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PADRÕES REPRODUTIVOS EM MYRTACEAE:
UMA ABORDAGEM ECOLÓGICA E FILOGENÉTICA

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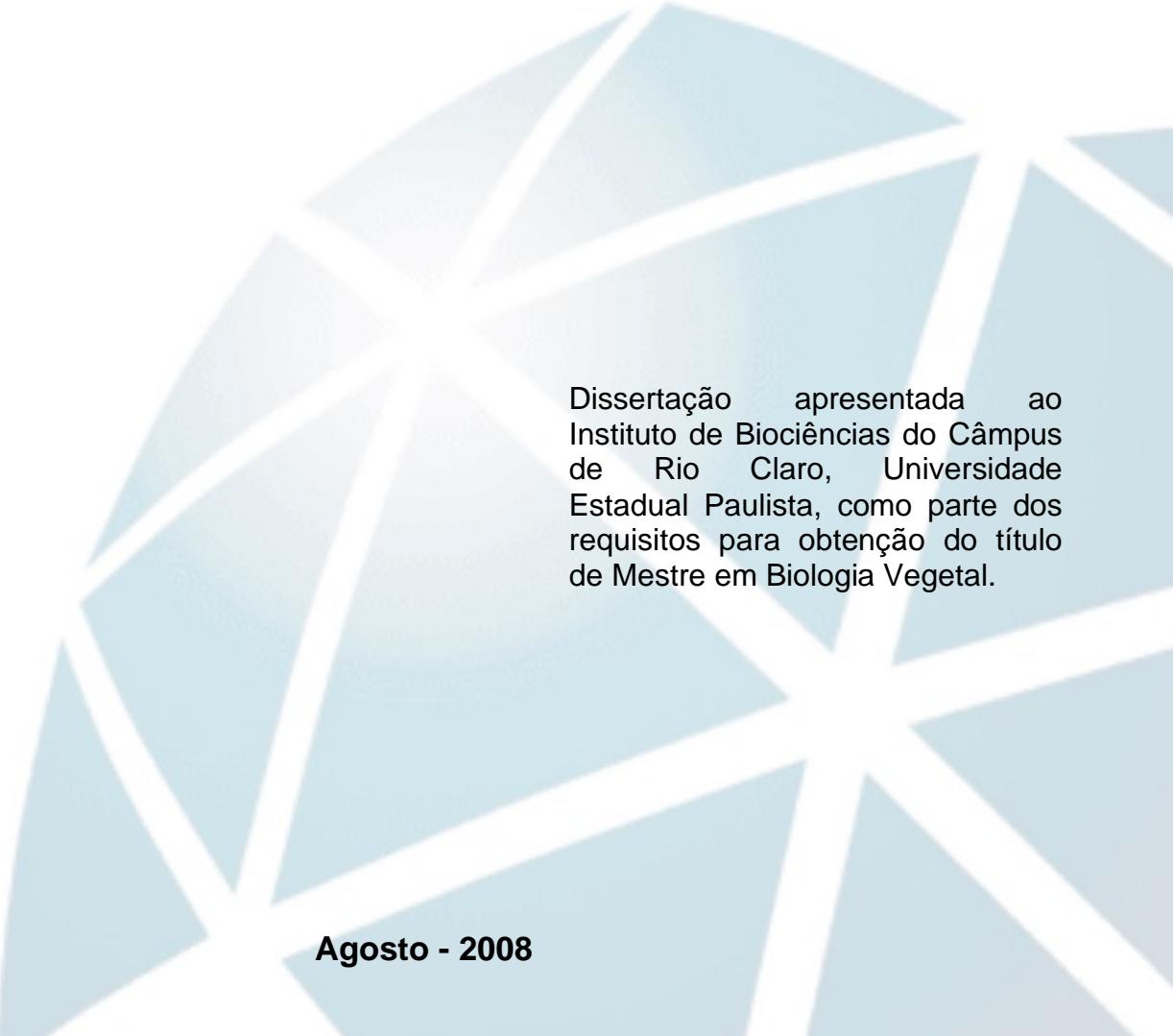
Dissertação apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Mestre em Biologia Vegetal.

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Rio Claro, 01 de agosto de 2008

"The obsession is a great substitute for talent"

(Steven Martin *apud* Nicholas Gotelli)

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eu estou com vocês eu sou apenas a menininha da casa. Valeu por todos os ensinamentos e principalmente por compreenderem a minha ausência em tantos e mais tantos momentos. Agradeço a outra metade da minha família (meus sogros Tânia Mara e Olavo, meu cunhado Thiago e minha vovó Myrthes) por além de me apoiarem e também compreender a minha ausência, agradeço por me aceitarem com muito carinho nessa família.

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SUMÁRIO

Resumo:

    O centro de origem e diversificação da tribo Myrteae (Myrtaceae) é a América do Sul. Esse grupo de plantas tem suprema importância na estrutura do ecossistema de Floresta Atlântica, apresentando uma ampla variação nos padrões fenológicos expressa em um grande número de espécies. Estas características permitem utilizar este grupo como modelo para avaliar a importância dos fatores filogenéticos e ecológicos atuando na reprodução das plantas. Os padrões reprodutivos de 34 espécies (550 indivíduos) de Myrteae foram investigados por 30 meses, em intervalos mensais, no sudeste do Brasil. Neste ambiente sem sazonalidade climática, o aumento no comprimento do dia foi o principal fator relacionado ao início da reprodução dessas plantas. Comparando o padrão fenológico observado contra os modelos nulos nós encontramos que a floração foi significantemente agrupada com um maior número de espécies apresentando botões florais e flores entre dezembro e janeiro. O padrão de frutificação foi ao acaso e não houve evidência de que os fatores climáticos limitassem a maturação dos frutos. Nós avaliamos também a inércia filogenética em algumas características reprodutivas morfológicas e fenológicas, através dos métodos de PVR (phylogenetic eigenvectors regression), e encontramos que as características morfológicas têm maior inércia filogenética do que as características fenológicas. Este resultado sugere que as características de história de vida das plantas são evolutivamente mais flexíveis do que as características morfológicas. Nós encontramos que o nicho reprodutivo das espécies (representado pelas condições climáticas ocorrentes no momento da reprodução) explica parte da variação nos padrões fenológicos de Myrtaceae, e a variação restante é explicada pela associação deste nicho com a filogenia não sendo possível separar a contribuição de cada um; essa variação compartilhada aponta a existência de um nicho reprodutivo filogeneticamente estruturado, que ocorre provavelmente em conseqüência da origem comum e diversificação das espécies de Myrteae na Floresta Atlântica. Nós investigamos a composição das espécies de aves e a estrutura das interações da rede de dispersão de sementes em Myrteae e registramos um total de 11 espécies de plantas e 42 espécies de frugívoros realizando 97 interações. A rede apresentou uma estrutura significativamente aninhada, com fracas interações e baixa assimetria. O fator que mais contribuiu para a quantitativa efetividade de dispersão de

sementes foi a freqüência de visitas. A probabilidade de dispersão de sementes foi intimamente associada com a morfologia da ave e da semente. As mais importantes espécies de aves que dispersam frutos de Myrtaceae são as espécies da família Turdidae. Do ponto de vista da conservação dos ecossistemas tropicais, em especial da Floresta Atlântica, este estudo evidencia a importância das aves de pequeno porte para a manutenção do processo de dispersão de sementes em ecossistemas ameaçados.

Abstract:

The centre of origin and diversification of Myrteae tribe (Myrtaceae) is in the South America. This group has supreme importance in flora and structure of threatened ecosystem of Atlantic Rain Forest, presenting a wide variation of phenological patterns express in a large species number. These characteristics allow utilizing this group as model for assess the importance of phylogenetic and ecological factors acting in the plants reproduction. Reproductive patterns in 34 Myrtaceae species (550 individuals) were investigated for 30-months at monthly intervals, in southeastern of Brazil. In this ambient without climatic seasonality, the increase in the day-length was the major abiotic factor related on start of reproduction. Comparing the phenology observed against null models we found that the flowering was significantly clumped, with a greater number of species showing flower buds and flowers between December and January. The fruiting pattern was random; there was no evidence of climatic factors limiting the maturation of fruits. We evaluated the phylogenetic inertia in some morphological and phenological traits, through PVR methods (phylogenetic eigenvectors regression), and found that morphological traits have more phylogenetic inertia than phenological ones. This result suggests that life history traits are evolutionarily more flexible than morphological traits. We found that the environment explained part of phenological patterns variation of these species, and remaining variation is accounted by environment and phylogeny association; this shared variation can be denominated reproductive niche structured phylogenetically, and it is probably consequence of their species origin and diversification in the Atlantic rain forest. We investigated birds species composition and interactions structure of Myrteae seed dispersal network. We registered a total of 11 plant species and 42 frugivore species carried out 97 interactions. The network revealed a significantly nested structure, weak interactions and low asymmetry. The factor that more contributed for the quantitative effectiveness of seed dispersal was the frequency of visits. The seed dispersal probability was closely associated with the morphology of birds and seeds. The most important seed dispersers of Myrtaceae were the Turdidae species. Of the standpoint of conservation of tropical ecosystems, in special of Atlantic rain forest, this study highlights the importance of small size birds for the maintenance of the dispersal process in threatened ecosystems.

INTRODUÇÃO GERAL

Uma das áreas da ecologia de plantas que mais tem recebido a atenção dos pesquisadores nos últimos anos é a fenologia, que investiga a periodicidade ou época de ocorrência de eventos biológicos repetitivos e sua relação com o clima e fatores bióticos (Lieth 1974). O estudo da fenologia das plantas envolve a observação, registro e interpretação da ocorrência dos eventos da sua história de vida, tais como: a expansão de botões florais e folhas, a abscisão das folhas, a floração, a frutificação, a dispersão de sementes e germinação (Fenner 1998).

