m. to 10 a.m. and from 3 p.m. to 5 p.m., periods at which there were uniform sky coverage and high contrast between the sky and the canopy. They were also oriented with magnetic north toward the top of the image, allowing superposition of the solar track (Joly & Martinelli 2010). The software Data Gap Analyzer 2.0 (Frazer *et al.* 1999) was used to convert the photographs into binary images and estimate the percentage of canopy opening by calculating the relative proportion of black and white pixels. From that, the percentage could be visually estimated (Joly & Martinelli 2010).

(5) Altitude of the centre of each sub-plot, obtained from topographic surveys previously made with a total station (Joly & Martinelli 2006). Sub-plots at lower altitudes are closer to watercourses (*person. observ.*), whose high humidity can have a positive, negative or neutral effect on seedling survival, mortality and recruitment. However, sub-plots at lower altitudes also have higher rock coverage (*person. observ.*), which should have a negative effect on seedlings due to reduced space to develop roots. Population response as a function of altitude is an indicative of microhabitat effect on seedling survival, mortality and recruitment.

(6) Elevation range of each sub-plot, calculated from the difference between the altitude of the highest corner and the altitude of the lowest corner of each sub-plot (Oliveira-Filho *et al.* 1994). Altitude values were obtained from topographic surveys previously made with a total

station (Joly & Martinelli 2006). In steeply sloping areas, where the canopy turnover rate is high (Martínez-Ramos *et al.* 1988), the probability of being damaged and killed by litterfall is higher than in areas of flat terrain (Mack 1998). Also, areas with greater elevation range difference may be more susceptible to landsliding, which should also result in higher seedling mortality. Population response as a function of elevation range should indicate how physical damage affects seedling survival, mortality and recruitment.

Data analyses

We used the bivariate O-ring statistics (Wiegand & Moloney 2004) and the pair-correlation function (Stoyan & Stoyan 1994) to determine whether mortality changed the spatial pattern of survivals at time 2 in relation to seedlings in time 1. The bivariate O-ring statistics for point patterns comprising type 1 and type 2 points (here type 1 represents dead individuals and type 2 survivals) is the expected density of survivals in a ring of radius r and width dw centred on an arbitrary dead plant. The O-ring statistics has the intuitive interpretation of a neighbourhood density and is especially sensitive to small-scale effects (Wiegand & Moloney 2004, Illian *et al.* 2008). The bivariate pair-correlation function $g_{12}(r)$ is the intensity normalized version of $O_{12}(r)$, *i.e.* $O_{12}(r) = \lambda_2 g_{12}(r)$, where λ_2 is the intensity of survivals in L1 and L2 (*i.e.* the number of survivals divided by the area of the plots; Stoyan & Stoyan 1994).

The appropriate null model to investigate the spatial structure in mortality of the survivals is random labelling, which identifies the spatial structures in the process that assigned a label 'mortality' to the individuals (Goreaud & Pelissier 2003, Wiegand & Moloney 2004). The fundamental question is to find out if the process that distributed the label was a random process. We used a Monte Carlo implementation of random labelling that involves random resampling of sets of n_1 dead individuals from the total of $(n_1 + n_2)$ dead and surviving individuals, *i.e.* we randomly shuffle the label ‘dead’ among the plants. In this case, random labelling implies that $g_{1+2,1+2}(r) = g_{11}(r) = g_{22}(r) = g_{12}(r) = g_{21}(r)$, where 1 symbolizes dead individuals, 2 survivals, and 1 + 2 symbolizes the joint pattern of dead and surviving individuals (Jacquemyn *et al.* 2010).

The observed summary statistics were contrasted to approximate (two-sided) 95% simulation envelopes for the null model. The simulation envelopes were created by calculating for each distance *r* the 5th lowest and highest values of the summary statistics from 199 Monte Carlo simulations of the null model. This yields an approximate 5% error rate (Illian *et al.* 2008). The analyses were done using the software Programita using 1 ring width (Wiegand & Moloney 2004, Jacquemyn *et al.* 2010).

Then, we used regression models in order to determine which of the predictor variables resulted in (1) the occurrence of more survivals after mortality events, (2) higher mortality rates of seedlings and (3) higher recruitment rates of seedlings in a given microhabitat. In the first case, the response variable was the number of survivals at time 2 in every sub-plot. The mortality and recruitment rates were calculated only for sub-plots with 10 or more seedlings at time 1, following the formula of population growth $N_t = N_0e^{rt}$. We consider N_t as the number of survivals at time 2 for the calculus of mortality rates and as the number of recruited individuals at time 2 for the calculus of recruitment rates, N_0 as the number of seedlings at time 1, *e* as the Neperian number, *r* as the mortality rate or the recruitment rate, and *t* as the number of months between time 1 and time 2 (eight for L1 and 19 for L2). The cut-off of 10 individuals was necessary in order to prevent overestimation of mortality and recruitment rates at sub-plots with very low numbers of seedlings at time 1. Because there were no sub-plots with 10 or more seedlings of *Mollinedia* at L2, it was removed from the analyses.

We used an ordinary least-squares (OLS) multiple regression between seedling survival, mortality rate or recruitment rate for the species studied at both L1 and L2 and the predictor variables in order to check the residuals for structure or spatial autocorrelation (Legendre & Fortin 1989). The residuals were evaluated with Moran's *I*, which is a widely used index of spatial autocorrelation that varies between -1 and +1, the expected value in the absence of significant spatial autocorrelation being around 0 (Cliff & Ord 1981). A correlogram presents the values of *I* as a function of distance classes. For a correlogram to be globally significant, at least one value of *I* has to be significant at an alpha level of less than α/k (Bonferroni criterion), where α represents the significance level (here, 0.05) and *k*, the number of distance classes considered. Once this is established, individual values of *I* can be declared significant at the 0.05 level. Complete spatial randomness, *i.e.* no spatial structure, is represented by a flat correlogram with no significant values of *I* (Legendre & Fortin 1989).

Because OLS is a basic, non-spatial regression analysis, when the R^2 is extremely high (above 0.886 in our analyses) and there are both no structure and spatial autocorrelation of the residuals, it is possible to assume that the response variable is not spatially autocorrelated (Beale *et al.* 2010). When these three criteria were met, we used the OLS multiple regression results in order to determine to which predictor variables seedling survival, mortality rate or recruitment rate was related.

In the cases where the residuals of the OLS multiple regression were structured and/or spatially autocorrelated, we used spatial eigenvector mapping (SEVM), one of the most flexible and statistically powerful spatial regression techniques (Bini *et al*. 2009). SEVM enables the selection of spatial filters that can be incorporated as covariates expressing "space" in a regression model. The spatial filters are eigenvectors correlated with the dependent variables that were extracted from a principal coordinates analysis of a symmetrical matrix expressing spatial relationships among spatial units (Bini *et al.* 2009, Beale *et al.* 2010). When no spatial filters were automatically selected during the analysis, we chose those that decreased the most the spatial autocorrelation of the residuals in the first distance classes (Rangel *et al.* 2010).

The selected spatial filters were then incorporated in a partial regression as a second predictor set. A partial regression quantifies the explanatory power due to individual sets of competing hypotheses as well as the magnitude of redundancy between the sets (Rangel *et al.* 2010). When adding spatial filters to the partial regression model, some variables presented multicollinearity (here, we considered multicollinears the variables with variance inflation factor higher than 6, as suggested by Bini *et al.* 2009). Because of that, we excluded them from the analyses in a stepwise fashion (Bini *et al.* 2009).

