

**DISPERSÃO DE SEMENTES E PROCESSOS DE LIMITAÇÃO
DEMOGRÁFICA DE PLANTAS EM AMBIENTES COM E SEM
BAMBUS NA FLORESTA PLUVIAL ATLÂNTICA**

DÉBORA CRISTINA ROTHER

Tese apresentada ao Instituto de
Biociências do Câmpus de Rio
Claro, Universidade Estadual
Paulista, como parte dos requisitos
para obtenção do título de Doutor
em Ciências Biológicas (Área de
Concentração: Biologia Vegetal)

Novembro - 2010

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Resumo geral

Em florestas tropicais, ainda são incipientes os estudos que tratam da influência dos bambus na dinâmica da vegetação. Pela grande capacidade de se expandir rapidamente no ambiente seja por crescimento vegetativo ou por produção massiva de sementes, os bambus promovem alterações significativas na estrutura das comunidades vegetais. Desta forma, esse estudo teve como objetivo avaliar o ciclo de vida das plantas em ambientes com (B) e sem bambus (SB) em uma área de floresta Atlântica densamente ocupada pelo bambu nativo *Guadua tigoara*. Os objetivos específicos deste estudo foram separados em capítulos. Para o capítulo 1, conhecer a composição de aves associadas aos ambientes com e sem bambus, identificar as aves que compõem a guilda de dispersores de sementes de *Euterpe edulis*, *Sloanea guianensis* e *Virola bicuhyba* e avaliar o potencial de dispersão das aves registradas em censos. Para o capítulo 2, avaliar o padrão espacial dos estágios iniciais da regeneração da comunidade de plantas nos ambientes B e SB. Finalmente para o capítulo 3, quantificar as perdas de propágulos e as probabilidades de transição entre cada etapa demográfica das três espécies de plantas selecionadas, e identificar os gargalos demográficos do recrutamento que podem colapsar a regeneração natural das três espécies de plantas nos ambientes B e SB. Verificamos que nos ambientes B foi registrado maior número de espécies de aves do que em ambientes SB. A maioria das aves registradas em censos nos dois ambientes foi insetívora, seguida por espécies frugívoras. A efetividade da dispersão de *Euterpe*, *Sloanea* e *Virola*, esteve restrita a um pequeno grupo de dispersores efetivos. As aves que mais contribuíram para a dispersão de *Virola* ocorreram mais freqüentemente em B. Este padrão foi similar para *Sloanea*, enquanto *Euterpe* apresentou um padrão misto, com algumas espécies de aves contribuindo para a dispersão em B e outras espécies em SB. Concluímos que um número considerável de espécies de aves frugívoras pode favorecer bordas de manchas de bambu e seu interior e que estes ambientes constituem elementos importantes da vegetação por funcionarem como áreas de abrigo e alimentação para muitas espécies de aves. Considerando o padrão espacial, verificamos que a comunidade de plantas da área estudada está com o recrutamento limitado nos dois ambientes como resultado da combinação de fatores bióticos e abióticos. Os bambus influenciam o padrão da chuva de sementes no complexo mosaico florestal quanto ao número de recrutas e riqueza de espécies de sementes. Além disso, os *hotspots* de recrutamento aparecem como extremamente dinâmicos e relacionados à expansão e declínio das manchas de *G. tigoara*. Os bambus promovem a heterogeneidade da floresta, mas as características de rápida colonização de *G. tigoara* e seu comportamento invasivo podem ser mais um fator de limitação do crescimento das comunidades vegetais sendo importante seu manejo. Quando avaliamos o ciclo de vida das plantas em nível populacional, verificamos que os propágulos das três espécies, quando protegidos da atividade de vertebrados, apresentaram maior probabilidade de chegar às fases posteriores do recrutamento. Assim, concluímos que a susceptibilidade à predação foi o principal gargalo demográfico durante as fases iniciais do estabelecimento. Os efeitos da presença do bambu no estabelecimento inicial são espécie-específica, pois nossos resultados indicam que o estabelecimento inicial de *Euterpe*, *Sloanea* e *Virola* na floresta Atlântica pode ser extremamente desigual, com uma profunda influência da heterogeneidade criada pelas manchas de bambu.

Palavras-chave: Frugivoria. Heterogeneidade. Limitação demográfica. Chuva de sementes. Estabelecimento. Bambus

General abstract

Studies about the bamboo influence in the plant dynamic process are still incipient. Given that bamboos are able to quickly expand in environment by either vegetative growth or massive seed production, bamboos promote significant changes in plant community structure. Thus, this work aimed at assessing the plant life cycles in bamboo (B) and non bamboo stands (NB) in an Atlantic forest area where the native bamboo *Guadua tagoara* occurs at high densities. The specific goals of this study were showed in chapters. For chapter 1, to know bird species associated with bamboo and non bamboo stands, identify the birds which belong to seed dispersers guild of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* and evaluate dispersal effectiveness and potential contribution to seed dispersal for the three plant species. For chapter 2, assess the spatial pattern of early regeneration stages of plant communities in B and NB stands. Finally, for chapter 3, quantify propagule losses as well as the probabilities of transition between each stage for all three plant species, and identify the demographic bottlenecks in recruitment that could collapse natural regeneration of the three plant species in B and NB stands. We verified that a higher number of bird species was registered in B stands than in NB. Most of registered birds in both B and NB stands were insectivorous followed by frugivorous species. The dispersal effectiveness of *Euterpe*, *Sloanea* and *Virola* depended on a restricted subset of effective bird dispersers. Birds which mostly contributed to the seed dispersal of *Virola* occurred more frequently in B. This pattern was similar for *Sloanea* while *Euterpe* exhibited a mixed pattern with some bird species contributing to the dispersal in the B stands and other species contributing in NB stands. We conclude that a substantial number of frugivorous bird species can favor borders of bamboo patches and their inner area. Moreover, these stands consist on important elements of vegetation as they function as refuge and feeding areas for several bird species. In relation to spatial pattern, we verified that plant community of the study area shows a limited recruitment in the two stands resultant of combining biotic and abiotic factors. Bamboo stands influenced seed rain patterns in the complex mosaics of Atlantic rainforest areas, with a variable importance across seasons on the abundance of recruits and species richness of the seed rain. Besides, the *hotspots* of recruitment were shown as extremely dynamic and related to the spread and decline of *G. tagoara* stands. Bamboos promote the forest heterogeneity, but the characteristics of rapid colonization of *G. tagoara* and its invasive behavior can be one additional factor for limiting the growth of plant community and thus its management is important. When we evaluate the life cycle of plants at population levels, we verify that protected from vertebrate activity, propagules of all three species had higher probability to reach subsequent stages of recruitment. Thereby we concluded that the susceptibility to predation was the main demographic bottleneck during the early stages of establishment. The effects of bamboo presence at the early establishment are species-specific because our results indicated that initial establishment of *Euterpe*, *Sloanea* and *Virola* at Atlantic forest can be extremely patchy, with a far-reaching influence of the heterogeneity created by successional bamboo patches.

Key words: Frugivory. Heterogeneity. Demographic limitation. Seed rain. Establishment. Bamboos.

INTRODUÇÃO GERAL

Os ciclos de regeneração de uma floresta trazem consigo uma série de etapas que vai desde a produção de sementes ao recrutamento dos juvenis, incluindo a dispersão de sementes, a chuva de sementes, a germinação e o estabelecimento de plântulas (Martínez-Ramos e Soto-Castro 1993). A regeneração natural das populações de plântulas depende em grande parte da dispersão de sementes (Jordano 1993, Gavin e Peart 1997, Wunderle 1997, Ganzhorn et al. 1999), que corresponde à etapa de ligação entre os adultos e o estágio de plântulas (Harper 1977, Wang e Smith 2002).

A dispersão pode transportar a semente para longe da planta-mãe (Janzen 1970) como também permitir a chegada de sementes a locais favoráveis para o estabelecimento das plântulas (Nathan e Muller-Landau 2000). A deposição das sementes longe de indivíduos coespecíficos representa um importante mecanismo de perpetuação das populações vegetais, uma vez que diminui a competição e a predação de sementes e o adensamento de plântulas, possibilitando a colonização de novas áreas (Janzen 1970, Connell 1971, Howe e Smallwood 1982, Oliveira-Filho et al. 1996, Silva e Tabarelli 2001).

No contexto da regeneração, a chuva de sementes é considerada o principal determinante da disponibilidade de propágulos na floresta (Alvarez-Buylla e García-Barrios 1991) e é determinada pelo fluxo de propágulos que resulta tanto do processo de dispersão local (autóctone) como das sementes provenientes de outras localidades (alóctones) (Martínez-Ramos e Soto-Castro 1993). Especialmente para este último, agentes dispersores exercem papel fundamental no transporte das sementes (Harper 1977, Fenner 1985, Martínez-Ramos e Soto-Castro 1993) e, conseqüentemente, no recrutamento das plantas, pois influencia a distribuição espacial das sementes na paisagem (Jordano e Godoy 2002).

Aproximadamente um terço das espécies de aves das florestas tropicais são frugívoras, contribuindo com grande parte do processo de dispersão das plantas (Snow 1981). Entretanto, além desse importante papel de dispersar sementes para longe da planta mãe (Christianini e Oliveira 2010) e aumentar a probabilidade de depositá-las em locais adequados para a germinação (Mckey 1975, Howe e Estabrook 1977), as aves diferem entre si quanto à efetividade na dispersão das sementes (Herrera e Jordano 1981, Schupp 1993, Jordano e Schupp 2000) por

desempenharem comportamentos específicos de acordo com as características do fruto de cada espécie de planta (Jordano e Schupp 2000).

Alguns estudos têm mostrado que o comportamento específico de forrageamento das aves influencia sua efetividade como dispersoras de sementes (Schupp 1993, Witmer e Van Soest 1998), juntamente com o número de visitas à planta mãe e o número de sementes dispersas pelas aves (Herrera e Jordano 1981, Schupp 1993, Jordano e Schupp 2000). Esses componentes quantitativos da dispersão constituem-se como os fatores fundamentais para compreendermos a relação planta-dispersor e um passo importante para avaliarmos as consequências dessa interação mutualística sobre os estágios subsequentes do recrutamento das plantas.

O processo de recrutamento das plantas, considerado como uma soma de estágios concatenados entre si e que proporcional e subsequentemente afetam a regeneração final (Clark et al. 1999), tem na fase semente-plântula sua etapa menos previsível (Schupp e Fuentes 1995, Clark et al. 1999), pois os estágios iniciais do processo de recrutamento são especialmente variáveis e afetados tanto em escala espacial como temporal (Schupp e Fuentes 1995, Schurr et al. 2008).

Múltiplos fatores afetam as etapas do ciclo de regeneração, que subsequentemente exercem influência sobre a dinâmica e a distribuição espacial das populações de plantas (Clark et al. 1999). Para espécies dispersas por animais, o estágio de plântula carrega as consequências dos padrões de movimento dos animais, enquanto os passos subsequentes do processo de recrutamento dependem, sobretudo, das condições do microhabitat e dos fatores que influenciam a probabilidade de sobrevivência de sementes e plântulas (Rey e Alcántara 2000).

Desta forma, fatores que determinam a perda de propágulos antes da dispersão são muito diferentes daqueles que agem depois desta. Na primeira fase predominam os efeitos intrínsecos à planta (por exemplo, baixa produção de sementes, aborto), enquanto na segunda um grande número de fatores bióticos e abióticos varia de forma complexa de acordo com a heterogeneidade ambiental (Jordano 2000).

Muitos fatores afetam o recrutamento das plantas, desde aqueles que limitam a produção ou a dispersão de sementes àqueles que influenciam a germinação das

sementes e o estabelecimento das plântulas (Jordano et al. 2004). Entre esses fatores podem ser incluídos fenômenos frequentemente dependentes da densidade como predação das sementes, herbivoria de plântulas, competição, ataque por patógenos ou estresse hídrico (Harms et al. 2000, Rey e Alcántara 2000) e também disponibilidade de micorrizas, de nutrientes do solo e de luz (Jordano et al. 2004).

O efeito de qualquer um desses fatores que leve à diminuição da probabilidade de sobrevivência, em qualquer das etapas, pode causar o que se chama gargalo demográfico (Jordano et al. 2004). Os gargalos demográficos resultam da ação de processos de limitação. Um processo, ou sua ação, limita a regeneração natural de uma espécie se sua anulação resulta em um aumento significativo dessa regeneração (Clark et al. 1998, Turnbull et al. 2000). Por exemplo, a interferência de fatores bióticos ou abióticos sobre a chuva de sementes em determinado ambiente pode gerar o que se chama de limitação de sementes. Isso ocorre quando as sementes não chegam a todos os locais potenciais de recrutamento e constitui-se em um dos fatores que com frequência limita o recrutamento em populações de plantas (Eriksson e Ehrlén 1992, Turnbull et al. 2000, Muller-Landau et al. 2002). Experimentalmente se pode demonstrar a limitação de sementes quando sementes são adicionadas nos locais potenciais de recrutamento e é verificado um incremento no número de propágulos recrutados (Jordano et al. 2004).

A limitação de sementes pode ser produzida pela limitação de fonte e/ou pela limitação de dispersão. A primeira é resultado da baixa disponibilidade de sementes no ambiente, seja porque a densidade da população adulta é muito baixa ou porque são produzidas poucas sementes. A limitação de dispersão ocorre quando, independente da quantidade de sementes produzidas, a quantidade de sementes dispersas é limitada pela atividade do dispersor, fazendo com que as sementes alcancem poucos dos vários locais de recrutamento possíveis (Muller-Landau et al. 2002). Segundo Schupp et al. (2002), a limitação de dispersão ocorre devido à baixa taxa de visitas dos dispersores às plantas com frutos e aos padrões de movimentação e comportamento alimentar dos dispersores.

A redução dos ambientes seguros para as plântulas ocuparem pode ser quantificada como limitação de estabelecimento. Neste caso, fatores de mortalidade

limitam o estabelecimento de novos indivíduos independentemente do número de sementes que chegam a uma determinada área (Jordano et al. 2004).

A importância relativa de cada fator de mortalidade pode variar de acordo com o tipo de ambiente, podendo ter como resultado uma discordância espacial no desempenho de cada estágio do ciclo de regeneração (Jordano e Herrera 1995, Schupp 1995, Schupp et al. 2002). A discordância entre estágios tem sido demonstrada em diferentes estudos para espécies mediterrâneas (Rey e Alcántara 2000, Gulías et al. 2004, Rodríguez-Peres e Traveset 2007) e está altamente relacionada às condições ambientais locais em vários estágios (Traveset et al. 2003, Rodríguez-Peres e Traveset 2007). As características favoráveis para as sementes podem, no entanto, ser desfavoráveis para as plântulas (conflito sementes-plântulas). Sementes pequenas, por exemplo, são mais facilmente dispersas pelo ambiente do que as sementes grandes, e têm maior probabilidade de escapar à predação. No entanto, sementes pequenas têm poucas reservas para o estabelecimento das plântulas e menor probabilidade de suportar as condições desfavoráveis de um ambiente (Schupp 1995).

A discordância entre o padrão da chuva de sementes e o de estabelecimento das plântulas em um ambiente é resultado de dois fatores: o padrão heterogêneo da dispersão das sementes e a variação ambiental que favorece a sobrevivência das plantas em determinados locais mais do que em outros (Schupp 1995). Conseqüentemente, ambientes que combinam elevado estabelecimento das plântulas com elevada consistência temporal do recrutamento podem ser considerados importantes *hotspots* de regeneração (Hampe et al. 2008).

Neste contexto, os temas relacionados à dispersão de sementes pelas aves, os gargalos demográficos do ciclo de regeneração das plantas, a discordância espacial da dispersão e os sítios de regeneração associados aos diferentes microhabitats serviram de base para o desenvolvimento do estudo de uma importante área de floresta Atlântica nos quais manchas de bambus são encontradas entremeadas à vegetação.

Bambus em florestas tropicais

No Novo Mundo são reconhecidas 356 espécies de bambus distribuídas em 38 gêneros, sendo o Brasil o país com maior diversidade e endemismo (Judziewicz et al. 1999). Dentre os gêneros que apresentam mais ampla distribuição geográfica e maior riqueza específica podem ser citados *Merostachys* Spreng., *Chusquea* Kunth (cerca de 40 espécies), *Guadua* Kunth (cerca de 16 espécies), *Olyra* L. e *Pariana* Aubl. (cerca de 18 espécies cada) (Filgueiras e Santos-Gonçalves 2004).

Os bambus estão distribuídos nos mais diversos biomas brasileiros especialmente na floresta Atlântica (Burman e Filgueiras 1993, Judziewicz et al. 1999) onde há uma elevada diversidade de ecossistemas e também alta riqueza de gramíneas, destacando-se espécies e gêneros endêmicos (Filgueiras e Santos-Gonçalves 2004).

Na floresta Atlântica ocorrem 65% das espécies nativas de Bambusoideae reconhecidas no Brasil (151 espécies; Filgueiras e Santos-Gonçalves 2004), sendo as florestas do sul e sudeste as regiões onde há maior diversidade e endemismo de espécies de bambus lignificados (Clark 1990). As montanhas do sudeste do Brasil, por exemplo, são consideradas como região de maior diversidade e endemismo de espécies de *Chusquea* no mundo (Clark 1997).

Bambus lignificados são aqueles que apresentam sistema subterrâneo bem desenvolvido, colmos ocos, florescimento cíclico com intervalos longos, padrão de floração gregária e são plantas monocárpicas que crescem por reprodução vegetativa por um número determinado de anos (Judziewicz et al. 1999, Filgueiras e Santos-Gonçalves 2004). O período pelo qual crescem vegetativamente varia de acordo com a espécie de bambu que, ao atingirem a maturidade fisiológica, florescem, produzem sementes e morrem (Janzen 1976, Soderstrom 1981).

Essas características do ciclo de vida dos bambus lignificados os tornam objeto de estudo bastante importante no contexto da dinâmica florestal, pois apesar de representarem o componente básico de diversos ecossistemas terrestres e desempenharem papéis ecológicos diversos (Viana e Filgueiras 2008), estão muitas vezes relacionados a ambientes perturbados da floresta Atlântica (Fantini e Guries 2000, Araujo 2008).

A rápida colonização por reprodução vegetativa e o comportamento invasivo (Wong 1991) são características de propagação que possibilitam o estabelecimento dominante dos bambus. Essa rápida ocupação dos ambientes pode exercer importantes interferências na dinâmica florestal, na regeneração florestal e na diversidade de espécies locais (Oliveira-Filho et al. 1994, Rother 2006, Lima 2007) por alterar a estrutura da vegetação local (Oliveira-Filho et al. 1994, Tabarelli e Mantovani 1999, Guilherme et al. 2004, Fantini e Guries 2007).

Os bambus parecem promover alterações estruturais na vegetação tanto por danos nas árvores maiores e plantas regenerantes como por alterações no micro-clima da floresta e elevada deposição de material na serrapilheira (Araujo 2008). Como consequência de seu estabelecimento, podem exercer influência sobre a vegetação sob diferentes formas: na abundância de sementes vindas através da dispersão (Rother et al. 2009), na regeneração de espécies arbóreas (Oliveira-Filho et al. 1994, Carvalho 1997, Fantini e Guries 2007), no crescimento de árvores (Oliveira-Filho et al. 1994) ou na sucessão florestal (Griscom e Ashton 2003, Lima 2007). Assim, os ciclos de vida, estrutura, evolução e ecologia dos bambus devem ser avaliados de maneira contextualizada dentro da floresta (Judziewicz et al. 1999).

No Brasil poucos estudos enfocaram a relação entre os bambus e a dinâmica florestal. Entre esses trabalhos podemos observar que ocorre uma concentração principalmente nas regiões norte, sudeste e sul. Oliveira (2000) verificou que árvores maiores são classes de tamanho mais raras em florestas do Acre ocupadas por *Guadua weberbaueri*. Silveira (2000), também na região norte do Brasil, observou que a composição florística local aparece reduzida em quase 40% do número de espécies como resultado da presença de *G. weberbaueri*.

Alguns autores como Oliveira-Filho et al. (1994), Carvalho (1997), Fantini e Guries (2007) e Campanello et al. (2007) acreditam que, uma vez estabelecidos, os bambus florestais podem restringir a regeneração florestal. Por sua elevada capacidade invasiva (Fantini e Guries 2000) os bambus podem ainda deslocar competitivamente as árvores e os arbustos pioneiros reduzindo a riqueza destes no local onde colonizam (Tabarelli e Mantovani 1997, 1999) ou até mesmo impedir a sucessão florestal por causar a mortalidade dos indivíduos jovens (Griscom e Ashton 2003). Mais recentemente, Budke et al. (2010) encontraram que a diversidade de

espécies aumenta em ambientes após o florescimento e morte massiva dos bambus.

Guilherme et al. (2004), Sanquetta et al. (2005), Rother (2006) e Lima (2007) enfocaram aspectos ecológicos da relação entre os bambus e a vegetação pelo acompanhamento da sobrevivência e recrutamento das espécies de plantas em ambientes ocupados por bambus. Vinha (2008) e Rother et al. (2009), por outro lado, estudaram a relação dos bambus com a composição e abundância de sementes provenientes da dispersão.

Apesar dos importantes trabalhos realizados nas últimas décadas, estudos sobre os bambus e sua relação com a estrutura e dinâmica florestal são ainda incipientes.

***Guadua tagoara* no contexto da dinâmica florestal**

Em algumas unidades de conservação, como o Parque Estadual Carlos Botelho – SP, a presença de bambus da espécie *Guadua tagoara* (Nees) Kunth vem se constituindo como um dos maiores problemas relacionados à redução da riqueza de espécies de plantas dos estágios mais avançados da regeneração. Alterações na dinâmica florestal onde *G. tagoara* está presente têm sido observadas, pois a espécie vem ocorrendo em elevada densidade em áreas onde encontram condições adequadas para seu estabelecimento e expansão (Fantini e Guries 2007, Terra 2007, Morokawa 2008) (Figura 1A).

Por ser uma espécie com elevado potencial invasivo, *G. tagoara* vem se tornando abundante em áreas nos quais ocorria naturalmente. Por ser considerada uma espécie pioneira e por ocupar rapidamente áreas perturbadas (Judziewicz et al. 1999), alguns autores associam a atual abundância do bambu *G. tagoara* à intervenção antrópica, como por exemplo, o corte do palmito juçara *Euterpe edulis*, fato que cria um ambiente adequado para seu crescimento e dispersão (Fantini e Guries 2000).

G. tagoara apresenta como característica marcante elevada produção de sementes, podendo formar bancos de plântulas disseminados pelo sub-bosque dos locais onde se encontram e nas áreas adjacentes (Rother 2006) (Figura 1B).

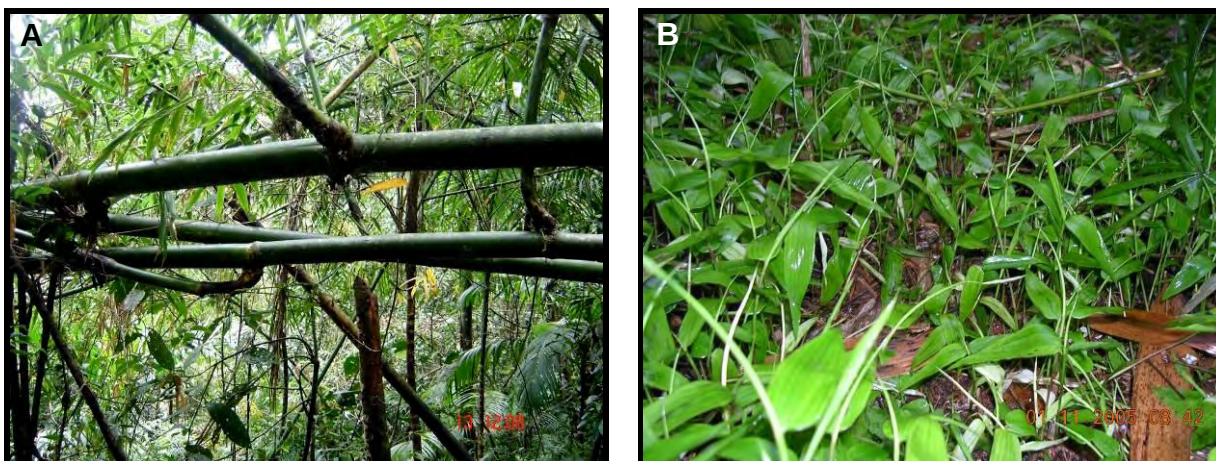


Figura 1 – Indivíduos adultos (A) e banco de plântulas (B) de *Guadua tagoara* no sub-bosque da parcela permanente do Parque Estadual Carlos Botelho, núcleo Sete Barras, SP.

A ocupação do espaço pelos bambus está ainda associada aos seus hábitos referentes à posição e forma de crescimento de seus colmos a partir dos rizomas como estratégia para obtenção de luz (Judziewicz et al. 1999). Em situações em que os bambus atingem e dominam o dossel florestal, observam-se alterações nas características estruturais da vegetação, ocasionando a homogeneização da cobertura florestal e possibilitando a identificação de grandes manchas com bambus em meio à vegetação mais densa (Nelson et al. 2006, Araujo 2008). Nestes ambientes, a estrutura da vegetação é caracterizada por dossel descontínuo, baixa densidade de indivíduos arbóreos de médio e grande porte e baixa diversidade florística (Oliveira-Filho et al. 1994, Tabarelli e Mantovani 1999, Guilherme et al. 2004, Fantini e Guries 2007).

OBJETIVOS

Apesar dos esforços para se compreender a dispersão de sementes (Howe e Smallwood 1982, Howe 1986, Schupp e Fuentes 1995, Levey et al. 2002), os tipos de gargalos demográficos do ciclo de regeneração das plantas (García et al. 2005, Clark et al. 2007) ou os fatores de mortalidade que atuam sobre os propágulos, poucos estudos comparativos foram realizados em florestas tropicais, onde a limitação do recrutamento é bastante difundida (Harms et al. 2000) e poucos são os estudos que relacionam diferentes tipos de ambientes às diferentes performances de sobrevivência das espécies vegetais. Estudos desta magnitude se concentram em

espécies mediterrâneas (Jordano e Herrera 1995, Rey e Alcántara 2000, Hampe e Arroyo 2002, Gómez et al. 2003, para mais detalhes ver Jordano et al. 2004).

Pelos motivos apresentados acima, juntamente com o fato das manchas de bambus serem ambientes pouco estudados e serem escassos os estudos disponíveis que analisam toda a série de eventos do ciclo de regeneração das espécies de plantas tropicais, o presente trabalho apresenta como objetivos: 1) conhecer a composição de aves associadas aos ambientes com e sem bambus, 2) identificar as aves que compõem a guilda de dispersores de sementes de três importantes espécies de plantas; para os ambientes com e sem bambus: 3) avaliar o potencial de dispersão destas aves registradas em censos; 4) avaliar o padrão espacial dos estágios iniciais da regeneração da comunidade de plantas; 5) quantificar as perdas de propágulos em cada etapa demográfica das três espécies de plantas selecionadas; 6) avaliar as probabilidades de transição entre uma etapa e outra do ciclo de regeneração das três espécies e 7) identificar os gargalos demográficos do recrutamento que podem colapsar a regeneração natural das três espécies de plantas.

Acreditamos que o conhecimento gerado neste estudo relativo à demografia das espécies vegetais de floresta Atlântica e especialmente aos fatores que limitam seu crescimento populacional nos diferentes tipos de ambientes, é ponto chave para o desenvolvimento de planos de conservação e restauração de populações. Isso se faz ainda mais importante pelo fato da floresta Atlântica se tratar de um dos biomas mais ameaçados do planeta e por ser considerada um *hotspot* para a conservação dado seu alto grau de espécies endêmicas (Myers et al. 2000).

ESTRUTURA DA TESE

Uma área de floresta Atlântica localizada no Parque Estadual Carlos Botelho (PECB), sul do estado de São Paulo com histórico de corte de palmitos juçara foi estudada com o objetivo de verificar a frugivoria e a dispersão de sementes de três espécies de plantas, avaliar o padrão espacial da chuva de sementes e das plântulas da comunidade de plantas e, por fim, avaliar os processos demográficos das plantas entre microhabitats sob bambus e microhabitats sob dossel de vegetação contínua. Esse trabalho representa o primeiro passo em relação ao

conhecimento dos padrões de recrutamento de populações de plantas em microhabitats distintos de uma mesma floresta. Para atingirmos esses objetivos precisamos conhecer a contribuição relativa de cada etapa demográfica no recrutamento final das plantas e como ocorrem as relações entre cada etapa (Schupp e Fuentes 1995, Nathan e Muller-Landau 2000). Diante da amplitude de temas a serem abrangidos, este estudo foi subdividido em três capítulos:

Capítulo 1. Plants and their fruit-eating birds in the Atlantic forest: a comparison among plant species and bamboo and non-bamboo stands.

Trabalhos como os realizados na Amazônia Peruana por Kratter (1997), por Zimmer et al. (1997) em Alta Floresta, Mato Grosso, e na região sul do Brasil por Santana e Anjos (2010) documentaram a associação de aves aos agrupamentos de bambus. Para *Guadua tagoara*, no entanto, trabalhos desta natureza ainda não foram realizados. A ausência de dados concretos da comunidade de aves que forrageia ou se refugia em ambientes com bambus *G. tagoara* foi, portanto o principal fator motivador deste capítulo. A partir do conhecimento gerado pelos censos das aves nos dois ambientes, relacionamos a guilda de aves frugívoras ocorrentes em cada ambiente com os dados de frugivoria de *Euterpe edulis*, *Sloanea guianensis* e *Virola bicuhyba*. Por fim, avaliamos neste capítulo quais espécies de aves se constituem como os dispersores mais efetivos das sementes destas três espécies de plantas.