A fenologia reprodutiva das plantas determina a futura sustentabilidade das espécies animais e vegetais (Boulter *et al.* 2006) porque, por exemplo, qualquer variação na data de floração pode influenciar os sucessos da polinização e consequentemente da dispersão de sementes, germinação e estabelecimento das plantas. Portanto, a época de ocorrência da reprodução afeta não somente as plantas mas também os animais que dependem dos seus recursos tais como flores e frutos (Newstron e Frankie 1994).

Tempo, duração e freqüência reprodutiva são parâmetros fenológicos que variam muito entre as espécies nas florestas tropicais (Bawa *et al.* 2003). A grande variedade de padrões de brotamento, floração e frutificação nessas florestas pode ser reflexo da diversidade de pressões seletivas bióticas e abióticas operando na comunidade (Fenner 1998). Decifrar as causas próximas e últimas da variação fenológica tem guiado, por um lado, a expectativa de que os padrões fenológicos são adaptativos, guiando a sincronização da atividade reprodutiva com a disponibilidade de fontes bióticas (polinizadores) e com o pico da disponibilidade de fontes abióticas (luz e água). Teorias alternativas são baseadas na evidência de que os padrões fenológicos não são adaptativos e são conservados entre taxa intimamente relacionados (Kochmer e Handel 1986).

Cada fenômeno fenológico pode ser estudado em diferentes níveis de organização. Por exemplo, pode-se estudar a fenologia de floração (ou frutificação) em uma comunidade inteira, ou em uma guilda de plantas que compartilham o mesmo polinizador (ou dispersor de sementes), ou em uma população de espécies particular, ou ainda, em maiores detalhes as flores ou frutos de uma única espécie; para cada nível de análise diferentes fatores e

forças seletivas influenciarão a ocorrência dos eventos (Fenner 1998, para maiores detalhes ver Primack 1985).

Numerosas hipóteses tem sido formuladas para considerar a influência de vários fatores na fenologia reprodutiva (ver revisão em: Wright e Van Schaick 1994, Fenner 1998, Bawa *et al.* 2003, Bolmgren *et al.* 2003) e caem dentro de quatro categorias: hipóteses climáticas, bióticas, filogenéticas e morfológicas. Cabe ressaltar que essas proposições não são excludentes, e podem ser complementares no entendimento dos padrões reprodutivos das espécies vegetais.

No grupo das hipóteses climáticas encontramos que a produção de flores pode coincidir com os dias mais longos em florestas úmidas tropicais (Wright e Van Schaick 1994, Morellato *et al.* 2000). Borchert *et al.* (2005) demonstraram que até mesmo pequenas mudanças no comprimento do dia podem estar relacionadas à floração em baixas latitudes. Stiles (1977) sugeriu que em florestas úmidas não sazonais, o relaxamento dos limites físicos na fenologia das plantas permite que as interações planta-polinizador e/ou planta-dispersor desempenhem um importante papel na evolução da época de ocorrência dos eventos reprodutivos nas plantas.

Dentre as hipóteses bióticas, as quais tem sido bastante estudadas desde o final da década de 70 (Stiles 1977, Waser 1979, Schemske 1981, Wheelwright 1985, Poulin 1999, Aizen e Vázquez 2006), destacam-se as hipóteses de competição e facilitação. Robertson (1895) foi um dos primeiros autores a sugerir que o tempo de floração seria modificado pela seleção natural para evitar a competição por polinizadores. A hipótese da competição assume que os vetores bióticos são fontes limitantes e que os eventos reprodutivos (de floração e frutificação) deveriam ser distribuídos ao longo do tempo ('staggered phenological'; Pleasants 1980) de modo a minimizar a competição entre as espécies permitindo sua coexistência; caso contrário poderia acarretar na exclusão competitiva de espécies concorrentes (Levin e Anderson 1970). A principal hipótese alternativa a esta é a da ação em massa ('mass action') a qual sugere que a facilitação seria mais importante que a competição. O agrupamento temporal dos períodos reprodutivos aumentaria o sucesso da polinização e dispersão de sementes e diminuiria o risco de predação difundindo esse risco através de um maior número de indivíduos (Rathcke 1983, Sakai 2002). Esta hipótese

assume que o risco de receber pólen de outras espécies é menor que o benefício alcançado pelo aumento da visitação por polinizadores (Boulter *et al.* 2006).

A categoria mais recente de hipóteses que têm sido proposta como limitante do padrão fenológico das plantas é a filogenética (Kochmer e Handel 1986; Johnson 1992; Ollerton e Lack 1992; Wright e Calderón 1995). Kochmer e Handel (1986) foram os primeiros autores a destacarem a importância do parentesco entre as espécies na expressão de seus padrões reprodutivos. Estes autores encontraram que certas famílias de angiospermas florescem na mesma época do ano em diferentes continentes (América do Norte e Ásia), demonstrando que a fenologia de floração é um caráter altamente conservado dentro de linhagens evolutivas.

Em 1987, Primack propôs um conjunto de hipóteses morfológicas para explicar as variações na reprodução das espécies, dentre todas as outras categorias mencionadas acima esse conjunto foi o menos testado e necessita de maior avaliação. Esse autor apontou que há uma íntima relação entre flores, frutos e sementes e que está relação tem implicações na fenologia e ecologia das plantas. A relação entre flores e frutos proposta por Primack (1987) prediz que espécies com grandes flores produzirão grandes frutos, pois grandes flores tem grandes ovários e as fontes contidas dentro dos ovários são incorporadas durante o desenvolvimento dos frutos após a fertilização; consequentemente espécies com grandes frutos terão grandes sementes ou um grande número de pequenas sementes por fruto. O tamanho do fruto e da semente terão implicações diretas na fenologia das plantas pois grandes frutos, os quais necessitam de um período maior para completar o seu desenvolvimento, irão florescer no início da estação apropriada para a floração (Primack 1987). Este autor formulou estas hipóteses para áreas temperadas, onde ocorre uma fria estação a qual limita o desenvolvimento dos frutos, estas hipóteses ainda necessitam ser testadas em ambientes tropicais.

Portanto, nas florestas tropicais não somente condições ambientais, como o comprimento do dia, mas também fatores bióticos que incluem interações com outros organismos como polinizadores e dispersores de sementes, podem ser agentes seletivos da fenologia das plantas (Rathcke e Lacey 1985, Sakai 2001). A intensidade e a forma como essas hipóteses afetam a fenologia das plantas seria melhor visualizada se demonstrada em

guildas de plantas relacionadas e em ambientes não sazonais (Stiles 1977, Fenner 1998), onde as limitações climáticas são mínimas e os padrões reprodutivos das plantas são provavelmente mais limitados por interações bióticas e filogenéticas.

A tribo Myrteae (*sensu* Wilson *et al.* 2005, Myrtaceae) representa um interessante sistema para avaliar estas hipóteses. A América do Sul é o principal centro de origem e diversificação das espécies de Myrteae (Lucas *et al.* 2007); essas espécies são dominantes na flora e estrutura dos principais ecossistemas da região Neotropical, há uma ampla variação nos padrões fenológicos expressa em um grande número de espécies, e ainda uma recente árvore filogenética ao nível de espécies foi proposta para a tribo (Lucas *et al.* 2007), a união desses fatores torna Myrteae um bom modelo para avaliarmos as tendências gerais e padrões evolutivos na fenologia das plantas (ao nível de espécies) e seu papel na estrutura dos ecossistemas.

Adicionalmente, dada a escassez de estudos em biologia reprodutiva desta importante família (Gressler *et al.* 2006), conhecer os dispersores de sementes e seu papel no ciclo de reprodução dessas espécies é também de extrema importância. A influência da fenologia nas interações entre plantas e dispersores de sementes é um dos parâmetros mais importantes na avaliação da integridade das interações bióticas, especialmente em sistemas ameaçados, e está entre as pesquisas prioritárias para a conservação de sistemas naturais (Bawa 1995).

Os animais dispersores, agindo como vetores que disseminam as sementes, podem desempenhar um importante papel na manutenção das populações de plantas (Harper 1977, Wang e Smith 2002). Neste contexto, a contribuição do dispersor ao sucesso da planta depende quantitativamente da frequência de visitas, da taxa de remoção de frutos e da probabilidade de manipular um fruto com sucesso (Schupp 1993, Godínez-Alvarez e Jordano 2007). Esses fatores foram avaliados para as interações entre aves e Myrtaceae com o objetivo de esclarecer quais espécies contribuem em maior intensidade para a manutenção dessas plantas na Floresta Atlântica.

A abordagem de redes complexas, a qual tem sido utilizada no estudo e interpretação de sistemas mutualísticos (planta-polinizador: Dupont *et al.* 2003; peixes-anêmonas marinhas: Ollerton *et al.* 2007; formiga-planta: Guimarães *et al.* 2006) foi

empregada aqui no contexto de efetividade de dispersão de sementes. Essa abordagem permite mais do que entender a relação entre cada par de espécies, visualizar o contexto global da força de interações existentes entre um grupo de espécies (Rico-Gray 2006). Essa perspectiva adicionalmente permite contextualizar quais características das aves e das plantas são responsáveis pela atual estrutura da rede de dispersão de sementes em Myrtaceae.

A tribo Myrteae (*sensu* Wilson *et al.* 2005, Myrtaceae)

A família Myrtaceae abrange mais de 130 gêneros e entre 3800 a 5800 espécies (Wilson *et al.* 2001) e é encontrada em todo o mundo, principalmente na América do Sul, África e Austrália (Govaerts 2008). A definição dos limites genéricos da família não era muito clara até 5 anos atrás, mas recentes trabalhos em filogenia molecular avançaram bastante na definição destes limites (Wilson *et al.* 2005, Lucas *et al.* 2005, Lucas *et al.* 2007).