In the cases where we did not find relation between seedling survival, mortality rate or recruitment rate, and the predictor variables and/or spatial filters, we explored the spatial structure of the response variables through Moran's *I* correlograms (Legendre & Fortin 1989). We used the software SAM version 4.0. (Rangel *et al.* 2010) to calculate the OLS regressions, the SEVM, the partial regressions and the Moran's *I*. Results were declared significant at the 0.05 level.

RESULTS

Mortality and spatial structure of survivals

Mortality was randomly distributed among dead and surviving individuals of the two species in L1 and L2 (Fig. 1). This means that the aggregated spatial pattern of seedlings in time 1 was maintained by survivals in time 2 instead of changing due to mortality.

Seedling survival

The number of individuals of *Faramea* that survived in L1 from time 1 to time 2 was related to the predictor variables ($p < 0.001$, $R^2 = 0.99$, $F_{6, 94} = 1247.54$). It was positively related to both initial seedling density ($p < 0.001$) and elevation range ($p = 0.005$), and negatively related to population basal area ($p = 0.028$). In L2, the number of individuals of *Faramea* that survived was also related to the predictor variables ($p < 0.001$, $R^2 = 0.95$, $F_{6, 94} = 274.37$). As well as in L1, it was positively related to initial seedling density ($p < 0.001$); however, the number of survivals presented only a marginally significant negative relation to population basal area ($p = 0.063$).

The number of individuals of *Mollinedia* that survived in L1 from time 1 to time 2 was related to the predictor variables ($p < 0.001$, $R^2 = 0.89$, $F_{6, 94} = 120.58$), being positively related to initial seedling density ($p < 0.001$). In L2, the number of individuals of *Mollinedia* that survived was also related to the predictor variables ($p < 0.001$, $R^2 = 0.89$, $F_{6, 94} = 124.08$). It was positively related to initial seedling density ($p < 0.001$) and also to population basal area ($p = 0.002$).

Seedling mortality

The mortality rate of *Faramea* in L1 was not related to any predictor variable nor to the spatial filter included in the partial regression model ($p = 0.785$, $R^2 = 0.32$, $F_{7, 9} = 0.54$). The mortality rate was spatially autocorrelated, although it only presented repulsion in the second distance class (Fig. 2). The mortality rate of *Faramea* in L2 was also not related to any predictor variable nor to the spatial filter included in the partial regression model ($p = 0.360$, $R^2 = 0.69$, $F_{6, 5} = 1.51$). However, differently from L1, the mortality rate was not spatially autocorrelated. The mortality rate of *Mollinedia* in L1 was not related to any predictor variable ($p = 0.672$, $R^2 = 0.14$, $F_{6,25} = 0.67$) and was not spatially autocorrelated.

Seedling recruitment

The recruitment rate of *Faramea* in L1 was not related to any predictor variable nor to the spatial filter included in the partial regression model ($p = 0.164$, $R^2 = 0.64$, $F_{7,9} = 2.07$). In L2, the recruitment rate of *Faramea* was also not related to any predictor variable ($p = 0.250$, $R^2 = 0.76$, $F_{7,4} = 2.12$). In both plots, the recruitment rate was not spatially autocorrelated.

The recruitment rate of *Mollinedia* in L1 was related to the predictor variables ($p = 0.02$, $R^2 = 0.44$, $F_{6,25} = 3.15$). It presented a marginally significant positive relation to population basal area ($p = 0.069$), a positive relation to percentage of canopy opening ($p = 0.036$) and a negative relation to elevation range ($p = 0.021$). However, the predictor variables explained only 44% of the variation of the recruitment rate of *Mollinedia*.

DISCUSSION

Seedling mortality due to distance and density-dependent mechanisms as well as microhabitat unsuitability is expected to decrease or increase the aggregation of populations of tropical tree species through ontogeny (Janzen 1970, Connell 1971, Condit *et al.* 2000, Dickie *et al.* 2007). However, none of the species studied presented any alteration in their spatial pattern due to mortality. The random distribution of mortality among individuals may occur because the distance and density-dependent mechanisms, and the microhabitat unsuitability act together and null each other's resulting spatial pattern. Alternatively, mortality factors that present different spatial structure (*e.g.*, interspecific competition) or that are not spatially structured at all may be more important to the species studied, resulting in the observed randomly distributed mortality among individuals.

Characteristics affecting seedling survival, mortality and recruitment that are not spatially structured include plant age and size, and physical damage caused by trampling. Also, spider webs on leaves seem to be a frequent source of loss of effective leaf area, which reduces photosynthesis and may lead to seedling mortality (Clark & Clark 1985). The non-spatially structured characteristics may be very idiosyncratic, with different degrees of importance to seedling fate accordingly to the species and to the site where it occurs.

Survival showed a negative distance and/or positive density-dependence for the species studied, with more surviving individuals in areas with higher initial seedling density. This result is contrary to many findings in the literature (*e.g.,* Janzen 1970, Connell 1971, Clark & Clark 1985, Schupp 1988, Wright 2002, Bell *et al*. 2006, Pigot & Leather 2008) and implies that intraspecific competition among seedlings, microenvironmental modification and/or action of plant natural enemies do not reduce the chance of survival in crowding sites. Actually, high-density sites are better for survival, which is due to facilitation or other positive interactions among seedlings of the same species, and thus constitute safe sites. Also, the high-density sites can correspond to favourable sites that are spatially restricted, even though we did not find relation between the number of survivals and environmental characteristics for both species. This may happen because factors determining favourable sites operate on a smaller scale than the one used in this study.

Besides initial seedling density, *Faramea* also presented fewer survivals in areas with greater population basal area. This indicates that intraspecific competition among individuals of different ontogenetic stages (rather than among seedlings) and/or pathogen attack caused by proximity to larger plants have an important influence on the distribution of individuals. Because intraspecific competition is unlikely to be a major factor contributing to seedling mortality in tropical forests (*e.g.,* Wright 2002, Bell *et al*. 2006), pathogen attack is probably the cause of mortality of seedlings of *Faramea* in areas with greater population basal area. Contrary to intraspecific competition, pathogen attack is regarded as a major mortality factor in tropical forests (Augspurger & Kelly 1984, Packer & Clay 2000).

Last, *Faramea* in L1 presented more survivals in areas with greater elevation range, which was not expected because physical damage is an important source of seedling mortality in tropical forests (Clark & Clark 1989, Mack 1998, Portela & Santos 2009), especially in steeply sloping areas (Mack 1998). We hypothesize that this pattern arises from a complex interaction between *Faramea*'s response to agents that cause physical damage and its competitive ability. Each species differs in its response (Clark & Clark 1989) and, if *Faramea* is more resistant to damage or recovers from it faster than do other species, it can outcompete them and indirectly benefit from physical damage. One possible reason we did not find relation between the number of survivals of *Faramea* and elevation range in L2 is that this plot is much flatter than L1 (Table 1), so that seedlings of this species do not gain any competitive advantage mediated by physical damage in steeply sloping areas.

Contrary to *Faramea*, *Mollinedia* in L2 presented more survivals in areas with greater population basal area, indicating that, for this species, pathogen attack does not contribute to seedling mortality. Instead, the presence of individuals of further ontogenetic stages benefits seedling survival through some positive interaction mechanism. It is possible we did not find relation between the number of survivals of *Mollinedia* and population basal area in L1 due to processes that operate distinctly for this species in the plots; these processes are likely to be mediated by soil and topographic characteristics that differ between L1 and L2 (Table 1). Dissimilar results among study sites for the same species have also been documented by other authors studying floristically and structurally similar sites in tropical forests (*e.g.,* Clark & Clark 1989, Martins & Santos *in prep.* a, b).