Capítulo 2. Spatial patterns of seed rain and seedling recruitment in a Brazilian tropical forest. A dispersão de sementes corresponde a um importante processo do ciclo de vida das plantas que pode ser espacialmente limitado ou pode apresentar discordância entre o local de chegada das sementes e os ambientes adequados para o estabelecimento das plântulas. Desta forma, a dispersão de sementes exerce forte influencia nas etapas subseqüentes do ciclo de vida das plantas e está altamente relacionada com as condições ambientais locais. Considerando que ambientes adequados para sementes germinarem podem ser inadequados para plântulas se estabelecerem (conflito semente-plântula), este capítulo avalia o padrão espacial das sementes e plântulas da comunidade de plantas nos ambientes com e sem bambus do Parque Estadual Carlos Botelho.

Capítulo 3. Bottlenecks in tropical plant regeneration: a comparative analysis of Brazilian Atlantic forest species in bamboo and non-bamboo stands. Neste capítulo nós estudamos os estágios críticos do ciclo de vida de *Euterpe edulis*,

Sloanea guianensis e *Virola bicuhyba* e os fatores que diminuem a probabilidade de sobrevivência dessas plantas entre uma etapa e outra nas fases iniciais do recrutamento nos ambientes com e sem bambus. O principal objetivo foi detectar os gargalos demográficos que afetam a vida das plantas, desde as sementes às plântulas estabelecidas, e qual ambiente se constitui como local adequado para uma população de plantas se estabelecer.

ÁREA DE ESTUDO

Parque Estadual Carlos Botelho

Este estudo foi realizado no PECB que possui área total de 37.797,43 ha e encontra-se na região sul do Estado de São Paulo. O PECB engloba parte dos municípios de São Miguel Arcanjo, Capão Bonito, Sete Barras e Tapiraí (entre 24°00' a 24°15'S e 47°55' a 48°05'W), com altitudes que variam entre 30 e 1000 m (Domingues e Silva 1988, Dias 2005) (Figura 2).

No PECB ocorre a floresta Ombrófila Densa (sub-montana nas encostas de planaltos e/ou serras e montana no alto de planaltos e/ou serras), um tipo de vegetação caracterizado pela presença de plantas arbóreas além de lianas lenhosas e epífitas em abundância que o diferencia de outras formações vegetacionais (Veloso e Oliveira-Filho 1992, Dias 2005). A característica ombrotérmica dessa formação está ligada aos fatores climáticos tropicais: elevadas temperaturas (médias de 25° C) e alta precipitação bem distribuída ao longo do ano, o que determina a inexistência de um período seco (Veloso e Oliveira-Filho 1992).

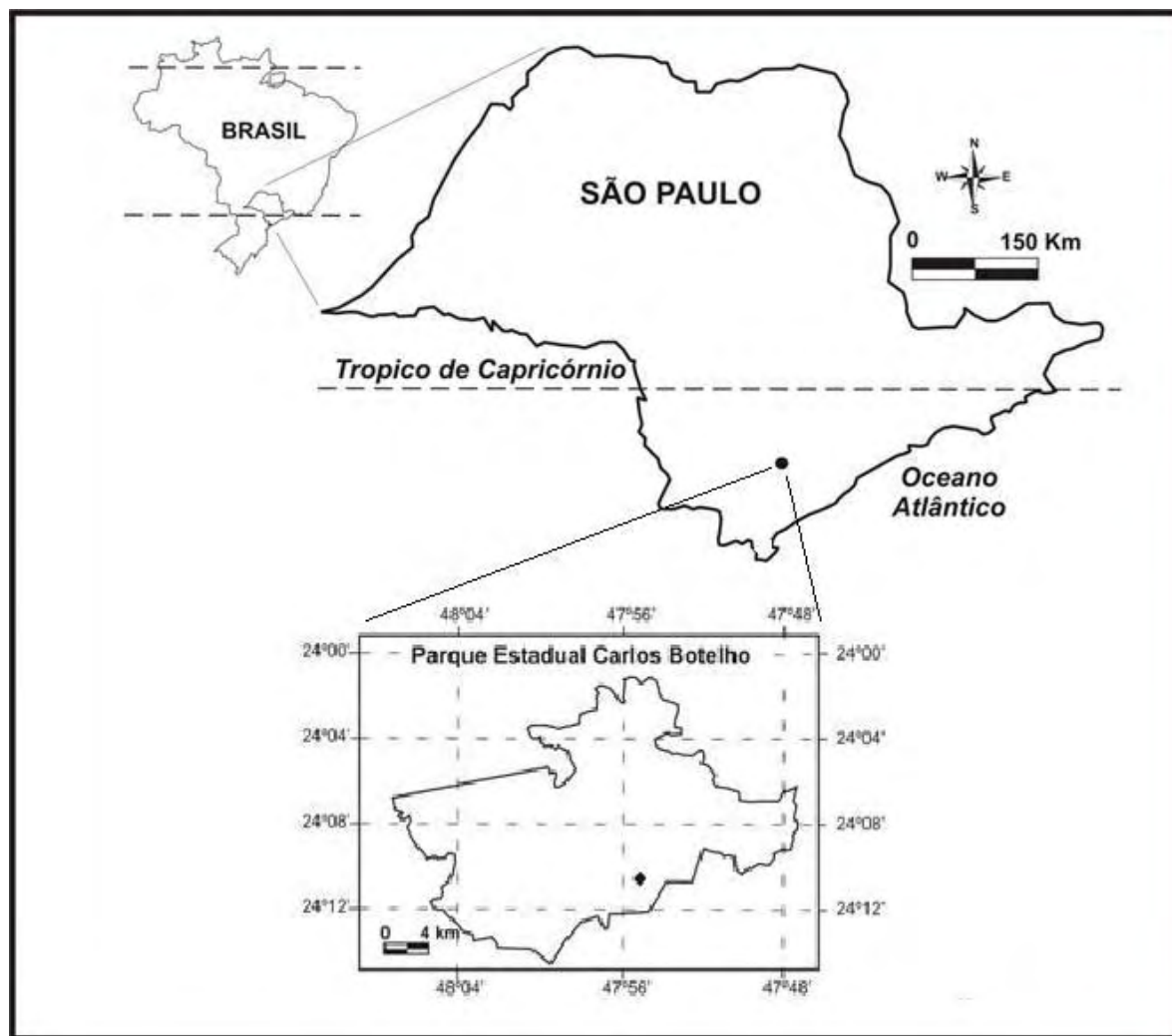


Figura 2 – Localização geográfica do Parque Estadual Carlos Botelho e da Parcela Permanente destacada como um ponto negro dentro da área do parque.

A área do PECB compreende duas unidades geomorfológicas: o Planalto de Guapiara, drenado pelos rios que formam a bacia hidrográfica do rio Paranapanema, e a Serra de Paranapiacaba, drenada pelos ribeirões Travessão, Temível e da Serra e pelos rios Preto e Quilombo, todos formadores da bacia do rio Ribeira de Iguape (Domingues e Silva 1988). Predominam no PECB as rochas graníticas que definem um relevo altamente acidentado que, associado aos elevados índices pluviométricos, definem morfogênese acelerada nas médias e nas altas vertentes, acumulando material nos sopés e canais fluviais (Domingues e Silva 1988).

O relevo define dois tipos climáticos diferentes, segundo a classificação de Köppen: A) clima quente úmido sem estiagem (Cfa) em áreas do Planalto de Guapiara com altitudes inferiores a 800 m na média e baixa escarpas da Serra de

Paranapiacaba; possui temperaturas inferiores a 18° C no mês mais frio e superiores a 22° C no mês mais quente e precipitação anual média de 1600 mm; B) clima temperado úmido sem estiagem (Cfb) nas partes mais elevadas da Serra de Paranapiacaba e que difere do anterior apenas pela temperatura média do mês mais quente, que não ultrapassa 22° C (Setzer 1946).

Projeto Parcelas Permanentes

Este estudo está vinculado ao Projeto temático "Diversidade, dinâmica e conservação em florestas do estado de São Paulo: 40 ha de parcelas permanentes" Biota/FAPESP (Processo N° 1999/09635-0). Para o desenvolvimento do projeto temático foi instalada uma parcela alocada em um trecho no Núcleo Sete Barras com altitude em torno de 300 m na vertente Atlântica da Serra de Paranapiacaba. Neste local foram montadas 256 subparcelas permanentes de 400 m² cada em uma parcela maior de 320 x 320 m, totalizando 10,24 ha de área amostrada (Figura 3).

Em cada subparcela foram amostrados, georreferenciados e identificados todos os indivíduos com perímetro à altura do peito (PAP) $\geq$ 15 cm. Foi feita principalmente, a caracterização do solo, da topografia e da luz, entre outros.

Para a vegetação foi feita uma caracterização das espécies ocorrentes (nas várias formas de vida) e sua estrutura foi caracterizada com dois levantamentos fitossociológicos, fisionômicos e silvigênicos. Na parcela permanente foi registrada uma riqueza florística de 205 espécies distribuídas em 44 famílias de plantas (Rodrigues 2005).

A parcela representa uma "amostra" da vegetação na região baixa do PECB, que se caracteriza por apresentar árvores com 20 - 30 m de altura média e pela ocorrência típica no sub-bosque de *Euterpe edulis* (palmito juçara) e bambus alto-escandentes da espécie *Guadua tagoara*, Cyatheaceae, Myrtaceae, Rubiaceae e Rutaceae (Rizzini 1979, Custódio-Filho 2002).

Em relação aos tipos de solo predominantes, a parcela permanente apresenta Cambissolo Háplico Distrófico latossólico típico, Cambissolo Háplico Distrófico léptico e Cambissolo Háplico Distrófico típico. Estes são solos medianamente profundos a profundos, pouco desenvolvidos, bastante homogêneos e que

apresentam atributos morfológicos (estrutura, textura e consistência) que favorecem a retenção de água (Rodrigues 2005).

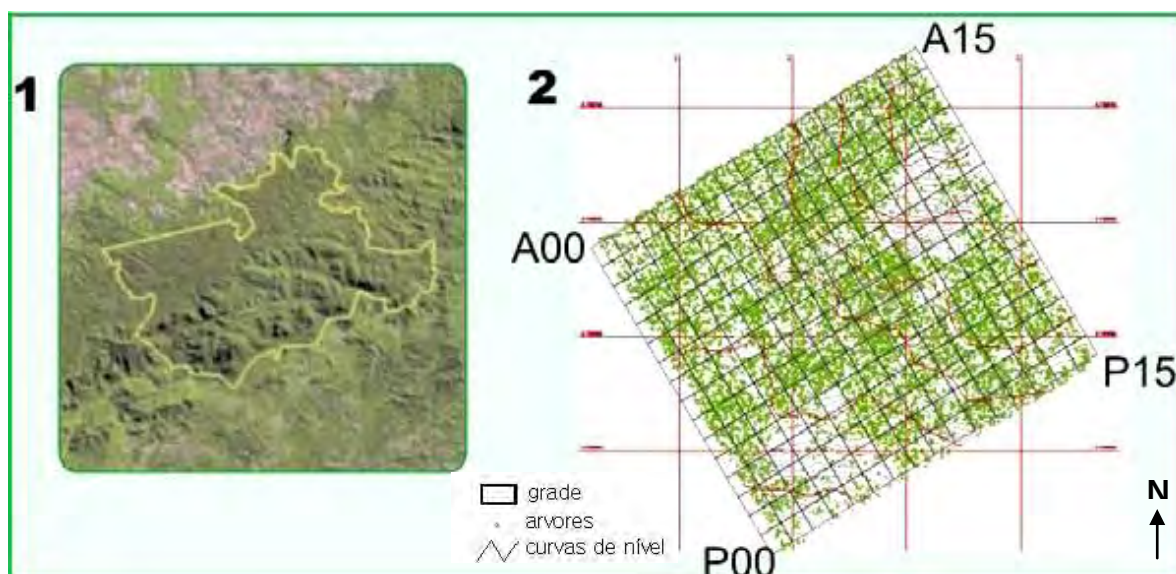


Figura 3 - Imagem de satélite (Landsat) do Parque Estadual Carlos Botelho (1) e detalhe da Parcela Permanente de 10,24 ha e subparcelas de 20 x 20 m (Retirado do 4º relatório temático do Projeto Parcelas Permanentes). As manchas claras em 2 são as áreas ocupadas pelo bambu *Guadua tagoara*.

Espécies alvo do estudo

As três espécies de plantas selecionadas para este estudo apresentam diferentes tipos e graus de limitação demográfica (Rother 2006, Rother et al. 2009), e os critérios para incluí-las no estudo foram: A) ornitocoria (dispersão de suas unidades de dispersão por aves); B) elevada abundância na parcela permanente como plantas adultas; C) sementes sem dormência e D) registro na chuva de sementes e parcelas de plântulas segundo os resultados de Rother (2006). As três espécies que se enquadraram nas características acima citadas foram: *Euterpe edulis* (Arecaceae), *Sloanea guianensis* (Elaeocarpaceae) e *Virola bicuhyba* (Myristicaceae).

***Euterpe edulis* Martius (Arecaceae)** é uma espécie de palmeira popularmente chamada de palmito juçara encontrada em elevada abundância na floresta Atlântica. Apresenta ampla distribuição geográfica, abrangendo desde o estado da Bahia até o Rio Grande do Sul, principalmente na floresta Ombrófila Densa, penetrando no interior pelas florestas de galeria da bacia do rio Paraná (Henderson 2000, Lorenzi et al. 2004). Presente no sub-bosque da floresta, cada indivíduo produz de uma a cinco

infrutescências anualmente com cerca de 3000 frutos cada (Mantovani e Morellato 2000). Seus frutos são drupas globosas contendo uma única semente com 13,5 mm de comprimento e 14,2 mm de largura (Pizo e Vieira 2004) coberta por uma fina camada de polpa de cor preta quando maduros (Galetti et al. 1999) e que contém 30,8% de água, 19,7% de lipídeos, 7,5% de proteína e 69,5% de carboidratos totais (peso seco) (Galetti et al. 2000). O período de frutificação se estende de abril a setembro com pico nos meses de junho e julho. Seus frutos servem de alimento para uma variedade de animais, incluindo aves e mamíferos, que dispersam efetivamente as sementes (Galetti et al. 1999). É uma espécie de grande interesse econômico por apresentar um meristema apical comestível que a torna alvo da extração ilegal. Na área de estudo e nas regiões adjacentes, *Euterpe edulis* vem sofrendo intensa redução de sua população (Galetti e Fernandez 1998, Rother 2006, Rother et al. 2009) (Figura 4).

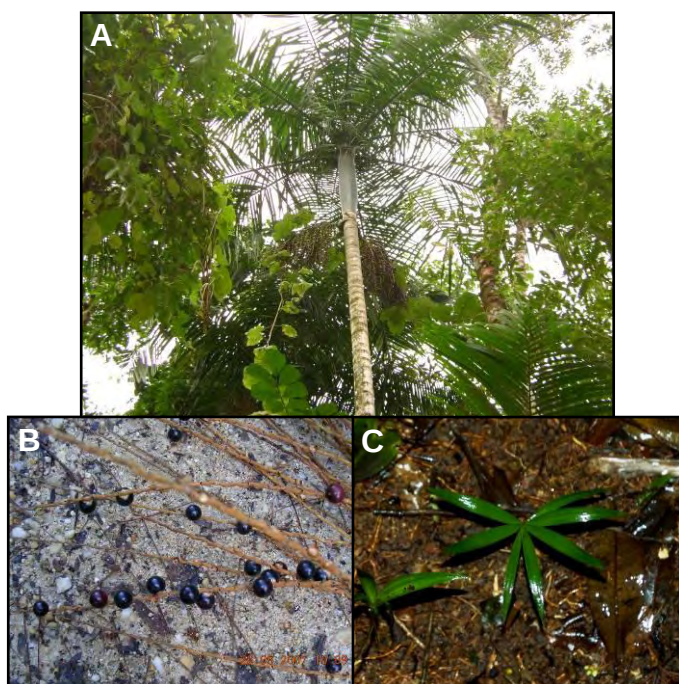


Figura 4 - Indivíduo adulto (A), frutos (B) e plântula (C) de *Euterpe edulis*.

***Sloanea guianensis* (Aubl.) Benth. (Elaeocarpaceae)** é uma espécie emergente (Foster e Janson 1985) que se distribui amplamente ao longo da floresta Atlântica, desde o nível do mar a 700 m de altitude. Encontra-se entre uma das espécies arbóreas mais altas deste tipo de formação florestal (Sanches 1994), atingindo mais de 20 m de altura (dado proveniente de estudo realizado em floresta tropical úmida no Parque Nacional do Manu, Peru - Foster e Janson 1985). O período de

frutificação varia entre anos, mas em geral ocorre entre os meses de dezembro e março (Zipparro 2004). O fruto é seco, deiscente, do tipo cápsula loculicida. Quando aberto, o fruto expõe uma semente com cerca de 10 mm de comprimento por 6 mm de largura. Cada semente é envolvida por arilo de cor vermelho-escuro que atrai a avifauna frugívora (Pinheiro e Ribeiro 2001) e que contém 90,9% de água, 2,5% de lipídeos, 6,9% de proteína e 87,7% de carboidratos totais (peso seco) (Galetti et al. 2000) (Figura 5).

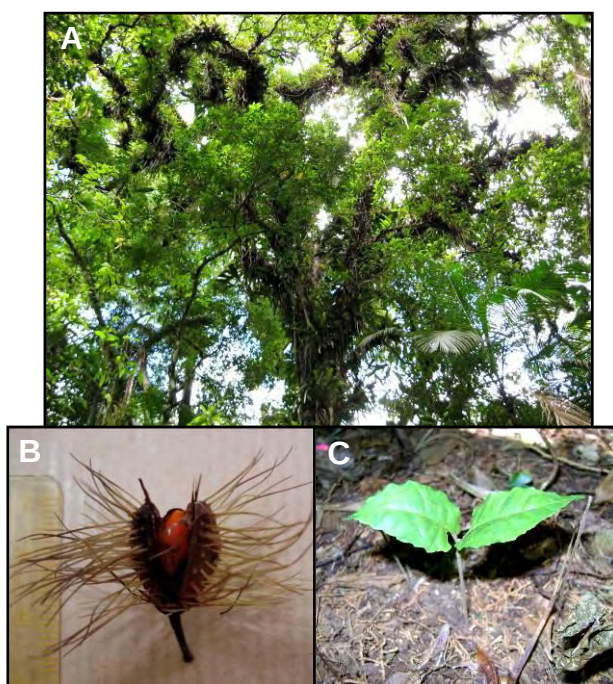


Figura 5 – Indivíduo adulto (A), fruto capsular com semente arilada (B) e plântula (C) de *Sloanea guianensis*.

***Virola bicuhyba* (Schott) Warb. (Myristicaceae)** é uma espécie de hábito arbóreo distribuída em florestas tropicais da América Central (Guatemala) à região sudeste do Brasil, e da costa oeste da Colômbia à costa Atlântica brasileira (Rodrigues 1980). As plantas são dióicas e atingem o dossel da floresta com altura variando entre 15 e 30 m. O período de frutificação ocorre entre os meses de julho e outubro (Zipparro 2004). Seus frutos são cápsulas deiscentes com cerca de 3,5 cm de comprimento por 2,5 cm de largura. Quando aberto, o fruto expõe um arilo de cor rosa, rico em lipídios que cobre toda a semente (Rodrigues 1980). Cada semente tem em média $2,14 \pm 0,21$ cm de comprimento, $1,50 \pm 0,1$ cm de largura e peso médio de $2,85 \pm 0,56$ g ($n = 494$ sementes) (Galetti et al. 2000). Possui arilo com 62,7 % de água, 61,8 % de lipídeo, 4,6 % de proteína e 32,1 % de carboidratos

totais (peso seco) (Pizo e Oliveira 2001). O arilo é de cor rosa e atrai grande número de frugívoros, especialmente aves de grande porte como tucanos e arapongas (Galetti et al. 2000) (Figura 6).

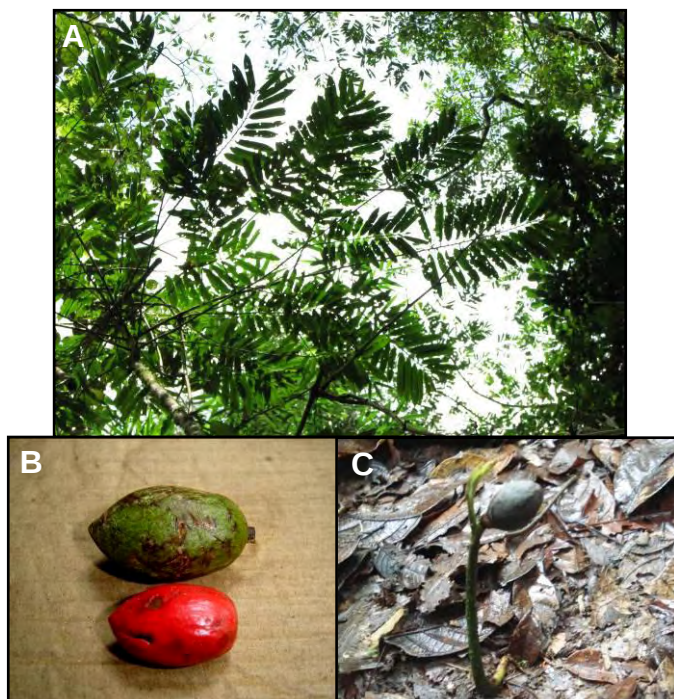


Figura 6 – Indivíduo adulto (A), fruto capsular e semente com arilo (B) e semente germinando (C) de *Virola bicuhyba*.

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PLANTS AND THEIR FRUIT-EATING BIRDS IN THE ATLANTIC FOREST: A COMPARISON AMONG PLANT SPECIES AND BAMBOO AND NON-BAMBOO STANDS

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Abstract

Many bird species have been linked to bamboo stands. Nevertheless there is a large gap in our knowledge of the birds associated with the bamboo *Guadua tagoara* that occurs in the Atlantic forest. Frugivorous birds associated with bamboo stands can be of primary importance for forest succession related to bamboo stand dynamics, determining seed rain density at the forest edges. We evaluated the bird community and the most common trophic guilds at Bamboo (B) and Non-bamboo (NB) stands in the Brazilian Atlantic forest. We also evaluated frugivory and dispersal effectiveness for three tree species: *Euterpe edulis* (Arecaceae), *Sloanea guianensis* (Elaeocarpaceae), and *Virola bicuhyba* (Myristicaceae). We then derived the potential contribution to seed dispersal of each bird species to the three focal plant species at each kind of stand. A total of 81 bird species were recorded, 74 species at B stands, and 55 species at NB stands. Most of these bird species were considered insectivores (49.4% of species), followed by frugivores (22.2%) and granivores (11.1%). Focal observations and spot censuses showed that 21 bird species ate fruits of *Euterpe*, while focal observations revealed 23 and 14 bird species interacting with *Sloanea* and *Virola* fruits, respectively. For both *Euterpe* and *Virola*, visitation rate was the variable which contributed more strongly to explain variance across frugivore species in the quantitative component (QC) of seed dispersal effectiveness, while the number of fruits manipulated/visit made the greatest contribution to QC in *Sloanea*. Birds that most contributed to seed dispersal of *Virola* tended to occur in B stands. This pattern is similar to *Sloanea*, while *Euterpe* presents a mixed pattern, with some bird species contributing to the dispersal in the B stands and other species contributing in NB stands. Variation in the quantitative component of dispersal was determined by feeding and fruit handling behaviors, and by visitation rates, which is related to species-specific traits and local abundance. This study reveals that effectiveness can vary depending on stand type, with the main dispersers in primary forest not being necessarily the main dispersers at forest edges with bamboo stands. Dispersal in *Euterpe*, *Sloanea* and *Virola* depended on a restricted subset of effective bird dispersers, suggesting that the successful regeneration and local population persistence of these three tree species are closely linked to the effective conservation of the frugivorous bird assemblage in both B and NB stands.

Key words: Frugivory. Fruit removal. Seed dispersal. Tropical forest. *Euterpe edulis*. *Sloanea guianensis*. *Virola bicuhyba*.

Introduction

Microhabitats have been a focus in studies of avian community ecology particularly because of the importance and implications of their differences to trophic relations (Urban and Smith 1989). Forest birds often select a breeding habitat on the basis of its vegetation structure, so patterns of microhabitat use have an important role in structuring bird assemblages (Smith and Shugart 1987). On the other hand, bird assemblages are of primary importance for the successful dispersal and regeneration of tropical forests and the maintenance of their successional dynamics. Therefore, microhabitat heterogeneity pervasively influences patterns of bird-plant interactions in the tropics. However, we still have a limited understanding of how landscape heterogeneity shapes variation in avian assemblages that interact with plants.

Bamboo stands appear as important elements in the composition of many tropical and temperate forests (Stotz et al. 1996, Judziwicz et al. 1999). In general, bamboo presents a significant vegetative growth succeeded by synchronous flowering followed by massive reproductive events by seeds (Janzen 1976). In forests where these plants occur, they form specific microhabitats resulting in a complex occupancy process closely related to forest succession and regeneration with multiple influences on population dynamics of birds and other animals (Olmos 1996).

The rapid colonization by vegetative reproduction and invasive behavior (Wong 1991) are traits that allow the dominant establishment of bamboos. Their rapid occupation of environments can have significant interference in forest dynamics, forest regeneration, and diversity of local species (Oliveira-Filho et al. 1994, Rother 2006, Lima 2007) by changing the local vegetation structure (Oliveira-Filho et al. 1994, Tabarelli e Mantovani 1999, Guilherme et al. 2004, Fantini e Guries 2007).

Possibly facilitated by anthropogenic (e.g., logging, palm [*Euterpe edulis*] heart extraction), and natural disturbances (e.g., landslides, treefall gaps), the bamboo *Guadua tagoara* dominates wide areas of the Atlantic forest in SE Brazil (Alves 2007), being considered a management problem inside forest reserves (Rother et. al 2009). *G. tagoara* exerts a strong influence on the vegetation dynamics in the area where it establishes due to its rapid expansion through vegetative growth (Judziwicz

et al. 1999). They may cause damage to trees and saplings, change forest microclimate and promote high deposition of material in the litter (Araujo 2008). In addition, patches of *G. tagoara* are characterized by a discontinuous canopy, low density of arboreal and mid-size individuals and low floristic diversity (Fantini and Guries 2007).

Bamboos are important for several bird species that inhabit preferentially dense bamboo stands and exploit their resources (i.e., bamboo seeds and associated fauna) (Olmos 1996, Vasconcelos et al. 2005, Santana and Anjos 2010). In the Atlantic forest, *Anabazenops dorsalis* (Sclater and Salvin 1880, Stotz et al. 1996, Kratter 1997), *Biatas nigropectus* (Areta 2007), *Anabazenops fuscus* (Rodrigues et al. 1994), *Haplospiza unicolor* (Olmos 1996), and most of *Drymophila* species (Menegaux and Hellmayr 1906, Parker et al. 1996, Sick 1997, Zimmer and Isler 2003) are specialist neotropical birds that show preference for bamboos. Eighteen out of 474 bird species recorded in the Alta Floresta region, eastern Brazilian Amazonia, were confined to bamboo stands within the forest (Zimmer et al. 1997), while at the Tambopata River, Peru, 25 bird species were confined to forest stretches dominated by the giant bamboo *Guadua weberbaueri* (Kratter 1997). This study showed that bamboo-dependent birds included a significant part (6%) of the total bird community in the area. There are some reports of omnivorous bird species seeking food (e.g., *Neopelma chrysolophum* foraging small fruits and small arthropods in southeastern Brazil, Sigrist 2006, Manhães 2007) or refuge (Reid et al. 2004) in bamboo-dominated habitats. Reid et al. (2004) related the preference of birds for bamboos as coverage or refuge, highlighting the importance of this microhabitat for shelter and nesting.

Despite efforts to establish a relationship between bamboo stands and birds, little is known about how often frugivorous birds use these environments. Their particular architecture and physiognomy and the fact that bamboo do not produce fleshy fruits are traits that likely make the bamboo stands unattractive to frugivorous birds (Stotz et al. 1996). Because frugivorous birds are critical for the reproduction and local distribution of many tropical plants (Snow 1965, Janzen 1970, Snow 1971, van der Pijl 1972), it is important to know how these birds use different microhabitats in a forest, especially bamboo-forest edges and bamboo stands where many non-bamboo plants have establishment constraints.

Frugivorous birds may perform high quality seed dispersal by disseminating seeds for long distances, by not damaging seeds, and moving seeds to safe sites (Mckey 1975, Howe and Estabrook 1977). However, different bird species may affect dispersal in different ways (Mckey 1975). Birds differ in the effectiveness of seed dispersal (Schupp 1993, Schupp et al. 2010), depending on how seeds are treated in their gut (Mckey 1975), the microhabitats types where seeds are dropped (Howe and Estabrook 1977), or the behavioral repertoire involved in the fruit removal (Howe 1980).

Previous studies showed that the foraging behavior of birds influences their effectiveness as seed dispersers (Sorensen 1984, Schupp 1993, Witmer and Van Soest 1998). However, effectiveness has both quantitative and qualitative components. The quantitative component refers to the number of visits to an individual or plant species, the number of seeds removed per visit, and the probability those seeds are handled so that they are dispersed away from the maternal tree (Schupp et al. 2010).