As Myrtaceae nativas do território brasileiro pertencem à tribo Myrteae, cujas características são (Landrum e Kawasaki 1997): árvores ou arbustos; folhas com estípulas, opostas, simples, com pontos translúcidos, nervura mediana geralmente proeminente, nervuras laterais geralmente facilmente visíveis, frequentemente proeminentes, poucas ou numerosas, retas ou curvas próximas à margem em direção ao ápice, frequentemente unidas com a nervura marginal; flores brancas (raramente rosas, vermelhas ou violetas); pétalas livres, 4-5 (raramente ausentes); muitos estames (raramente poucos); ovário ínfero; fruto carnoso, 1-a muitas sementes. Suas flores são polinizadas principalmente por abelhas e besouros (Lughadha e Proença 1996; Gressler *et al.* 2006) e seus frutos carnosos são procurados por diversas espécies de frugívoros (Pizo 2002; Gressler *et al.* 2006), sendo um importante recurso para a manutenção dos animais na Floresta Atlântica. Apesar da importância dessa família na estrutura desse bioma, há poucos estudos sobre a biologia reprodutiva de suas espécies. A maioria das informações sobre floração provém, predominantemente, de estudos em nível de comunidade que incluem apenas algumas espécies (Morellato *et al.* 1989; Gressler *et al.* 2006).

Objetivo Geral

O principal objetivo deste trabalho foi estudar a fenologia de algumas espécies da família Myrtaceae ao longo de um gradiente vegetacional de Floresta Atlântica. E entender como está estruturada a rede de interações entre espécies de Myrtaceae e as aves que utilizam seus frutos como alimentos.

Objetivos específicos:

CAPÍTULO 1 - entender a importância dos fatores bióticos, morfológicos e filogenéticos em adição aos fatores abióticos que atuam nos padrões fenológicos reprodutivos de Myrtaceae.

CAPÍTULO 2 - descrever as conseqüências imediatas da atividade das aves frugívoras e entender seu papel na efetiva dispersão de sementes de Myrtaceae.

Material e Métodos

Área de Estudo

Este estudo foi desenvolvido na Ilha do Cardoso (Parque Estadual da Ilha do Cardoso - PEIC; figura 1), situado no extremo sul do estado de São Paulo, no município de Cananéia (47°54'75''W, 25°03'88''S). Faz parte do complexo estuarino lagunar de Iguape-Cananéia-Paranaguá, considerado o terceiro do mundo em termos de produtividade pela União Internacional de Conservação da Natureza (IUCN).
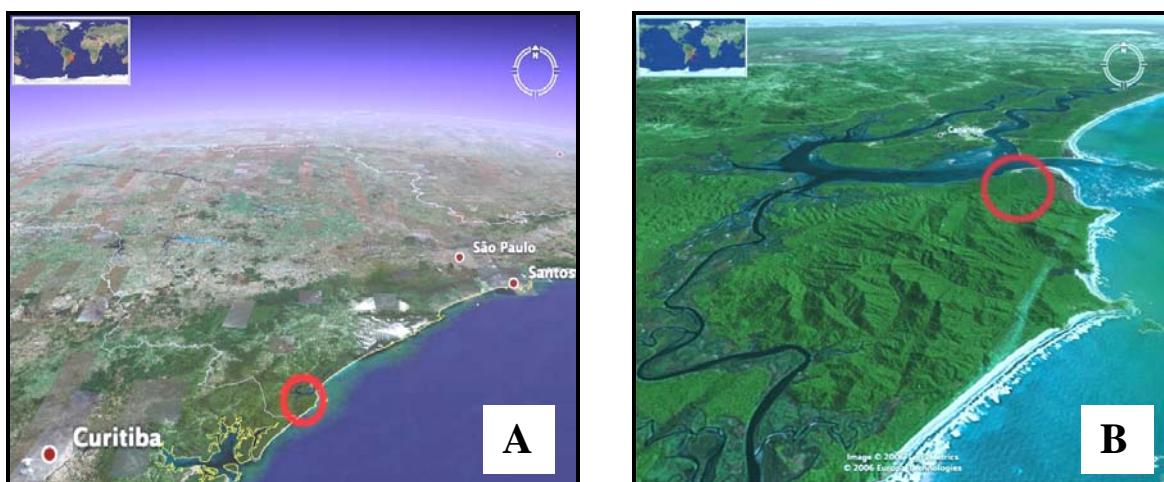
Figura 1. Localização do Parque Estadual da Ilha do Cardoso (PEIC), município de Cananéia, São Paulo, Brasil. **(A)** Visão geral da região sul de São Paulo, o círculo vermelho indica a localização do PEIC. **(B)** Visão detalhada do PEIC, o círculo vermelho indica a localização do Núcleo Perequê, na restinga do Pereirinha, local onde a pesquisa foi desenvolvida. Fonte: Google Earth.

O PEIC é uma ilha continental de 15.100 ha, a qual é exclusivamente composta de vegetação de Floresta Atlântica (Bernardi *et al.* 2005). A topografia da ilha do Cardoso é predominantemente montanhosa na sua porção central, com elevações acima de 800 metros. A sua vegetação foi estudada em projetos enfocando a restinga (de Grande e Lopes 1981) e a produção de uma flora geral (Barros *et al.* 1991). A fauna da ilha apresenta diversas espécies de aves e mamíferos frugívoros, incluindo aves ameaçadas de extinção como a jacutinga (Galetti *et al.* 1996).

O presente estudo foi desenvolvido ao longo da vegetação de restinga do Parque Estadual da Ilha do Cardoso (figura 2). Essa formação é constituída por um mosaico vegetacional contínuo abrangendo as seguintes fisionomias (seguindo Couto e Cordeiro 2005): vegetação sobre cordões arenosos (Fig. 2A e 2B) e floresta de transição restinga-encosta (Fig. 2C). Apesar de existirem diferenças florísticas e micro-climáticas peculiares a cada fisionomia estudada, em conceito amplo elas compõem uma única formação. O objetivo deste estudo está ligado à descrição fenológica e das interações animal-planta ao longo da vegetação de restinga, portanto, caracterizar as diferenças pertinentes a cada mosaico não foi o alvo deste estudo.

Figura 2. Três fisionomias constituintes da vegetação de restinga do Parque Estadual da Ilha do Cardoso (Cananéia/SP) nas quais foram estudadas as espécies de Myrtaceae do presente trabalho. **(A)** Vegetação de escrube em estágio avançado de regeneração; **(B)** Florestas baixa e alta de restinga e **(C)** Floresta de transição restinga-encosta.

Características gerais da vegetação estudada, seguindo Couto e Cordeiro (2005):

1. Vegetação sobre cordões arenosos:

1.1. Escrube em estágio avançado de regeneração (Fig. 2A): possui estratos predominantes herbáceos e arbustivos abertos podendo formar moitas intercaladas com espaços desnudos ou aglomerados contínuos que dificultam a passagem. A altura das plantas pode chegar a 3 metros e diâmetro caulinar a cerca de 3 centímetros. Há predominância de trepadeiras de algumas espécies

como *Davilla rugosa* e *Smilax* spp. Sub-bosque ausente e pouca serrapilheira, ou ausente. O substrato é arenoso seco e de origem marinha. As espécies indicadoras são: *Dalbergia ecastaphylla*, *Dodonea viscosa*, aroeirinha (*Schinus terenbinthifolius*); araçá-de-praia (*Psidium cattleianum*), *Gaylussacia brasiliensis*; mojoleiro (*Abarema* sp); maria-mole (*Guapira opposita*) e *Erythroxyllum* sp.

1.2. Floresta baixa de restinga: fisionomia arbórea com dossel aberto, estrato inferior aberto e árvores emergentes. Apresenta estratos predominantes arbustivo e arbóreo. As árvores em geral possuem de 3 a 10 metros de altura, sendo que as emergentes chegam a 15 metros, com grande número de plantas com caules ramificados desde a base. É grande a quantidade e diversidade de epífitas, com destaque para as bromeliáceas, orquidáceas, aráceas, pteridófitas, briófitas e liquens. Há uma camada fina de serapilheira (entre 4 e 5 cm), com grande quantidade de folhas não decompostas. Grande diversidade de espécies vegetais, podendo haver predominância de mirtáceas: guamirim (*Myrcia* spp), araçá-de-praia (*Psidium cattleianum*), murta (*Blepharocalyx* sp), guamirim (*Gomidesia* spp), pitanga (*Eugenia* spp). Presença de palmáceas: guaricangas (*Geonoma* spp), tucum (*Bactris setosa*), brejaúva (*Astrocaryum aculeatissimum*). As espécies indicadoras são as mirtáceas e além delas *Geonoma schottiana*, *Clusia criuva* e pinta-noiva (*Ternstroemia brasiliensis*). O substrato arenoso é de origem predominantemente marinha, seco e com raízes formando trama superficial.

1.3. Floresta alta de restinga: fisionomia arbórea com dossel fechado e estrato predominante arbóreo, variando entre 10 e 15 metros, as emergentes podem atingir 20 metros. Diâmetro caulinar variando de 12 a 25 cm, com algumas plantas ultrapassando 40 centímetros. Apresenta alta diversidade e quantidade de epífitas; espessa camada de húmus e serapilheira. No sub-bosque: plantas jovens do estrato arbóreo, arbustos como: *Weinmannia paulliniifolia*, pinta noiva (*Ternstroemia brasiliensis*), *Erythroxylum* sp, *Amaioua intermedia*, guaricangas e tucum. Poucas plantas no estrato herbáceo. As espécies

indicadoras são: *Clusia criuva*, canelinha-do-brejo (*Ocotea pulchella*), guanandi (*Callophyllum brasiliensis*), *Psidium cattleianum*, guaricanga (*Geonoma schottiana*), palmito-juçara (*Euterpe edulis*). A família de plantas arbóreas que apresenta maior número de espécies é Myrtaceae com 18 espécies (Sugyama 1998). O substrato arenoso é de origem predominantemente marinha, podendo haver deposição de areia e argila de origem continental, ocorrendo inundações ocasionais em determinadas áreas.