Although we found fewer survivals of *Faramea* in areas with greater population basal area, which seems to be a result of mortality caused by pathogen attack, there was no relation between this predictor variable and mortality rate of this species. Moreover, mortality rate of *Faramea* in the two plots and of *Mollinedia* in L1 could not be explained by any of the predictor variables nor by spatial filters, which means it does not respond to spatially structured characteristic or that the spatial scale evaluated in this study was not suitable as to identify factors influencing the spatial distribution of mortality rates. Actually, mortality rates were not spatially structured themselves, being randomly distributed in the plots. The only exception was a repulsion among mortality rates in the second distance class for *Faramea* in L1, a pattern that can also be mediated by soil and topographic characteristics that differ between the plots. Therefore, some unknown mortality factor results in high mortality rates in an area and in low mortality rates in the adjacent area within L1. Further studies should aim at determining the causes of seedling mortality in order to understand how they influence the demographics of *Faramea* and *Mollinedia*.

The recruitment rate of *Faramea* was also randomly distributed in the plots and did not respond to spatially structured characteristics. Alternatively, the spatial scale evaluated may not have been suitable. Future investigations should aim at understanding which characteristics lead to the recruitment of seedlings to further ontogenetic stages and how they affect plant demography (Meiners & Handel 2000). The recruitment of *Mollinedia* in L1 was beneficiated by higher population basal area, once more indicating that the presence of individuals of further ontogenetic stages leads to some positive interaction mechanism instead of negative effects due to intraspecific competition and/or pathogen attack. *Mollinedia* also recruited more in areas with higher percentage of canopy opening, which is in accordance with many studies about tropical tree species (*e.g.*, Augspurger & Kelly 1984, Whitmore 1996, Kobe 1999). Nevertheless, elevation range had a negative impact on recruitment rate of this species, most likely due to physical damage in steeply sloping areas (Mack 1998). Probably, other non-spatially structured characteristics or factors operating on smaller spatial scales also influence the recruitment rate of *Mollinedia*, since population basal area, percentage of canopy opening and elevation range explained only 44% of the variation of such rate.

Knowing which microhabitats are important for seedling fate enables better experimental designs in order to untangle the factors that result in seedling survival, cause seedling mortality or benefit seedling recruitment. Here, we employed advanced spatial analysis techniques in order to show that mortality occurs randomly among seedlings and does not modify their aggregated spatial pattern, which should be maintained through further ontogenetic stages. We can predict where more survivals are found in the forest: they are located especially in areas with higher seedling density. However, it is not possible to indicate where mortality operates at higher rates, because it occurs randomly in the forest. Also, we could not determine where recruitment occurs at higher rates due to idiosyncratic characteristics of the species: while *Faramea* presents randomly distributed recruitment rates, *Mollinedia* presents relation to three predictor variables.

Therefore, characteristics that are not spatially structured seem to have a great importance especially to mortality rates of the species studied. Alternatively, factors operating on a different spatial scale than the one used in this study may be more important to mortality and recruitment of the species.

ACKNOWLEDGMENTS – Valeria F. Martins held a scholarship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) while carrying out this study (Process Number 142295/2006-0) and Flavio A. M. Santos was supported by a grant from the CNPq (Process Number 207132/2004-8). The research was supported by the State of São Paulo Research Foundation (FAPESP) as part of the Thematic Project "Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar - Functional Gradient" (Process Number 03/12595-7), within the BIOTA/FAPESP Program, The Biodiversity Virtual Institute (http://www.biota.org.br). This research has been authorized by COTEC/IF 44.924/2006 and IBAMA 12170-1 permits. The authors wish to thank Joselino Vieira dos Santos and Manuel Vieira de Assunção for help during fieldwork; Christiane Corrêa and Rafael Costa for part of the hemispheric photographs, and Gisele Garcia for the analysis of the hemispheric photographs. We are also much indebted to Thorsten Wiegand, José Alexandre F. Diniz-Filho and Thiago Fernando L. V. B. Rangel for help with data analysis; Thosten Wiegand also commented the manuscript.

LITERATURE CITED

Alves, L.F. 2000. Estrutura, dinâmica e alometria de quatro espécies arbóreas tropicais. Doctoral thesis, Universidade Estadual de Campinas, Campinas.

Alves, L.F.; Vieira, S.A.; Scaranello, M.A.; Camargo, P.B.; Santos, F.A.M.; Joly, C.A. & Martinelli, L.A. 2010. Forest structure and abovegroung biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). Forest Ecology and Management 260: 679-691.

Augspurger, C.K. & Kelly, C.K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects for dispersal distance, seedling density, and light conditions. Oecologia 61: 211–217.

Beale, C.M.; Lennon, J.J.; Yearsley, J.M.; Brewer, M.J. & Elston, D.A. 2010. Regression analysis of spatial data. Ecology Letters 13: 246-264.

Bell, T.; Freckleton, R.P. & Lewis, O.T. 2006. Plant pathogens drive density-dependent seedling mortality in a tropical tree. Ecology Letters 9: 569-574.

Bever, J.D. 1994. Feedback between plants and their soil communities in an old field community. Ecology 75: 1965–1977.

Bini, L.M.; J. Diniz-Filho, A.F.; Rangel, T.F.L.V.B.; Akre, T.S.B.; Albaladejo, R.G.; Albuquerque, F.S.; Aparicio, A.; Araújo, M.B.; Baselga, A.; Beck, J.; Bellocq, M.I.; Böhning-Gaese, K.; Borges, P.A.V.; Castro-Parga, I.; Chey, V.K.; Chown, S.L.; Marco Jr., P.; Dobkin, D.S.; Ferrer-Castán, D.; Field, R.; Filloy, J.; Fleishman, E.; Gómez, J.F.; Hortal, J.; Iverson, J.B.; Kerr, J.T.; Kissling, W.D.; Kitching, I.J.; León-Cortés, J.L.; Lobo, J.M.; Montoya, D.; Morales-Castilla, I.; Moreno, J.C.; Oberdorff, T.; Olalla-Tárraga, M.Á.; Pausas, J.G.; Qian, H.; Rahbek, C.; Rodríguez, M.Á.; Rueda, M.; Ruggiero, A.; Sackmann, P.; Sanders, N.J.; Terribile, L.C.; Vetaas, O.R. & Hawkins, B.A. 2009. Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. Ecography 32: 193-204.

Clark, D.B. & Clark, D.A. 1985. Seedling dynamics of a tropical tree – impacts of herbivory and meristem damage. Ecology 66: 1884-1892.

Clark, D.B. & Clark, D.A. 1989. The role of physical damage in the seedling mortality regime of a neotropical Rain Forest. Oikos 55: 225-230.

Cliff, A.D. & Ord, J.K. 1981. Spatial processes: models and applications. Pion Limited, London, UK.

Condit, R.; Ashton, P.S.; Baker, P.; Bunyavejchewin, S.; Gunatilleke, S.; Gunatilleke, N.; Hubbell, S.P.; Foster, R.B.; Itoh, A.; LaFrankie, J.V.; Lee, H.S.; Losos, E.; Manakaran, N.; Sukumar, R. & Yamakura, T. 2000. Spatial patterns in the distribution of tropical tree species. Science 288: 1414–1418.

Connell, J.H. 1971. On the role of natural enemies in pre- venting competitive exclusion in some marine animals and in rain forest trees. *In:* Den Boer, P.J. & Gradwell, G.R. (Eds.) Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp 298–310.

CPTEC – Centro de Previsão de Tempo e Estudos Climáticos 2010. Dados metereológicos, hidrológicos e ambientais de Plataformas de Coletas de Dados no PESM Picinguaba. http://satelite.cptec.inpe.br/PCD/metadados.jsp?uf=25&id=30887&tipo=AGROMET. 08 Apr. 2010.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72: 1066–1075.