Avian frugivore species in an assemblage frequently vary in effectiveness, so that only a few species actually contribute most dispersal (Schupp et al. 2010). The number of visits may be influenced by the abundance of the frugivore at that particular habitat, and by its diet (i.e., how often it relies on fruits). The amount of seeds removed per visit depends on body mass and on the behavior used to manipulate the fruits. Concerning this aspect, frugivorous birds may be classified as swallowers (potential dispersers), chewers (low probability of dispersing large seeds) or pulp predators (Moermond and Denslow 1985, Levey 1987, Snow and Snow 1988, Jordano and Schupp 2000). Regarding swallowers, body size and bill width tend to be positively correlated with the number of seeds removed (Jordano 1992, Jordano and Schupp 2000). These visitation and consumption subcomponents of the quantitative component of dispersal effectiveness show ample variation across species in frugivore assemblages, but their relative contributions have been rarely assessed with empirical data (Schupp et al. 2010).

The second, qualitative component of dispersal effectiveness is a function of the treatment given to seeds by frugivorous (Izhaki and Safriel 1990, Godínez-Alvarez et al. 2002, Traveset et al. 2007), and the seed deposition pattern that defines the seed shadow (Izhaki et al. 1991, Pizo and Simão 2001, Loiselle and

Blake 1999, Jordano and Schupp 2000, Calviño-Cancela 2002, Holbrook and Loiselle 2007, Schupp et al. 2010).

This chapter evaluates and compares the bird community and the most common feeding habits at Bamboo and Non-bamboo stands representing structurally and compositionally different forest patches in a Brazilian Atlantic forest. We also evaluate the quantitative component of seed dispersal effectiveness for three arboreal, bird-dispersed tree species: *Euterpe edulis* Martius (Arecaceae), *Sloanea guianensis* (Aubl.) Benth. (Elaeocarpaceae), and *Virola bicuhyba* (Schott) Warb. (Myristicaceae). We then relate the bird species recorded at the two stands and their putative contribution to seed dispersal of the focal tree species at each stand. All plants here studied have fruits that are eaten by a great number of birds, have large fruit production, represent a range of seed sizes, and have different nutritional profiles, important traits to be attractive and dispersed by birds.

Methods

Study site

Fieldwork was conducted at the lowlands of the Carlos Botelho state park – PECB (24° 00'-24° 15' S, 47° 45'-48° 10' W), a reserve with over 37,000 ha of well-preserved Atlantic rain Forest (*sensu* Morellato and Haddad 2000) located in the state of São Paulo, SE Brazil. Combined with other adjacent reserves, the park forms a continuous block of 120 thousand ha, one of the largest in the whole Atlantic Forest. The study site is covered by tall (20-30 m) lowland old-growth forest with an opened understory where the palms *Euterpe edulis* and *Geonoma* spp., and arborescent ferns (Cyateaceae) are common. Myrtaceae, Lauraceae, Rubiaceae, Fabaceae and Sapotaceae are the richest plant families (Dias, 2005). The average temperature is 21.1° C (range 17.4-25.2° C), and the site receives an average annual rainfall of 2000 mm. Rains are well distributed throughout the year, but a rainiest and hottest season occurs from December to March (DAEE/SP 2009).

Data were collected in a permanent plot, in an old trail crossing the forest, and along a roadside. It was subdivided in 256 subplots of 20 x 20 m in which all trees with DBH $\geq$ 15 cm were tagged, measured, mapped and identified (Rodrigues 2005). At the 10.24 ha permanent plot we studied the frugivory and seed dispersal of the focal plant species, and the composition of the assemblage of frugivorous birds. Spot censuses were carried out by walking along the Figueira's trail (approximately 2-km

long, 4-m wide) and the Serra da Macaca's roadside, a dirty road that crosses the park. The spot censuses consisted of short (typically < 3min) scans of the tree canopy to record the activity of frugivorous birds. The advantage is the increased probability of recording rare, typically large-bodied, frugivores that show extremely low visitation rates (Howe 1981).

Approximately 3 ha of the permanent plot are covered by patches of *Guadua tagoara* (Nees) Kunth, a large-sized, semi-scandent woody bamboo native from the Brazilian Atlantic rain forest (hereafter bamboo or B stands) interspersed with areas without bamboos (non-bamboo or NB stands) forming a mosaic throughout the plot. As a result of the bamboo presence, B stands have a greater canopy opening and thicker ground litter than NB stands (Rother 2006).

Trees

Euterpe edulis Martius or "palmito juçara" is a dominant palm species in the understory or subcanopy of the Atlantic Forest (269 individuals.ha⁻¹ at the permanent plot; unpubl. data). Each tree produces from one to five infructescences annually with about 3000 fruits each (Mantovani and Morellato 2000). Fruits are globose, containing a single rounded seed (mean 13.5 mm length, 14.2 mm width; Pizo and Vieira 2004) covered by a thin layer of black pulp when mature. Fruit maturation in the study site generally extends from April to September, peaking in June-July (Galetti et al. 1999, Rother 2006). *E. edulis* fruits are eaten by several frugivores, especially birds (Galetti et al. 1999). Ongoing illegal harvesting for palm-heart poses a serious threat to many *E. edulis* populations (Galetti and Fernandez 1998).

Sloanea guianensis (Aubl.) Benth. is one of the highest trees in the Atlantic forest, with more than 20 m height (Sanches 1994, Foster and Janson 1985). The fruit is a dry, dehiscent capsule, which splits upon ripening to expose a single seed (about 10 mm length, 6 mm of width) covered by a red aril attractive to birds (Pinheiro and Ribeiro 2001). Fruit maturation varies annually, but in the study site generally extends from December to March (Zipparro 2004).

Virola bicuhyba (Schott) Warb. is a dioecious tree ranging from 15 m to 30 m height. Fruits are dehiscent capsules containing a single large seed (21.4 mm length, 15,0 mm width) covered by a rose, lipid-rich aril eaten by large birds like toucans and cotingas (Galetti et al. 2000). Fruit maturation extends from July to October (Zipparro 2004).

Census data

At the permanent plot, birds heard and observed were recorded using point counts. Five points with 30 m radius were set at B and NB stands, spaced 100 m from each other. Each point was sampled between 6:00 to 9:00 h in periods of ten min each (Raman 2003). Points were monthly sampled between May 2008 and April 2009 except October 2008 due to weather conditions. The diet classification of bird species followed Motta-Junior (1990), and the taxonomic classification and nomenclature of species followed Sick (1997).

Seed removal

To quantify the visitation rates of potential seed dispersers, and the amount of seeds removed from plants, focal observations were conducted on 46 individuals of *Euterpe edulis*, five of *Sloanea guianensis* and five of *Virola bicuhyba*. All plants observed were located at Non-bamboo stands due to the difficult to be encountered in the Bamboo stands. From now on these plant species are referred to only by their genus.

Observation sessions were made between 06:00 and 18:30 h. Each tree was watched for a minimum of 4 h. *Euterpe* was watched from April 2008 to August 2008, yielding a total of 276 h of observation. *Sloanea* was watched on December 2007 and December 2008, totalling 28 h of observation, and *Virola* was watched from August 2008 to October 2008 during 77.3 h. Fruit-eating birds were identified, counted, and the number of fruits they removed (= ingested), dropped, regurgitated and touched (= ingested + dropped + fruits with partial consumption of pulp) were recorded. An estimate of the removal effectiveness of the different species was achieved by combining visitation and seed removal rates (Schupp 1993, Schupp et al. 2010).

Profiting from the local abundance of *Euterpe*, and to augment our frugivory records on this species, we used two complementary methods besides focal observations. We made spot census by walking along the Figueira trail and the roadside yielding a total of 34 h of observation. In addition, non-systematic, haphazard recordings were made for all birds seen feeding on *Euterpe* fruits out of focal observations or spot census, totalling 1.45 h.

Data analysis

Census data

Species cumulative curves and richness estimators (Chao 2, Jackknife 1, Jackknife 2, Bootstrap), were performed for frugivorous and non frugivorous birds recorded at B and NB stands to check the sufficiency of the samples. The aim was to estimate how many species were expected in a random sample of birds from census collection and to compare the two stand types. For this, we used the function `specpool` in library `vegan` in R package v. 2.9.2 (R Development Core Team 2009) which estimates the extrapolated species richness in a species pool, or the number of unobserved species. Function `specpool` is based on incidences in sample sites, and gives a single estimate for a collection of sampling sites (data matrix). To compare bird species richness between B and NB stands we generated rarefaction curves using the library `vegan`. We plotted rarefaction curves (with 95% confidence intervals) standardized for the average number of individuals recorded per month and visually compared richness in each stand (Gotelli and Colwell 2001). Species richness estimators for B and NB stands were evaluated from census data. For this, we used Permutational Multivariate Analysis of Variance using Distance Matrices with the function `adonis` in library `vegan` with 9999 permutations (R package v. 2.9.2; R Development Core Team 2009).

Seed removal

For each tree species, the number of visits/10 h of observations, the number of fruits touched/visit and dispersal probability (ingested fruits as a fraction of the total number of touched fruits) were used to calculate the Quantitative Component (QC) of seed dispersal. In order to graphically compare the QC profile among plant species, we constructed separate curves for *Euterpe*, *Sloanea* and *Virola*. The QC values of each bird species was log-transformed and plotted in a bi-dimensional plane sorted from highest to lowest value (Magurran, 1988). In order to evaluate the relative influence of each of the three subcomponents of the QC (number of visits /10 h, fruits touched/visit and dispersal probability) we first estimated the Relative Dispersal Contribution of each bird species as the proportion of the total QC contributed by each bird species. We then performed a multiple regression (lmg estimates, library `relaimpo`; R package v. 2.9.2, R Development Core Team 2009) of each subcomponent on QC. This procedure yields the fraction of variance in QC explained

by each subcomponent and the bootstrapped confidence intervals for these relative contributions.

Potential contribution to dispersal

We contrasted B and NB stands in relation to the putative contribution of each bird species to seed removal of each plant species using the abundances of birds at each stand as revealed by the census data, and the amount of seeds removed by each species according to the focal observations. The contribution to dispersal (PCD) was defined as

$$PCD = (n/N)*(c/C)$$

where

n = number of fruits ingested by a given bird species

N = total number of fruits ingested by all bird species

c = number of contacts with a given frugivorous bird species in the stand (B or NB)

C = total number of contacts with all frugivorous bird species in the stand

To compare the potential contribution of bird species to dispersal, the PCD value obtained for each bird species was plotted in a bi-dimensional plane for each plant species for B and NB stands.

Results

Census data

A total of 81 bird species were recorded in the census for both stands, with 74 species in B stands (528 contacts), and 55 species in NB stands (538 contacts) (Table 1). Most of these bird species were considered insectivores (49.4% of species), followed by frugivores (22.2%) and granivores (11.1%). A relative high percentage of omnivorous species was recorded (17.3%). Frugivorous birds were more common at NB (27.3%) than at B stands (21.6%) considering all feeding habits.

The rarefaction curves did not reach an asymptote until the last censused month in both stands (Figure 1), although the final estimates were within the confidence interval of the estimates obtained with 11 months of sampling. Different estimators were consistent in indicating higher species richness for B compared to NB stands (Table 1). Observing the shape of rarefaction curves, an increment in the number of census in NB stands would not significantly increase the number of species reached in B stands. Despite richness differences, census data did not show differences in bird species composition between B and NB stands ($R^2 = 0.06$, $F =$

1.42, $p = 0.14$). The six most commonly observed species at B stands were *Ramphodon naevius* (62 contacts), *Saltator fuliginosus* (30), *Trogon viridis* (28), *Drymophila ferruginea* (23), *Habia rubica* (23), *Turdus albicollis* (22), and *Chiroxiphia caudata* (21). At NB *Saltator fuliginosus* (58), *Ramphodon naevius* (55), *Turdus albicollis* (46), *Trogon viridis* (35), *Habia rubica* (25), *Tinamus solitarius* (23), and *Cacicus haemorrhous* (20) were the most common species.

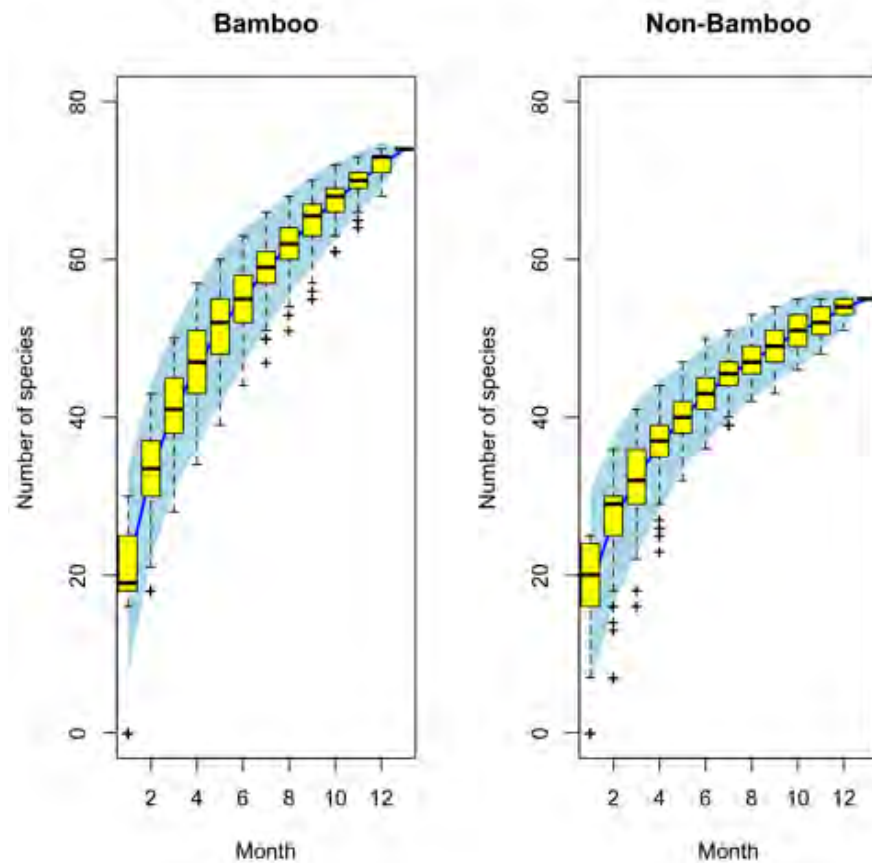


Figure 1 – Cumulative curve (rarefaction) for number of bird species recorded in Bamboo and Non-Bamboo stands in the permanent plot located in the Carlos Botelho State Park, SP. The blue envelope represents the confidence interval for $N=100$ permutations. Box plots represent the median, 50% and 90% percentiles, and outlier values for the estimated number of species at each month.

Table 1 – Species richness estimators for Bamboo (B) and Non-bamboo (NB) stands in the permanent plot located in the Carlos Botelho State Park, SP.

	Species	Chao ($\pm$ SE)	Jack1 ($\pm$ SE)	Jack2	Boot ($\pm$ SE)	Months
B	74	98.14 ($\pm$ 12.47)	98 ($\pm$ 8.59)	109.14	85.06 ($\pm$ 4.68)	13
NB	55	75.64 ($\pm$ 13.48)	70.7 ($\pm$ 6.35)	79.65	62.03 ($\pm$ 3.39)	13

Seed removal

Focal observations and spot censuses showed that 21 bird species ate the fruits of *Euterpe*, while focal observations revealed 23 and 14 bird species interacting

with *Sloanea* and *Virola* fruits, respectively (Table 2). The most recorded species at *Euterpe* were *Selenidera maculirostris*, *Trogon viridis*, *Turdus albicollis* and *Turdus flavipes*. Some species (e.g., *Procnias nudicollis* and *Aburria jacutinga*) had low number of records in *Euterpe* but removed a great number of fruits due to the particular behavior of spending a long time feeding on the canopy where they ingest many fruits. *Euphonia pectoralis*, *Euphonia* sp., *Habia rubica*, *S. maculirostris*, *Tangara cyanocephala* and *T. seledon* were the most important birds feeding on *Sloanea* fruits. It is noteworthy that the birds recorded with higher frequency in *Sloanea* were small birds (except *S. maculirostris*), predominantly from the Emberezidae family (except *S. maculirostris* and *H. rubica*). *T. viridis* and *T. flavipes* were the most frequent visitors to *Virola*. Together with *Turdus leucomelas* they touched a large number of fruits (Table 2).

Table 2 - Fruit-eating birds recorded visiting *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* trees. The number of fruits “touched” is the sum of fruits ingested, dropped, and fruits with partial consumption of pulp.

Birds	Plants	<i>Euterpe</i>		<i>Sloanea</i>		<i>Virola</i>	
		Number of visits	Number of fruits touched	Number of visits	Number of fruits touched	Number of visits	Number of fruits touched
<i>Aburria jacutinga</i> (Spix, 1825)*		7	76			1	6
<i>Attila rufus</i> (Vieillot, 1819)				2	9		
<i>Baryphthengus ruficapillus</i> (Vieillot, 1818)		19	29			4	4
<i>Brotogeris tirica</i> (Gmelin, 1788)*		2	2	1	2		
Undetermined 1				2	1		
<i>Dacnis cayana</i> (Linnaeus, 1766)				3	5		
<i>Euphonia pectoralis</i> (Latham, 1801)				4	11		
<i>Euphonia</i> sp.				4	12		
<i>Habia rubica</i> (Vieillot, 1817)				2	11		
Undetermined 2				1	1		
<i>Orthogonys chloricterus</i> (Vieillot, 1819)		2	7	1	3	2	2
<i>Pachyramphus castaneus</i> (Jardine and Selby 1827)				1	5		
Parulidae Family				4	3		
Undetermined 3				1	1		
<i>Pitangus sulphuratus</i> (Linnaeus, 1766)*		1	2				
<i>Procnias nudicollis</i> (Vieillot, 1817)		5	49				
<i>Pyroderus scutatus</i> (Shaw, 1792)		6	7				
<i>Pyrrhura frontalis</i> (Vieillot, 1817)*		2	13				
<i>Ramphastos dicolorus</i> (Linnaeus, 1766)		3	14				
<i>Ramphastos</i> sp.						1	1
<i>Ramphastos vitellinus</i> (Lichtenstein, 1823)		1	8			1	1

Plants	<i>Euterpe</i>		<i>Sloanea</i>		<i>Virola</i>	
	Number of visits	Number of fruits touched	Number of visits	Number of fruits touched	Number of visits	Number of fruits touched
<i>Birds</i>						
<i>Saltator fuliginosus</i> (Daudin, 1800)			2	2		
<i>Selenidera maculirostris</i> (Lichtenstein, 1823)	26	166	7	10	6	6
<i>Tachyphonus coronatus</i> (Vieillot, 1822)*	2	2	2	3		
<i>Tangara cayana</i> (Linnaeus, 1766)			2	2		
<i>Tangara cyanocephala</i> (Statius Muller, 1776)			2	8		
<i>Tangara seledon</i> (Statius Muller, 1776)*	5	6	3	7		
<i>Tangara</i> sp.	1	1	1	1		
<i>Tersina viridis</i> (Illiger, 1811)					8	8
<i>Thraupis cyanoptera</i> (Vieillot, 1817)			2	3		
<i>Thraupis palmarum</i> (Wied, 1823)					2	2
<i>Trogon viridis</i> (Linnaeus, 1766)	73	75			26	26
<i>Turdus albicollis</i> (Vieillot, 1818)	52	110			3	5
<i>Turdus amaurochalinus</i> (Cabanis, 1851)*	2	12				
<i>Turdus flavipes</i> (Vieillot, 1818)	93	172	3	3	23	35
<i>Turdus leucomelas</i> (Vieillot, 1818)	4	8	1	3	6	18
<i>Turdus rufiventris</i> (Vieillot, 1818)*	3	6			2	2
<i>Turdus</i> sp.					5	5
<i>Tytira cayana</i> (Linnaeus, 1766)			1	2		

*Recorded only during spot censuses in *Euterpe*.

For both *Euterpe* and *Virola*, visitation rate was the variable which contributed more strongly (more than 80% and more than 60%, respectively) to variation in QC of seed dispersal effectiveness across species, while the number of fruits manipulated/visit made the greatest contributions to QC variation in *Sloanea* (Figure 2).

The number of bird species with large QC was low, as observed in the last isoline of Figure 3. These bird species with a large number of fruits removed per visit and high visitation rate contributed with high QC values. Birds that had high QC to *Euterpe* were *S. maculirostris* and *T. flavipes*; to *Sloanea* were *Euphonia* sp., *E. pectoralis* and *Habia rubica*, while to *Virola* the birds with higher QC values were *T. flavipes* and *T. viridis* (Figure 3).

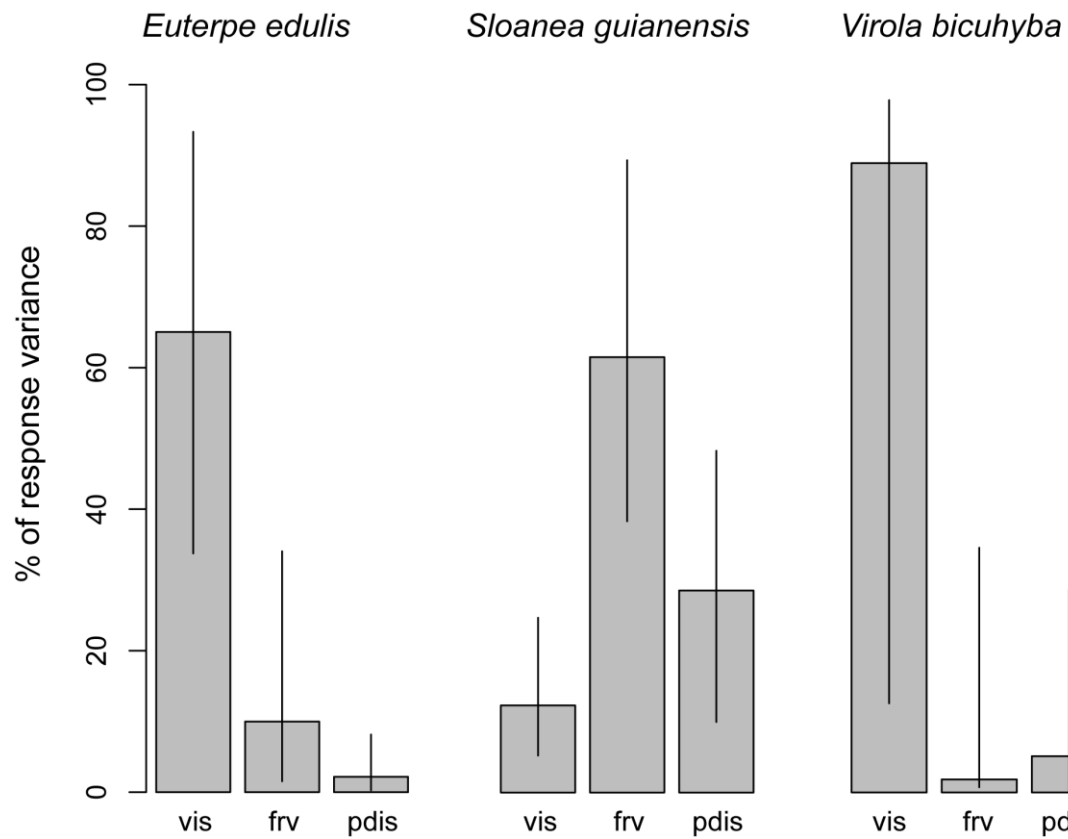


Figure 2 - Relative importance of each variable (vis, number of visits/10 h; frv, number of fruits manipulated/visit; pdis, probability that a handled fruit will be dispersed) determining the quantitative component (QC) of seed dispersal for the three plant species studied. Bars indicate the relative contribution of each variable to the total variance in QC explained: *Euterpe edulis*, $R^2 = 77.2\%$; *Sloanea guianensis*, $R^2 = 92.2\%$; and *Virola bicuhyba*, $R^2 = 95.9\%$. Bar plots represent the lmg estimates of these relative contributions (see Methods), with their bootstrapped confidence intervals.

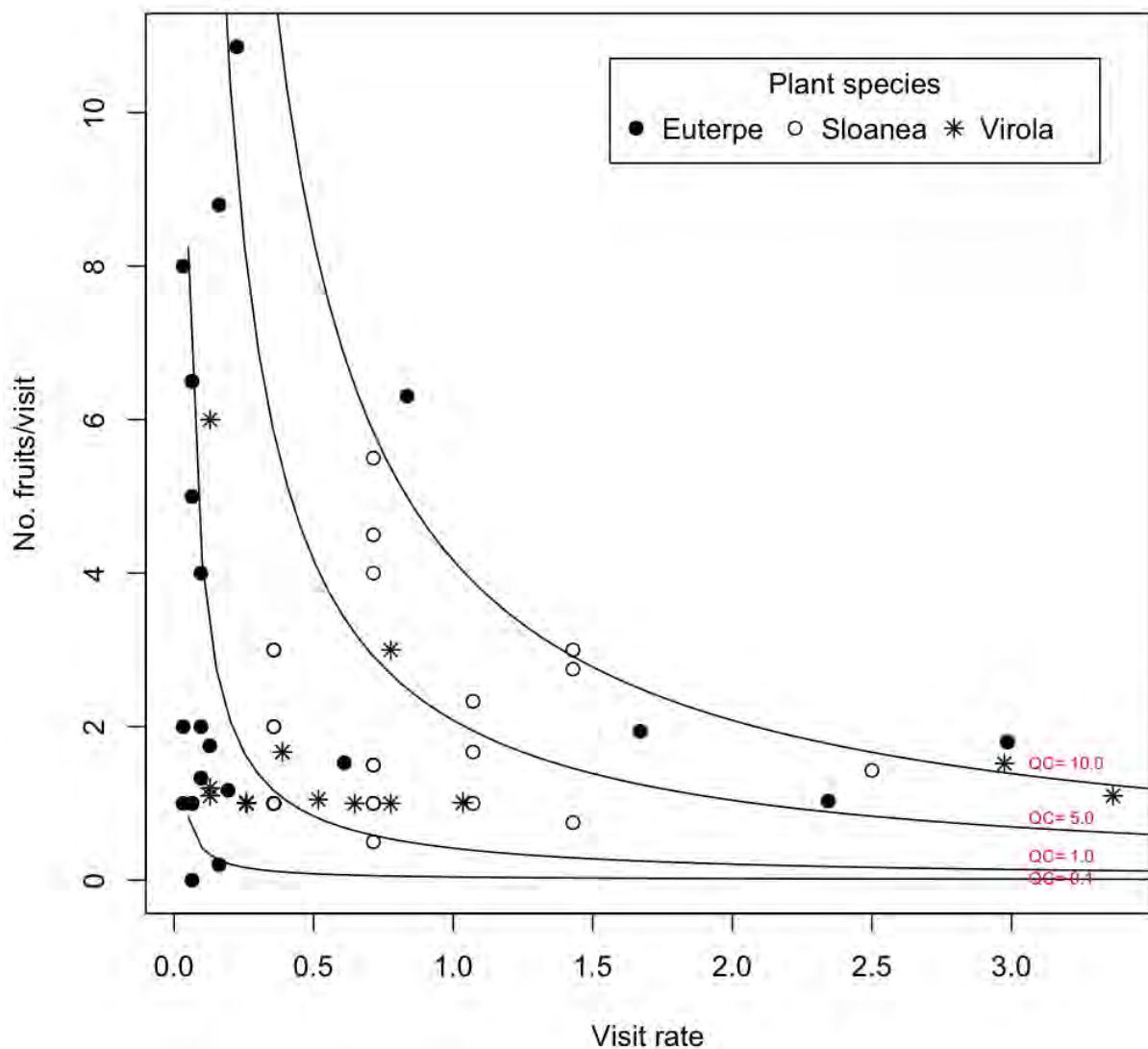


Figure 3 – Variation in the quantitative component (QC) among frugivorous bird species eating *Euterpe edulis*, *Sloanea guianensis*, and *Virola bicuhyba*. Symbols represent individual bird species and their relative position in the plane defined by the two main variables determining the QC of effectiveness: visitation rate and the number of fruits consumed per visit. Isolines depict areas with the same QC value for the quantitative component.

Visitation rate per bird species and fruits touched/visit are variables that contributed significantly to the Relative Dispersal Contribution, being positively related in the model. Dispersal probability also contributed to the quantitative component of *Sloanea* and *Virola* seed dispersal, but it did not so for *Euterpe*. Interestingly, dispersal probability in *Sloanea* was the only variable that negatively influenced the relative dispersal contribution to seed dispersal (Table 3).

Table 3 - Correlates of foraging variables (explanatory variables) and the Relative contribution to seed dispersal (response variable) for the fruit-eating bird species that visited *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* trees. Dispersal probability is defined as ingested fruits/touched fruits. The Relative contribution to seed dispersal is the proportional dispersal contributed by each species.

	Visitation rate			Fruits touched/visit			Dispersal probability		
	F	Beta	p	F	Beta	p	F	Beta	p
<i>Euterpe</i>	49.97	0.86	0.000	10.00	0.38	0.005	0.24	0.06	0.63
<i>Sloanea</i>	15.16	0.69	0.000	24.53	0.72	0.000	5.26	-0.42	0.03
<i>Virola</i>	223.89	0.95	0.000	7.95	0.18	0.018	8.36	0.18	0.016

Compared to the other plant species, *Virola* had a reduced bird assemblage which effectively dispersed its seeds. *T. flavipes* and *T. viridis* were the dominant species in relation to QC values, followed by *T. leucomelas*. Considering all bird species together for all three plant species studied, *T. flavipes* presented the greatest relative importance to *Euterpe* and *Virola* seed dispersal (Figure 4).