2. Floresta de transição restinga-encosta: Essa formação ocorre ainda na planície, em íntimo contato com as formações acima descritas, desenvolvendo-se sobre substratos mais secos e de origem continental, podendo estar em contato e apresentar grande similaridade com a floresta ombrófila densa de encosta, porém pertencente ao complexo de vegetação de restinga. Possui fisionomia arbórea com dossel fechado e estrato predominante arbóreo com altura variando entre 12 e 18 metros, com as emergentes podendo ultrapassar 25 metros. Grande amplitude diamétrica com diâmetros variando de 15 a 30 centímetros, alguns podendo ultrapassar 40 centímetros. A diversidade e quantidade de epífitas é elevada. A camada de húmus e serapilheira é espessa. No sub-bosque são encontradas plantas jovens do estrato arbóreo e arbustos como: *Psychotria nuda*, *Amaioua intermedia*. É grande a diversidade de espécies no estrato arbóreo, dominância de: mirtáceas, lauráceas (*Ocotea* spp e *Nectandra* spp), *Didymopanax* sp, *Pera glabrata*, *Euterpe edulis*, *Pouteria*, *Machaerium* spp. Na comunidade arbórea a família que apresenta maior número de espécies é Myrtaceae com 16 espécies (Pinto 1998). O substrato é arenoso, com deposição variável de areia e argila de origem continental.

Clima:

O clima da Ilha do Cardoso é subtropical úmido (C*fa*) sob a classificação climática do sistema de Köppen (Köppen 1923); sempre úmido, sem estação seca e com temperatura média superior a 20°C. Dados meteorológicos para o período de 30 anos (1956-1985) foram coletados da estação de Cananéia (5 km distante do local de estudo) e foram obtidos com o Instituto Oceanográfico da Universidade de São Paulo (USP). A precipitação média anual para o clima normal é de 2248 mm (Fig. 3), com uma estação super-úmida ocorrendo nos meses de setembro a maio quando a precipitação mensal está acima de 100 mm, e uma estação úmida ocorre de junho a agosto quando a precipitação é menos freqüente e pode chover abaixo de 100 mm/mês. A temperatura média anual é de 21.3 °C (Fig. 3). Dados meteorológicos para o período de estudo (do ano de 2005 a 2007) foram obtidos da estação meteorológica localizada no local do estudo, a qual pertence à Escola Superior de Agricultura "Luiz de Queiroz" da Universidade de São Paulo (ESALQ - USP). Durante o período de estudo as temperaturas foram muito estáveis em todos os anos (média de 21.9°C) e a precipitação em 2007 (1702 mm) foi abaixo da média de 30 anos (Fig. 4B). Os dados de comprimento do dia são para a latitude de 25°C e seguem Pereira *et al.* (2001), o maior comprimento do dia ocorre em dezembro (13.47 h) e o mais curto em junho   (10.55 h) (Fig. 4A).
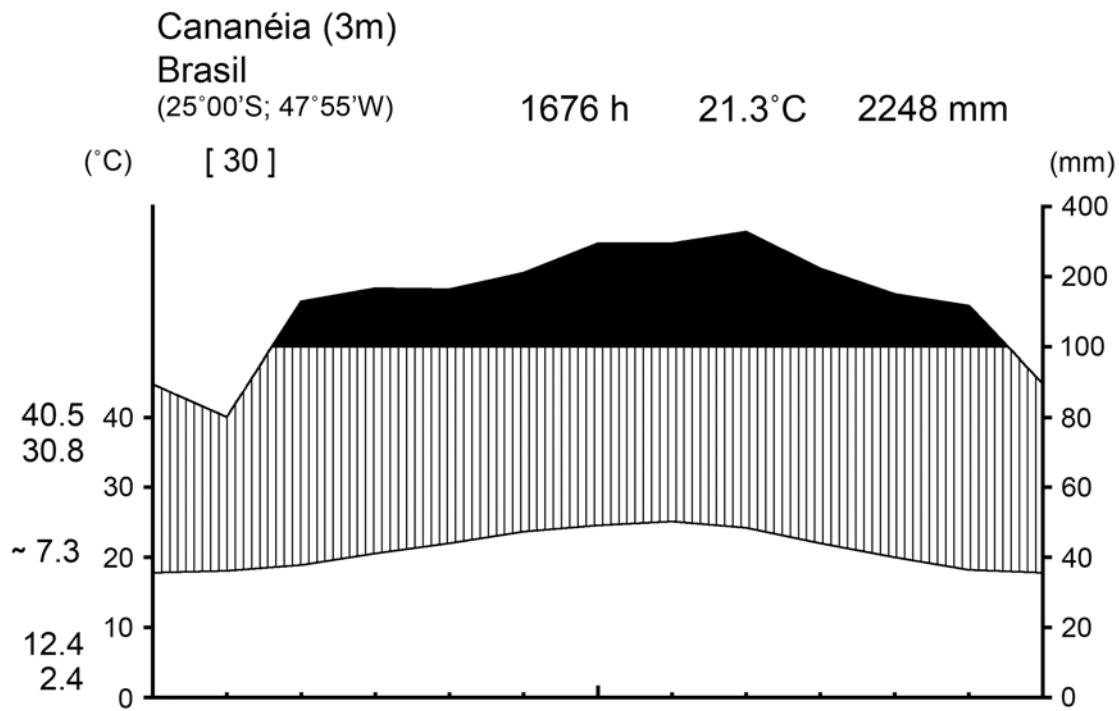
Figura 3. Diagrama ecológico do clima elaborado de acordo com Walter (1973). Os meses do ano estão representados no eixo horizontal de julho a junho. Eixo vertical da esquerda representa a temperatura (˚C) e o eixo da direita representa a precipitação (mm). Este diagrama cobre o período de 1956 a 1985 para a cidade de Cananéia, estado de São Paulo, Brasil. A área preta representa o período super-úmido e a área rachurada o período úmido. Fonte dos dados: Instituto Oceanográfico da USP.
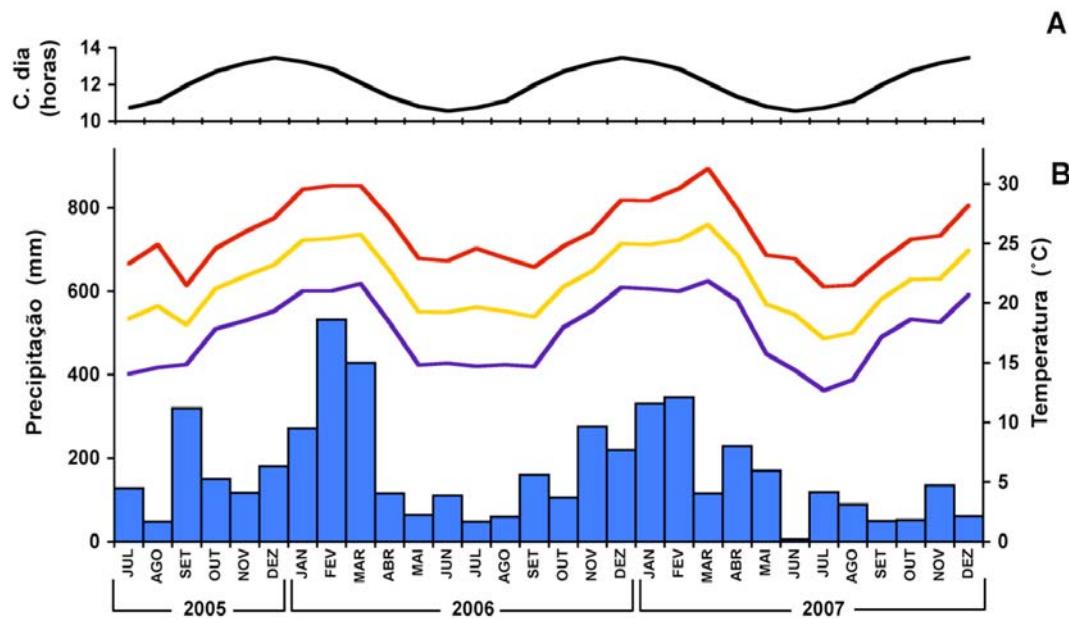
Figura 4. Dados climatológicos do PEIC, Cananéia/SP, para o período de julho de 2005 até dezembro de 2007. **(A)** Comprimento do dia em horas. **(B)** Distribuição da precipitação total mensal (barras) e das temperaturas média mensais (linha amarela), média das máximas (linha vermelha) e média das mínimas (linha roxa). Fonte: Projeto Parcelas Permanentes (Biota Fapesp) Esalq/USP Piracicaba.

Métodos

    Seleção das espécies amostradas – Dois métodos de amostragem foram empregados: transecções e trilhas. Em cada ambiente foram demarcadas 10 transecções de 25 metros de comprimento e 4 metros de largura. Esses transectos estavam distanciados 10 metros da trilha de pesquisa (pré-existente) e seguiam em direção ao interior da mata (perpendicularmente à trilha). O critério de inclusão das plantas variou entre os ambientes devido às características vegetacionais de cada lugar:

    1) Escrube em estágio avançado de regeneração: foram marcadas com placas de alumínio seguindo a ordem de aparecimento todas as mirtáceas independente do tamanho. Esse critério foi adotado para poder definir a partir de que altura cada espécie de mirtácea seria considerada reprodutiva.

    2) Florestas alta e baixa de restinga e Floresta de transição restinga-encosta: todas as mirtáceas que possuíam altura equivalente ou superior a 50 cm de altura do chão foram marcadas com placas de alumínio seguindo a ordem de aparecimento. Esse critério foi adotado para poder definir a partir de que altura cada espécie de mirtácea seria considerada reprodutiva.

    Aliado ao método de transecções foram observadas também as árvores nas trilhas de pesquisa pré-existentes destes 3 ambientes. A utilização desses dois métodos permitiu que um número maior de indivíduos por espécie fosse amostrado, tornando a análise final dos dados fenológicos mais robusta e precisa.