Dickie, I.A.; Schnizter, S.A.; Reich, P.B. & Hobbie, S.E. 2007. Is oak establishment in old fields and savanna openings context dependent? Journal of Ecology 95: 309–320.

Fenner, M. 1987. Seedlings. New Phytologist 106(suppl): 35–47.

Frazer, G.W.; Canham, C.D. & Lertzman, K.P. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs - Users manual and program documentation. Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.

Gatsuk, L.E.; Smirnova, O.V.; Vorontzova, L.I.; Zaugolnova, L.B. & Zhukova, L.A. 1980. Age stages of plants of various growth forms: a review. Journal of Ecology 68: 675-696.

Gómez-Aparicio, L.; Gómez, J.M. & Zamora, R. 2005. Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate. Journal of Ecology 93: 1194–1202.

Goreaud, F. & Pelissier, R. 2003. Avoiding misinterpretation of biotic interactions with the intertype K12-function: population independence vs. random labelling hypotheses. Journal of Vegetation Science 14: 681–692.

Hampe, A.; García-Castaño, J.L.; Schupp, E.W. & Jordano, P. 2008. Spatial-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. Journal of Ecology 96: 668-678.

Hanley, M.E.; Fenner, M. & Edwards, P.J. 1995. The effect of seedling age on the likelihood of herbivory by the slug *Deroceras reticulatum*. Functional Ecology 9: 754-759.

Herrera, C.M.; Jordano, P.; López-Soria, L. & Amat, J.A. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological

Monographs 64: 315–344.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201-228.

Illian, J.; Penttinen, A.; Stoyan, H. & Stoyan, D. 2008. Statistical analysis and modelling of spatial point patterns. John Wiley & Sons, Chichester.

Jacquemyn, H.; Endels, P., Honnay, O. & Wiegand, T. 2010. Evaluating management interventions in small populations of a perennial herb *Primula vulgaris* using spatio-temporal analyses of point-patterns. Journal of Applied Ecology 47: 431-440.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104: 501–528.

Joly, C.A. & Martinelli, L.A. (Coord.) 2006. First report "Composição Florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar". Thematic Project Biota/FAPESP 03/12595-7.

Joly, C.A. & Martinelli, L.A. (Coord.) 2007. Second report "Composição Florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar". Thematic Project Biota/FAPESP 03/12595-7.

Joly, C.A. & Martinelli, L.A. (Coord.) 2010. Fifth report "Composição florística, estrutura e funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar". Thematic Project Biota/FAPESP 03/12595-7.

Joly, C.A.; Martinelli, L.A.; Alves, L.F.; Vieira, S.A.; Tamashiro, J.Y.; Aidar, M.P.M.; Camargo, P.B.; Assis, M.A. & Bernacci, L.C. 2008. As Parcelas Permanentes do Projeto Temático Biota Gradiente Funcional: Composição Florística, Estrutura e Funcionamento da Floresta

Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar, Estado de São Paulo, Brasil. *In:* Sanquetta, C.R. (Ed.) Experiências de monitoramento no bioma Mata Atlântica com o uso de parcelas permanentes. RedeMAP: Rede de Parcelas Permanentes dos Biomas Mata Atlântica e Pampa & Funpar, Curitiba, Brasil, pp. 109-148.

Kitajima, K. & Fenner, M. 2000. Ecology of seedling regeneration. *In:* Fenner, M. (Ed.) Seeds. Cabi publishing, Wallingford, UK, pp. 331–359.

Klimas, C.A.; Kainer, K.A. & Wadt, L.H.O. 2007. Population structure of *Carapa guianensis* in two forest types in the southwestern Brazilian Amazon. Forest Ecology and Management 50: 256-265.

Kobe, R.K. 1999. Light gradient portioning among tropical tree species through differential seedling mortality and growth. Ecology 80: 187-201.

Lacerda, M.S. 2001. Composição florística e estrutura da comunidade arbórea num gradiente altitudinal da Mata Atlântica. Doctoral thesis, Universidade Estadual de Campinas, Campinas.

Legendre, P. & Fortin, M.-J. 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107–138.

Mack, A.L. 1998. The potential impact of small-scale physical disturbance on seedlings in a Papuan rainforest. Biotropica 30: 547-552.

Martínez-Ramos, M.; Sarukhan, J. & Pinero, D. 1988. The demography of trees in the context of forest gap dynamics: the case of *Astrocaryum mexicanum* at Los Tuxtlas tropical rainforest. *In:* Davy, D.J.; Hutchings, M.J. & Watkinsons, A.R. (Eds.) Plant population ecology. Blackwell Scientific, Oxford, England, pp. 293-313.

Martins, S.C. 2010. Caracterização dos solos e serapilheira ao longo do gradiente altitudinal da Mata Atlântica, estado de São Paulo. Doctoral thesis, Centro de Energia Nuclear na Agricultura da Universidade de São Paulo, Piracicaba.

Martins, V.F. & Santos, F.A.M.S. *in prep.* a. Density of seed sources, seed dispersal, post-dispersal processes and the aggregation of tree species in a tropical forest.

Martins, V.F. & Santos, F.A.M.S. *in prep.* b. Uncoupled seed-seedling spatial relationship does not uncouple seed and adult distributions in a tropical forest.

Meiners, S.J. & Handel, S.N. 2000. Additive and nonadditive effects of herbivory and competition on tree seedling mortality, growth, and allocation. American Journal of Botany 87: 1821-1826.

Morellato, L.P.C. & Haddad, C.F.B. 2000. Introduction: The Brazilian Atlantic Forest. Biotropica 32: 786–792.

Morellato, L.P.C.; Talora, D.C.; Takahasi, A.; Bencke, C.S.C.; Romera, E.C. & Ziparro, V. 2000. Phenology of Atlantic rain forest trees: a comparative study. Biotropica 32: 811-823.

Myers, N.; Mittermeier, R.A; Mittermeier, C.G.; Fonseca, G.A.B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 852-858.

Norghauer, J.M.; Malcolm, J.R. & Zimmerman, B.L. 2006. Juvenile mortality and attacks by a specialist herbivore increase with conspecific adult basal area of Amazonian *Swietenia macrophylla* (Meliaceae). Journal of Tropical Ecology 22: 451-460.

Oliveira-Filho, A.T. & Fontes, M.A.L. 2000. Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. Biotropica 32: 793-810.

Oliveira-Filho, A.T.; Vilela, E.A.; Carvalho, D.A. & Gavilanes, M.L. 1994. Effects of soils and topography on the distribution of tree species in a Tropical Riverine Forest in South-Eastern Brazil. Journal of Tropical Ecology 10: 483-508.

Packer, A. & Clay, K. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404: 278-281.

Pedroni, F. 2001. Aspectos da estrutura e dinâmica da comunidade arbórea na Mata Atlântica de Planície e Encosta em Picinguaba, Ubatuba, SP. Doctoral thesis, Universidade Estadual de Campinas, Campinas.

Pigot, A.L. & Leather, S.R. 2008. Invertebrate predators drive distance-dependent patterns of seedling mortality in a temperate tree *Acer pseudoplatanus*. Oikos 117: 521-530.

Portela, R.C. & Santos, F.A.M. 2009. Mortality and mechanical damage of seedlings in different size fragments of the Brazilian Atlantic Forest. Tropical Ecology 50: 267-275.

Rangel, T.F.; Diniz-Filho, A.F. & Bini, L.M. 2010. SAM: a comprehensive application for Spatial Analysis in Macroecology. Ecography 33: 46-50.

Rey, P.J.; Ramírez, J.M.; Sánchez-Lafuente, A.M. & Alcántara, J.M. 2006. Seed- vs. microsite-limited recruitment in a myrmecochorous herb. Plant Ecology 184: 213-222.