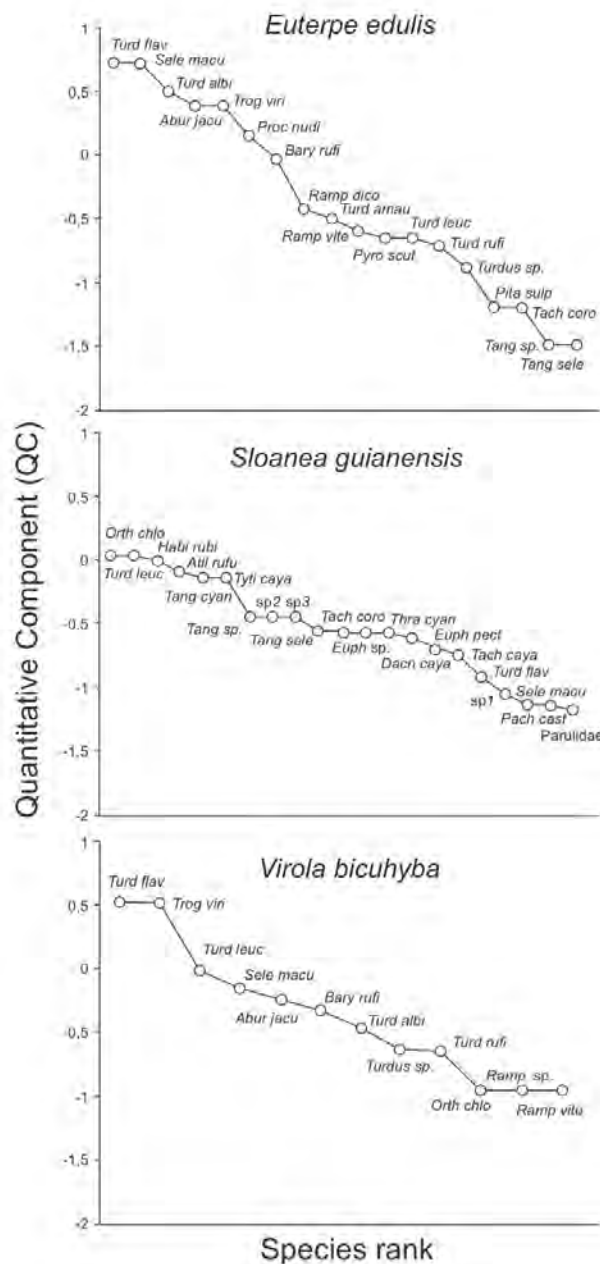


Figure 4 - Quantitative component curves of the Relative contribution to seed dispersal by the fruit-eating birds visiting *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* in the Carlos Botelho state park (PECB), Sete Barras, SP. In the horizontal axis, species are ranked from the largest to the lowest quantitative component. Codes for the bird species: *Abur jacu* (*Aburria jacutinga*), *Atil rufu* (*Attila rufus*), *Bary rufi* (*Baryphthengus ruficapillus*), *Dacn caya* (*Dacnis cayana*), *Euph pect* (*Euphonia pectoralis*), *Habi rubi* (*Habia rubica*), *Orth chlo* (*Orthogonys chloricterus*), *Pach cast* (*Pachyramphus castaneus*), *Parulidae* (*Parulidade Family*), *Pita sulp* (*Pitangus sulphuratus*), *Proc nudi* (*Procnias nudicollis*), *Pyro scut* (*Pyroderus scutatus*), *Ramp dico* (*Ramphastos dicolorus*), *Ramp sp.* (*Ramphastos sp.*), *Ramp vite* (*Ramphastos vitellinus*), *Sele macu* (*Selenidera maculirostris*), *Tach coro* (*Tachyphonus coronatus*), *Tang caya* (*Tangara cayana*), *Tang cyan* (*Tangara cyanocephala*), *Tang sele* (*Tangara seledon*), *Tang sp.* (*Tangara sp.*), *Thra cyan* (*Thraupis cyanopectera*), *Trog viri* (*Trogon viridis*), *Turd albi* (*Turdus albicollis*), *Turd amau* (*Trurdus amaurochalinus*), *Turd flav* (*Turdus flavipes*), *Turd leuc* (*Turdus leucomelas*), *Turd rufi* (*Turdus rufiventris*), *Turd sp.* (*Turdus sp.*).

Potential contribution to dispersal

Combining the bird census and the QC data enabled us to estimate the population-level contributions of each frugivore species to overall dispersal. *Turdus albicollis* and *Trogon viridis* were the bird species that potentially contributed the most to the dispersal of *Euterpe* seeds in both B and NB stands. Comparing stand types, *T. albicollis* had a greater potential contribution at NB, while *T. viridis* had a similar contribution in both stands. *T. flavipes* and *P. nudicollis* potentially contribute more to dispersal at NB, while *S. maculirostris* had a greater contribution to seed dispersal at B stands. Although *T. flavipes* and *S. maculirostris* had ingested a large amount of *Euterpe* fruits, they both had a reduced number of contacts. As a result, the PCD value of these two species was low. *E. pectoralis* and *S. maculirostris* contributed the most to the potential dispersal of *Sloanea* at B stands, while *T. coronatus* and *T. flavipes* had greater contribution at NB stands despite their low PCD values. In relation to *Viola*, *T. viridis* was the most important bird species in the potential contribution to dispersal in both kinds of stands (Figure 5). The bird species that most contributed to seed dispersal of *Sloanea* and *Viola* was different from the species highlighted in the QC analyses (Figure 4). Such discrepancies resulted from the number of contacts with each bird species at each stand.

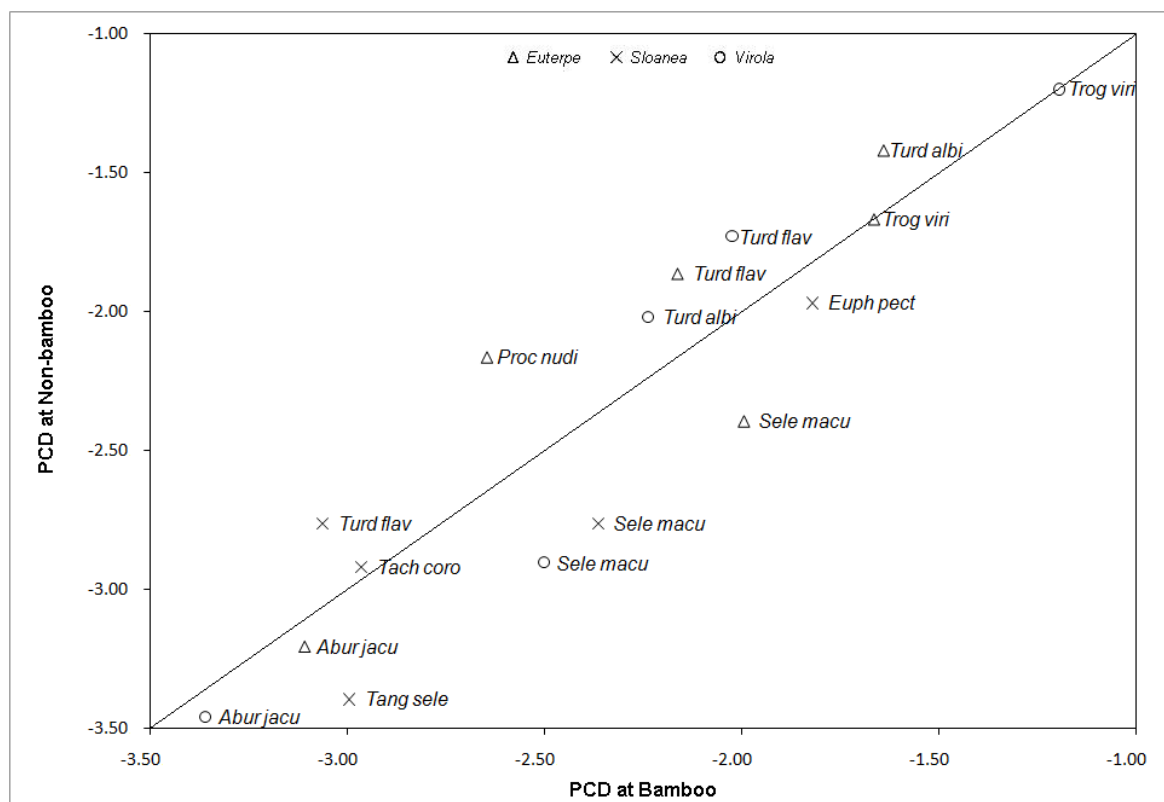


Figure 5 – Potential contribution to seed dispersal (PCD) of each frugivorous bird species recorded eating fruits of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* at Bamboo and Non-bamboo stands in the Carlos Botelho state park, Sete Barras, SP. PCD values were represented on a logarithmic scale to better visualize species with low PCD values. Diagonal line represents the equal potential contribution to the seed removal at both stands. Species positioned above diagonal line have greater PCD at NB stands and species positioned below diagonal line have greater PCD at B stands. For a given bird species, differences between stands are proportional to the perpendicular distance of the point that represents the bird to the diagonal line. Codes for the bird species: *Euph pect* (*Euphonia pectoralis*), *Proc nudi* (*Procnias nudicollis*), *Sele macu* (*Selenidera maculirostris*), *Trog viri* (*Trogon viridis*), *Turd albi* (*Turdus albicollis*), *Turd flav* (*Turdus flavipes*).

In sum, birds that most contributed to seed dispersal of *Virola* tended to occur in B stands. This pattern is similar to *Sloanea*, while *Euterpe* presents a mixed pattern. Therefore, the removal of fleshy fruits by birds is potentially not greatly affected at B stands.

Discussion

The Atlantic forest is admittedly the biome with one of the highest diversity of birds in Brazil, with many endemic species (Goerck 1997, Sick 1997, Marini and Garcia 2005) restricted to very specific physiognomic and abiotic conditions. The structure of the vegetation is indeed an important feature that may locally influence the structure of bird communities, including the species richness (Wiens 1989, Develey and Martersen 2006) and composition (Terborgh and Weske 1969,

Shahabuddin and Kumar 2006). Based on this background we expected to find important differences in the structure of the bird communities between B and NB stands because they represent different habitats with distinct biotic and abiotic characteristics (Rother 2006).

We found a similar species composition between stands despite variation in species richness, however with differences in the relative importance of feeding guilds. Insectivorous birds were the most common for both B and NB stands followed by strictly frugivorous birds. NB stands, however, had more species of frugivorous birds than B stands. This result is interesting because plants are extremely important for birds as foraging substrate, and as a direct source of food (Gomes et al. 2008). In Jurubatiba National Park, southeastern Brazil, 71.4% of birds are frugivorous (fruits consumed in at least one observation) (Gomes et al. 2008), and in the lowland humid forest in Costa Rica the frugivorous birds represent 30% of the total bird fauna (Blake and Loiselle 1992). Frugivorous birds are important in the natural regeneration of the forests by acting as seed dispersers for 60 - 95% of woody plant species (Howe and Smallwood 1982, Jordano 1992, Morellato and Leitão-Filho 1992), thus assisting in the maintenance of the floristic heterogeneity of the vegetation (McKey 1975, Julliot 1997).

Frugivorous birds, however, have different behaviors when interacting with their plants that serve as food source. Differences in fruit and seed handling behaviors classify birds as effective dispersers or not. In addition, the plant - bird disperser interaction involves more factors than just the treatment that birds give to the fruit, which makes this interaction even more complex. Differences in the quality of seed deposition sites and seed viability are also important factors for the dispersal effectiveness, and integrate the range of qualitative components that must be considered into the context of the system plant/bird dispersers (Schupp 1993, Jordano and Schupp 2000, Schupp et al. 2010). However, variation in the quantitative component largely determines the patterns of seed rain by determining the amount of seeds taken away from trees by dispersers.

Considering the quantitative component of seed dispersal we found ample variation among the bird species that visited the studied plants. Only four bird species (*Orthogonys chloricterus*, *S. maculirostris*, *T. flavipes* and *T. leucomelas*) were observed visiting and removing fruits of all the three studied plants. For the plant community this is a favorable result because it denotes great local bird diversity

whose different feeding behaviors allow the diversification of forms used to select fruits and subsequently disperse the seeds. Bird diversity and different forms of treating the fruits optimize the processes of dispersal (Pizo 1997, 2004) because more fruits dispersed involve a lower dissemination limitation of seeds (Schupp et al. 2002, Muller-Landau et al. 2002). Similarly, in the well-studied seed dispersal system of *Prunus mahaleb*, ample variation in fruit handling behaviors was noted, which greatly influenced the quantitative component of seed dispersal (Jordano and Schupp 2000): irrespective of visitation frequency and feeding rates some species are inefficient dispersers because most seeds are dropped in situ.

The estimates of the quantitative component of birds visiting the three tree species varied in different levels: among plants, among bird species, and within species of bird visitors. *S. maculirostris*, *T. viridis*, *T. albicollis*, and *T. flavipes* were very effective in dispersing *Euterpe* by removing large number of fruits away from the mother plant. *T. viridis*, *T. albicollis* and *T. flavipes* however, were very effective due to frequent visitation to the plants. Ramphastidae, which commonly visits *Euterpe* with high frequency, showed a low visitation rate, despite of high number of fruits removed in few visits. This could be most likely a result of the high availability of *Euterpe* ripe fruits in the study area. *T. flavipes*, however was the most important bird disperser of *Euterpe* at Carlos Botelho as reported for other forests (Côrtes 2006, Fadini et al. 2009).

Sloanea had the highest richness of bird species interacting with their fruits, and QC values with low range variability (0.067 to 1.071) if compared to *Euterpe* and *Virola* (Appendix A). This reduced QC variability across species resulted in a very distinct QC curve for *Sloanea*. This could result from the similarities among the variable values (visit rate, number of fruits manipulated/visit and dispersal probability) that compose the QC for bird species recorded in *Sloanea*. On the other hand, birds with larger QC values for *Sloanea* did not coincide with the most important birds to *Euterpe* and *Virola*. Additionally, bird species with highest relative contribution to *Sloanea* seed dispersal (*Orthogonys cloricterus*, *Turdus leucomelas*, *Habia rubica*, *Attila rufus*, *Tangara cyanocephala* and *Tytira cayana*) were bird species with smaller body size than most of the birds recorded for *Euterpe*, and were species with a low or nil contribution to the seed dispersal for both *Euterpe* and *Virola*.

Compared with the number of fruits removed, visitation rate was the most important variable to the seed dispersal process of *Euterpe*. Also, this was the most

important component for the dispersal effectiveness of *Virola*. Similarly, visitation rate was the most important component to the seed dispersal effectiveness of *P. mahaleb*, a well-studied zoochorous species from Mediterranean (Jordano and Schupp 2000). Both *Euterpe* and *Virola* share a relatively large fruit and an assemblage dominated by large-bodied species. Thus most variation in QC for these species was associated to variation in visitation, since most species in the assemblage share fruit handling behaviors.

A different case occurred when bird species removed many fruits in a single visit. For instance, *S. maculirostris* and *P. nudicollis* removed large number of *Euterpe* fruits but spent long time on the plant, regurgitating seeds under it in a very restricted area (Galetti et al. 2000, Pizo and Simão 2001). As a result, a large number of fruits was wasted due to the accumulation of regurgitated seeds under the mother plant where the seeds and seedlings may experience higher mortality (Howe and Estabrook 1977, Wenny 2000). This high mortality under the parental plant is due to predation by specialist predators and parasites that respond to the density and focus their activities where resources are common and abundant (Janzen 1970, Connell 1971). Besides predation, seedlings under the mother plant are subject to intraspecific competition for light or nutrients (Howe and Smallwood 1982, Howe 1986).

S. maculirostris and *P. nudicollis* are important species to the dispersal of *Euterpe* by contributing to high fruit removal. Similar results were found by Côrtes (2006) at the Cardoso Island. The behavior of these birds characterizes what is called restricted dissemination (Jordano and Godoy 2002, Schupp et al. 2002). Birds restrict the location of the foraging areas to sites they have high availability of ripe fruits, restricting the seed movement to those patches where ripe fruits are available concurrently (Herrera and Jordano 1981). Both *S. maculirostris* and *P. nudicollis* are also able to contribute long-distance dispersal events, despite concentrate their foraging at certain places with high fruit availability.

Some studies have evidenced that directed dispersal could be more common than previously noted (Nathan and Müller-Landau 2000). For example, seeds of *Ocotea endresiana* are preferentially dispersed to gaps by *Procnias tricarunculata* and their seedlings had a high survival in that site conditions (Wenny and Levey 1998, Wenny 2000). Our study, on the other hand, showed a waste of *Euterpe* seeds under mother plants when they are removed by *S. maculirostris* and *P. nudicollis*.

In relation to *Sloanea*, the variable most important to QC was the number of fruits manipulated per visit. *Euphonia* sp., *Euphonia pectoralis*, *Habia rubica*, *S. maculirostris*, *Tangara cyanocephala* and *T. seledon* were the most important birds feeding on *Sloanea* fruits, all of them are small birds, predominantly of the Thraupidae family (except *S. maculirostris* and *H. rubica*). Thraupidae form an abundant, diverse, and an important group of tropical fruit-eating birds (Levey 1987). The species in this assemblage, contrasting with the *Euterpe* case, show extensive variation in fruit handling behavior, yet more similar visitation patterns. The small size of the *Sloanea* fruits can be related to the small bill size of birds in the Thraupidae family. This congruence possibly made the Thraupidae the most important group among all *Sloanea* seed dispersers. Despite fruit mandibulation be a typical behavior of Thraupidae before ingesting, which often lead to the dropping of seeds (Levey 1987), seed waste was not registered for most birds during observations of *Sloanea* trees except for *T. seledon* that was observed discarding seeds under the mother plant after removing their aril.

For many plants only a reduced number of bird species is responsible for most of the "dispersal service" (Schupp et al. 2010) because there are several factors that ultimately limit and define the dispersers assemblage. Bird assemblages vary among plant species as a result mainly of size and structure of fruits (Pratt and Stiles 1985). This relation is exemplified in our study by *Euterpe* and *Virola* that have attracted birds of large size (*A. jacutinga*, *P. nudicollis*, *S. maculirostris*, and *Ramphastos* spp.), while a group consisting of small birds predominated in the dispersal of *Sloanea*. The conclusion that smaller birds eat smaller fruits is supported, among others, by studies developed at Trinidad (Snow and Snow 1971) and Costa Rica (Skutch 1980). Our analysis reveals that these differences in assemblage composition across tree species determine ample differences in dispersal services and effectiveness. Only a reduced subset of species in these assemblages can be considered reliable dispersers in terms of both visitation and fruit handling behaviors.

The *Turdus* thrushes, for example, illustrate great variation within the genus in seed dispersal effectiveness according to the plant species with which they interacted. For *Euterpe* *T. flavipes* was the most effective *Turdus* species and is also the bird most effective in the dispersal of *Virola*. To *Sloanea* *T. leucomelas* was the species that contributed the most to the effectiveness in seed dispersal.

Muscicapidae is viewed as a very important bird family that disperses seeds in viable conditions (Murray 1988). Some studies reported the family Muscicapidae as one of the most effective in dispersing *Euterpe* seeds in pristine (Laps 1992, Cortes 2006, Fadini et al. 2009), and fragmented forests (Matos and Watkinson 1998, Cerisola et al. 2007). Unlike *Euterpe*, detailed investigations regarding the seed dispersal of *Sloanea* and *Virola* are few and deserve special attention when discussing the relationship between plants and their seed dispersal agents.

Comparisons among congeneric species may, however add up to the lacking knowledge about the seed dispersal of *Virola* species (e.g., Russo 2003). Studies developed at Peru and Panama allowed some authors to conclude that morphological similarities among the fruits of *V. calophylla*, *V. sebifera*, and *V. nobilis* were fairly consistent with disperser assemblage composition, with a few exceptions (Russo 2003). Ramphastidae (toucans and araçaris) and Trogonidae were the most frequent families in the visitation of *V. sebifera* and *V. nobilis* (Howe 1981, Howe et al. 1985). At Carlos Botelho, *T. viridis* was most frequent, but surprisingly toucans and araçaris were not common visiting *Virola*. Russo (2003) showed that in regard to *V. calophylla*, the primate *Ateles paniscus* was the species with highest frequency of visits, with higher seed removal per visit and higher total seed removal. We had no record of primates feeding on *Virola bicuhyba*, and birds are the main dispersers of this Atlantic forest *Virola*.

When we considered the abundances of birds and the QC to derive the potential contribution to seed dispersal our results revealed differences in the frugivore assemblages that disperse seeds of the three plant species at B and NB stands. This result highlights the importance of considering how landscape heterogeneity might influence variation in dispersal effectiveness among species, an aspect that remains understudied in plant-frugivore mutualisms (Schupp et al. 2010). The contribution to seed dispersal and the composition of the frugivorous bird assemblage visiting a given plant are related to the abundances of the birds in the forest and varies according to their specific abundance at each stand. Cortês (2006) showed that bird abundance indirectly influences the quantitative component because it largely determines visitation rate, though it was negatively correlated to dispersal rate. So, the abundance of each species can influence more strongly the real contribution to seed dispersal than the number of seeds that each bird species

disperses during each foraging visit to fruiting plants, as the *Euterpe* and *Virola* examples illustrate.

The local abundance of frugivorous birds has been shown to be the main factor affecting the composition and bird visitation patterns to plants in various study systems (Schupp 1993, Jordano and Schupp 2000). In this context, the maintenance of bird populations should be a key aspect for conservation of plant populations that depend on these birds for their dispersal and successful natural regeneration in different environments.

Frugivorous species have species-specific patterns of treating the seeds and disperse them to different microhabitats. However, microhabitats differ in their conditions for plant recruitment, an aspect related to the quality component of seed dispersal effectiveness. Then, differences in the deposition conditions by each bird species are as important as the differences in the specific microhabitat conditions to the germination, establishing and plant recruitment (Schupp 1993, Jordano and Schupp 2000, Schupp et al. 2010). An important conclusion of this study is that the effective dispersal of *Euterpe*, *Sloanea* and *Virola* at Carlos Botelho are restricted to a very small range of effective bird dispersers. At the landscape scale, losses of this restricted assemblage of dispersers could result in substantial changes in the composition and diversity of the forest (Wright et al. 2007, Terborgh et al. 2008, Holbrook and Loiselle 2009) and alterations of the successional dynamics in bamboo stands.

The high number of bird species in B stands was an unexpected result from this study, revealing that a sizeable number of frugivorous species might favour edges of bamboo patches or even their interior. This result is extremely interesting since environments with bamboos are often considered unattractive to fauna, especially to frugivorous birds (Stotz et al. 1996), and a negative influence to the forest dynamic when they occur abundantly (Sanquetta et al. 2006). Many studies have, however shown that stands with bamboos constitute important elements of the vegetation as well as potential shelter areas, providing food for many bird species during the fruiting season, as well as animal prey for insectivorous birds (Olmos 1996, Kratter 1997, Reid et al. 2004, Vasconcelos et al. 2005). Despite of negatively affect tree regeneration in forested habitats (Griscom and Ashton 2003, Guilherme et al. 2004, Rother et al. 2009), bamboo provides a rich environment for insects, birds and some mammals. Insects find sufficient food in the bamboos, and they in turn act

as food for birds while mammals that need fruit, may access to other types of forest (Janssen 2000).

Our results suggest that the structure of native bamboo stands plays an important role in the dynamics of the Atlantic forest by determining critical aspects of plant-bird interactions of great relevance to forest regeneration. Bamboo stands constitute a critical and extremely important element for the maintenance of bird species, not only for those foraging specifically in this habitat type but for those that use them as a shelter against predators or for nesting. Edges at the bamboo-forest interface can be critical patches for the recruitment of tree species and for the maintenance of the floristic heterogeneity of the vegetation.

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Appendix A – Quantitative component data for frugivorous species in the three plant species studied at Carlos Botelho state park. Quantitative component = Dispersal probability X Fruits manipulated/visit X visitation rate.

Species	Dispersal probability	Fruits touched/visit	Visitation rate	Quantitative component
<i>Euterpe edulis</i>				
<i>Aburria jacutinga</i>	1.0000	10.86	0.225	2.440
<i>Baryphthengus ruficapillus</i>	1.0000	1.53	0.610	0.931
<i>Brotogeris tirica</i>	1.0000	1.00	0.064	0.064
<i>Orthogonys chloricterus</i>	0.0000	0.00	0.064	0.000
<i>Pitangus sulphuratus</i>	1.0000	2.00	0.032	0.064
<i>Procnias nudicollis</i>	0.8980	8.80	0.161	1.413
<i>Pyroderus scutatus</i>	1.0000	1.17	0.193	0.225
<i>Pyrrhura frontalis</i>	1.0000	6.50	0.064	0.417
<i>Ramphastos dicolorus</i>	0.8571	4.00	0.096	0.385
<i>Ramphastos vitellinus</i>	1.0000	8.00	0.032	0.257
<i>Selenidera maculirostris</i>	0.9880	6.31	0.835	5.266
<i>Tachyphonus coronatus</i>	1.0000	1.00	0.064	0.064
<i>Tangara seledon</i>	0.1667	0.20	0.161	0.032
<i>Tangara sp.</i>	1.0000	1.00	0.032	0.032
<i>Trogon viridis</i>	1.0000	1.03	2.344	2.408
<i>Turdus albicollis</i>	0.9182	1.94	1.670	3.243
<i>Turdus amaurochalinus</i>	0.8333	5.00	0.064	0.321
<i>Turdus flavipes</i>	0.9709	1.80	2.986	5.362
<i>Turdus leucomelas</i>	0.8750	1.75	0.128	0.225
<i>Turdus rufiventris</i>	1.0000	2.00	0.096	0.193
<i>Turdus sp.</i>	1.0000	1.33	0.096	0.128
<i>Sloanea guianensis</i>				
<i>Atila rufus</i>	0.5000	4.50	0.714	0.804
<i>Brotogeris tirica</i>	1.0000	2.00	0.357	0.714
<i>Dacnis cayana</i>	0.3333	1.67	1.071	0.198
<i>Euphonia pectoralis</i>	0.2500	2.75	1.429	0.246
<i>Euphonia sp.</i>	0.2500	3.00	1.429	0.268
<i>Habia rubica</i>	0.5000	5.50	0.714	0.982
<i>Orthogonys chloricterus</i>	1.0000	3.00	0.357	1.071
<i>Pachyramphus castaneus</i>	0.2000	1.00	0.357	0.071
<i>Parulidade</i>	0.2500	0.75	1.429	0.067
<i>Saltator fuliginosus</i>	0.5000	1.00	0.714	0.179
<i>Selenidera maculirostris</i>	0.1429	1.43	2.500	0.073
sp1	0.5000	0.50	0.714	0.089
sp2	1.0000	1.00	0.357	0.357
sp3	1.0000	1.00	0.357	0.357
<i>Tachyphonus coronatus</i>	0.5000	1.50	0.714	0.268
<i>Tangara cayana</i>	0.5000	1.00	0.714	0.179
<i>Tangara cyanocephala</i>	0.5000	4.00	0.714	0.714
<i>Tangara seledon</i>	0.3333	2.33	1.071	0.278
<i>Tangara sp.</i>	1.0000	1.00	0.357	0.357
<i>Thraupis cyanopectera</i>	0.5000	1.50	0.714	0.268
<i>Turdus flavipes</i>	0.3333	1.00	1.071	0.119
<i>Turdus leucomelas</i>	1.0000	3.00	0.357	1.071
<i>Tytira cayana</i>	1.0000	2.00	0.357	0.714
<i>Virola bicuhyba</i>				
<i>Aburria jacutinga</i>	0.8333	6.00	0.129	0.647
<i>Baryphthengus ruficapillus</i>	1.0000	1.00	0.517	0.518
<i>Orthogonys chloricterus</i>	0.5000	1.00	0.259	0.129
<i>Ramphastos sp.</i>	1.0000	1.00	0.129	0.129
<i>Ramphastos vitellinus</i>	1.0000	1.00	0.129	0.129

Species	Dispersal probability	Fruits touched/visit	Visitation rate	Quantitative component
<i>Selenidera maculirostris</i>	1.0000	1.00	0.776	0.776
<i>Tersina viridis</i>	0.0000	1.00	1.035	0.000
<i>Thraupis palmarum</i>	0.0000	1.00	0.259	0.000
<i>Trogon viridis</i>	1.0000	1.00	3.364	3.364
<i>Turdus albicollis</i>	0.6000	1.67	0.388	0.388
<i>Turdus flavipes</i>	0.7714	1.52	2.975	3.493
<i>Turdus leucomelas</i>	0.4444	3.00	0.776	1.035
<i>Turdus rufiventris</i>	1.0000	1.00	0.259	0.259
<i>Turdus</i> sp.	0.4000	1.00	0.647	0.259

2

SPATIAL PATTERNS OF SEED RAIN AND SEEDLING RECRUITMENT IN A BRAZILIAN TROPICAL FOREST

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Abstract

Several factors decrease plant survival due to loss of propagules throughout their lifecycles. Among these factors, the dispersal process can be spatially limited in terms of distance and extension. Dispersal limitation can thus result in short distance and aggregated (contagious) seed distributions. In addition, the arrival of seeds may not coincide with suitable environments for seed survival and, consequently, for seedlings. We assess the spatial pattern of seed and seedling establishment in the Atlantic rainforest, using seed traps and seedling plots during two different periods in two different microhabitats. Physical and chemical variables of soil and light were used to characterize the microhabitats of regeneration as well as to evaluate the landscape pattern of regeneration. Seed density patterns showed temporal and spatial discordance with seedling density. Stand type (mature forest vs. bamboo-dominated stands) was related to differences in seed species richness and seedling abundance for 2004-2005 and to differences in seed abundance and richness in 2007-2009. Seedling species richness was independent of stand type and consistent for both two periods. Spatial autocorrelation patterns showed by seed rain, seedling establishment, and seedling richness ranged between periods. Thus, abundance and richness of plant recruits at the seed and seedling stages respond differently according to local conditions and time. Comparing the two periods, abundance and richness showed spatial autocorrelation in 2004-2005 while only seed richness varied spatially in 2007-2009. Sand was an important soil characteristic to explain variation of seed and seedling abundance as well as for seedling richness in the permanent plot. The plant community at both stands types evidences marked recruitment limitation as a result of the interplay between biotic and abiotic factors. Forest mosaics are species reservoirs. Because bamboo stands promotes heterogeneity in the forest, they are important components of the landscape. However, in high density at the forest, bamboos can be one more limiting recruitment factor to plant community. In this case, their management is essential.