    Observações fenológicas - Mensalmente os transectos foram percorridos e as espécies de Myrtaceae observadas com auxílio de binóculos. Durante as observações de cada indivíduo foram registradas as seguintes fenofases: botão floral, flor aberta (antese), fruto verde e fruto maduro (Galetti *et al.* 2004), as quais foram registradas e quantificadas pelo método de Fournier (1974), onde a partir dos valores obtidos em campo através de uma escala intervalar semi-quantitativa de cinco categorias (0 a 4) foi calculada a

porcentagem de intensidade de cada fenofase. Através da porcentagem de Fournier os picos fenológicos podem ser evidenciados com maior precisão e refinamento representando melhor o comportamento fenológico das espécies (Bencke e Morellato 2002; San Martin-Gajardo e Morellato 2003). A identificação das espécies amostradas foi realizada com base em exsicatas confeccionadas a partir da coleta de ramos das plantas. A identificação das espécies de Myrtaceae foi feita por especialistas (ver agradecimentos) e 'vouchers' das espécimes foram depositados no Herbarium Rio Clarense (HBRC), da UNESP – Universidade Estadual Paulista: (HBRC48585 a HBRC48590 e HBRC48685 a HBRC48765).

Morfometria de flores e frutos - para essas análises foram coletados aproximadamente 20 frutos e 20 flores de cada espécie, de pelo menos 3 indivíduos adultos. Foi registrado, para cada fruto (Fig. 5): 1. comprimento e diâmetro do diásporo (mm); 2. peso fresco (g); 3. peso da semente (g); 4. peso da polpa (g); 5. número de sementes por diásporo. E para cada flor: 1. altura do gineceu (mm); 2. altura dos estames (mm); 3. diâmetro da corola (mm); 4. distância entre extremidades opostas dos estames (mm); 5. comprimento do pedicelo (mm).
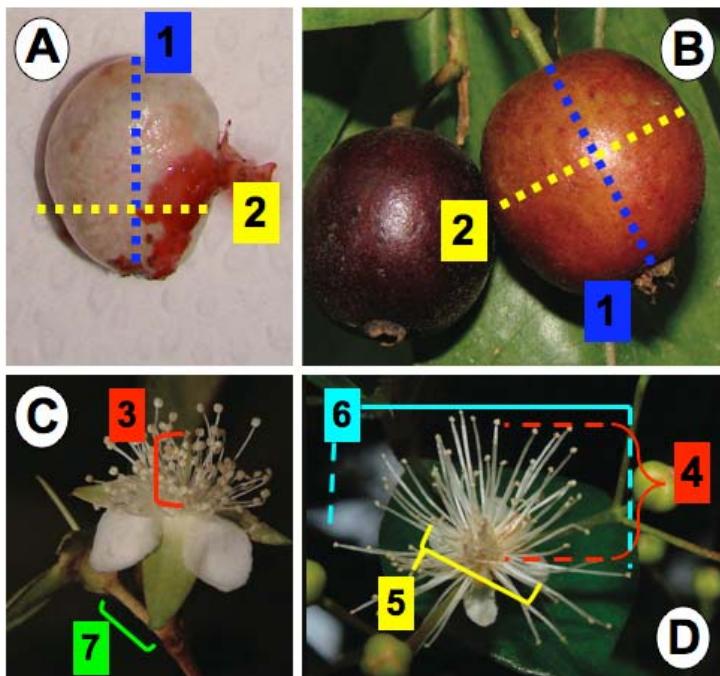
Figura 5. Medidas morfológicas coletadas de semente (**A**), fruto (**B**) e flor (**C** e **D**) das espécies de Myrtaceae, no PEIC, Cananéia/SP.

Legenda:

Fruto e semente:
  (1) Comprimento;
  (2) Diâmetro;

Flor:
  (3) Altura do gineceu;
  (4) Altura dos estames;
  (5) Diâmetro da corola;
  (6) Distância entre extremidades opostas dos estames;
  (7) Comprimento do pedicelo.

Interação com os frugívoros - Foram realizadas observações focais em alguns indivíduos em frutificação a fim de identificar as aves frugívoras que interagiram com as mirtáceas. Durante as observações, com auxílio de binóculos (8x40), foi registrada a espécie da ave visitante e seu comportamento alimentar. Foi respeitada uma distância mínima do observador até a planta para evitar qualquer influência nas interações planta-animal, mas sem prejudicar a visibilidade e a identificação das espécies consumidoras. As espécies de plantas estudadas são dispersas principalmente por aves, portanto as observações se restringiram aos horários de atividades desses animais: do amanhecer até às 12 horas e a partir das 13 horas até o entardecer.

Os dados mensurados durante as observações foram: o horário da visita, a espécie visitante, o número de indivíduos, o tempo de permanência na árvore, o número de frutos consumidos e detalhes do comportamento (por exemplo: modo de apanhar e manipular os frutos) (Galetti *et al*. 2004).

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CAPÍTULO 1

REPRODUCTIVE PATTERNS IN MYRTACEAE:

AN ECOLOGICAL AND PHYLOGENETIC PERSPECTIVE

Reproductive patterns in Myrtaceae:

an ecological and phylogenetic perspective

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Abstract:

The reproductive patterns in Myrtaceae, a major plant family of the Atlantic rain forest, were investigated from an ecological and phylogenetic perspective. During 30-months 34 Myrtaceae species (550 individuals) were observed monthly for changes on flowering and fruiting, in the Atlantic rain forest southeastern of Brazil. Under low seasonal climate, the increase in the day-length was the major abiotic factor related to the onset of reproduction in Myrtaceae. By comparison of the phenological structure observed against null models we found that the flowering was significantly clumped, with a greater number of species showing flower buds and flowers between December and January. The fruiting pattern was random; there was no evidence of climatic factors limiting fruit maturation. We evaluated the phylogenetic inertia in some reproductive parameters, through PVR (phylogenetic eigenvectors regression) methods, and found that reproductive morphological characteristics have more phylogenetic inertia than phenological ones; suggesting that life history traits are evolutionarily more flexible than morphological traits. Fruit and flower size did not affect the species sequence of flowering or fruiting, but fruits that require more time for its maturation flowered at the end of appropriate season. We demonstrate that the shared influence of the phylogenetic and environmental factors acting about the phenology is high, pointing the existence of a reproductive niche phylogenetically structured in Myrtaceae. This pattern can be consequence of rapid evolutionary rate together with a long permanence of the flora in wet and warm conditions, which may have obscure previously existing phylogenetic. We demonstrated the importance of considering this partition among phylogeny and environmental factors in phenological studies, since leave it aside biologically may lead to equivocated conclusions. The conclusions we have draw open new avenues to further studies, addressing the importance of each factor in the determination of species' phenological responses. The methods analyses applied allow a better understanding the patterns of

evolution and general trends in the reproductive phenology of Myrtaceae, and can be employed to study dominant families in other high diversity forest, contributing to the knowledge of the evolution and functioning of these complex ecosystems.

Key-words: phenological patterns, Myrtaceae, mutualism, facilitation, competition, phylogenetic, morphological characters, fruit, flower, resource availability, niche conservatism, evolution.

Introduction

Production of flowers and fruits by plants sustains a large assembly of animals, such as pollinators, seeds dispersers and predators, herbivores and pathogens (van Schaik et al. 1993). These plant-animal interactions, especially when involving mutualistic partners, have been paramount in the generation of Earth's biodiversity (Ehrlich and Raven 1964, Bascompte and Jordano 2007), and are responsible for much of the angiosperm diversification (Grant 1949, Stebbins 1981, Eriksson and Bremer 1992, Ricklefs and Renner 1994, Dodd et al. 1999, Verdu 2002).

Many factors influence the availability of flowers, fruits and leaves in the community, shaping the reproductive and leafing patterns, such as: climate (Opler et al. 1976; Wright and van Schaick 1994, Johnson 1993), herbivory (Aide 1988, Brody 1997), competition or attraction for pollinators (Waser 1979, Schemske 1981, Aizen 2006) or dispersers (Stiles 1977, Wheelwright 1985, Poulin 1999), fruit-size (Primack 1987), seed mass (Mazer 1989) and phylogeny (Kochmer and Handel 1986, Wright and Calderón 1995, Smith-Ramírez 1998, Marco and Páez 2002, Debussche et al. 2004).

The relative importance of each one of these factors can vary according to the studied ecosystem. For instance, proximate factors are more relevant in areas such as tropical deciduous forest, where the annual rainfall is very seasonal and plant phenology is driven by water availability (Bullock 1990). Other aspects may be more important in habitats with no water stress such as day-length in tropical aseasonal forest (Wright and van Schaick 1994, Morellato et al. 2000). Stiles (1977) suggested that in aseasonal tropical rain forests, the relaxation of physical limits on reproductive time of species allow plant-pollinator and/or disperser interactions to play a major evolutionary role in timing plant phenology.

Unlike the abiotic factors, which have been well studied and largely accepted as limiting the reproduction of plants in some ecosystems, hypotheses related to the biotic

vectors, such as facilitation and competition, still generate controversy. In accordance with competition hypotheses species sharing pollinators or seed dispersers should undertake a phenological displacement to minimize overlap, reduce competition, and consequently have more effective pollination and seed dispersal (Pleasants 1980). A staggered phenological structure allows the coexistence of species; otherwise this could lead to competitive exclusion (Levin and Anderson 1970). Other authors suggested that a high temporal overlap in the production of flowers and fruits in species that share similar flower or diaspore morphologies, could attract a larger number of pollinators and seed dispersers (the facilitation hypothesis), thereby increasing fruit set and seed dispersal (Moeller 2004, Thies and Kalko 2004). An aggregated phenological structure could lead the coexistence of species by increasing the likelihood of successful pollination and seed dispersal, decreasing the risk of predation upon each flower by spreading the risk across more individuals (Rathcke 1983, Sakai 2002).