Russo, S.E. & Augspurger, C.K. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7: 1058–1067.

Schupp, E.W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51: 71–78.

Sentelhas, P.C.; Marin, F.R.; Ferreria, A.S. & Sá, E.J.S. 2003. Banco de dados climáticos do Brasil. http://www.bdclima.cnpm.embrapa.br/resultados/balanco.php?UF=&COD=492. 08 Apr. 2010.

SMA – Secretaria do Meio Ambiente. 1996. Atlas das unidades de conservação do estado de São Paulo. Parte 1 – Litoral, Secretaria do Meio Ambiente & CESP, São Paulo.

SOS Mata Atlântica/INPE/ISA. 1998. Atlas da evolução dos remanescentes florestais e ecossistemas associados ao domínio da Mata Atlântica no período 1990–95. SOS Mata Atlântica/INPE/ISA, São Paulo, SP.

Stoyan, D. & Stoyan, H. 1994. Fractals, random shapes and point fields. Methods of geometrical statistics. Wiley, Chichester.

Whitmore, T.C. 1996. A review of some aspects of tropical rainforest seedling ecology with suggestions for further enquiry. *In:* Swaine, M.D. (Ed.). The ecology of tropical forest tree seedlings. Man an the Biosphere Series 17: 3–39, UNESCO, Paris.

Wiegand, T. & Moloney, K.A. 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104: 209–229.

Willson, M.F. 1993. Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107/108: 261-280.

Wright, S.J. 2002. Plant diversity in tropical forests: a review of the mechanisms of species coexistence. Oecologia 130: 1-14.

Table 1: Mean ± standard deviation of values of soil characteristics, canopy opening and topographic characteristics for two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. For further explanation on data, please refer to the text.

	L1	L2
pH $CaCl_2$	3.67 ± 0.35	3.58 ± 0.25
P (mg x kg^{-1})	17.27 ± 7.21	122.50 ± 48.44
S (mg x kg^{-1})	30.19 ± 12.13	9.34 ± 6.40
H+Al (mmolc x kg^{-1})	128.50 ± 53.29	17.86 ± 9.31
SB (mmolc x kg^{-1})	13.59 ± 6.87	22.11 ± 12.85
C (%)	5.00 ± 1.19	4.03 ± 2.46
N (%)	0.38 ± 0.09	0.29 ± 0.17
Clay	40.90 ± 8.41	22.05 ± 7.72
Silt	10.62 ± 3.94	5.64 ± 2.15
Clay+silt (%)	51.52 ± 10.22	27.69 ± 9.34
Canopy opening (%)	7.50 ± 1.84	7.00 ± 2.09
Altitude (m)	45.49 ± 4.85	73.22 ± 4.90
Elevation range (m)	3.42 ± 1.34	2.59 ± 1.24

Table 2: Number of seedlings of *Faramea picinguabae* and *Mollinedia schottiana* at two 1-ha plots (L1 and L2) of Lowland Atlantic Rainforest. Extracted from Martins & Santos (*in prep.* a).

Species	L1	L2
Faramea	539	319
Mollinedia	1403	127

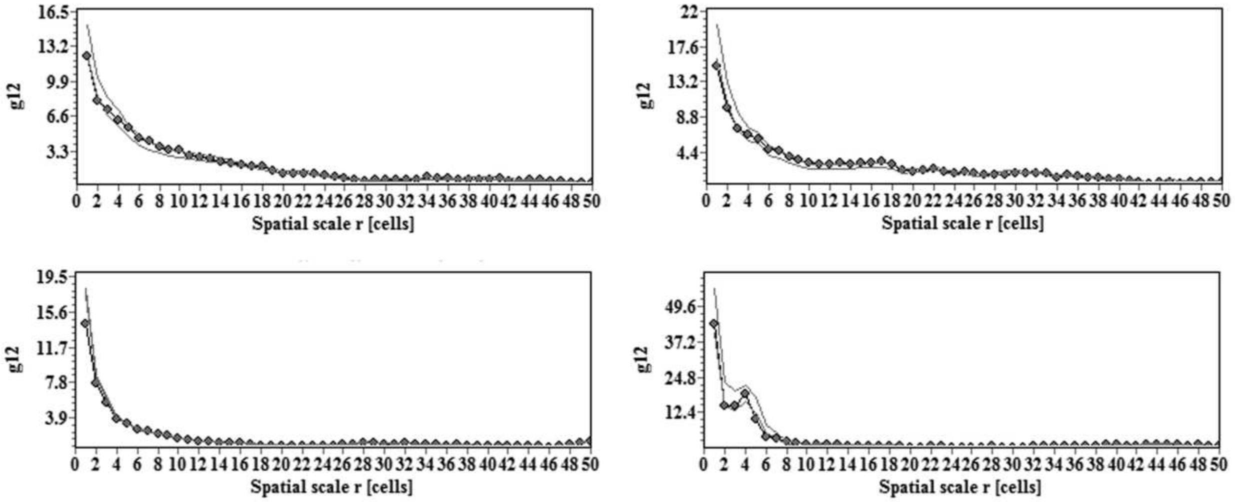


Fig. 1: Analysis of survival for individuals of *Faramea* (top) and *Mollinedia* (bottom) in two 1-ha plots (L1 at the left side and L2 at the right side) of Lowland Atlantic Rainforest. The observed test statistics (dots) and simulation envelopes (grey solid line) being the 5th lowest and highest values of the test statistics taken from the 199 simulations of the null model of random labelling.

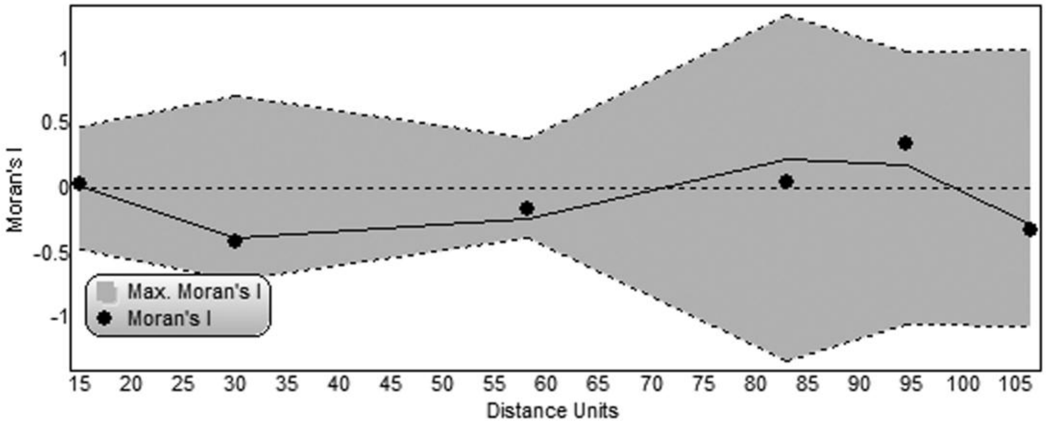


Fig. 2: Correlogram of the mortality rate of seedlings of *Faramea* in L1, an 1-ha plot in the Lowland Atlantic Rainforest. The only significative *I* is in the second distance class (p = 0.006).