Key words

Microhabitats, spatial heterogeneity, seed dispersal, seedling establishment, *hotspots*, Bamboo stands.

Introduction

Spatial pattern of seed deposition had been scarcely included in dispersal studies given that seed dispersal has not been associated to recruitment limitation before (Gómez-Aparicio et al. 2007). Schupp and Fuentes (1995), however, concluded through the combination of observational and experimental studies that there is a close and important spatial relationship between seed dispersal and seed sources in different microhabitats within heterogeneous landscapes. Because of such relationship and the fact that seed dispersal is the first demographic process and the single mobile stage of the plant lifecycle (Nathan and Muller-Landau 2000), seed dispersal patterns have been identified in many demographic studies as an essential aspect to understand the plant regeneration dynamics (Jordano and Herrera 1995, Rey and Alcántara 2000, Hampe 2004). In addition, seed dispersal defines an initial template for subsequent demographic processes, thereby influencing gene flow patterns and, consequently, the genetic structure within and between populations (Ouborg et al. 1999).

Plant recruitment process is considered as a sum of stages related to each other that affects the final regeneration (Clark et al. 1999). The seed-seedling transition is the least predictable stage in plant recruitment (Schupp and Fuentes 1995, Clark et al. 1999). Such unpredictability occurs because early stages of the recruitment are especially variable and prone to density-dependent processes at various spatial and temporal scales (Schupp and Fuentes 1995, Schurr et al. 2008). As suggested by Schupp and Fuentes (1995), it is crucial to study the plant lifecycle as a series of events that permit the identification of critical transitions related to the dispersal processes that determine consequences for final recruitment.

On a local spatial scale, plant population dynamics are largely determined by seed movement (Ouborg et al. 1999), a process pervasively influenced by spatially variable environmental factors (Schurr et al. 2008). Both plant fecundity and seed dispersal are subject to ample spatial variation. The spot where an adult plant is established obviously affects its seed production (Schurr et al. 2008), while the surrounding environment can influence seed dispersal at least in two ways: first, for animal-dispersed species, the disperser behavior, its habitat preferences and predator avoidance are biotic influences that can lead to aggregated seed deposition in specific environments, with lasting consequences for the subsequent stages of recruitment (Wenny and Levey 1998, Jordano and Schupp 2000, Wenny 2001).

Second, the seed deposition of anemochorous species may be affected by wind conditions and topography (Tackenberg 2003), as well as by seed collision with obstacles (Schurr et al. 2008). After seed arrival in a given site, there are different physical (e.g., nutrient availability, water and light) and biotic conditions (e.g., seed predators, herbivores and pathogens) which will further affect the post dispersal stages of recruitment. Consequences of the environmental heterogeneity on plants are therefore relative because their effect depends on the specific life stage considered (Russell and Schupp 1998).

Heterogeneous patterns of seed arrival can also be generated by microhabitat structure, because vegetation acts as a primary barrier for seed dispersal (Nathan et al. 2002). Bullock and Moy (2004) found that higher seed density reached forested microhabitats than low grassland. Established plants on forested microhabitats acted as seed sources as well as a physical barrier to seeds from neighboring plants, leading to high seed density in these areas. In short, differences in seed density reaching deposition sites exert relevant demographic effects on plant recruitment (Nathan and Muller-Landau 2000).

The processes involved in each stage of the regeneration cycle (e.g., pre- and post-dispersal seed predation, seed dispersal, herbivory, pathogens action) may be, however, independent of each other and in most cases may lead to high local specificity of the regeneration success. This specificity largely results from variable qualities of specific microhabitats for different recruitment stages, leading to spatial discordances between the initial seed rain and final recruitment (Jordano and Herrera 1995, Schupp 1995). The ultimate plant recruitment success and its variation among habitats can be differentiated by understanding how each stage is independent from each other but highly dependent on local conditions.

Spatial discordances in recruitment frequently derive from contrasted influences of biotic and abiotic factors at each stage of the regeneration cycle. These factors include: seed dispersers, seed predators, competitors, pathogens, herbivores and microclimatic conditions of light, nutrients and water availability, which are temporally and spatially heterogeneous (Schupp 1995, Rodríguez-Pérez and Traveset 2007). The uncoupling between stages has been demonstrated in various studies for Mediterranean species (Jordano and Herrera 1995, Rey and Alcántara 2000, Alcántara et al. 2000, Gullás et al. 2004, Rey et al. 2004, Rodríguez-Pérez and Traveset 2007), and is highly related to local environmental conditions at various

stages (Traveset et al. 2003, Rodríguez-Pérez and Traveset 2007). Suitable sites for seeds may nevertheless be unsuitable to seedlings (seed-seedling conflict). Small seeds, for instance, are more easily spread in the environment than large seeds, and have a relative higher probability to escape from predation. Small seeds however have low nutritional reserves for seedling establishment and therefore less chance to withstand on unsuitable environments (Schupp 1995).

The uncoupling between seed rain and established seedling patterns in a given environment results from two factors: extremely heterogeneous pattern of seed dispersal in different landscape patches, and environmental variation which favors plant survival in some patches more than in others (Schupp 1995). Accordingly, environments that combine high plant establishment with high temporal recruitment consistency may be considered important *hotspots* of plant regeneration (Hampe et al. 2008).

Concepts related to spatial discordance of seed dispersal and regeneration sites associated with different microhabitats served as a framework for the study of an area of Atlantic rainforest where bamboo patches define a distinct patchiness and heterogeneity in the vegetation. Some bamboo species are at high densities in certain regions of the Atlantic forest where environmental and historical (e.g., forest perturbation) conditions are appropriated for their establishment and expansion (Fantini and Guries 2007, Terra 2007, Morokawa 2008). This is the case of the bamboo *Guadua tagoara* (Nees) Kunth, a species that may grow within the forest, in secondary forests edges (Judziewicz et al. 1999, Fantini and Guries 2007), and gaps (Smith et al. 1981, Tabarelli and Mantovani 1999, Alves 2007, Araujo 2008, Lima and Gandolfi 2009).

The local occupancy by bamboos is associated with the position and shape of their culms growth from rhizomes in a way for getting light (Judziewicz et al. 1999). In situations where bamboos reach and dominate forest canopy, the vegetation structure is consequently changed leading to forest cover homogenization and large bamboo patches amidst vegetation (Nelson et al 2006, Araujo 2008). At bamboo-dominated sites, vegetation structure is characterized by a discontinuous canopy, low density of medium and large arboreal individuals, and low floristic diversity (Oliveira-Filho et al. 1994, Tabarelli and Mantovani 1999, Guilherme et al. 2004, Fantini and Guries 2007). However, little is known about how bamboo presence limits the initial stages of recruitment of non-bamboo plants.

In this paper we emphasize the importance of studying seed and seedling spatial patterns across different environments and periods. This knowledge is essential for understanding the complete scenario of all processes involved in the recruitment dynamic in a bamboo-dominated forest patch. Our main goal is to compare the spatial pattern of seed rain and seedling recruitment in a local scale at a Brazilian Atlantic forest site. The density and spatial distribution of seeds and seedlings were monitored in two microhabitats that are structurally and compositionally different (Bamboo and Non-bamboo stands). Specifically, the key questions of this study are: (i) are there spatial autocorrelations for seed and seedling distributions?; (ii) are there spatial autocorrelations for seed and seedling species richness? Moreover, considering two periods and Bamboo and Non-bamboo stands: (iii) are there specific environmental characteristics associated with *hotspots* of recruitment? and (iv) are *hotspots* of recruitment spatially-related to Bamboo stands?

Material and Methods

Study area and the permanent plot

This study was developed in an area of Tropical Lower Montane Atlantic Forest, in the Carlos Botelho State Park (PECB). This reserve is part of one of the largest and most preserved Atlantic Forest remnants in Brazil, being recognized in 1999 as the natural heritage site by UNESCO. The Atlantic forest is characterized by high species diversity and high endemism levels, with plant species richness estimated at 20,000, of which 6,000 are endemic (Mittermeier et al. 2004). These characteristics included this biome in the 25 world's hotspots for biodiversity conservation (Myers et al. 2000, Laurance 2009).

The study was conducted in a permanent plot located at an altitude of ca. 300 m on the Atlantic side of the Serra de Paranapiacaba. On this site, 256 permanent sub-plots of 400 m² were established within a larger plot of 320 x 320 m, totaling 10.24 ha. At each sub-plot, all plant individuals with perimeter at breast height (PAP) ≥ 15 cm were sampled, georeferenced and identified. Soil, topography, climate, and light were the environmental traits surveyed within the plot (see Rodrigues 2005).

The permanent plot is formed by high (20 - 30 m), old-growth lowland forest, with an opened understory interspersed by patches of the bamboo *Guadua tagoara* (Rother et al. 2009). The vegetation is characterized by typical occurrence in the understory of *Euterpe edulis* (Palm), high scandent bamboos, and plants of the

families Ciatheaceae, Rubiaceae and Rutaceae (Rizzini 1979, Custódio-Filho 2002). The mean temperature during the study period was 21.1° C (ranging between 17.4 - 25.2° C), and a mean of 3,384 mm of rainfall.

Seed rain and seedling sampling

Seed rain and seedling recruitment of the plant community were quantified during two periods (2004 - 2005 and 2007 - 2009) in both Bamboo and Non-bamboo stands by using seed traps and seedling plots. From 2004 to 2005, traps and each adjacent plot of 1m² were placed at 40 points per stand type. From 2007 to 2009, a total of 61 sampling points received a trap and an adjacent plot, both of 0.25 m², from which 31 were in Bamboo and 30 in Non-bamboo stands. Seed rain was sampled from June 2004 to June 2005 and from November 2007 to March 2009. Seedlings were sampled from June 2004 to July 2005 and from January to November 2008. Traps were emptied once a month and the seeds collected were counted and identified to the lowest taxonomic level possible (see Rother et al. 2009 for details). Plots were sampled monthly for 2004-2005 period and bimonthly for January to November 2008. Seedlings were tagged, counted and identified to the lowest taxonomic level possible (see Rother et al. 2009 for details).

Environmental variables

Data from physical and chemical soil traits of the permanent plot data bank were crossed with biological data from seeds and seedlings of each sampling point. The soil data bank included the following physical traits: granulometry, porosity, soil density, sand, silt and clay, and for chemical traits: pH, organic matter, P, K, Ca, Al and Mg (see Rodrigues 2005 for details).

Hemispherical photos were made for each sampling point in January 2008. Photos were taken in totally overcast days (to avoid the sunlight reflection on the lens), with a digital camera (Coolpix 4500, Nikon, Tokio, Japan) using a fisheye lens (aperture of 180° – FC-E8), to indirectly characterize light and radiation conditions, and canopy structure (Jennings et al. 1999). From each image obtained by hemispheric photography, six indexes of solar radiation and canopy structure were obtained: proportion of direct light (DSF), proportion of indirect light (ISF), global radiation (GSF), effective leaf area index (LAI), effective groundcover by the canopy (GndCover) and the proportion of the sky hemisphere that was visible (VisSky). We

used the HemiView 2.1.x (AT Delta-T Devices Ltd., Cambridge, UK) for photo analysis. Photos were previously treated in the Paint Program version 6.0 to remove artifacts such as reflexes that could interfere with the analyses.

Data analysis

The basic dataset included the coordinates $x - y$ of each seed trap and its respective seedling plot, the seed and seedling abundance for the plant community at each sampling point, seed and seedling species richness, data from physical and chemical soil characteristics, light conditions and canopy structure. We investigated spatial patterns in the data by generating Moran's I spatial correlograms (Moran's I x distance classes between sampling points) for the abundance and richness of seeds and seedlings to evaluate the intensity of spatial autocorrelation in each distance class (Diniz-Filho et al. 2003). Moran's I index ranges from -1 to +1 and quantifies the degree of autocorrelation between two points, being positive in a direct correlation and negative when opposite. This index was used to test whether the points with traps located at variable distances show more similarity in the abundance or richness of seeds than expected by chance. The same index was estimated for seedling abundance and richness data for both periods. Data from each period was analyzed separately. The distance at which the value of spatial autocorrelation crosses the expected value, indicates the range of the patch size or simply the spatial range of the pattern (Fortin et al. 2002, Aparicio et al. 2008).

To verify whether the abundance and richness of seeds and seedlings vary between stands (Bamboo and Non-bamboo) to both periods we fit linear mixed models by Restricted Maximum Likelihood (REML) using Generalized Least Squares (GLS), which allows the errors to be correlated and to have unequal variances. The Akaike information criterion (AIC) was used to compare statistical models and to choose the most informative one. The AIC has become a standard criterion to select the best fitting models when dealing with autoregressive problems. It is calculated to evaluate the relative support of the data for each model, expressed as the Akaike weight. This value is interpreted as the probability of the model being the best approximating model given the model set (Diniz-Filho et al. 2008). The smallest AIC value is selected as the best for fitting the model based on observed data (Crawley 2002).

Finally, we used multiple regression analysis to investigate whether environmental variables could explain the seed and seedling abundance and richness patterns. We first calculated Pearson's correlation for all possible pairs of variables of soil and light (only for 2007 - 2009 period), and excluded those showing high correlation with at least another variable to avoid multicollinearity problems among explanatory variables (Booth et al. 1994). For cases in which Moran's I was significant, we included spatial variables as predictor variables in all models. We also included stand type as a predictor variable for those cases where we found differences between bamboo and non-bamboo stands. The Akaike information criterion (AIC) was used to compare multiple regression models and to choose the most informative one. All analyses were performed in R package v. 2.9.2 (R Development Core Team 2009).

Results

Temporal and spatial discordance in seed and seedling density

Seed rain and seedling establishment density varied between periods and stands (Table 1). When we consider the time scale, seed rain was denser in non-bamboo stands (NB, hereafter) in the 2004-2005 period. On the other hand, this relationship was inverse to 2007-2009. In this period higher seed density reached bamboo stands (B, hereafter). Interestingly, despite the lower seed density recorded at bamboo stands in 2004-2005, more seedlings established in these environment.

In 2007-2009, seed rain in B stands increased by approximately 20-fold compared with that of 2004-2005, and was nearly 3.5-fold the seed density recorded in NB. However, the pattern for established seedlings was markedly different. Recruitment in the Bamboo stands appears very reduced in 2007-2009, despite the intense seed rain that occurred in these stands. However, seed densities recorded at B in 2007-2009 were the result of just four traps which received disproportionately high seed abundance. Only these four traps accounted for 12,546 seeds in B stands.

Table 1. Seed and seedling density for Bamboo (B) and Non-bamboo (NB) stands and on two study periods (2004-2005 and 2007-2009).

Period	Seed rain density (seeds/m ²) ± sd	Seedling density (seedlings/m ²) ± sd
2004-2005		
B	117.70 ± 161.74	15.20 ± 15.54
NB	303.90 ± 759.43	8.30 ± 6.57
2007-2009		
B	2525.03 ± 1045.40	53.94 ± 6.80
NB	719.73 ± 186.50	54.00 ± 8.83

In summary, the seed density patterns showed a marked discordance with seedling density patterns for both temporal and spatial scales (Figure 1).

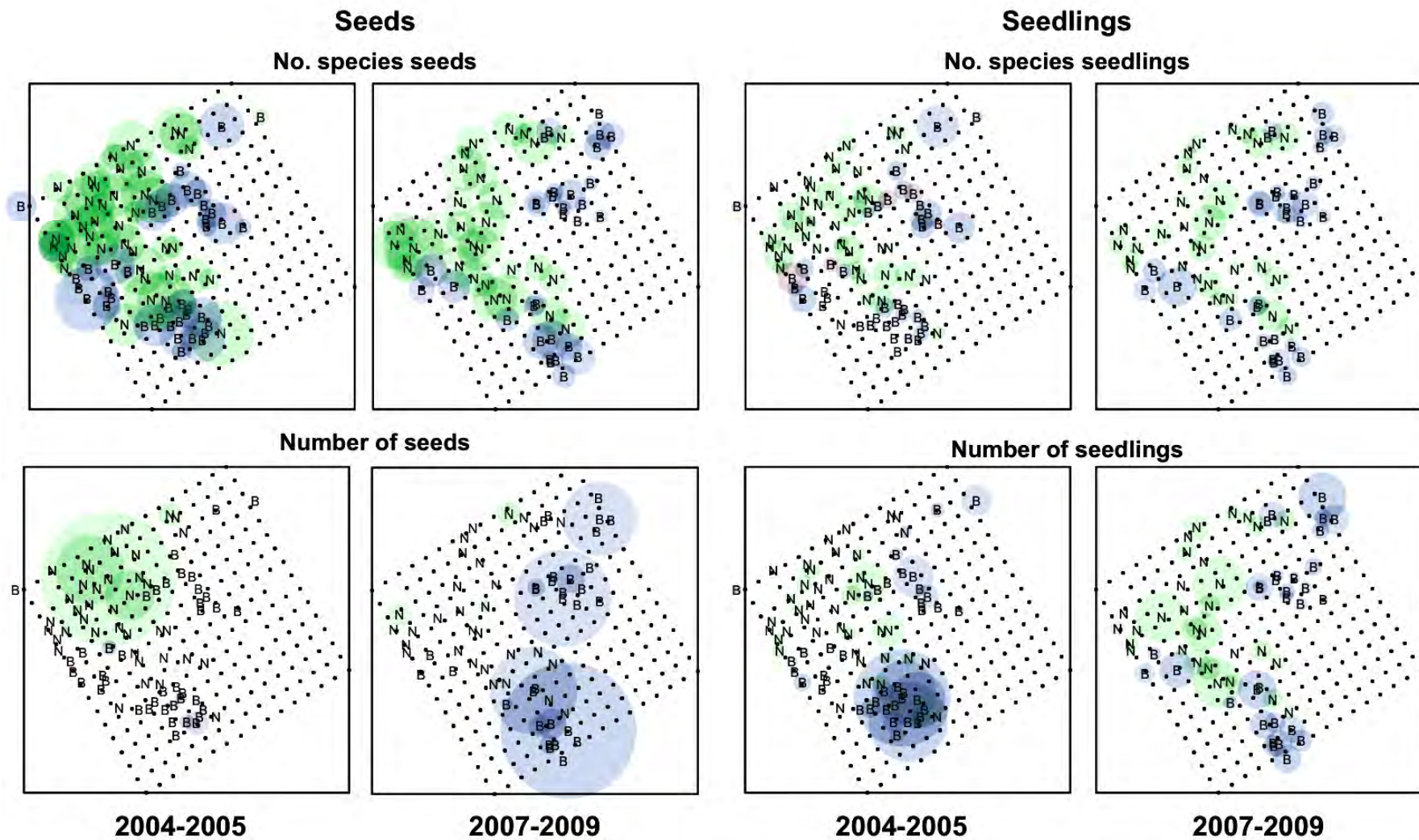


Figure 1. Bubble plots of seed rain and seedling density and seed and seedling richness separated by study period. Blue bubble for Bamboo stands and green bubble for Non-bamboo stands.

Hotspots of recruitment

Seed rain did not differ between NB and B stands in 2004-2005 although a higher number of seeds were recorded at NB. Over the same period, seedling establishment was significantly higher in B than NB stands (GLS: seedling and site effects, $t = 2.44$, $p = 0.017$). For 2007-2009, seed abundance differed between stands (GLS: seed and site effects, $F = 5.42$, $p = 0.023$). Bamboo stands received the majority of dispersed seeds. Stand type, however, did not influence seedling establishment on that period (GLS: seedling and site effects, $t = 0.008$, $p = 0.994$).

Seed richness was significantly affected by stand type in both periods (GLS: seed species and site, for 2004-2005, $t = 4.30$, $p = 0.00$; for 2007-2009, $t = -2.33$, $p = 0.023$). Nevertheless, seedling richness was similar for both stand and period comparisons.

Surprisingly, the seed and seedling abundances presented no consistency among periods concerning the effect of the stand type. However, we observed a consistent temporal trend (influence on seed richness and no influence of stand type on seedling richness) for seed and seedling richness. In other words, we found no differences between the two habitat types for seed rain and seedling establishment abundance between periods while the pattern for species richness was consistent for stand types.

In short, stand type was related to differences in seed richness and seedling abundance for 2004-2005 and to differences in seed abundance and richness in 2007-2009. Seedling richness was independent of stand type and consistent for the two study periods.

Spatial autocorrelations in seed and seedling abundance and diversity

For 2004-2005, the autocorrelation pattern for seeds was spatially- dependent at distance class 1. Pairs of traps distant approximately 25.47 m showed a significant similarity in seed abundance (Figure 2a). In relation to seedlings, we also observed spatial autocorrelation between plots located within short distances from each other ($p < 0.05$) (Figure 2b). For seed richness, the spatial pattern is also spatially dependent among traps located 90.87 m from each other (Figure 2c). While seedling richness exhibited spatial dependence at longer distance classes (Figure 2d).

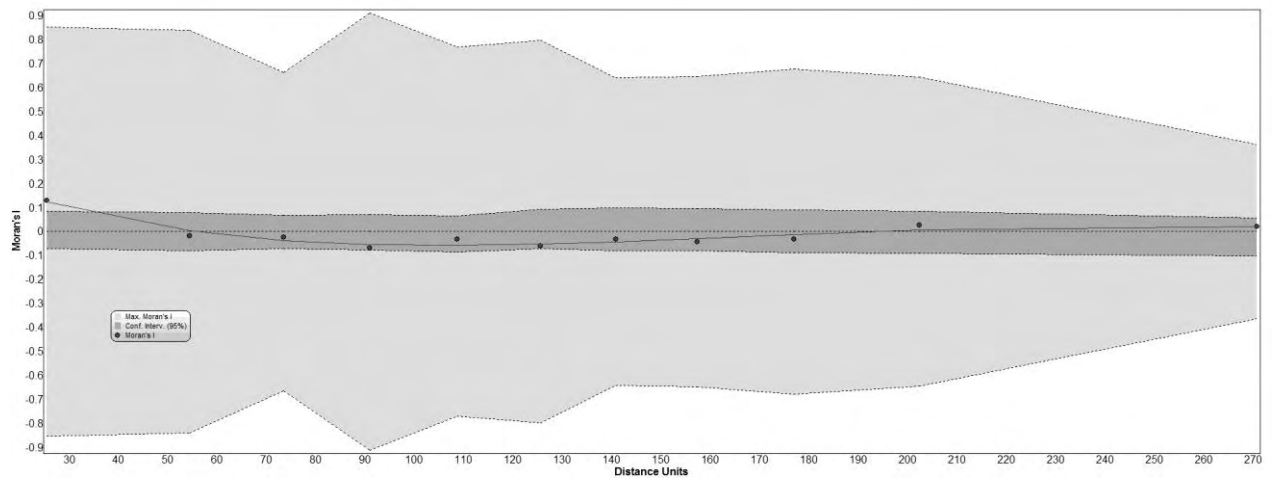
All results from 2007-2009 were contrary to those found in the previous period. Seed rain, seedling establishment and seedling richness showed no spatial

autocorrelation on the permanent plot (Figure 3a, 3b and 3d, respectively). Seed richness, however, was spatially-dependent, especially at shorter distance classes (24.85 m and 64.70 m) (Figure 3c). Traps located within these distances had similar seed richness.

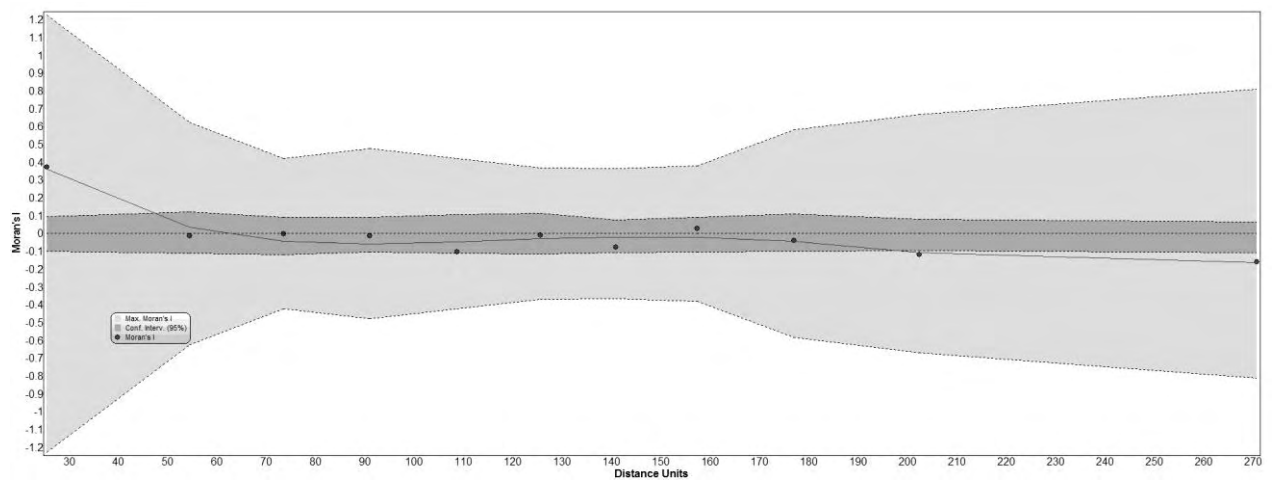
Spatial autocorrelation patterns displayed by seed rain, seedling establishment, and seedling richness ranged between the two study periods. This result suggests that each variable (abundance and richness) responds differently according to local environmental conditions and time (spatial and temporal variation, respectively).

The pattern of spatial autocorrelation for large distances was random in all cases (Moran's I values approaching to zero). Besides different responses of seeds and seedlings towards environmental characteristics, inconsistencies between periods can be resulting from undetermined species, especially for seedling richness. Seeds and seedlings not identified in both periods may have influenced our results because only species identified to genus or species entered in the analysis.