Initially there was not an appropriated statistical treatment to test these biotic hypotheses. Patterns of flowering and fruiting were identified only qualitatively, based on graphic analyses of distribution of flowers and fruits along time (e.g. Snow 1965, Heithaus et al. 1975, Stiles 1977). Lack of total overlap between neighbor species in time constituted sufficient evidence for the segregation of reproductive times induced by competition (Fleming and Partridge 1984). From the decades of 80 and 90, null models have been applied to test these hypotheses (Armbruster 1986, Gotelli and Graves 1996, Gotelli 2001). These models enable compare data of flowering or fruiting obtained in the field with reproductive sequences generated at random. This technique allows determining if observed phenological overlap is less than (or greater than) that expected by chance, testing the hypotheses of competitive displacement (or facilitation through mass action).

Besides climate and biotic vectors, the reproductive morphological traits may also affect the time of flower and fruits in plant community. Primack (1987) hypothesize that there is a

close relationship among flowers, fruits and seeds, with implications to the phenology and ecology of plants. The relation between flowers and fruits proposed by Primack (1987) predicts that species with large flowers almost always have large fruits, because large flowers have large ovaries ("correlation pleiades" Berg 1960) and the resources contained within the ovary are incorporated into the developing fruit after fertilization; consequently, species with large fruits present either large seeds or large numbers of small seeds per fruit (Primack 1987). The fruit and seed size have direct implications in the plant phenology, since species with large fruits will require a greater period of time for fruit maturation than species with small fruits; thus, species that need more time for fruit maturation will flower in the beginning of the season appropriate for flowering (Primack 1987). Primack (1987) hypothesize this relation for temperate areas, where a cold season occurs, which limit the development of fruits, this hypothesis still need to be tested in tropical areas.

Finally, another perspective was to evaluate the role of phylogeny in the reproductive pattern displayed by species. Flowering phenology represents a highly conserved character within evolutionary lineages (Kochmer and Handel 1986). The role of common ancestry and the constraints associated with phylogenetic relatedness in the variation and evolution of phenological traits (Harvey and Pagel 1991) should not be left aside when testing abiotic or biotic hypotheses (Marco and Paéz 2002, Boulter et al. 2006). Kochmer and Handel (1986) were the first to summarize hypotheses and test the influence of phylogeny among plant families from distinct geographic localities. They demonstrated that phylogeny is a constraint on plant flowering.

The hypotheses of competition or facilitation among coexisting species, as well as the influence of morphology and relatedness in the phenological expression of the plants would be more convincing if demonstrated for a guild of related plants. Additionally, such influences should be easier to be finding in aseasonal environments (Stiles 1977, Fenner

1998), where the climatic constraints are minimum, and plant phenological patterns are more likely limited by biotic interaction or phylogenetic constraints.

The tribe Myrteae (*sensu* Wilson et al. 2005, Myrtaceae) represents an interesting system to evaluate theses hypothesis (abiotic, biotic and phylogenetic) acting in the phenological patterns. South-America is the main centre of origin and diversification of Myrteae species (Lucas et al. 2007); the tribe has supreme importance in the flora and structure of many ecosystems, some among the most threatened in the world, such as the Atlantic rainforest (Mori et al. 1983, Oliveira-Filho and Fontes 2000); and the variation of phenological patterns expressed in the great number of species makes Myrteae a good model to understand general trends and patterns of evolution in the phenology at species level and its role in the structure of ecosystems.

We examined, during 30-month study, the reproductive phenological patterns of the Myrtaceae community in the Atlantic rain forest, from the point of view of its phylogenetic affinities and the constraints imposed by climate and biotic factors. We seek to understand the importance of biotic and phylogenetic factors in addition to abiotic factors on phenological patterns, utilizing a species level phylogeny tree (Lucas et al. 2007), and detailed field observations of flowering and fruiting phenologies, and seed dispersers. Previous works addressing this questions covered family or genera levels of comparisons and usually focused only on flowering (Kochmer and Handel 1986, Wright and Calderón 1995). To our knowledge, this is the first work addressing phenological patterns using phylogenetic comparative methods, a resolved phylogeny within a single family, based on detailed phenological observations of flowering and fruiting. We asked the following:

1) Is the reproductive activity of Myrtaceae seasonal? Are the flowering and fruiting patterns related to changes in abiotic factors (precipitation, temperature, and day length)?

2) Is the reproductive phenology of Myrtaceae shaped by phylogeny? Does relatedness affect the timing and duration of reproduction? What is the relative importance of the ecological (environmental factors) and phylogenetic component determining the reproductive patterns?

3) Do coincident ('aggregated') or divergent ('segregated') patterns occur in flowering and fruiting among species that share pollinators or dispersers? Such patterns may be a result of competition or facilitation?

4) Are there any influences of reproductive characters morphology in the phenology of the species?

METHODS

Study area

This study was conducted in the Parque Estadual da Ilha do Cardoso (PEIC), São Paulo state, southeastern Brazil (situated 47˚54'75''W, 25˚03'88''S). PEIC is a protected continental island of 15,100 ha, which is composed exclusively of Atlantic rain forest vegetation (Bernardi et al. 2005). The PEIC flora has been studied in detail (Barros et al. 1991, Mello and Mantovani 1994, Sugyama 1998). The climate is subtropical humid (C*fa*) under the Köppen system of climatic classification (Köppen 1923), ever wet with no dry season and mean temperature is superior to 20˚C. Meteorological data from 30-years period (1956-1985) are of the city of Cananéia station (5 Km from the study area) and were obtained from the Oceanographic Institute of the University of São Paulo (USP). The average annual rainfall to the normal climate is 2248 mm, with one rainy season from September to May when monthly rainfall is over 100 mm, and a less rainy season from June to August when rainfall is less frequent and may fall under 100 mm/month. The mean annual temperature is 21.3 ˚C (Fig. 1). Data from the study period (from 2005 to 2007 year) were obtained from the meteorological station located at the study site, which belongs to the Escola Superior de

Agricultura "Luiz de Queiroz" from University of São Paulo (ESALQ-USP). During the study period the temperatures were very stable accross years (21.9˚C mean) and the rainfall in 2007 (1702 mm) was below the 30-year average. The data on day length are for the latitude of 25˚ and follow Pereira et al. (2001), the longest day length occur in December (13.47 h) and the shortest in June (10.55 h).

Study species

The Myrtaceae family encloses more than 130 genera and 3800 to 5800 species (Wilson et al. 2001) and is found all over the world. Definition of the generics limits of Myrtaceae is not clear yet. The work on molecular phylogeny of the family in the last 5 years has advanced in the definition of generic boundaries within the family (Wilson et al. 2005, Lucas et al. 2005, Lucas et al. 2007). Myrtaceae is one of the most important families of Brazilian forests (in term of species diversity and number of individuals), and is among the dominant families in the threatened biome of Atlantic Forest (Mori et al. 1983, Oliveira-Filho and Fontes 2000). Brazilian Myrtaceae belongs to the tribe Myrteae, whose main distinctive feature is the production of fleshy indehiscent fruits (Wilson et al. 2001). From this point the term family or Myrtaceae refers to the tribe Myrteae, unless mentioned.

The flower morphology is very conservative, but the flower size is variable among species, while inflorescence types and flowering strategies are extremely diverse (Lughadha and Proença 1996). The flowers are hermaphrodite, petals white or cream, stamens numerous and ovaries inferior (Landrum and Kawasaki 1997). Petals and/or stamens may act as attractants, but the stamens (Plate 1) are generally the most conspicuous structures in the open flower (Lughadha and Proença 1996). Scent also appears to play a role in attraction and one-day flowers are the norm in the tribe; pollen is the principal reward available to visitors and

among them the bees (Apoidea) are the most common pollinators (Lughadha and Proença 1996, Gressler et al. 2006).

In contrast to the wide interspecific variation in morphological traits of the fruits (fruit size, colour and number of seeds), species are very similar in the composition of the fruit pulp, being rich in carbohydrates and water (Pizo 2002, E. Cazetta *personal communication*). These fruits are an important resource for the maintenance of animals in Atlantic Forest (Pizo 2002); and birds (Plate 1) and monkeys are the major Myrtaceae seed dispersers over all Neotropical region (Gressler et al. 2006). Besides of the importance of this family in the structure of endangered tropical ecosystems, studies about the reproductive biology of Myrtaceae species are scarce. A deeper understanding of the reproductive biology of this group may represent an invaluable contribution toward their conservation.

The identification of Myrtaceae species was made by specialists (see acknowledgements) and voucher specimens of studied plants are deposited in the Herbarium Rio Clarense (HRCB) of the UNESP – University of São Paulo State (HBRC48585 to HBRC48590 and HBRC48685 to HBRC48765).

Flowering and fruiting

We monitored the reproductive phenology of 550 marked adult individuals, representing 34 species, distributed on nine genera (see Appendix A). The number of individuals studied per species varied in accordance with species abundance in the area, ranging from 1 to 73 individuals (mean of 16 individuals). Observations were carried out on reproductive phenophases: flower buds, flowers (anthesis or flowering itself), immature fruits and mature fruits (prepared for dispersal or fruiting itself) at monthly intervals from July 2005 to December 2007. On each monthly observation, we estimate the intensity of phenophases in

each individual applying Fournier's percent index of intensity, which consist in an interval scale varying from 0 to 4, with a 25% interval between classes 1-4 (Fournier 1974).

For each observed individual we calculated five phenological variables per reproductive phenophase: a) onset date; b) peak date; c) duration (number of months the individual remained in the phenophase); d) time of flower development; e) fruit maturation (the difference in months between the first date of flower bud or immature fruit and the first date of the following phenophase, flower or mature fruit). When one individual presented more than one phenological event over the 30-months of observation, we calculated the mean phenological variable. Then, based on the individual phenological variables we calculated the average phenological variable to represent each species, to minimize the effects of extrinsic sources of variability.

Since the species flowered or fruited year-round, and there was not a start or end date of reproduction (i.e. there was not a true zero point) the use of a circular scale instead of a linear one was more appropriated. The year was represented by a rotation of 360° with arbitrary origin (by convention 1st January equals 0° or 360°). This technique has been widely used on phenological studies (see Morellato *et al.* 2000, Boulter *et al.* 2006). We calculated for each phenological variable ('a' and 'b') described above the mean angle (a) or mean date (converted from mean angle), the vector *r* (the concentration around the mean angle) and the circular standard deviation (Zar 1996).