CONSIDERAÇÕES FINAIS

Estudos prévios mostram que a maioria das espécies arbóreas tropicais ocorre principalmente com forte agregação em escalas que variam de poucos metros até algumas centenas de metros (*e.g.*, Hubbell 1979, Forman & Hahn 1980, Condit *et al.* 2000, Plotkin *et al.* 2000, Boll *et al*. 2005, Klimas *et al.* 2007). Devido a eventos de dispersão local, suas sementes também são agregadas no ambiente (Janzen 1970, Connell 1971, Clark *et al*. 1999, Nathan & Muller-Landau 2000, Nathan *et al*. 2000). De fato, encontramos que as sementes das três espécies estudadas e que todos os estádios ontogenéticos de *Faramea* e *Pourouma* apresentam agregação (com exceção dos adultos de *Pourouma*, devido ao baixo número de indivíduos amostrados nas áreas de estudo). Este padrão é facilmente visualizado no campo. Porém, as plântulas e os adultos de *Mollinedia* ocorreram ora agregados, ora de forma aleatória, dependendo da análise espacial empregada.

A função K e a SADIE utilizam formas muito diferentes para determinar o padrão espacial das populações. De forma geral, a função K usa, em seu cálculo, o número acumulado de indivíduos presentes em diferentes raios a partir de uma planta focal; este raio foi de 1 m para plântulas e de 5 m para adultos de *Mollinedia*. Já a SADIE mede o esforço necessário para rearranjar de forma homogênea os indivíduos da população, os quais se distribuem em áreas mais densas e menos densas. Neste estudo, cada unidade amostral onde o número de indivíduos foi contado foi de 10 m por 10 m. Assim, é possível obter resultados distintos com ambas análises, devido a um efeito da escala utilizada.

No caso das plântulas e adultos de *Mollinedia* em L1 e das plântulas desta espécie em L2, os agrupamentos ocorrem com força máxima em escala menor do que a utilizada na SADIE.

Assim, eles são detectados pela função K, mas não pela SADIE, que capta o padrão aleatório de distribuição dos agrupamentos nas áreas de estudo. Este padrão corresponde ao observado no campo. Já para os adultos de *Mollinedia* em L2, a força máxima de agregação ocorre na classe de distância de 50 m, que é a metade do tamanho dos lados de cada parcela de 1 ha. Assim, na SADIE, metade das unidades amostrais doariam indivíduos à outra metade, de forma que o esforço de cada unidade para gerar homogeneidade espacial não seria muito grande. Provavelmente, isto resultou no padrão aleatório dos adultos de *Mollinedia* em L2 quando utilizamos a SADIE. Assim, plantas que ocorrem agregadas em escalas muito pequenas ou muito grandes podem apresentar padrão espacial aleatório quando o padrão de pontos é transformado em contagens na SADIE.

Nós utilizamos somente a função K para determinar o padrão espacial dos outros estádios ontogenéticos de *Mollinedia*, os quais se mostraram agregados principalmente nas primeiras classes de distância. Como os estádios ontogenéticos das três espécies estudadas apresentaram padrão espacial agregado, principalmente em escalas pequenas, podemos dizer que os resultados apresentados neste trabalho estão de acordo com outros estudos que mostram que espécies arbóreas tropicais são geralmente agregadas (*e.g.*, Hubbell 1979, Forman & Hahn 1980, Condit *et al.* 2000, Plotkin *et al.* 2000, Boll *et al*. 2005, Klimas *et al.* 2007).

A densidade das fontes de semente é considerada um dos fatores que potencialmente influenciam a estrutura espacial de espécies arbóreas (Bleher *et al.* 2002). Porém, mais uma vez nós encontramos resultados distintos quando o mesmo conjunto de dados foi analisado utilizando-se diferentes métodos. Com a função K, *Pourouma* (a espécie dióica que ocorre em baixa densidade) apresentou, de uma forma geral, a maior agregação dos estádios ontogenéticos, a mais forte associação espacial entre plântulas e adultos (também encontrada para *Faramea*), e o menor decréscimo na agregação ao longo da ontogenia, o que está de acordo com nossas expectativas. Porém, quando utilizamos a SADIE, a maior agregação de plântulas e adultos, e a mais forte associação entre estes estádios foi encontrada para *Faramea* (a espécie homóica - *sensu* Cruden & Lloyd 1995 - que ocorre em alta densidade).

Nas áreas de estudo, adultos de *Pourouma* apresentam altura de até 20 m e são indivíduos com copa farta; já adultos de *Faramea* atingem 8 m e apresentam uma copa pequena, com poucos galhos e folhas; a situação intermediária ocorre para *Mollinedia*. Além disto, os diásporos de *Pourouma* são maiores e provavelmente são dispersos por aves maiores do que as que consomem os diásporos de *Faramea* e também de *Mollinedia.* Assim, o espalhamento das sementes e, consequentemente, das plântulas é muito maior em torno de um adulto de *Pourouma* (zona de influência) do que de um de *Faramea*. Na SADIE, isto poderia significar muitas unidades amostrais doando indivíduos de *Pourouma* às outras, enquanto o contrário ocorreria para *Faramea.* Assim, o esforço de cada unidade para gerar homogeneidade espacial na população de *Faramea* seria maior do que para *Pourouma*, resultando na maior agregação de plântulas e adultos, e na mais forte associação entre estes estádios ontogenéticos de *Faramea*. Porém, na Fig. 3 do segundo capítulo, observamos que *Pourouma* é a única espécie que apresenta distribuição das sementes coincidindo com a dos adultos, indicando uma limitação de dispersão. Assim, os fatores que explicam as diferenças encontradas quando os dados são analisados utilizando-se a função K e a SADIE ainda precisam ser investigados.

Quando utilizamos a SADIE, encontramos que *Pourouma* foi a única espécie a apresentar um decréscimo na agregação ao longo da ontogenia, de forma a não se possível comparar a redução na agregação das três espécies para se detectar a influência da densidade das fontes de semente na estrutura espacial das mesmas. O resultado encontrado indica que, além da densidade das fontes de semente, outros fatores, como dispersão e processos pós-dispersão, também influenciam a estrutura espacial das populações estudadas.

A menor agregação dos estádios ontogenéticos e a mais fraca associação entre plântulas e adultos não foi encontrada para *Faramea*, mas sim para *Mollinedia* (a espécie dióica cujos indivíduos femininos ocorrem em densidade intermediária), tanto quando usamos a função K, como quando usamos a SADIE. O maior decréscimo na agregação ao longo da ontogenia também foi encontrado para *Mollinedia*, ao se utilizar a função K. Novamente, estes resultados indicam que, juntamente com a densidade das fontes de semente, dispersão e processos pós-dispersão também influenciam a estrutura espacial das populações estudadas. Desta forma, a influência da densidade das fontes de semente na estrutura espacial das populações de espécies arbóreas pode ser: (1) um artefato do método utilizado para a análise do padrão, (2) altamente dependente da escala espacial utilizada na análise e/ou (3) mascarado por outros fatores que também afetam a maneira com que os indivíduos se distribuem no ambiente.

A estrutura espacial de espécies arbóreas também é influenciada pela dispersão de sementes (Nathan & Muller-Landau 2000, Bleher *et al.* 2002). A agregação comumente observada em espécies arbóreas tropicais (*e.g.*, Hubbell 1979, Forman & Hahn 1980, Condit *et al.* 2000, Plotkin *et al.* 2000, Boll *et al*. 2005, Klimas *et al.* 2007) é geralmente atribuída à dispersão (Condit *et al*. 2000, Svenning 2001, Svenning & Skov 2005), que parece explicar o padrão espacial das três espécies estudadas: suas sementes se concentraram sempre próximas às fontes de semente; além disto, plântulas e fontes de semente também estiveram sempre associadas. No entanto, apenas em metade das vezes sementes e plântulas estiveram associadas, o que é explicado pelos processos propostos do modelo de Janzen-Connell. Porém, como a mortalidade não desacoplou espacialmente a distribuição das fontes de semente da distribuição das sementes, podemos dizer que o padrão espacial das espécies estudadas é explicado pelo modelo de Hubbell (1980).