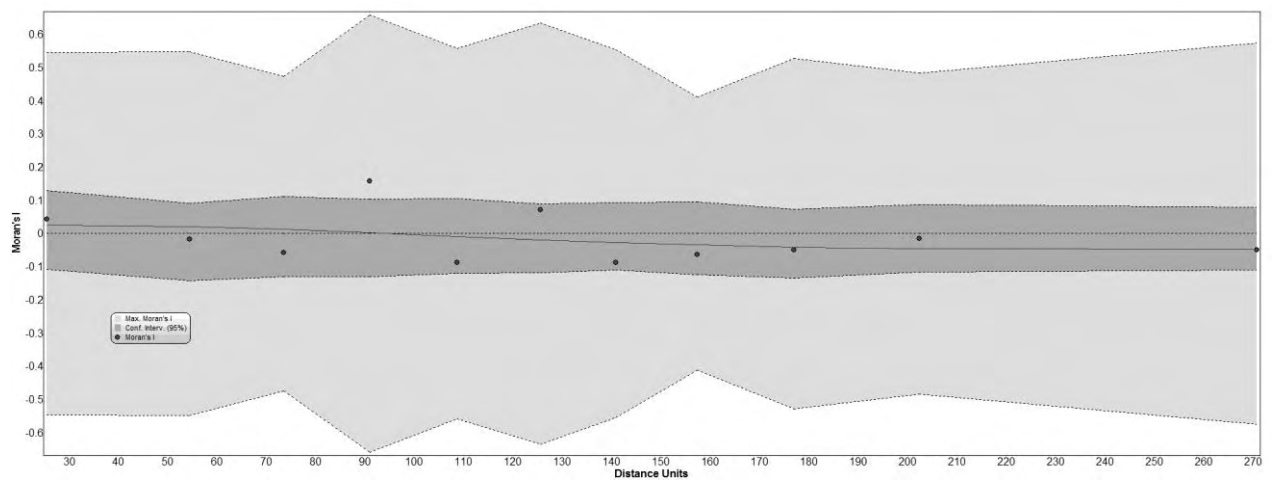
(a)



(b)



(c)



(d)

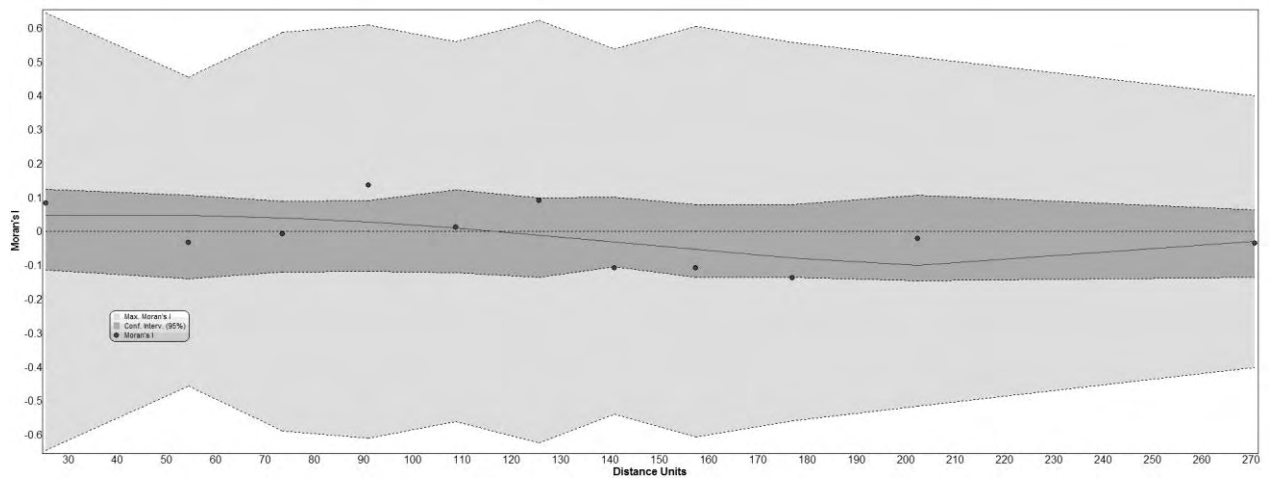
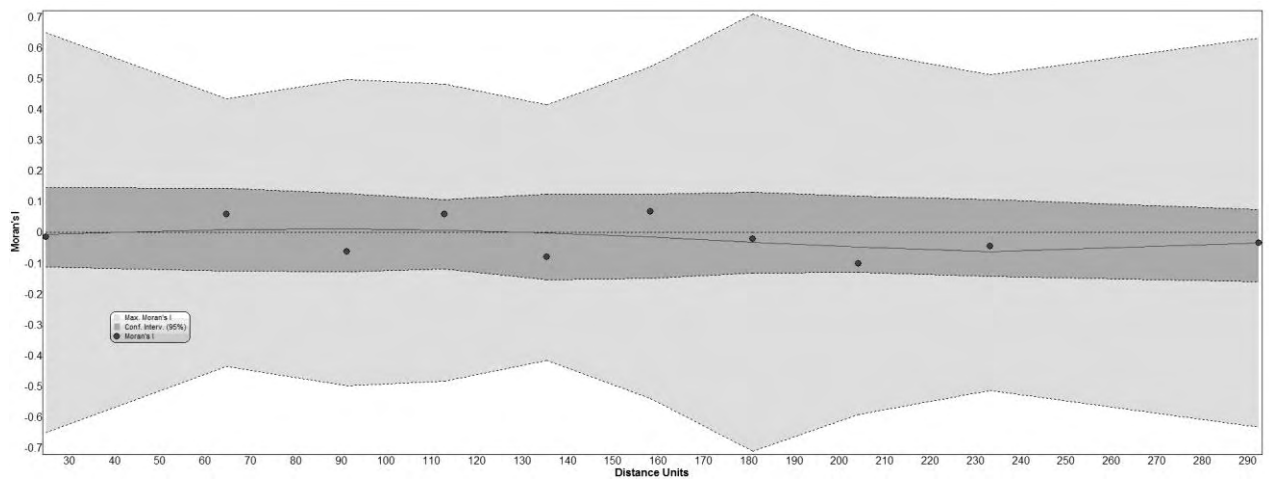
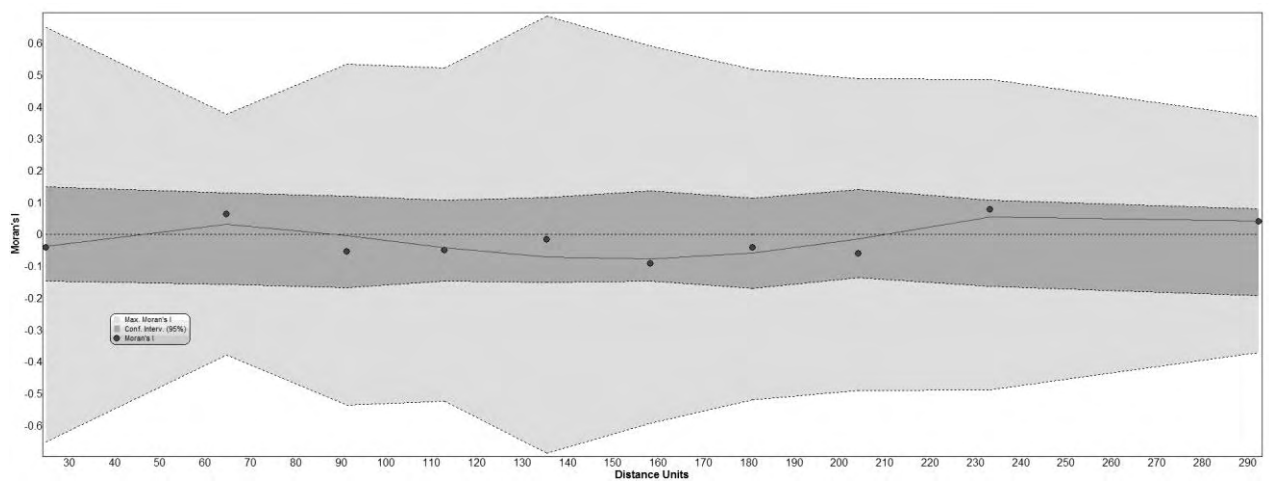


Figure 2. Spatial correlograms using Moran's I for seed rain abundance (a), seedling abundance (b), seed richness (c) and seedling richness (d) (circles), in 2004–2005. All spatial correlograms were estimated for distance classes in meters.

(a)



(b)



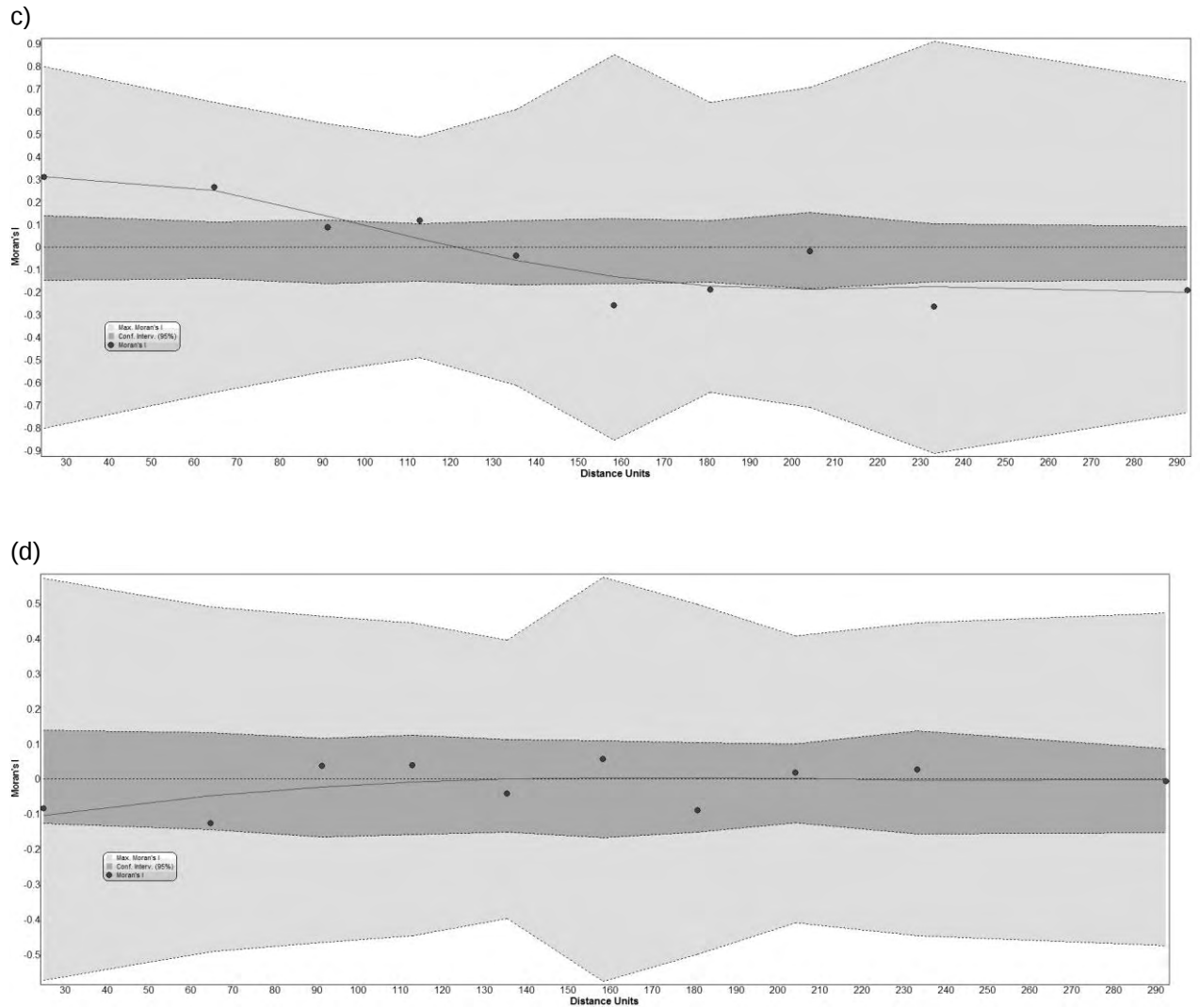


Figure 3. Spatial correlograms using Moran's I for seed rain abundance (a) seedling abundance (b), seed species richness (c) and seedling species richness (d) (circles), in 2007–2009. All spatial correlograms were estimated for distance classes in meters.

The spatial patterns of seed rain and seedling recruitment showed a significant clumping at the plot scale (Figure 3), both in terms of abundance and species richness, with only a few sampling locations concentrating most recruit abundance and diversity of species.

Relating seed and seedling patterns with environmental traits

The relationships between seed and seedling abundance and richness with environmental variables are summarized in Table 2. In 2004-2005, seed and seedling abundance, and seed and seedling richness had spatial autocorrelation, while only seed richness was spatially-dependent in 2007-2009.

In relation to the 2004-2005 period, the variance explained by all models based on seeds number was extremely low ($r^2 = 8.1\%$) (Table 2A). This result indicates that environmental variables used in the models were not able to explain the spatial autocorrelation for seed abundance shown by Moran's I. Variables as slope and sand content contributed to explain only 21.7% of seed richness variation in the permanent plot.

Models fitted for seedlings abundance ($r^2 = 39.6\%$) were better than those obtained for seeds abundance. Among the environmental variables, variation in seedling abundance was largely explained by variation in sand content followed by organic matter content. Variables as slope, pH, organic matter and sand contributed to explain only 23.5% of variation in seedling richness. In other words, all models failed to successfully explain the spatial autocorrelation of seedling species richness (Table 2A).

Considering the period 2007-2009, the model that best explained ($r^2 = 0.464$) the spatial autocorrelation of seed richness had Ca and site as the most important variables. The model with these two variables explained 46.4% of the seed richness variation (Table 2A).

For 2007-2009, when we considered only non-spatial autocorrelation models (Table 2B), the model which included P, effective groundcover by the canopy (GndCover) and site explained 18.7% of variation in seed number. Regarding seedlings, models including pH, clay and GndCover explained 19.4% of the variation among points. Finally, the model including P, Al, sand, silt, the proportion of the sky hemisphere that was visible (VisSky) and site as the most important variables explained 27.1% of the variation in seedling richness (Table 2B).

It is worth noting that in 2004-2005 all parameters showed spatial autocorrelation while only seed richness varied spatially in 2007-2009. Except for seed richness (2007-2009), sand was an important environmental trait for variation of seed and seedling abundance and for seedling richness in the permanent plot.

Table 2. Models for abundance and species richness of seeds and seedlings in relation to environmental variables for two periods (2004-2005 and 2007-2009).

A) Spatial autocorrelation	2004-2005			2007-2009		
	Variables	r^2	AIC	Variables	r^2	AIC
Seed abundance	8, 15, 16, 17	0.081	133.054	-	-	-
Seed richness	1, 8, 16, 17	0.217	-64.778	6, 15, 16, 17	0.464	-65.442
Seedling abundance	1, 3, 8, 9, 16, 17	0.396	31.431	-	-	-
Seedling richness	1, 2, 3, 8, 16, 17	0.235	-27.452	-	-	-
B) Non-spatial autocorrelation	2004-2005			2007-2009		
	Variables	r^2	AIC	Variables	r^2	AIC
Seed abundance	-	-	-	4, 14, 15	0.187	89.442
Seed richness	-	-	-	-	-	-
Seedling abundance	-	-	-	2, 10, 14	0.194	-3.148
Seedling richness	-	-	-	4, 7, 8, 9, 11, 15	0.271	-63.006

Environmental variables used in the models: (1) slope, (2) pH, (3) Organic matter, (4) P, (5) K, (6) Ca, (7) Al, (8) Sand, (9) Silt, (10) Clay, (11) VisSky - proportion of the sky hemisphere that was visible, (12) DSF - proportion of direct light, (13) LAI – effective leaf area index, (14) GndCover - effective groundcover by the canopy, (15) site, (16) X, and (17) y.

Discussion

Temporal and spatial discordance in seed and seedling density

Variations between years in seed rain and early establishment are usually common and spatial concordance between stages is frequently weak mainly due to extremely variable mortality factors which cause seedling losses (Schupp and Fuentes 1995, Clark et al. 1999, Hampe et al. 2008). A fundamental issue in plant demography studies is whether the initial spatial configuration of the seed rain is a good predictor of later seedling establishment (spatial concordance) (Jordano and Herrera 1995, Schupp and Fuentes 1995). For animal-dispersed species, reliable frugivores would disperse sizeable amounts of seeds to predictably good quality microsites for later establishment. However, these two essential components of seed dispersal effectiveness do not frequently covary across species in frugivore assemblages (Schupp et al. 2010), and would create spatial discordances between the process of seed dissemination and the process of establishment. Our results showed that seed rain pattern was not concordant with the resulting established seedlings both spatially and temporally. Here seed rain was not a good predictor of seedling establishment, because concordance occurs when seed rain spatial pattern

is more heterogeneous than post-dispersal losses (Hampe et al. 2008). That is, either the stage-specific survival probabilities are spatially coupled along stages or the high seed density which reaches some microsites obscures variation in seed and seedling mortality, despite density-dependence (Harms et al. 2000).

Discordance between stages has been demonstrated in several studies for Mediterranean species (Jordano and Herrera 1995, Alcántara et al. 2000, Rey and Alcántara 2000, Gulías et al. 2004, Rodríguez-Pérez and Traveset 2007) and it is highly related to variation in local environmental conditions at various stages (Traveset et al. 2003, Rodríguez-Pérez and Traveset 2007). Favorable conditions for seed can be unfavorable for seedling (seed-seedling conflict). Small seeds, for example, are more easily dispersed than large seeds, and are more likely to escape from predation. Small seeds, however, have low nutritional reserves for seedling establishment and they are less likely to survive at adverse environmental conditions (Schupp 1995).

Plant recruitment process is considered a sum of concatenated stages connected among themselves in a manner that subsequently affect the final regeneration (Clark et al. 1999). The seed-seedling transition is the least predictable phase on the recruitment process (Schupp and Fuentes 1995, Clark et al. 1999) because it ties up the post-dispersal of seeds in the ground and the multiple influences associated with germination. These early stages of recruitment are especially variable and affected both at multiple spatial and temporal scales (Schupp and Fuentes 1995, Schurr et al. 2008).

The extensive discordance found in our study can be explained by the combination of two factors. First is habitat patchiness, where plants experience a high diversity of pressures that create abrupt transitions in recruitment quality (and survival prospects) across microsites over relatively reduced scales. Second, the strong pressure exerted by post-dispersal mortality factors on seedling establishment (chapter 3, Rother et al. 2010 - unpublished data). This highlights the central role of establishment limitation characterized by an extremely low probability of reaching the established seedling stage as a result of reducing the occurrence of relatively safe environments. So, mortality factors might limit the establishment of new individuals regardless of the number of seeds arriving in the area (Jordano et al. 2004).

Hotspots of recruitment

Several works have reported the recruitment associated to landscape heterogeneity (e.g., Jordano and Herrera 1995, Schupp 1995, Schupp and Fuentes 1995, Wenny and Levey 1998, Wenny 2001) due to the importance of microhabitats characteristics influencing seed rain and establishment. Interestingly, despite the temporal inconsistency for seed arrival and establishment, stand type was an important factor in our study to explain variation in seed richness in both periods. Annual variations in the local fruit production (both in timing, frequency and intensity) are commonly reported in the literature for the Atlantic rainforest (Ziparro 2004), and support the lack of consistency found in our results for seed rain abundance between the two study periods.

Reproductive phenological patterns may be influenced by numerous abiotic factors such as rainfall, temperature and day length (Ashton et al. 1988, Morellato et al. 1989, 2000), dispersal (Wheelwright 1985, Morellato and Leitão-Filho 1992), phylogeny (Kochmer and Handel 1986), and the activity of pollinators and seed dispersers (Snow 1965). In addition, seed rain is influenced by a set of other factors potentially more important, including distribution, density and fertility of parent-plants (Clark et al. 1998b) as well as landscape features around seed traps (Schneider and Sharitz 1988) and proximity and neighborhood effects (Morales and Carlo 2008).

In addition to the temporal variation affecting recruitment success, seedlings are dependent on a set of influences (i.e., biotic factors: herbivory, competition, trampling by animals, pathogens, and abiotic factors: humidity, light, soil nutrients) and new recruits need to overcome these barriers to ensure their survival (Rey and Alcántara 2000). More important than the number of seeds arriving at a particular site, it is the microhabitat quality that will determine the seedling establishment (Jordano et al. 2004), as some microhabitats really represent dead ends for recruitment.

Environments that combine a high annual intensity and consistency for the early stages of plant establishment represent potential *hotspots* (Hampe et al. 2008). In the current study, seedlings found better conditions for establishment success in B stands in the period 2004-2005 although seed arrival was higher in NB stands. In the second study period, however, establishment was similar in both stands. Considering that the two stands showed inconsistency on establishment, our model indicates that B and NB stands did not represent *hotspots* for recruitment: the level of the

community, the inherent variation in each of these types of microsites erodes any general difference in quality for recruitment. At the population level, however, species could provide different answers regarding the types of stands and periods.

Negative relationships between seed rain and seedling establishment associated with low plant survival at different recruitment stages results in a limited recruitment. In the current study, plant community appears limited, especially for subsequent dispersal stages in both stands. Resource availability, suitable environmental conditions (i.e., years with high rainfall, gaps, etc.), and a high probability of recruiting in a given stand during these conditions are determinant factors for a successful establishment. However, *hotspots* are hardly detectable in short-term research projects (Clark et al. 1999, Howe and Miriti 2004, Hampe et al. 2008).

Spatial autocorrelations in seed and seedling abundance and diversity

The spatial pattern of recruitment is largely dependent on the initial seed dissemination established by the seed rain. However, this initial “template” for recruitment can be erased to a variable extent by the influence of successive post-dispersal factors such as seed predation, germination and seedling mortality (Herrera et al. 1994, Nathan et al. 2000, García 2001) as well as microhabitat characteristics (Webb and Peart 2000). Discordance between seed rain and seedling establishment patterns in an environment is the result of two factors: the heterogeneous pattern of seed dispersal and environmental variation that favors extremely variable plant survival depending on local microsite characteristics (Schupp 1995).

Seed rain, seedling establishment and species richness varied spatially in the studied periods. This means that abundance and species richness of seedlings respond differently according to environmental conditions. These different responses were observed in the study area in both spatial (over short-distances) and temporal scales.

Associations between species and variables of the physical environment produce more evident patterns with respect to distribution and organism abundance (Whittaker 1956, Webb and Peart 2000). At points close to each other we found greater similarity for seed and seedling abundance and species richness. This result reveals the fact that close points are at sites where forest composition is more similar. As a result of predominant dispersal over short-distances and infrequent

long-distance dispersal events, seed arrival and seedling establishment show aggregated distributions: a few nearby spots or microsites consistently get high recruit density. But our study reveals that these *hotspots* need not be necessarily concordant for seeds and seedlings. Especially for richness, inconsistencies found between periods can be the consequence of undetermined species and differences in seed predation and post-dispersal germination rate between stands (García-Castaño 2001), which can vary from year to year.

Relating seed and seedling patterns with environmental traits

Spatial ecology promotes novel approaches for studying seed dispersal, helping to elucidates processes of spatial pattern formation and their implications in plant recruitment success (Nathan and Muller-Landau 2000). Seed dispersal often depends on environmental variables which are altered in space and/or show spatially-explicit variation (Clark et al. 1999, Schurr et al. 2008). For animal-dispersed species, the spatial distribution of seedlings can be pervasively conditioned by the animals movement patterns (Julliot 1997, Russo 2005, Russo et al. 2006), while subsequent steps of the recruitment process depend mainly on the microhabitat conditions and factors that influence probability of seed and seedling survival (e.g., Rey and Alcántara 2000). In wind-dispersed species, seed deposition may be affected by wind conditions and topography (Tackenberg 2003), as well as the collision of seeds with obstacles (Schurr et al. 2008). Seed morphology influences not only how seeds move, but also where seeds stop (Levine and Murrell 2003).

Thus, within the plant community, seed dispersal patterns vary among populations, species and individuals at different distances from parental plant, microhabitats and also periods. In our study, we noted that all recruitment variables varied spatially in 2004-2005, while only seed richness varied in 2007-2009. Aparicio et al. (2008) investigated the influence of habitat structure, physical environment and human disturbance on plant richness in all forest patches interspersed within an agricultural matrix in the Guadalquivir River basin, Spain. These researchers found weak associations between species richness and the physical environment. However, they observed that richness decreased with disturbance levels within each environment and increased in the most forested areas.

A correlation between species distributions and soil and topography variables has been successively demonstrated in numerous studies on tropical forests (e.g., Clark et al. 1998a, Oliveira-Filho et al. 2001, Carvalho et al. 2005, John et al. 2007). At a local scale, topography has been considered the most important variable for spatial distribution and structure of tropical forests. Topography commonly alters soil properties, especially water regime and fertility.

We found associations between abundance and richness of the variables of recruitment in face of specific physical and/or chemical traits from environment. Interestingly, seed and seedling abundance and seedling richness were distributed in patches influenced by sand percentage in the soil. Organic matter also influenced the spatial dependence of abundance and richness of seedlings. In the literature, organic matter is cited as an important factor in forest regeneration by promoting plant growth and therefore increasing the biomass (Jumpponen et al. 1998). According to Tomé Júnior (1997), sites enriched by organic matter occur in lowlands with water excess (oxygen deficiency), being more harmful for decomposing microorganisms than plants that produce biomass. In this system, gains become greater than losses, therefore, accumulating organic matter. Gil-Solórzano et al. (2009) studied a sand deposit on crop fields formed by ashes from the volcano Parícutín in Michoacán, Mexico. The authors suggest that the nature of the organic matter accumulated in the soil can have a significant effect on composition of the seedling community. This result supports the Egger hypothesis (Egger 1963) according to which the lack of organic matter in soil prevents the vegetation development in sandy substrates of volcanic origin. In any case, the interactions between soil properties and seed limitation can be difficult to track due to their lasting effects, as evidenced by Ehrlén et al. (2006).

Along with dispersal, the response of seed species richness to environmental variation can be determined by a set of specific natural history traits such as flowering time, longevity, vegetative propagation, life-form, etc (Tilman et al. 1994). Some species perform better than others in certain environments. Individual performance also varies depending on levels of physical disturbance (Butaye et al. 2001), predator density, herbivores and competitors, and all these factors show ample variability from year to year.

A series of important processes of life history occur in the transition from seed delivery to the adult stage. Interactions between species and environmental factors

strongly influence these transitions and can significantly change the predicted model for dispersal (Schupp and Fuentes 1995, Nathan and Muller-Landau 2000, Wang and Smith 2002). Thus, our results suggest that the plant community dynamics on the permanent plot is under the combined influence of stand conditions, interactions between individuals and the seed rain pattern. All these factors vary from year to year and have important consequences for plant recruitment by regulating the abundance, distribution and species diversity.

Knowledge of seed dispersal spatial patterns within the landscape is of great relevance for understanding the role of forest mosaics as reservoirs of plant diversity. In this context, different habitats play an important role on tropical forests regeneration and diversity maintenance. Thus, B stands are certainly important components of the landscape since species are sensitive to environmental variables in an interactive and not separated way, besides apart from constituting an environment of competition between species (Botrel et al. 2002). In regard to *G. tagoara*, this species presents great biomass allocation for necessary its functions at initial establishment, what makes it competitive and favors its rapid colonization (Pellegrini et al. 2007). Bamboos form specific microhabitats resulting in a complex occupancy process closely related to forest succession and regeneration. In view of that, general conclusions about species distribution in relation to environmental variables should be made only after a sufficient number of replications of the same recruitment patterns in many areas (Botrel et al. 2002). Our results indicate that bamboo stands are influential in shaping seed rain patterns in the complex mosaics of Atlantic rainforest areas, with a variable importance across seasons on the quantitative values (abundance) of recruits and species richness of the seed rain. Hotspots of recruitment in these forests appear as dynamic as the vegetation physiognomy related to the spread and decline of bamboo stands.

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3

BOTTLENECKS IN TROPICAL PLANT REGENERATION: A COMPARATIVE ANALYSIS OF BRAZILIAN ATLANTIC FOREST SPECIES IN BAMBOO AND NON-BAMBOO STANDS

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Abstract

We studied the critical life stages and processes in the early recruitment of three tropical tree species, *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba*, of the Brazilian Atlantic forest in different microhabitats. We evaluated transition probabilities among the early stages involved in regeneration from seed to seedling survival to determine the overall probability of a seed in a fruit becoming an established individual in a population. The relative importance of each mortality factor was evaluated to determine the overall loss of propagules affecting the recruitment processes. We combined observational studies of seed rain and seedling emergence with experimental seed addition, in situ. Observations of seed rain and seedling establishment, and seed addition experiments were performed in disturbed, bamboo-dominated microhabitats and in old-growth forest environments. Our results showed that the addition treatment significantly increased the number of surviving seedlings for all three species. However, for *Sloanea* and *Virola* this effect depended strongly on protecting seeds artificially, since both species suffer very high seed and seedling losses due to post-dispersal seed predators and herbivores. The most favorable microhabitats for seeds and seedlings of *Euterpe* and *Virola* were the worst for seeds and seedlings of *Sloanea*. When protected from vertebrate activity, propagules of all three species had higher probability to reach subsequent stages of recruitment, suggesting that susceptibility to predation during the early stages of establishment can be more crucial than microhabitat differences as determinants of successful regeneration. Moreover, the seed trap data combined with experimental seed addition revealed that differences among the study species in the relative importance of dispersal vs. establishment limitation are mediated by their variable responses to patch heterogeneity created by bamboo stands.

Key words

Life stages, mortality factors, survival probability, tropical forest, *Euterpe edulis*, *Sloanea guianensis*, *Virola bicuhyba*.

Introduction

Regeneration process in a forest involves a series of stages from seed production to recruitment of juveniles, including seed dispersal, seed germination and seedling establishment (Martínez-Ramos and Soto-Castro 1993, Jordano and Herrera 1995, Clark et al. 1999, Rey and Alcántara 2000). This process concatenates the early consequences of seed dissemination with the early stages of seedling regeneration and strongly affects vegetation structure (Wang and Smith 2002). Multiple factors influence these stages and determine the dynamics and spatial distribution of plant populations (Clark et al. 1999).

Seed dispersal is particularly an important phase because it connects the end of adult reproductive cycle and seedling stage (Harper 1977, Wang and Smith 2002), and includes its consequences for survival and establishment of seeds and seedlings. For animal-dispersed species, seed dispersal bridges the consequences of animal movement patterns with their effects. These effects occur due to influences of the seed-delivery microhabitat on the survival probability of dispersed propagules. Thus, the frequent dichotomy of seed and recruitment limitation processes is really artefactual as both define how the final establishment is limited (Clark et al. 2007).

The steps of recruitment process subsequent to dissemination (seed arrival) depend on the microhabitat conditions and the factors affecting growth and mortality on both seeds and seedlings. There are many mortality factors that can act on these stages being seed predation, herbivory, pathogen attack, and water stress the most common (Harms et al. 2000, Rey and Alcántara 2000), and any of these early life-history events can be bottlenecks for recruitment. The relative importance of each mortality factor can vary according to microhabitat conditions, resulting in spatial discordance in performance of each stage of regeneration (Jordano and Herrera 1995, Schupp 1995, Schupp et al. 2002). Either disproportionately high mortalities at a given stage or marked discordances (uncoupling) among the recruitment probabilities of successive stages can lead to regeneration bottlenecks, i.e., demographic transitions where the survival prospects for propagules are zero or close to zero.

Despite recent efforts to understand how generalized are these types of demographic bottlenecks (García et al. 2005, Clark et al. 2007), few comparative studies have been carried out in tropical rainforests, where recruitment limitation is pervasive (Harms et al. 2000).

Seed dispersers play a key role by providing dispersal services as mobile agents or mobile links, and disseminating seeds throughout distinct habitat patches in heterogeneous landscapes (Lundberg and Moberg 2003, Kremen et al. 2007). These mobile links served by mutualistic interactions between plants and frugivores markedly contribute to plant persistence in fragmented landscapes and to ecosystem resilience. These occur especially when outcome of interactions mediates transfer of seeds from mature habitats into successional patches (Murray 1986, Silva et al. 1996, Bengtsson et al. 2003) allowing ecosystem reorganization (Bengtsson et al. 2003).