Seasonality, Climate and phenology

To evaluate the existence of seasonality in the reproductive patterns of Myrtaceae we tested the distribution of mean dates of onset and peak (phenological variables 'a' and 'b') for all phenophases applying circular statistics (Rayleigh test, Z) as described in Morellato et al. (2000). If the mean angle is significant, and the pattern is seasonal, the concentration around

the date of the mean angle denoted by r (length vector) is considered a measure of the degree of seasonality (Morellato et al. 2000). The vector r varies from 0 (when phenological activity is distributed uniformly all over the year) to 1 (when phenological activity is concentrated around one single date of year or mean angle) (Zar 1996). All circular distributions tested presented circular normality (Kuiper test, p>0.15).

To test if the phenological patterns were related to abiotic factors we applied the multiple linear regression (Zar 1996). The number of species in each reproductive phenophase along 30-months was the dependent variable and mean temperature, precipitation and day length were the independent variables. One multiple regression was computed to each reproductive phenophase. The relation between the phenology and previous climate was tested with a time lag of 1 to 3 months; as no significant results were found we omitted these results. The normality, homogeneity and linearity of data were tested through a residual analysis, and it was not necessary to transform the data. We also compared the number of species in each phenophase with the normal climate (30-years) and the same relations were detected, and these results were also omitted.

Phylogeny and phenology

To evaluate if the phenological patterns are a consequence of the phylogenetic relationships among species we applied phylogenetic eigenvector regression (PVR, Diniz et al. 1998), which estimates the phylogenetic inertia in the traits evaluated. The objective of this technique is to describe the vectors that can be used as predictors in multiple regression. The vectors are obtained from a principal coordinate analysis (PCA) of the matrix that expresses the phylogenetic relationship among species. Only few vectors are necessary to describe all the relationships in the matrix, thus stepwise models are used to determine the vectors to be retained during the multiple regressions. The adjusted R square (the adjusted coefficient of

determination – R^2_a) can be interpreted as an estimate of the degree of phylogenetic effect or phylogenetic inertia. Traits under analysis (phenological eigenvectors) were regressed on phylogenetic eigenvectors retained in such a way that estimated values express phylogenetic trends in data and residuals express independent evolution for each species. However, the phylogenetic portion of total variance in the phenological variables may contain a phylogenetic component related to ecology, called "phylogenetic niche conservatism" (Harvey and Pagel 1991). Related species may present traits or behaviors that are alike because they occupy similar niches during evolutionary history, and the traits will be related to phylogeny and ecology (environment) in possibly different proportions. To separate what proportion of the phenological variation of species is attributed exclusively to phylogeny, to environment, or to both factors combined, we utilized the partition method proposed by Desdevises et al. (2003). However, we consider the interpretation of R^2_a (backwards of R^2) because it provides an unbiased estimate of the real contribution of a set of explanatory variables (environment and phylogeny) to the dependent variable (phenology) (Legendre and Legendre 1998). To perform the PVR including the partitioning of the variation, it was necessary to obtain the phylogenetic, environmental and phenological eigenvectors. The computation took the following steps:

Step 1- Phylogenetic eigenvectors: The phylogenetic tree used in our study was elaborated by Lucas et al. (2007) to tribe Myrteae on the specie-level using molecular information. Fourteen out of 34 species studied in the PEIC were referred on this tree, thus subsequent adjustments to accommodate more 14 species were needed, summing 28 species in the analyses. The additional 14 species from PEIC belonging to monophyletic groups were included as politomies in the ancestral nodes: *Myrcia sect. Gomidesia* (4 species added), *Eugenia* (7 species added), *Calyptranthes* cf. *rubella* was added to the ancestral point of this genus; and the same procedure was taken for two species of *Campomanesia*. We compute two

matrices of phylogenetic distances between species: in the first all branches were scaled to one unit length, and in the second matrix we considered the same topology but we add an estimative of branch lengths also based in the paper of Lucas et al. (2007). From each matrix of phylogenetic distances, we obtained the phylogenetic eigenvectors for each species through principal coordinate analysis. The results of use of both phylogenetics information were qualitatively identical; we reported only results for the model where the branch lengths were considered.

Step 2 - Phenological eigenvectors: Due to the circularity of phenological data it was necessary to apply a transformation that linearizes the dates to be used as the predicted variables in the future regressions. Initially, we compute a matrix of phenological distance between pairs of species, in a way the difference between the dates of two species were represented by the smallest angular distance between them. A total of eight matrices were constructed (onset and peak to each phenophase). From each matrix we extracted vectors of the ordination of species through eigenvector analysis. We considered only the first vector for each species, because it always accounted for more that 67% of the species phenological variance. To ensure that these vectors represented well the original dates we transformed the vectors in a matrix of distance (utilizing Euclidian distance) and associated this matrix with the original matrix of phenological distance; in all cases the association between matrices were greater than 71% (Mantel test). Hence, we conclude that the first eigenvectors were an efficient linear representation for the phenological distance (circular) between species.

Step 3 - Environmental eigenvectors: To obtain the ordination of species relative to the environmental gradient occupied we utilize a canonical correspondence analysis (CCA, ter Braak 1986). CCA is specifically usefull to extract latent environmental gradients from ecological data set because it selects ordination axes that represent the dispersion of species along an environmental gradient (ter Braak 1986). To carried out CCA we used two matrices,

in the first the species were represent by columns and the 30-months of study by lines; the second matrix had three columns, each one representing one environmental variable (total monthly precipitation, mean monthly temperature and day length) and the 30-months of study by lines. We utilized just the first and second ordination axes because they represented better the species response to the environmental variables measured.

The first multiple regression evaluated the effects of climatic factors (environmental eigenvectors) on the traits of interest (phenological eigenvectors). The variation due to phylogeny was determined through a second multiple regression on the phenological eigenvectors with phylogenetic eigenvectors. The third multiple regression looked at the effects of environment and phylogeny on phenology, using the phylogenetic eigenvectors that had a significant effect from the previous analysis. The variation due to environment is equal to the R^2_a from the third analysis minus the R^2_a from the second. The variation from phylogeny is equal to the R^2_a from the third analysis minus R^2_a from the first. In addition, the variation from both is equal to the R^2_a from the second minus R^2_a resultant of subtraction of R^2_a from the third minus R^2_a from the first. The residual variation, not accounted for phylogeny or environment, is equal to 1 minus the sum of the previous three computations (to more detail see Legendre and Legendre 1998, Desdevises et al. 2003, McCarthy 2007).

We performed pairwise comparisons among distance matrices using Mantel tests (1967) to evaluate the association between: phylogenetic *versus* phenological distances (16 tests) and environmental *versus* phenological distances (16 tests); and the results were in general similar, thus we presented just the PVR results.

Reproductive phenological patterns: aggregated, segregated or random

Given that the flower morphology of 34 species studied are very similar and that other studies suggests that Myrtaceae are visited by the same guild of pollinators (Lughadha and

Proença 1996, Gressler et al. 2006) we assumed the occurrence of competition by pollinators in the flowering season. And yet, based on registers of consumption of fruits by birds in ten Myrtaceae species in the PEIC (V. G. Staggemeier unpublished data), we assumed that competition by seed dispersers also could occur.

We tested if the reproductive patterns were segregated, random or aggregated over time through null model analysis. We quantify temporal niche overlap among all species in accordance with the model of mean pairwise overlap by Pleasants (1990). An overlap index was calculated for each pairwise combination of species, and the mean observed value to all species was compared with 100 simulated values. The overlap index utilized was Czekanowski (Feinsinger et al. 1981). Graphically, this index represents the intersection area of the phenological histograms of two species, being symmetric and ranging from 0 to 1. For two species "1" and "2" with activity "P_{1i}" and "P_{2i}" the overlap index (O) is:

$$O_{12} = O_{21} = 1 - 0,5 * \sum_{i=1}^{n} | P_{1i} - P_{2i} |$$

To elaborate the simulated communities we used Monte Carlo simulations. In the simulations the onset of flowering and fruiting were randomized while the duration and shape of phenological curve was preserved. Evidence consistent with staggered (or aggregated) flowering and fruiting times occurred when the observed reproductive overlap was smaller (or greater) than 95 simulated values (Wright and Calderón 1995).

Primack hypothesis:

We collected and measured flowers and fruits of the Myrtaceae species (approximately 20 flowers and 20 fruits of at least 3 individuals) on flowering or fruiting during the study. For each flower we measured: pistil length (from receptacle to stigma),

stamen length (from receptacle to anther), corolla diameter, distance between opposes stamens and pedicel length. For each fruit we measured: length, diameter and mass of fruit and seed, number of seeds per fruit and pulp mass. Initially, to establish if the morphological traits (flower, fruit and seed) were more conservative than the phenological characteristics (duration and time of development for each phenophase) we quantified the phylogenetic inertia existent in theses trait through PVR (Diniz-Filho et al. 1998), the traits were log-transformed before the analyzes. To evaluated Primack's hypothesis we computed the regressions of log-morphologies with the phylogenetic eigenvectors and retained residuals. These residuals were used to test the hypothesis because they express independent evolution of each species (Diniz-Filho et al. 1998). To establish the flowering sequence of species, we considered only the species flowering in the more favorable period, defined from onset mean date of flower bud for the Myrtaceae community plus or minus one standard deviation (corresponding to the period from October to March). The range of restriction was 180˚, 70.6% of species flowered in this period. The mean angles for each species were converted in Julian days, to compute the linear regression between the sequence of flowering and the variables of interest.