Apesar das espécies estudadas serem arbóreas e apresentarem frutos carnosos dispersos por aves, a relação espacial positiva entre fontes de semente e diásporos distribuídos no ambiente também deve ser encontrada para espécies com diferentes formas de vida e de dispersão. Isto é esperado devido ao formato leptocúrtico da curva de dispersão (muitas sementes localizadas próximas às fontes de semente e poucas carregadas a maiores distâncias da planta parental), independentemente da síndrome de dispersão dos diásporos (Houle 1995, Nathan *et al.* 2000). Assim como para espécies arbóreas com frutos carnosos, as com outras formas de vida e de dispersão também não apresentam um padrão claro na relação espacial entre sementes e plântulas. Por exemplo, já foram encontradas relações espaciais discordantes entre estes dois estádios de recrutamento (*sensu* Hampe *et al.* 2008) para espécies arbóreas anemocóricas (*e.g.*, Augspurger 1983, Houle 1992), bem como relações espaciais concordantes (*e.g.*, Houle 1998). Ambos padrões também foram relatados para sementes e plântulas de gramíneas na costa da Califórnia (Peart 1989). Infelizmente, são poucos os estudos que relacionam espacialmente estes estádios de recrutamento, sendo necessários mais trabalhos que analisem espécies com diferentes formas de vida e de dispersão. Além disto, é raro o uso de técnicas de análise espacial (*e.g.*, Houle 1998, Hampe *et al.* 2008), que devem ser empregadas em estudos futuros para o controle da autocorrelação espacial dos dados envolvendo distribuição de sementes e plantas, possibilitando, assim, uma interpretação mais realista dos fenômenos ecológicos (Hampe *et al.* 2008).

Por último, a relação espacial entre plântulas e adultos deve ser positiva se processos pós-dispersão não atuarem com alta intensidade, levando à mortalidade de plântulas em locais específicos e ao seu recrutamento em outros. Aparentemente, os processos pós-dispersão não atuam no sentido de desacoplar espacialmente os adultos das plântulas em florestas tropicais, onde as populações comumente têm padrão espacial agregado (Hubbell 1979, Forman & Hahn 1980, Condit *et al.* 2000, Plotkin *et al.* 2000, Boll *et al*. 2005, Klimas *et al.* 2007). Porém, pode ocorrer desacoplamento em outros ecossistemas, dependendo das características do ambiente e das espécies de planta.

Os processos pós-dispersão são o último grupo que potencialmente influencia a estrutura espacial de espécies arbóreas (Nathan & Muller-Landau 2000, Bleher *et al.* 2002). Tais processos podem alterar a agregação entre os diferentes estádios ontogenéticos (Janzen 1970, Connell 1971, Hubbell 1979, Condit *et al.* 2000, Harms *et al.* 2000, Dickie *et al.* 2007). Quando utilizamos a função K, *Faramea* manteve a agregação constante ao longo da ontogenia em L2 e apresentou uma maior agregação de estádios ontogenéticos subsequentes em L1. Com a SADIE, a agregação de adultos foi maior do que a de jovens nas duas áreas de estudo. Estes resultados indicam que os processos propostos por Hubbell (1980) parecem ser mais importantes do que os propostos no modelo de Janzen-Connell. Além disto, pode ser que *Faramea* só sobreviva nas áreas onde luz, umidade, temperatura, propriedades físicas e químicas do solo, e interações positivas são propícias (Hubbell 1979, Hutchings 1997, Itoh *et al.* 1997, Condit *et al.* 2000, Dickie *et al.* 2007).

Por outro lado, *Mollinedia* apresentou uma diminuição na agregação ao longo da ontogenia quando utilizamos a função K, mas manteve a agregação constante com a SADIE. Já *Pourouma* teve a agregação diminuída em ambas as análises. A diminuição da agregação indica que os processos propostos no modelo de Janzen-Connell são importantes, ocorrendo mortalidade dependente de distância e densidade devido à ação de competição intraespecífica, modificação do microambiente e inimigos naturais das plantas (Janzen 1970, Connell 1971, Condit *et al.* 2000, Harms *et al.* 2000, Wiegand *et al.* 2007). Como observamos desacoplamento espacial entre jovens e imaturos de *Pourouma* em L1, e entre imaturos e adultos de *Mollinedia* e *Pourouma* nas duas áreas de estudo, o auto-debaste, que leva à mortalidade dependente de densidade de indivíduos maiores (Hubbell 1979, Forman & Hahn 1980, Sterner *et al*. 1986, Condit *et al.* 2000, He & Duncan 2000, Plotkin *et al.* 2000, Getzin *et al*. 2006), parece ser um processo importante para estas duas espécies. Tal importância é reforçada pelo maior decréscimo na agregação ao longo da ontogenia de *Mollinedia* ao se utilizar a função K, como esperado para uma espécie mais densa sujeita ao auto-desbaste; também é reforçada pelo menor decréscimo na agregação ao longo da ontogenia de *Pourouma* ao se utilizar a mesma análise, o que está de acordo com o esperado para uma espécie menos densa sujeita ao auto-desbaste (Murrell 2009). No entanto, o desacoplamento dos estádios mais avançados das duas espécies não impediu que os adultos estivessem associados a sementes e plântulas.

Apesar das taxas de mortalidade serem maiores no estádio de plântula (Fenner 1987, Kitajima & Fenner 2000), a mortalidade neste estádio ocorreu aleatoriamente no ambiente e não modificou o padrão espacial agregado das populações das três espécies nas áreas de estudo. Nossos resultados mostraram que, após eventos de mortalidade, há uma proporção maior de plântulas em locais onde originalmente elas se encontravam em maior densidade (perto das fontes de semente, onde mais sementes são depositadas durante os eventos de dispersão), o que é contrário a muitos estudos (*e.g.,* Janzen 1970, Connell 1971, Clark & Clark 1985, Schupp 1988, Maetô & Fukuyama 1997, Wright 2002, Bell *et al*. 2006, Pigot & Leather 2008). Isto indica que mortalidade dependente de distância e densidade não reduz a chance de sobrevivência em áreas com alta densidade de plântulas. Tais áreas são, na verdade, melhores para a sobrevivência, provavelmente devido à facilitação ou interações positivas entre plântulas da mesma espécie. Além disto, a mortalidade e o recrutamento das plântulas das espécies estudadas não se relacionaram com nenhuma das características do ambiente avaliadas (densidade inicial de plântulas, área basal da população, área basal da comunidade, abertura de dossel, altitude e amplitude de inclinação), mesmo com a alteração na agregação tendo indicado possíveis fatores que aumentariam a chance de mortalidade ou sobrevivência das mesmas. Assim, mortalidade e recrutamento parecem ser influenciados por características que não são espacialmente estruturadas. Alternativamente, fatores que operam em uma escala espacial diferente da utilizada neste estudo podem ser mais importantes para a mortalidade e o recrutamento das espécies.

Este estudo separou a influência de diferentes fatores e processos que estruturam uma população no espaço. Encontramos que as populações estudadas são agregadas e que este padrão espacial não pode ser atribuído à densidade das fontes de semente. Por outro lado, a agregação é explicada pela dispersão de sementes, uma vez que adultos ocorrem associados a sementes e plântulas. Os processos pós-dispersão alteram a agregação das populações ao longo da ontogenia, mas não modificam seu padrão espacial após os eventos de mortalidade no estádio de plântula. Apesar do auto-desbaste desacoplar estádios ontogenéticos mais avançados, ele não atua com força suficiente para que adultos se dissociem de sementes e plântulas. Não é possível prever onde a mortalidade e o recrutamento ocorrem em maiores taxas no ambiente, mas a sobrevivência é maior em áreas com alta densidade de plântulas, como próximo aos adultos reprodutivos. Desta forma, os processos propostos por Hubbell (Hubbell 1980) parecem ser os mais importantes atuando nas populações das três espécies estudadas.