Bamboo-dominated stands are a particular microhabitat in forests around the world. Bamboos have been showed to influence forest structure and dynamics by casting a dense shade in the forest understory (Guilherme et al. 2004). Bamboo stands therefore provide preferred microhabitats for seed predators (Iida 2004), physical damage to seedlings and saplings (Griscom and Ashton 2006), and also alter patterns of seed limitation (Rother et al. 2009). As a result, large tracts of bamboo-dominated forests may occur, as in southwestern Amazonia, where approximately 180,000 km² of forest are dominated by *Guadua weberbaueri* and *G. sarcocarpa* (Nelson 1994; Griscom and Ashton 2003). In the Atlantic forest in SE Brazil, the endemic bamboo *Guadua tigoara* dominates wide areas, being considered a management problem inside forest reserves (Araujo 2008).

Previous studies have addressed the effects of bamboos on the seed rain (Rother et al. 2009), seedling establishment, and sapling performance of non-bamboo species (Griscom and Ashton 2006). However, it is still unknown if bamboo microhabitat conditions can affect propagule losses at each sequential demographic stage and demographic bottlenecks inherent to each stage for non-bamboo species.

Here we compared seed rain, abundance of early established seedlings (germination), and seedling survival of three Atlantic forest plant species (*Euterpe edulis*, *Virola bicuhyba* and *Sloanea guianensis*) between bamboo and non-bamboo stands. We evaluated how these three stages are connected through recruitment cycle of the focal plant species as a series of transition probabilities which depend on mortality factors. These factors determine the overall loss of propagules by affecting the three main recruitment processes (dispersal, germination and seedling survival).

To assess limitation processes that can act as demographic bottlenecks for effective recruitment, we combined seed addition experiments (Turnbull et al. 2000;

Munzbergová and Herben 2005) and subsequent seedling establishment, with an observational approach based on seed traps and seedling plots that has been successfully used in previous studies (e.g. Dalling et al. 2002, Muller-Landau et al. 2002, Gómez-Aparicio et al. 2007, Mendoza et al. 2009). Combining these two approaches is fundamental to understand recruitment limitation and to interpret seed addition experiments (Clark et al. 2007). This is a central issue when attempting to assess factors affecting limitation of local densities, where the magnitudes of limitation at both seed and seedling stages need to be evaluated. Moreover, we might expect that coexisting species in a forest might differ in their relative positions along a seed-to-establishment limitation gradient (Muller-Landau et al. 2002) yet these positions depend on the particular microhabitat type of the forest. These aspects of patch heterogeneity in limitation strength remain virtually unexplored in tropical forests.

We ultimately aimed to identify the most important stages limiting recruitment of non-bamboo plant species at forest patches under influence of bamboos, or not, and which of these forest patches represent suitable sites for species recruitment.

Material and methods

Study area and plant species

The field work was conducted in a 10.24-ha permanent plot set at the Carlos Botelho State Park, a reserve with over 37,000 ha of the Atlantic forest (*sensu* Morellato and Haddad 2000) located in the state of São Paulo, southeast of Brazil. The study site (24° 10' S, 47° 56' W; 350-450 m a.s.l.) is covered by high (20-30 m) old-growth lowland forest with an open understory where the palm *Euterpe edulis* (269.8 individuals.ha⁻¹; unpubl. data), species of the genera *Geonoma* and *Psychotria*, and arborescent ferns (Cyateaceae) are especially common. Myrtaceae, Lauraceae, Rubiaceae, Fabaceae and Sapotaceae are the richest plant families overall (Dias 2005). During the period of study, the mean temperature was 21.1° C (range 17.4-25.2° C), and the site received a mean of 3,384 mm of rainfall. Rains are well distributed throughout the year, but a rainiest and hottest season occurs from December to March.

Approximately 3 ha of the permanent plot are covered by *Guadua tagoara* (Nees) Kunth, a large-sized, semi-scandent woody native bamboo from the Brazilian Atlantic forest. They form patches (hereafter bamboo or B stands) interspersed with

areas without bamboos (non-bamboo or NB stands) forming a mosaic throughout the plot. As a result of the bamboo presence, B stands have a greater canopy opening and thicker ground litter than NB stands (Rother 2006).

The three plant species selected for this study (*Euterpe edulis*, *Virola bicuhyba* and *Sloanea guianensis*) are all bird-dispersed species naturally occurring in the Atlantic forest. In the study site, they occur at B and NB stands as seeds, seedlings and adults (Rother 2006).

Euterpe edulis Martius (Arecaeae) is a dominant palm found in the understory of the Atlantic forest. Given that its palm-heart has been over-harvesting, *E. edulis* populations have declined (Galetti and Fernandez 1998). Each individual produces between one and five infructescences annually, bearing on average over 3,000 fruits each (Mantovani and Morellato 2000). Fruits are globose with a single rounded seed (13.5 mm length, 14.2 mm width; Pizo et al. 2006) covered by a thin layer of black pulp when mature. Period of fruit maturation generally extends from April to September, peaking between June-July (Galetti et al. 1999, Rother 2006). *E. edulis* has their fruits eaten and seeds dispersed by many bird species (Galetti et al. 1999, Côrtes 2006, Fadini et al. 2009).

Sloanea guianensis (Aubl.) Benth. (Elaeocarpaceae) is one of the tallest arboreous species in the Atlantic rainforest (Sanchez 1994), with more than 20 m height (personal observation). Period of fruit maturation generally extends from December to March (Ziparro 2004). Its fruit is a dry capsule that dehisces upon ripening to expose a single seed (10 x 6 mm) covered by a red aril attractive to frugivorous birds (Pinheiro and Ribeiro 2001).

Virola bicuhyba (Schott) Warb. (Myristicaceae) is a dioiceous tree reaching 15-30 m height. Period of fruit maturation extends from July to October (Ziparro 2004). Fruits of *V. bicuhyba* are dehiscent capsules containing a single seed (21.4 x 15.0 mm) surrounded by a lipid-rich aril that attracts medium to large frugivorous birds like toucans and cotingas (Rodrigues 1980, Galetti et al. 2000). From now on we refer to these species only by their generic names.

Seed rain and seedling plots

Seed traps of 0.25 m² spaced by at least 20 m from each other were haphazardly set at each kind of stand. An equal number of similar-sized seedling plots were located beside each seed trap, totaling 61 seed traps and 61 seedling

plots being 30 points at Non-bamboo and 31 at Bamboo stand. Seed traps were wooden boxes lined with a fine fabric (1 mm mesh) and suspended 10 cm above the ground. Traps had the material collected monthly (from November 2007 to January 2009) and seeds counted and identified to the lowest possible taxonomic level. Seedlings were individually marked with a numbered tag and identified monthly from January 2008 to November 2008. This design was chosen to evaluate how seed rain density is correlated with the realized establishment limitation (the proportion of sites receiving seeds at which establishment does not occur) (Muller-Landau et al. 2002).

Seed addition experiments

We conducted seed addition experiments by combining two factors, seed density and seed predation, in replicated experimental plots with two levels each. For the Control level we used the naturally occurring seed density of each species, as determined by the concurrent study of seed rain. Seed addition level involved sowing an augmented density of seeds relative to the Control. For all species except *Virola* we increased by three-fold the density of seeds naturally occurring in the seed rain in order to set up the Addition treatment. Low seed availability of *Virola* allowed only a two-fold increase of the naturally occurring seed rain in the Addition treatment of this species. For *Euterpe*, four and seven seeds were used in Control and 12 and 21 seeds in Addition treatment for NB and B stands, respectively. For *Sloanea*, two and six seeds were used for Control and Addition treatments, respectively, in both B and NB stands. Finally, for *Virola*, two and four seeds were used for Control and Addition treatment at each type of stand. The influence of seed predation upon seedling establishment was tested using wire cages (1.2 cm mesh size, 25 x 25 cm) that protected the seeds from vertebrate seed predators (Excluded treatment), and contrasted with unprotected seeds (Open treatment).

Treatments were arranged in 40 100 x 100 cm experimental units or blocks, each one containing a full combination of the two treatment factors: seed density and seed predation. Twenty blocks were placed randomly at B and NB stands. Leaf litter was removed from each block area and seeds of each species were sown according to their natural seed dispersal period. Seeds of *Euterpe* were sown in July 2007, *Sloanea* in December 2008, and *Virola* in September 2008. Seed viability was prior tested to sowing by floating on water. Only potentially viable seeds (i.e., those that did not float) were used. Each seed was marked with a small stick to be relocated in

subsequent monthly census after the initial sowing. Data on seed predation, seedling emergence, herbivory and seedling survival were monthly collected for each species until seedlings had reached 15 cm high.

Data analysis

Bottlenecks in regeneration

Transition probabilities (TP) were used to quantify the survival probability at each stage involved in regeneration and the cumulative probability of a seed becoming an established seedling. Also, TP analysis gives information about the spatial distribution of recruitment considering B and NB stands (see e.g., Rey and Alcántara 2000). To estimate TP, we used data from seed traps and seedling plots to evaluate: 1) dispersed seeds; 2) total seed rain; 3) emerging seedlings; 4) established seedlings, and 5) total seedling recruitment. “Dispersed seeds” corresponded to the intact seeds without their pulp or aril collected in seed traps. “Total seed rain” was the total number of seeds collected in the whole sampled area (i.e. B and NB stands pooled). As soon as seedlings emerged, they were considered as “emerging seedlings”, while seedlings surviving until the last observation were considered as “established seedlings”. Finally, “total seedling recruitment” is the sum of all seedlings recorded at B and NB stands.

Diagrams of the recruitment dynamics were built for each plant species showing TP at each stage and cumulative recruitment probability for each stand. To construct diagrams, data from seed traps and seedling plots were used. In some cases, the number of seedlings in the plots exceeded the number of initial seeds recorded in the corresponding seed trap. In these cases, we used the estimated germination rate obtained from the seed addition experiments to retrocalculate the number of seeds expected to result in the recorded number of seedlings. Thus, we divided the recorded number of emerging seedlings by the germination rate using the mean value for the ADD and CONTROL treatments of the OPEN replicates in the seed addition experiments. We used the specific values obtained from experiments in B and NB stands to retrocalculate values for each habitat type.

Factors limiting recruitment

From seed addition experiments we estimated the number of seeds and seedlings lost due to biotic and abiotic factors for each treatment within each type of

stand. At first, we calculated the proportion of seeds or seedlings affected by a given mortality factor ($M_1, \dots, M_n$). Secondly, we obtained the probability of survival after the mortality factor action as $1 - M_n$. Then the cumulative probability was obtained as the product of the transition probabilities of the specific process involved at each stage.

The analysis included a comparison of recruitment stages in B and NB stands and the factors that could result in demographic bottlenecks. In the transition from seeds to the early seedlings stage (emerging seedlings), we considered four categories representing demographic mortality factors on the recruitment: 1) herbivory, 2) pathogens, 3) lost to drought, and 4) others. "Herbivory" refers to seed loss by herbivore damage on the endosperm and embryo tissues; "Pathogens" accounts for seed loss due to fungi activity; "Lost to drought" include seed loss due to desiccation, and for "Others" we considered seeds lost by factors involving ants and mammals (especially rodents), mammal trampling or movement of seeds by rainfall.

For the transition from emerging seedlings to established seedling stage, we considered the same four categories with some differences. "Herbivory" is the loss of a seedling due to herbivore damage on the meristem tissues; "Pathogens" is the seedling loss due to fungal activity; "Lost to drought" is the seedling loss to water deficit in the soil, and "Others" includes seedling loss by mammal trampling or seedling disappearance due to unknown causes.

To evaluate the relative importance of each mortality factor to determine the overall mortality of propagules, from dispersed seed to established seedling, we regressed the total number of seeds germinating and seedlings established recorded in the treatment on the loss attributed to each of mortality factors.

We fitted a multiple regression model with library `relaimpo` in R package v. 2.9.2 (R Development Core Team 2009). Thereby, we quantified the relative importance of each individual regressor's (mortality factor) contribution to the overall recruitment at the early stage (number of emerging seedlings) and to the total loss of propagules throughout the recruitment period (up to the final number of seedlings surviving), i.e., the "seed to early seedling" and "early seedling to established seedling" stages, and which of all regressors contributed to the full model R^2 (Grömping 2006). The technique is based on computer-intensive methods to average regressors effects over resampled orderings of the independent variables. Multiple models with multiple orderings of the regressor variables are tested and this provides a reasonable decomposition of the model variance. The analysis yields a "natural"

decomposition of the model R^2 in linear regression models and provides metrics for the relative influence of each predictor on the dependent variable, as well as bootstrap estimates for the confidence intervals of the metrics (Grömping 2006). This analysis was performed in two ways. First, mortality levels for each factor were regressed on the number of seeds germinating in each plant species at B and NB stands. Second, the mortality levels for each factor were regressed on the total loss of propagules during the recruitment of the three species in the stands.

Generalized models were used to estimate the significance of treatment effects on overall seedling emergence and seedling survival of each species. To perform this analysis, the number of emerging seedlings and alive in each plot was related to the initial number of seeds sown and grouped by stand type, seed addition treatment, and exclusion treatment. We used zero-inflated count models, a special procedure for data with an excess frequency of zeroes, like the type of data we typically get when using seed traps and seedling plots. We used a log link function and we also specified a negative binomial distribution for this type of data, as it has both a super-excess of zeroes and also some sampling points where the number of seeds or seedlings is extremely high (i.e., a 'fat-tailed' distribution of the number of seeds/trap and/or the number of seedlings/plot). Therefore, we fitted the data of number of emerging seedlings and number of seedlings surviving per replicate treatment to test differences between B and NB stands. For this analysis, the library `pscl` in R package v. 2.9.2 (R Development Core Team 2009) was used.

To test the overall significance of each model we used likelihood ratio tests for comparing the fitted models with a null model of no effects (i.e., the intercept-only model). Note that the model outputs do not indicate in any way if the zero-inflated models represent an improvement over a standard negative binomial regression. We determined this by running the corresponding standard negative binomial model (library `MASS` in R package) and then performing a Vuong test (library `pscl`; R package) of the two models. We report the results from the zero-inflated models since in all cases but one (the fit of the final number of *Sloanea* seedlings surviving) they result in better fits than the regular negative binomial model.

Results

Bottlenecks in the regeneration

Comparing the three species, *Euterpe* presented a higher seed density (18.6 ± 0.8 seeds/m²) than *Sloanea* and *Virola* (8.1 ± 1.0 and 0.79 ± 0.1 seeds/m², respectively) (Figure 1). While the seed rain of *Euterpe* is relatively thorough (21.3% of the traps had at least one seed recorded; 11.5% of the plots with at least one seedling surviving), *Sloanea* and *Virola* show more restricted seed dissemination (18.0 and 11.5% of the traps with at least one seed; 3.3% and 1.6% of the plots with at least one seedling surviving, respectively).

The three species differ when considering the dispersal and recruitment patterns at B and NB stands (Table 1). We recorded a significantly higher *Euterpe* seed density in NB stands, whereas B stands were better for the emergence and survival of seedlings (Figure 1). For *Sloanea*, seed dispersal to B stands was extremely limited. Only 0.008% of the total *Sloanea* seed rain (8.1 ± 1.0 seeds/m²) in the permanent plot was dispersed to B stands, resulting in 0.1 ± 0.03 dispersed seeds/m². Therefore, seed dispersal was a potentially critical link to *Sloanea* regeneration in B stands (Figure 1).

The total of *Virola* seed rain was very low in both kinds of stands. At B stands, however, seeds had a 75% probability to be dispersed, but this did not translate in significant differences in the seed rain. On the other hand, NB stands showed a collapse in the *Virola* regeneration cycle by a failure of seeds to be dispersed (Figure 1).

Table 1 - Differences in density of seeds and seedlings of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* in Bamboo (B) and Non-bamboo (NB) stands.

Stage	<i>Euterpe</i>	<i>Sloanea</i>	<i>Virola</i>
Seeds dispersed	B<NB *	B<NB **	B>NB ^{NS}
Seedling emergence	B>NB *	B<NB ~	B>NB ^{NS}
Seedling survival	B>NB *	B<NB ^{NS}	B>NB ^{NS}

Significances of the differences in densities between B and NB stands were tested with a generalized linear model for zero-inflated data: *, $P < 0.05$; **, $P < 0.01$; ~, $0.05 < P < 0.10$; ^{NS}, non-significant.

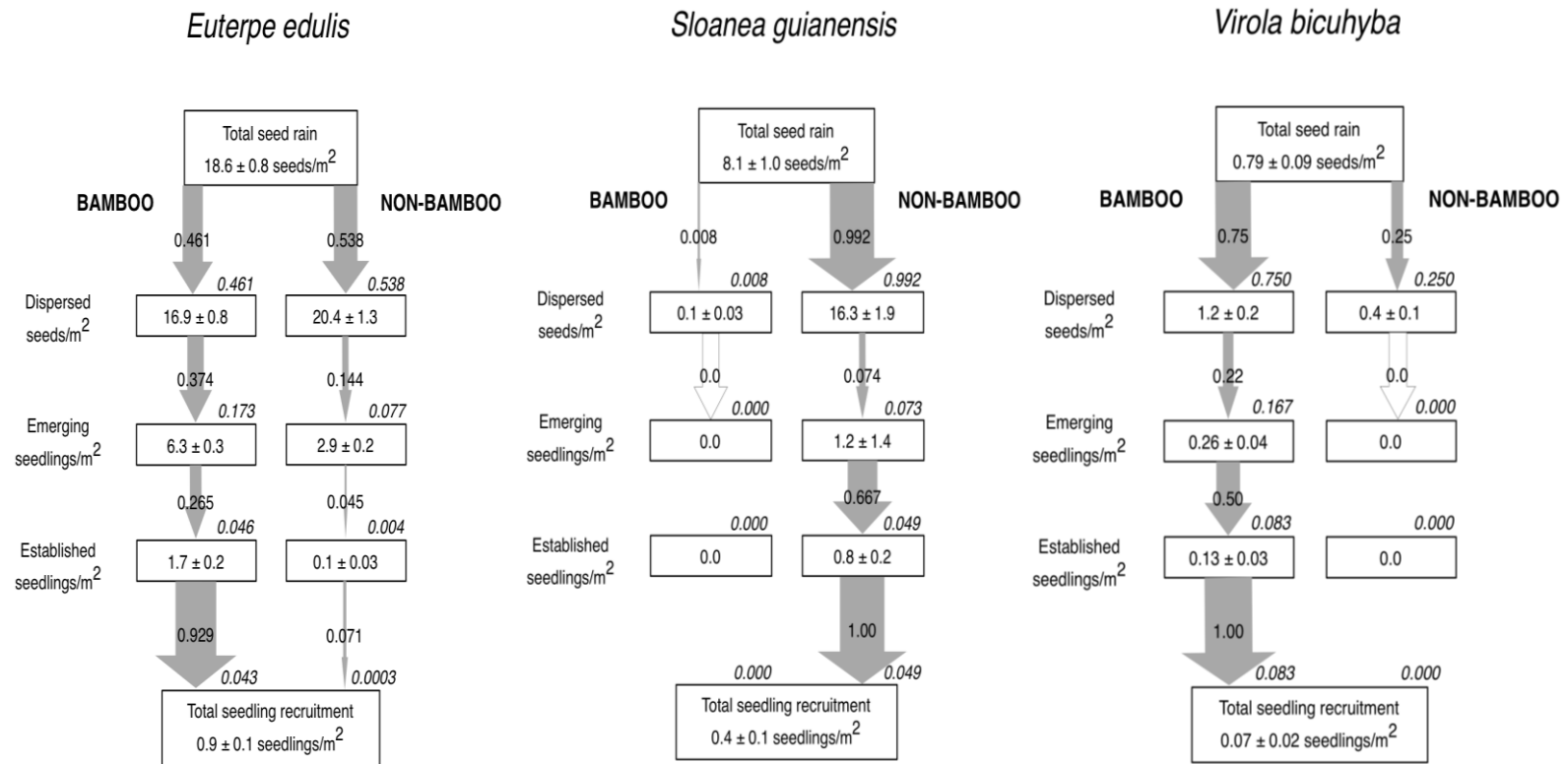


Figure 1 - Diagram of recruitment dynamics of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba*, showing the transition probabilities at each stage and the cumulative probability for each microhabitat.

Differences in the final recruitment at B and NB stands were resulted from the cumulative action of stage-specific transition probabilities that markedly differ between stands and among species (Figure 1). The cumulative probability of recruitment (Figure 2) indicates that *Euterpe*, *Sloanea* and *Virola* seeds had a low probability of reaching the seedling survival stage in both B and NB stands. Interestingly, there was a clear separation between the trends of cumulative recruitment in “Open” and “Closed” treatments, independently of the stand type. The exclusion of post-dispersal seed predators, herbivores, and mammal trampling or removal in the Closed treatments resulted in a higher probability of survival until the stage of established seedlings, which could lead to increased regeneration. The difference between Open and Excluded treatments was more marked for *Sloanea*, whose seed survival rate increased 10% in sites protected by cages (Figure 2). Therefore the action of vertebrate herbivores and seed predators makes all species susceptible to deepening demographic bottlenecks throughout the course of the regeneration cycle.

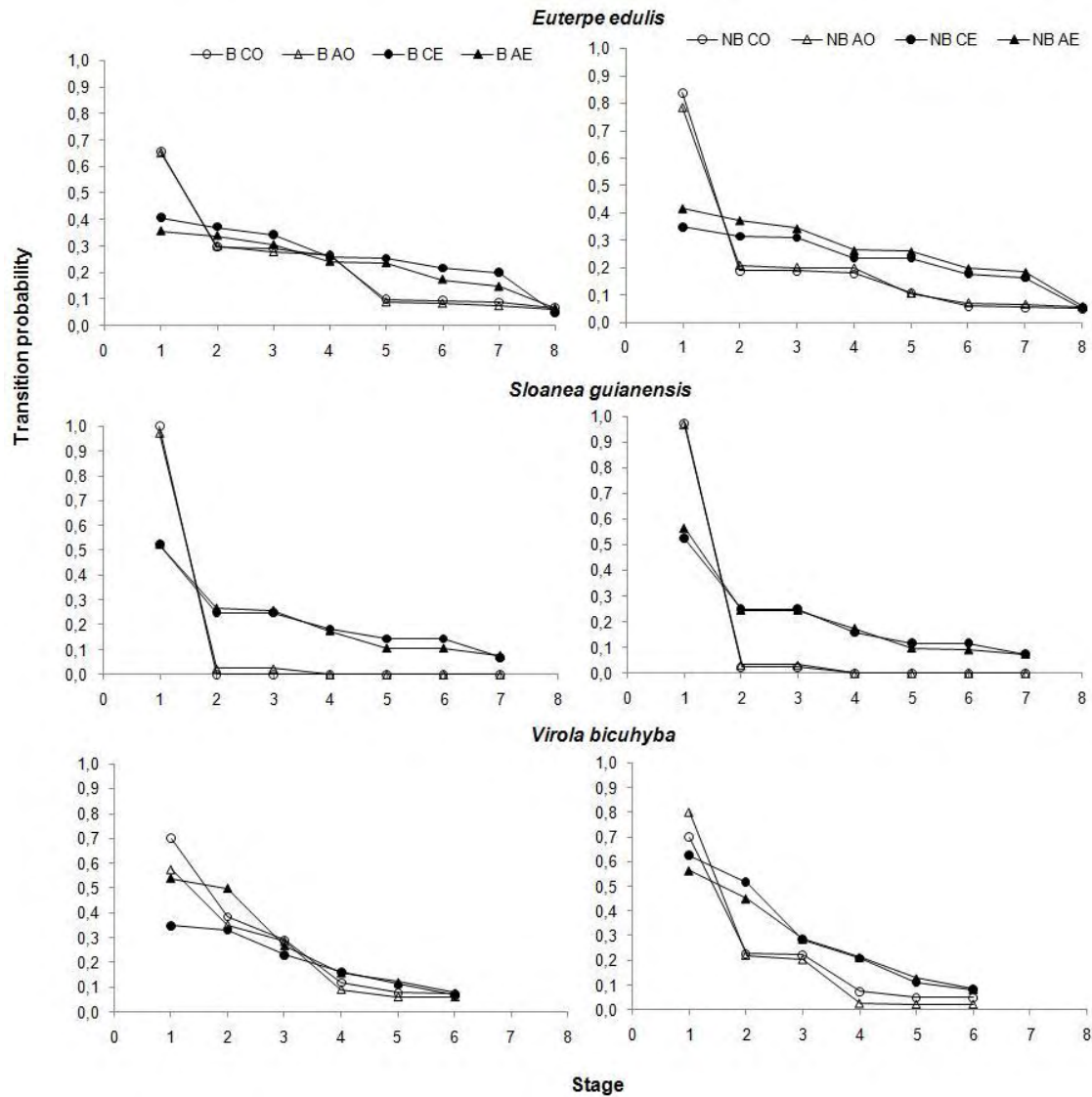


Figure 2 – Cumulative probabilities of a seed reaching the seedling survival stage under demographic bottlenecks in the regeneration cycle. Probabilities were estimated from the initial number of seeds sown in each treatment combination. Numbers in the abscissa axis represent approximately sequential stages where the action of different mortality factors on “seed to early seedling” and “early seedling to established seedling” transitions takes place. For *Euterpe edulis*, to early seedling: (1) germination, (2) others, (3) herbivory, (4) pathogens, and to survivor seedlings: (5) others, (6) herbivory, (7) pathogens, (8) final survival. For *Sloanea guianensis*, to early seedling: (1) germination, (2) others, (3) pathogens, and to survivor seedlings: (4) others, (5) herbivory, (6) lost to drought, (7) final survival. For *Virola bicuhyba*, to early seedling: (1) germination, (2) others, (3) herbivory, and to survivor seedlings: (4) others, (5) herbivory, (6) final survival. Panels on the left show the trends for Bamboo stands and those on the right, for Non-bamboo stands. Open symbols indicate Open treatments (Add or Control) and closed symbols indicate Excluded treatments (Add or Control). For Bamboo stands: (BCO) control open, (BAO) add open, (BCE) control excluded and (BAE) add excluded. For Non-bamboo stands: (NB CO) control open, (NB AO) add open, (NBCE) control excluded and (NB AE) add excluded.

Mortality factors limiting recruitment

We assessed the relative importance of each factor determining loss of propagules in two ways. First, by regressing the number of emerging seedlings after germination (early establishment) with the mortality at each stage. Second, by regressing the total mortality of propagules recorded throughout the sequential recruitment stages on the stage-specific mortality. These approaches emphasize, on one hand, how mortality factors determine early establishment and, on the other, which mortality factors largely determine the total loss of propagules during the establishment stages. The relative importance of each mortality factor to the number of seeds germinating is shown in Table 2, which summarizes the decomposition of total R^2 . The “Others” factor was the one that greatly contributed to pre-germination losses, i.e., mortality due to various factors causing loss of seeds prior to germination and/or seedling emergence (basically seed loss in the soil, not including loss to post-dispersal seed predators and pathogens). This result was consistent across all three species and for both B and NB stands. Among the species studied, however, seed germination of *Sloanea* was more strongly suppressed by “Others” factor. This could have been caused by high mammal trampling or removal or displacement of seeds by rainfall at B stands (with a relative contribution to R^2 of 0.9894). At NB stands, all mortality of *Sloanea* was attributed to the “Others” factor because seeds were completely absent in the first monitoring stage of the experiment.

Seed loss caused by herbivory damage to the endosperm and embryo tissues had a limited contribution for pre-germination losses in all three species. *Virola bicuhyba* presented high values for the “Herbivory” factor, especially at B stands (relative contribution to R^2 : 0.4300). Seed loss to fungi activity was recorded only for *E. edulis* seeds and had a low contribution to total seed mortality in both B and NB stands.

Table 2 – Relative importance of each mortality factor to the number of seeds of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* successfully germinating at Bamboo and Non-bamboo stands. Total R^2 is the total variance in number of seeds germinating accounted for by the combination of all mortality factors; figures for each factor indicate the proportional effect (contribution to total R^2) of each mortality factor.

Microhabitat	<i>Euterpe</i>	<i>Sloanea</i>	<i>Virola</i>
Bamboo			
Total R^2	61.4 %	71.9 %	65.1 %
Others	0.7326	0.9894	0.5700
Herbivory	0.1546	0.0106	0.4300
Pathogens	0.1128	-	-
Non-bamboo			
Total R^2	65.7 %	*	77.1 %
Others	0.7270	*	0.7342
Herbivory	0.1942	*	0.2658
Pathogens	0.0788	-	-

* all the mortality was attributed to the “others” factor for *Sloanea* in Non-bamboo stands

The decomposition of R^2 for the total loss of propagules during the recruitment showed that the factors varied in degree of importance for each species as well as according to stand type (Table 3). For *Euterpe* and *Virola*, “Others” was the most relevant factor that contributed to early seedling mortality and mortality of established seedlings in both B and NB stands (relative contribution to $R^2 > 0.15$ and 0.30 for these two stages of recruitment, respectively). This combination of mortality sources in fact contributed to approximately one third of the overall mortality of any species at B or NB stands, with a slight trend for a more limited effect (< 0.28) in the seed to early seedling transition (Table 3). Losses caused by herbivory were sizeable but quite variable among species, stands, and for the two transitions considered, with no clear patterns. However, the relative contribution of losses to herbivory was more limited for the small-seeded *Sloanea* (0.03), and larger for the large-seeded *Euterpe* and *Virola* (> 0.10). While in *Euterpe* most mortality was caused by losses to “Others” and “Herbivory”, in *Virola* the relative contribution of different mortality causes was more even, with most effects in any stand having ~ 0.25 - 0.35 relative contribution (Table 3).

In B stands, mortality of *Sloanea* propagules in the transition from seed to early seedling stage was largely dependent on the “Others” factor. This factor had a high relative importance by the decomposition of R^2 , what indicates that despite “Herbivory” had some influence in the total loss of propagules, loss due to mammal trampling or to

other unaccounted factors were the most important mortality cause for seeds and seedlings of *Sloanea* at B stands. From early seedling to the established seedling stage, propagule loss was largely caused by “Others” (0.2995) and “Lost to drought” (0.2719) factors. In NB stands, all mortality of *Sloanea* was attributed to “Others” factor because seeds were completely absent in the first monitoring most likely due to runoff.

Thus, the total loss of propagules during recruitment was strongly dependent on the associated action between stand type and mortality factor.

Table 3 – Relative importance of each mortality factor to the total loss of propagules during the recruitment of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* in Bamboo and Non-bamboo stands. Total R^2 is the total variance in number of seeds or seedlings lost (total mortality) caused by the combination of all mortality factors. Figures for each factor indicate the proportional effect (contribution to total R^2) of each mortality factor to overall mortality.

Stand and Stage	Factor	<i>Euterpe</i>	<i>Sloanea</i>	<i>Virola</i>
Bamboo				
Total R^2		48.4 %	70.5 %	48.4 %
Seed to early seedling	Others	0.1529	0.3994	0.3060
	Herbivory	0.0997	0.0292	0.2020
	Pathogens	0.0267	-	-
Early seedling to established seedling	Others	0.3802	0.2995	0.3485
	Herbivory	0.1900	-	0.1435
	Pathogens	0.1505	-	-
	Lost to drought	-	0.2719	-
Non-bamboo				
Total R^2		47.1 %	*	42.8 %
Seed to early seedling	Others	0.2555	*	0.2781
	Herbivory	0.2595	*	0.2650
	Pathogens	0.0349	-	-
Early seedling to established seedling	Others	0.3357	*	0.2650
	Herbivory	0.0735	-	0.1572
	Pathogens	0.0409	-	-
	Lost to drought	-	*	-

* all the mortality was attributed to the “others” factor for *Sloanea* in Non-bamboo stands

Seed addition experiments and recruitment limitation

The seed addition experiments allowed a proper test of recruitment limitation effects due to post-dispersal seed predation and herbivory, on one hand, and to seed

limitation (i.e., limited number of dispersed seeds) on the other. We used two separate models to fit the number of emerging seedlings (i.e., early establishment limitation) and the number of seedlings established (i.e., late establishment limitation) under conditions of different stand types (B and NB), seed addition treatment, and predator/herbivore exclusion (Table 4).

Table 4 - Summary of GLM model fits (with zero-inflated distributions) for the early (number of emerging seedlings) and late (number of established seedlings) recruitment success indicators of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* in Bamboo and Non-bamboo stands. Effects - M: microhabitat (stand type; Bamboo or Non-bamboo); A: seed addition; E: exclusion of post-dispersal seed predators and vertebrate herbivores. Treatment significance indicates the significant effects and one-, two-, and three-way interaction terms (indicated by dots) for each recruitment variable and species.

	<i>Euterpe</i>		<i>Sloanea</i>		<i>Virola</i>	
	χ^2 , df	Effect significance	χ^2 , df	Effect significance	χ^2 , df	Effect significance
Emerging seedlings	154.0*** 3, 7	M***; E***; A***- M•E•A*	57.3*** 3, 11	E**; A* - -	35.8*** 3, 11	- M•E~ M•E•A*
Established seedlings	114.0*** 3, 7	M*; E~; A*** M•A***; M•E* -	37.5** 3, 11	All ^{NS}	31.6** 3, 11	All ^{NS}

Significance of the likelihood-ratio tests comparing the fitted model with a null model and specific tests for each effect and interaction. Only the significant terms are shown: *, $P \leq 0.05$; **, $P < 0.001$; ***, $P < 0.0001$; ~, $0.05 < P < 0.10$; ^{NS}, non-significant.

In *Euterpe*, the regression model for the number of emerging seedlings was significant for the three main effects (stand type, exclusion, seed addition), and the three-way interaction (microhabitat x exclusion x seed addition). Hence, the number of seeds germinating depended significantly on the type of microhabitat and on both the exclusion and addition treatments, but always considering the type of stand. This result is mainly due to the higher percentage of *Euterpe* seedlings emerged in B stands (Table 5), where the exclusion treatment was highly effective in reducing mortality (Figure 3). The exclusion treatment was no longer significant for the final recruitment of established seedlings (it was in fact only marginally significant). It seems that mortality of seedlings diluted the effect of exclusion and made the final recruitment similar in open treatments and in those where seed predators were excluded.

There were still differences between microhabitats, however, B stands showed a higher number of surviving seedlings. The addition treatment was also highly significant in determining the final number of established seedlings. Both the addition and exclusion

treatments had effects dependent on microhabitat type, with more marked positive effects on final recruitment at B stands (Figure 4).

The results for *Sloanea* showed an absence of emerging seedlings in the open control treatment at B stands, and a lack of final recruitment in Open treatments (Table 5). Thus, the results showed a highly significant effect of the exclusion treatment on both early seedlings emergence and later establishment. This result demonstrates that, when protected, seeds of *Sloanea* had a much higher probability of emerging and surviving to establishment for both stand types (Figures 3, 4). The influence of seed addition in increasing seedling establishment is limited when seeds are exposed to predators and herbivores.

Similarly to *Sloanea*, we did not obtain *Virola* surviving seedlings in the open control treatment at NB stand (Table 5). Despite this, excluded seeds had higher probabilities of reaching the emerged seedling stage, especially at NB stands (Table 5, Figure 3).

Therefore, for all three species, an increase in initial seed rain density resulted in enhanced recruitment at both stands. So, the addition treatment increased the number of emerged seedlings in all species (Figure 3).

Table 5 - Percentage of seedlings (relative to the initial number of seeds sown) of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* emerging (A) and surviving (B) in Bamboo (B) and Non-bamboo (NB) stands. Treatments - C: control, A: add, O: open, and E: excluded.

Stage	Stand	Treatment	<i>Euterpe</i>	<i>Sloanea</i>	<i>Virola</i>
(A) Seedling emergence	B	CO	5.98	0.00	6.42
		AO	18.06	1.96	18.18
	NB	CO	1.62	0.65	6.42
		AO	6.48	1.31	8.56
	B	CE	10.34	12.42	13.90
		AE	33.62	37.25	19.79
	NB	CE	6.48	12.42	8.02
		AE	17.43	33.99	18.72
(B) Seedling survival	B	CO	3.09	0.00	2.50
		AO	6.44	0.00	0.00
	NB	CO	0.26	0.00	0.00
		AO	1.80	0.00	0.00
	B	CE	16.24	23.26	25.00
		AE	38.66	37.21	32.50
	NB	CE	9.02	16.28	10.00
		AE	24.48	23.26	30.00

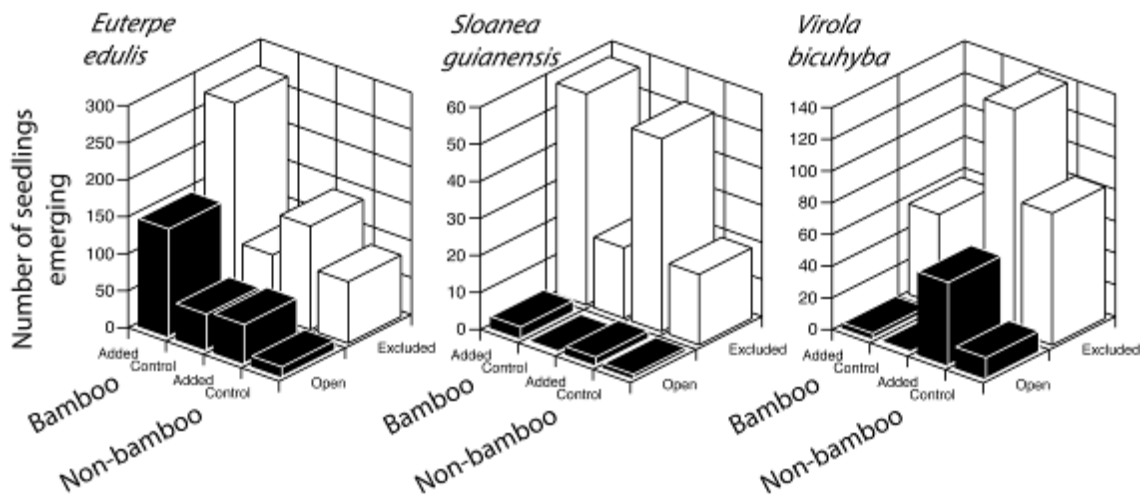


Figure 3 - Number of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* emerging seedlings in bamboo and non-bamboo stands in relation to a combination of seed addition treatment ("Added" vs. "Control") and the exclusion of post-dispersal seed predators ("Excluded" vs. "Open").

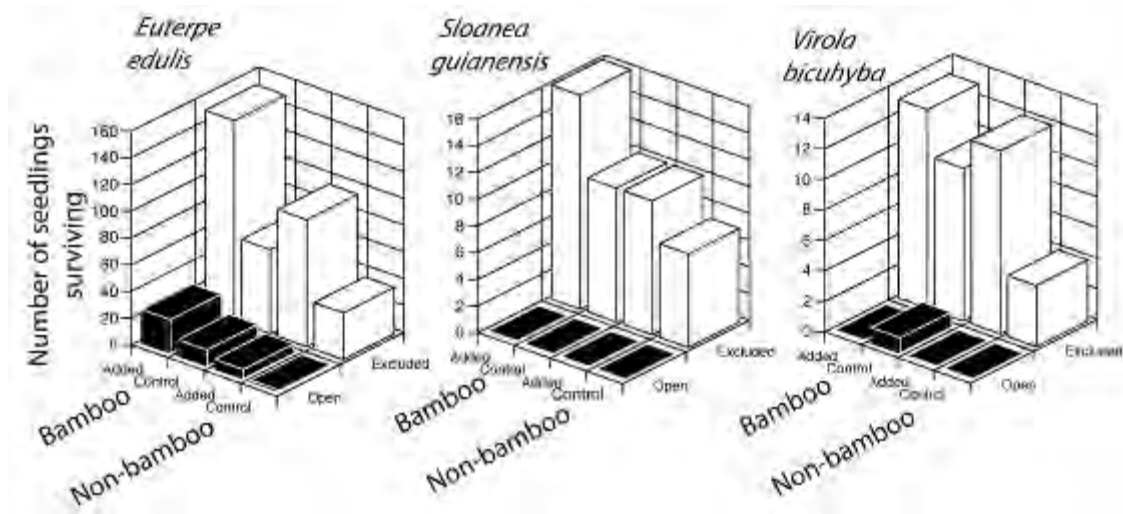


Figure 4 - Number of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba* surviving seedlings in bamboo and non-bamboo stands in relation to a combination of seed addition treatment ("Added" vs. "Control") and the exclusion of post-dispersal seed predators ("Excluded" vs. "Open").

In sum, the Addition treatment increased significantly the number of surviving seedlings for all three species. However, for *Sloanea* and *Virola* this effect strongly depended on seed exclusion, since both experience very high seed and seedling losses due to post-dispersal seed predators and herbivores. The most favorable microhabitat for seeds and seedlings of *Euterpe* and *Virola* was the least favorable for *Sloanea*.

When protected from vertebrate action, propagules of all three species had increased probability to reach subsequent stages of recruitment.

Discussion

Demographic bottlenecks and factors limiting recruitment

Our results highlight the crucial role of landscape heterogeneity in determining seed to seedling regeneration limitation in tropical woody species. Stands dominated by bamboo in the Atlantic rainforest can dramatically influence successful recruitment of woody species. Our analyses aimed at combining observational (seed trap and seedling plots monitoring) with experimental (seed addition) approaches to evaluate the relative roles of seed dispersal and recruitment limitation in successful seedling establishment, as well as to identify regeneration bottlenecks operating in this habitat mosaic. Density of propagules and recruitment stage in which propagules are more limited can vary among species and with stand type (microhabitat type). In addition, at each stage, density of propagules varies with plant species, being influenced by factors affecting the suitability of sites for establishment (Muller-Landau et al. 2002, Jordano et al. 2004). However, susceptibility to predation can be more crucial than microhabitat differences in determining survival of some species (Molofsky and Fisher 1993). While observational data from seed traps and seedling plots can effectively help in assessing recruitment limitation patterns (Muller-Landau et al. 2002), when combined with seed addition experiments under controlled conditions in distinct microhabitats they can be conclusive about key stages that limit establishment.

In the recruitment dynamics, *Euterpe* total seed rain and dispersed seed density were slightly higher at NB stands, whereas B stands presented higher densities of emerging and established seedlings. It appears that dispersal of *Euterpe* seeds is not limited by the interaction with seed dispersers in NB. However, success in the subsequent establishment stages is strongly constrained by mortality factors in this stand. Insects and rodents cause significant post-dispersal predation of *Euterpe* seeds (Pizo and Simão 2001). At NB stands, the proportion of propagule losses in the transition from seed to early seedling stage was similar between “others” and “herbivory” mortality factors, what is in accordance with von Allmen et al. (2004) that studied a

nearby site. This suggests that bamboo stands can significantly limit the seed rain of this palm, but proportionate good conditions for germination and seedling establishment (e.g., due to limited activity of post-dispersal seed predators in this stand type).

In regard to *Sloanea*, seed dispersal was extremely limited at B stands. Despite both stands showed marked propagule losses, mortality factors contributed to greater propagule losses in the initial life cycle of *Sloanea* in NB than B stands. The stage of established seedling of *Sloanea* was particularly collapsed at NB stand, where the probability of recruitment in the preceding stages was clearly high (Figure 1). It seems that plant-insect herbivores interactions are preserved in NB, and demographic bottlenecks are more intense in this environment in the transition from seed to early seedling. NB stands appear to have microhabitat differences that may favour individuals within the *Sloanea* population. Other studies have shown that seed survival might differ among distinct microhabitats if seed predators use them non-randomly (Kiltie 1981, Willson 1988, Whelan et al. 1991). In addition, a survey of results reported in the literature showed no consistent habitat or microhabitat patterns in seed survivorship (Willson 1988). In wet forests, the amount and seasonality of rainfall varies strongly. Drought periods may cause plant stress and consequently decrease seedling survival (Engelbrecht et al. 2005). However, drought was not an important mortality factor for seedlings of all studied species in both stands.

Leaf litter can influence seed and seedling performance by reducing soil temperature and water evaporation, what can result in increased local humidity or reduced water infiltration from rain to soil (Santos and Valio 2002). The influence of leaf litter varies during the first year of the life of some species, inhibiting initial emergence but, at the same time, enhancing early seedling survival (Ibáñez and Schupp 2002). Thus, leaf litter may affect seeds on the forest floor increasing their predation rate, altering germination patterns (Schupp 1988, Molofsky and Augspurger 1992, Santos and Valio 2002), and seedling development (Santos and Valio 2002).

With regard to *Sloanea* recruitment, leaf litter removal when the seed addition experiment was set may have facilitated location of seeds by predators and therefore contributed to their removal, as suggested by Zipparro et al. (2005). On the other hand, the leaf litter that naturally accumulated at both stands during the experiment was not

removed. We know that B stands accumulate more litter than NB stands (Rother 2006). Thus, we would not expect to find higher seedling density of *Sloanea* in B because small seeds are better adapted to surviving in sites with low amounts of litter (Gross 1984, Molofsky and Augspurger 1992, Kostel-Hughes et al. 2005).

For shade-tolerant species such as *Sloanea*, survival depends more on biotic than on abiotic conditions (Molofsky and Fisher 1993). In contrast, seedlings from larger seeds have a store of provisions that enhances establishment chances under adverse conditions (Leishman and Westoby 1994), as in sites with a thick litter layer (Gross 1984, Winn 1985, Leishman and Westoby 1994). Therefore, large-seeded species such as *Euterpe* and *Virola* are expected to perform better in the seed to early seedling transition and achieve higher seedling survival at B stands where leaf litter was higher than NB stands (Rother 2006).

Previous studies showed that the impact caused on seed survival of *Virola* spp. by insects was lower than vertebrates (De Steven and Putz 1984, Asquith et al. 1997, Zipparro et al. 2005). Mammals, particularly rodents, are considered the main predators of *Virola* spp. seeds in tropical forests (Zipparro et al. 2005, Forget et al. 2006, Notman and Gorchoy 2001). In the current study, *Virola* life cycle was extremely constrained by seed rain in both B and NB stands. Nevertheless, seeds in B had 75% of probability to be dispersed, suffering however considerable loss to post dispersal events that may be attributed to mammal (especially rodents) removal, mammal trampling and seed displacement by rainfall (Marthews et al. 2008). Interestingly, there was a total collapse of the *Virola* regeneration cycle in NB stand caused by propagule failure after seed dispersal. The possible reason for the propagule failure may be attributed to biotic factors, mainly insect predation and terrestrial mammal removal or predation. In a nearby site, Zipparro et al. (2005) found intense predation on *Virola* seeds by a Nitidulidae beetle, but noted that predation by vertebrates was the main cause of seed death.

Previous studies have shown that predation of unprotected seeds reduced seedling abundance and consequently recruitment in tropical forests (De Steven and Putz 1984, Sork 1987, Schupp 1990, Asquith et al. 1997, Notman and Gorchoy 2001, Zipparro et al. 2005). Our results indicated that seeds disappeared before germinating.

Ant and mammal (especially rodents) removal, mammal trampling or seed displacement by rainfall were more important mortality agents than seed predation by pathogens, being the main causes of seed and seedling reduction in all species at both stands. This assertion is evidenced by the fact that cage-protected seeds survived better and produced more seedlings than unprotected. Biotic factors, therefore, limited the early recruitment of *Euterpe*, *Sloanea* and *Virola* at the study site irrespective of stand type.

For the studied species, an increase in initial seed rain density resulted in higher recruitment at both stands, unequivocally identifying a significant dispersal limitation. Moreover, the addition treatment increased the number of emerged seedlings and improved seedling survival for all three species. This shows that seedling establishment is a more limited stage than seed availability or survival which contrasts with Clark et al. (2007). These authors found that establishment limitation is stronger than seed limitation because most added seeds fail to recruit to seedling stage.

At both stands there was no spatial concordance in different phases of the life cycle (Traveset et al. 2003). Nevertheless seeds of the three studied plant species had a low probability of reaching established seedling stage except under protected conditions. Plants experience strong pressure from the feeding and trampling activities of herbivores, what often result in a marked limitation of regeneration (Plumptre 1993). Although unprotected sites were susceptible to deepening demographic bottlenecks throughout the course of the regeneration cycle, the highest probability of seed and seedling survival in the addition treatment resulted in low limitation in both stands for the three species. This identifies the central role of dispersal limitation that is resultant by a failure of enough seeds to reach specific sites and have profound effects in the final stages of establishment.

Success in regeneration can indicate to what extent a specific microhabitat represents a suitable site and how this varies according to species. The potential regeneration patches in different microhabitats can be envisioned as a gradient of variable recruitment probabilities between the “unsafe” and “safe” extremes. The most favorable stands for seeds and seedlings of *Euterpe* and *Virola* were bamboo-dominated patches, which represented the least favorable for *Sloanea* individuals. Therefore, absence of bamboos favors *Sloanea* recruitment. The positive effects for

Euterpe and *Virola* might be associated to bamboo patch size and/or border effects, for instance if the edge of bamboo stands is favored by frugivores after feeding on nearby fruiting individuals. The data on seed rain support this for *Virola* but not for *Euterpe*. However, for both species, bamboo stands facilitated germination success and seedling emergence.

Bamboo effects on the early recruitment therefore are species-specific. Nevertheless, negative effects appear to be more prominent at larger sized classes and later stages of plant recruitment, mainly due to physical damage caused by litter and culms that fall on saplings and cause their mortality (Griscom and Ashton 2003). Bamboo growth dynamics proportionate an environment where saplings and young trees within bamboo stand have a high probability of being physically damaged (Griscom and Ashton 2003). Therefore, an early facilitation of the germination and seedling emergence (e.g., due to edge effects caused by bamboo stand) can switch to negative influences at later stages when bamboo patch expands and the recruits get trapped in a large bamboo-covered area. Experimental research is necessary to evaluate plant survival in the subsequent stages (e.g., older saplings) in order to test the physical effects of bamboo on the final recruitment.

Our results indicate that the early recruitment of these relevant trees and palm species in the Atlantic rainforest can be extremely patchy, with a far-reaching influence of the heterogeneity created by successional bamboo patches. While the seed trap data suggested pervasive seed limitation for all the three species studied, the experimental analysis and monitoring of subsequent stages indicated a very heterogeneous outcome in terms of recruitment prospects depending on tree species and stand type. The combination of observational monitoring of the seed rain and the experimental analysis of post-dispersal seed predation and seedling establishment proved to be essential for understanding the delayed consequences of dispersal limitation processes in this forest.

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CONCLUSÃO GERAL

No capítulo 1 verificamos que nos ambientes com bambu foi registrado, surpreendentemente, maior número de espécies de aves do que em ambientes sem bambu. A maioria das aves registradas em censos nos dois ambientes foi insetívora, seguida por espécies frugívoras. Concluimos que um número considerável de espécies de aves frugívoras pode favorecer bordas de manchas de bambu e seu interior e que estes ambientes constituem elementos importantes da vegetação por funcionarem como áreas de abrigo e alimentação para muitas espécies de aves, especialmente para as espécies insetívoras (Olmos 1996, Kratter 1997, Reid et al. 2004, Vasconcelos et al. 2005).

A guilda de aves que consomem frutos de *Euterpe* foi composta por 21 espécies, enquanto 23 espécies foram registradas para *Sloanea* e 14 para *Virola*. Entretanto, somente um subconjunto reduzido de espécies dessas assembléias pode ser considerado como reais dispersores em termos de visitaç o e comportamento de manipula o dos frutos.

Dentre as espécies de aves registradas, uma conclus o importante deste estudo   que a efetividade da dispers o de *Euterpe*, *Sloanea* e *Virola*, est  restrita a um pequeno grupo de dispersores efetivos. Na escala da paisagem, perdas de aves destes grupos de dispersores poderiam resultar em mudan as substanciais na composi o e diversidade da floresta (Wright et al. 2007, Terborgh et al. 2008, Holbrook e Loiselle 2009) e altera es da din mica sucessional, especialmente nos ambientes com bambu.

A abund ncia local de aves frug voras tem recebido importante aten o por ser considerada o principal fator que afeta a composi o e os padr es de visita o  s plantas (Schupp 1993, Jordano e Schupp 2000). Desta forma, a manuten o das popula es de aves deve ser considerada como um aspecto chave para a conserva o das popula es de plantas que dependem destas aves para sua dispers o e sucesso na regenera o natural. Isso se faz importante tamb m para ambientes com bambu, pois como vimos anteriormente, os bambus abrigam grande n mero de esp cies de aves.

Em *Euterpe* e *Virola*, a taxa de visitação foi a variável que contribuiu mais fortemente para a efetividade de dispersão das sementes, enquanto o número de frutos manipulados por visita teve maior contribuição na dispersão das sementes de *Sloanea*. Interessantemente, as aves que mais contribuíram para a dispersão de *Virola* ocorreram mais freqüentemente nos ambientes com bambus. Este padrão foi similar para *Sloanea*, enquanto *Euterpe* apresentou um padrão misto, com algumas espécies de aves contribuindo para a dispersão no bambu e outras espécies contribuindo para maior dispersão nas áreas sem bambu.

Este estudo revelou que a efetividade da dispersão pode variar de acordo com o tipo de ambiente, com os principais dispersores da floresta primária não sendo, necessariamente, os principais dispersores das bordas da vegetação com bambus.

No capítulo 2 verificamos que o estabelecimento na parcela permanente se apresentou como um processo restrito espacialmente. O padrão espacial da chuva de sementes foi discordante com o padrão das plântulas estabelecidas nos ambientes com e sem bambus e nos períodos estudados. Esse fato resulta na limitação do estabelecimento e tem profundas conseqüências para os estágios subseqüentes do ciclo de regeneração das plantas. Independente do número de sementes que chegaram aos ambientes com e sem bambus, fatores como a predação pós-dispersão (para mais detalhes ver capítulo 3) limitaram o estabelecimento de novos indivíduos. Os ambientes onde as sementes chegaram foram inadequados para as plântulas se estabelecerem (conflito semente-plântula).

Apesar da inconsistência temporal na chegada de sementes e estabelecimento das plântulas, o tipo de ambiente foi fator importante na riqueza de espécies de sementes em ambos os períodos. Em nosso estudo, as plântulas da comunidade encontraram melhores condições para o sucesso de estabelecimento em ambientes com bambu no período 2004-2005, apesar da abundância de sementes ter sido predominante em ambientes sem bambus. No período subseqüente, no entanto, o estabelecimento foi semelhante nos dois ambientes. Considerando que os dois ambientes mostraram inconsistência no estabelecimento (não apresentaram elevado estabelecimento nos dois períodos) nossos resultados indicam que tanto ambientes

com bambus como ambientes sem bambus não representam *hotspots* para o recrutamento. O sucesso no recrutamento foi altamente dependente das condições locais.

Os padrões de dependência espacial encontrados em nosso estudo para a dispersão a curta distância e o estabelecimento de plântulas são comuns aos sistemas de dispersão das plantas (García 2006). Observamos que na área de estudo estes padrões são resultantes da combinação de alguns fatores: estrutura heterogênea da paisagem onde ambientes estruturalmente diferentes se dispõem em mosaicos, fatores de mortalidade que limitam o crescimento populacional das plantas nos diferentes tipos de ambientes e, ainda pouco estudada na parcela permanente, a atividade dos dispersores movendo sementes.

Nossos resultados indicam que os bambus influenciam o padrão da chuva de sementes no complexo mosaico florestal no que diz respeito ao número de recrutas e riqueza de espécies de sementes. Além disso, os *hotspots* de recrutamento nessa floresta aparecem como extremamente dinâmicos e relacionados à expansão e declínio das manchas de *G. tigoara*. É importante salientar que os bambus promovem a heterogeneidade da floresta, mas as características de rápida colonização de *G. tigoara* e seu comportamento invasivo podem ser mais um fator de limitação do crescimento das comunidades vegetais sendo importante seu manejo, neste caso.

Neste contexto, ressaltamos a importância de se estudar a série de estágios interdependentes do recrutamento das plantas (Jordano e Herrera 1995) a partir dos padrões espaciais da chuva de sementes e das plântulas associados às características ambientais. Essas se constituem como importantes ferramentas para se compreender detalhadamente a dispersão e suas consequências.

Em relação ao capítulo 3, nossos resultados mostraram que no tratamento de adição o número de plântulas sobreviventes aumentou significativamente para as três espécies. No entanto, em *Sloanea* e *Virola* este efeito foi fortemente dependente da proteção das sementes com gaiolas de exclusão de predadores. Essas duas espécies sofreram perdas muito elevadas de sementes e plântulas devido aos predadores de sementes pós-dispersão e aos herbívoros.

Os ambientes mais favoráveis para as sementes e plântulas de *Euterpe* e *Virola* foram os menos favoráveis para *Sloanea*. Propágulos das três espécies, quando protegidos da atividade de vertebrados, apresentaram maior probabilidade de chegar às fases posteriores do recrutamento. A partir desses resultados concluímos que a susceptibilidade à predação se constitui como o principal gargalo demográfico durante as fases iniciais do estabelecimento. Além disso, esta susceptibilidade à predação pode ser mais importante do que as diferenças entre ambientes como determinantes do sucesso da regeneração.

Os dados da chuva de sementes combinados com os dados experimentais de adição de sementes revelaram que diferenças entre as espécies estudadas em relação à importância relativa da dispersão vs. limitação de estabelecimento são mediadas por suas respostas que variam segundo a heterogeneidade ambiental criada pelas manchas de bambu.

Os efeitos da presença do bambu no estabelecimento inicial são espécie-específica. No entanto, efeitos negativos parecem ser mais proeminentes em classes de tamanho maiores e as fases posteriores do recrutamento de plantas, principalmente devido a danos físicos causados pelas folhas e radículas que caem sobre as plântulas e causam sua mortalidade (Griscom e Ashton 2003). Estudos experimentais se fazem necessários para avaliar a sobrevivência das plantas nas fases subseqüentes (por exemplo, juvenis) para testar os efeitos físicos do bambu no recrutamento final.

Nossos resultados indicam que o estabelecimento inicial de *Euterpe*, *Sloanea* e *Virola* na floresta Atlântica pode ser extremamente desigual, com uma profunda influência da heterogeneidade criada pelas manchas de bambu e que a combinação dos métodos observacional e experimental foi essencial para compreendermos as conseqüências da limitação da dispersão nesta floresta.

A variedade de técnicas experimentais e de análises disponíveis atualmente nos oferecem a oportunidade de estudar a dispersão em toda a gama de processos no qual está envolvida a fim de explicar como uma população se regenera, como se forma e como a diversidade biológica se estrutura nos diferentes tipos de ambientes.

O conhecimento gerado neste estudo relativo à demografia das espécies vegetais de floresta Atlântica e especialmente aos fatores que limitam seu crescimento populacional nos diferentes tipos de ambientes, é, portanto, ponto chave para o desenvolvimento de planos de conservação e restauração de populações.

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