Se o modelo de recrutamento de Hubbell (Hubbell 1980) se aplicar à maior parte das espécies arbóreas de florestas tropicais, a comunidade deve se estruturar em agrupamentos de coespecíficos com poucos metros de raio; estes agrupamentos estariam intercalados com outros, cada um composto por indivíduos de outra espécie. Assim, os fatores e processos que estruturam as comunidades arbóreas tropicais devem ser avaliados em escalas espaciais correspondentes ao tamanho dos agrupamentos (alguns metros de raio), e não somente na escala correspondente à zona de influência de cada indivíduo.

LITERATURA CITADA

Augspurger, C.K. 1983. Offspring recruitment around tropical trees: changes in cohort distance with time. Oikos 40: 189-196.

Bell, T.; Freckleton, R.P. & Lewis, O.T. 2006. Plant pathogens drive density-dependent seedling mortality in a tropical tree. Ecology Letters 9: 569-574.

Bleher, B.; Oberrath, R. & Böhning-Gaese, K. 2002. Seed dispersal, breeding system, tree density and the spatial pattern of trees – a simulation approach. Basic and Applied Ecology 3: 115-123.

Boll, T.; Svenning, J.C.; Vormisto, J.; Normand, S.; Grández, C. & Balslev, H. 2005. Spatial distribution and environmental preferences of the piassaba palm *Aphandra natalia* (Arecaceae) along the Pastaza and Urituyacu rivers in Peru. Forest Ecology and Management 213: 175–183.

Clark, D.B. & Clark, D.A. 1985. Seedling dynamics of a tropical tree – impacts of herbivory and meristem damage. Ecology 66: 1884-1892.

Clark, D.B.; Palmer, M.W. & Clark, D.A. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology 80: 2662–2675.

Condit, R.; Ashton, P.S.; Baker, P.; Bunyavejchewin, S.; Gunatilleke, S.; Gunatilleke, N.; Hubbell, S.P.; Foster, R.B.; Itoh, A.; LaFrankie, J.V.; Lee, H.S.; Losos, E.; Manakaran, N.; Sukumar, R. & Yamakura, T. 2000. Spatial patterns in the distribution of tropical tree species. Science 288: 1414–1418.

Connell, J.H. 1971. On the role of natural enemies in pre- venting competitive exclusion in some marine animals and in rain forest trees. *In* Den Boer, P.J. & Gradwell, G.R. (eds.)

Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, pp 298–310.

Cruden, R.W. & Lloyd, R.M. 1995. Embryphytes have equivalent sexual phenotypes and breeding systems: why not a common terminology to describe them? American Journal of Botany 82: 816-825.

Dickie, I.A.; Schnizter, S.A.; Reich, P.B. & Hobbie, S.E. 2007. Is oak establishment in old fields and savanna openings context dependent? Journal of Ecology 95: 309–320.

Fenner, M. 1987. Seedlings. New Phytologist 106(suppl): 35–47.

Forman, R.T.T. & Hahn, D.C. 1980. Spatial patterns of trees in a Caribbean semievergreen forest. Ecology 61: 1267–1274.

Fundação SOS Mata Atlântica 2011. Mata Atlântica. www.sosmatatlantica.org.br. 23 April 2011.

Getzin, S.; Dean, C.; He, F.; Trofymow, J.A.; Wiegang, K. & Wiegang, T. 2006. Spatial pattern and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. Ecography 29: 671-682.

Hampe, A.; García-Castaño, J.L.; Schupp, E.W. & Jordano, P. 2008. Spatial-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. Journal of Ecology 96: 668-678.

Harms, K.E.; Wright, S.J.; Calderon, O.; Hernandez, A. & Herre, E.A. 2000. Pervasive density-dependent recruitment enhances seedlings diversity in a tropical forest. Nature 404: 493-495.

He, F. & Duncan, R.P. 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. Journal of Ecology 88: 676-688.

Houle, G. 1992. Spatial relationship between seed and seedling abundance and mortality in a Deciduous Forest of North-Eastern North America. Journal of Ecology 80: 99-108.

Houle, G. 1995. Seed dispersal and seedling recruitment: the missing link(s). Écoscience 2: 238-244.

Houle, G. 1998. Seed dispersal and seedling recruitment of *Betula alleghaniensis*: spatial inconsistency in time. Ecology 79: 807-818.

Hubbell, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299–1309.

Hubbell, S.P. 1980. Seed predation and coexistence of tree species in tropical forests. Oikos 35: 214-229.

Hutchings, M.J. 1997. The structure of plant populations. *In* Crawley, M.J. (ed.) Plant Ecology. Blackwell Science, Oxford, pp. 325–358.

Itoh, A.; Yamakura, T.; Ogino, K.; Lee, H.S. & Ashton, P.S. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia. Plant Ecology 132: 121-136.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501–528.

Kitajima, K. & Fenner, M. 2000. Ecology of seedling regeneration. *In* Fenner, M. (ed.) Seeds. Cabi publishing, Wallingford, pp. 331–359.

Klimas, C.A.; Kainer, K.A. & Wadt, L.H.O. 2007. Population structure of *Carapa guianensis* in two forest types in the southwestern Brazilian Amazon. Forest Ecology and Management 50: 256-265.

Maetô, K. & Fukuyama, K. 1997. Mature tree effect of *Acer mono* on seedling mortality due to insect herbivory. Ecological Research 12: 337-343.

Murrell, D.J. 2009. On the emergent spatial structure of size-structured populations: when does self-thinning lead to a reduction in clustering? Journal of Ecology 97: 256-266.

Nathan, R. & Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal: their determinants and consequences for recruitment. Trends in Ecology and Evolution 15: 278–285.

Nathan, R.; Safriel, U.N.; Noi-Meir, I. & Schiller, G. 2000. Spatiotemporal variation in seed dispersal and recruitment near and far from *Pinus halepensis* trees. Ecology 81: 2156–2169.

Peart, D.R. 1989. Species interactions in a successional grassland. I. Seed rain and seedling recruitment. Journal of Ecology 77: 236-251.

Pigot, A.L. & Leather, S.R. 2008. Invertebrate predators drive distance-dependent patterns of seedling mortality in a temperate tree *Acer pseudoplatanus*. Oikos 117: 521-530.

Plotkin, J.B.; Potts, M.D.; Leslie, N.; Manokaran, N.; LaFrankie, J. & Ashton, P.S. 2000. Species-area curves, spatial aggregation, and habitat specialization in tropical forests. Journal of Theoretical Biology 207: 81–99.

Schupp, E.W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51: 71–78.

Sterner, R.W.; Ribic, C.A. & Schatz, G.E. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. Journal of Ecology 74: 621-633.

Svenning, J.C. 2001. Environmental heterogeneity, recruitment limitation and the mesoscale distribution of palms in a tropical montane rainforest (Maquipucuna, Ecuador). Journal of Tropical Ecology 17: 97–113.

Svenning, J.C. & Skov, F. 2005. The relative roles of environment and history as controls of tree species composition and richness in Europe. Journal of Biogeography 32: 1019–1033.

Wiegand, T.; Gunatilleke, C.V.S.; Gunatilleke, I.A.U.N. & Okuda, T. 2007. Analyzing the spatial structure of a Sri Lankan tree species with multiple scales of clustering. Ecology 88: 3088-3102.

Wright, S.J. 2002. Plant diversity in tropical forests: a review of the mechanisms of species coexistence. Oecologia 130: 1-14.