RESULTS

Phenology and climate

Most species began to blossom during the super humid season, when the maximum day-length occurs (Fig. 2). The dates of onset and peak of flower bud and flower were significantly seasonal (Table 1), and both were associated in great intensity with day length and in lower intensity with temperature (Table 2). Only the onset of immature fruit was seasonal, occurring in later January. The other fruiting variables (peak of immature fruit, onset and peak of mature fruit) were not seasonal. Only 57.2% of the variance in immature

fruit was explained by climate and there was no climatic restriction limiting the occurrence of mature fruits over year (Fig. 2).

Phenology and Phylogeny:

When we did not consider the partition variation between phylogenetic and environmental components, we found that both factors influenced the phenological expression (Table 3), but the environmental components with greater intensity. However, when the variation was partitioned we found that the influence of phylogeny was absent or very weak. The climatic environment was the factor controlling the phenological patterns of species. The high variation shared between environment and phylogeny revealed the existence of an reproductive niche phylogenetically structured (Table 3).

Flowering and fruiting patterns: aggregated, segregated or random

We found an aggregated flowering pattern p=0.03. The flowering overlap among species is higher than expected by random (Fig. 3A) indicating possibly low competitive pressure. The fruiting pattern did not differ from random, thus fruits are available around the year, although in different intensity (Fig. 3B).

Primack's hypothesis

The phylogenetic inertia was elevated in the morphological characteristics in general (Table 4). Morphological traits (flower, fruit and seed) were more conservative than the phenological traits (duration and development time of each phenophase), except for flower bud duration and flower development time (Table 5).

When we did consider star phylogeny there was a positive relation between flower and fruit size, but when we did consider hierarchical phylogeny, the relation disappeared (Table

6). Large fruits have more seeds, in accordance with the Primack's hypotheses. Larger flowers and fruits did not require more time to development than did smaller flowers and fruits, and flower and fruit size also did not affect the flowering sequence of species. However, when considered hierarchical phylogeny, we found that fruits with larger seeds required more time to maturation (Table 6). We found that fruits that require more time for maturation flowered at the end of the appropriated season (Table 6). However when we regressed (considered hierarchical phylogeny) the flowering sequence against seed log-diameter and log-development time of mature fruit, we found that only the development time of fruit affected the flowering sequence of species (R^2_a: 0.22; for development time: $\beta=0.64$ and $p=0.018$).

DISCUSSION

Our 30-month study of the phenology of 34 Myrtaceae species in the Atlantic rain forest showed strong seasonality in flowering, with a peak in December and January. The higher percentage of species in flower buds and flowers coincided with the longest day-length, corroborated the predictions of van Schaick et al. (1993). Borchert et al. (2005) have demonstrated that even small changes on day-length may be a cue for flowering in low latitudes.

It is interesting to note that day-length, rather than temperature, seems to be the flowering trigger for Myrtaceae species. This can be explained by stability of the climatic factors in rain forest, these habitats are characterized by absent of water stress and absent of extreme variations in the temperature, what it becomes the day-length an factor particularly important acting as an initial impulse to phenological reproductive cycle of the plants (Bollen and Donati 2005), being able to be the unique reliable mechanism to induce the major synchrony in the species flowering in these habitats (Borchert et al. 2005). Moreover how

much greater the distance in relation to equatorial line, is expected that the seasonality in the day length acquire more importance, consequence of the greater variation in the solar angle along year (Borchert et al. 2005).

The flowering during the warmest and wet season presented as advantages the increase in light availability, in the quantity of nutrients accessible to plants through decomposition (Morellato 1992) and the activity of pollinators during this period (Morellato and Leitão-Filho 1996, Sakai 2001).

We found that the flowering was significantly clumped. The climatic factors explained the clumped pattern. However, others factors can be associated with this pattern. The plants can flower at the same time because pollinators are more abundant in determined moment or the greater availability of flowers can attract more pollinators ("mass action" hypothesis) increasing the success of the pollination and decreasing the predation risk in individual flowers through spreading the risk for others individuals (Rathcke 1983, Sakai 2002).

Although the segregation of flowering time reduce overlap in shared pollinators, the converse is not necessarily true (Gotelli and Graves 1996) like presented in some studies, the high overlap necessarily not imply in competition between plants (Thompson 1982, Rathcke 1988, Gross et al. 2000, Moeller 2004). Moreover, sympatric species with similar floral characteristics that co-flowering can presented mechanisms that minimize possible competitive effects, such as differentiation in the chemical composition of scent which is noted by bees (Dobson 1996) or temporal segregation daily in the offer of resource (e.g. pollen; Stone et al. 1998). Knudssen (1999) found that *Geonoma* species had floral scents differentiation and he suggested that this characteristic could be responsible by isolated reproductive in sympatric species co-flowering in this genus. Stone et al. (1998) in an *Acacia* african community found that the activity of shared pollinators can be structured throughout the day as a result of temporal patterns of pollen release across species. The high overlap also

can benefit rare species in the community because then the "magnet effects" can occur, where the species more abundant attract pollinators that also visited the rare species (Thompson 1978, Schemske 1981). Separating the evidence in support of each of these competing drivers (climatic or pollinators) is accrediting difficult and require a best knowledge of pollinators and pollination of these plants. Hence, our study is important for pointing the direction of flowering in Myrtaceae, opening space to further works to evaluated in detail the plant-pollinator relationships in the period of high flowering overlap in the community. Ideally, these studies should include experimental tests because without direct experimental evidence, statistical inferences about the existence or not of competition will always be open to question (Fleming and Partridge 1984).

A different picture emerges from the fruiting patterns in Myrtaceae. Fruiting peaks were relatively short with a uniform distribution throughout the year without a clear seasonality at the community level. Such kind of year-round fruit production is also reported from other aseasonal tropical Atlantic rain forest (Morellato et al. 2000, San Martin-Gajardo and Morellato 2003, Marques et al. 2004), indicating that in these habitats the conditions to development and ripening of the fruits are little restrictive around the year. The general effect of this random fruiting pattern is to assure a continuous food resource to vectors, favoring its local fidelity and potentially increasing the reliability of dispersers' agents.

The continuous availability of fruits is a necessary part of the mutualism between plant and disseminator (Fenner 1998). The success of seed dispersal, which is essential for long term survival of plant population, largely depends on correspondence between fruit maturation and abundance of frugivores and hence, timing of fruiting is important for plant dynamics (Herrera 1985, Stiles 1980). The spacing of fruiting time among species can benefit plants, especially the ones producing large fruit crops that are consumed by residents dispersers, principally the ones that exhibit territoriality (Stapanian 1982) which was the case

of Myrtaceae in the Cardoso Island (V. G. Staggemeier, *unpublished dates*). Whellwright (1985) and Smith-Ramírez (1998) also found, through null model analysis that observed fruiting patterns were indistinguishable from randomized patterns in its studies area.

We found that fruit and flower morphological characteristics had a larger phylogenetic component than did phenological traits, suggesting that life-history traits are evolutionarily more flexible than morphological traits, likely because the environmental contribution is greater to phenology. Similar pattern was described by Morales (2000) comparing morphological (seed and flower size among others) and demographic (germination time, growth rate, establishment among others) characteristics; he found that the morphological characteristics were less flexible than demographic characteristics, which also have a greater environmental influence. The evolution of fleshy fruits is phylogenetically conserved character (Jordano 1995, Bolmgrenn and Erikson 2005) and this tendency indicates that species remain in the same part of the niche space (Harvey and Pagel 1991, Lord et al.1995), accounting to the elevated inertia found in the Myrtaceae fruit morphology.

In relation to Primack's hypotheses, we found relation between fruit and flower size only when star phylogeny was considered, indicating that, in fact, large flowers do not produce necessarily large fruits. Hence, we reject the first Primack's hypothesis tested. The relation between number of seeds and fruit size exists independent of species relatedness namely, larger fruits have more seeds in accordance with the second Primack's hypotheses. Larger Myrtaceae flowers and fruits did not require necessarily more time to complete its development. However, fruits with larger seeds require more time to maturation. This result was evident only when we considered hierarchical phylogeny, stressing what other authors have showed: the species relatedness can mask the existing patterns. Primack postulated that in temperate environment larger fruits must flower first in the appropriate season for flowering. The morphological characteristics of Myrtaceae did not account for the sequence

of flowering of species, demonstrating that in habitats with no stress climatic plants with different fruits size can be found flowering in any date. However, species that need more time for fruit maturation, flowered in the end of appropriate season for flowering, making mature fruit available around the year, even when the most species flower at the same period.

The phenological patterns when analyzed from the environmental and phylogenetic standpoint demonstrate that does not exist an exclusively phylogenetic pressure, but the environment influence the phenology independent of relatedness among species. Additionally, the shared influence of both two factors is high pointing the existence of an reproductive niche phylogenetically structured. This may be explained by two complementary hypotheses, one related to the rapid evolutionary changes that occur to Myrtaceae and the other, related to the origin and diversification of actual flora in the southeastern Brazil (Lucas et al. 2007). A rapid evolutionary rate together with a long permanence of the flora in wet and warm conditions may have obscure previously existing phylogenetic trends in phenological patterns of this family. These hypotheses explain the lack of phylogenetic trends when phenology is considered in relation to the environmental and phylogenetic variables simultaneously.

This was the first study to contemplate the partition of phenological response in one phylogenetic component, one environmental component and shared influence of both. We demonstrated the importance of considering this partition in phenological studies, since leave it aside biologically may lead to equivocated conclusions, you can assign that phylogeny has an important role in determining the phenological structure of the community when in fact it is not possible to distinguish it due to environmental influences.

This result open new avenues for studying the reproductive response of same species that have evolved under different selective pressures (same species occurring at different geographical locations or altitude) similar to the analyses by Kochmer and Handel (1986) and

Boulter et al. (2006). Kochmer and Handel (1986) argued that if phylogenetic constraints are global properties of families, and if phylogenetic constraints are stronger than local selective pressures, the species of a family should flower on similar dates regardless of their geographic locations.

The conclusions we have draw open new avenues to further studies, addressing the importance of each factor in the determination of species' phenological responses. The methods of analysis we use can be employed for the best represented families of other ecosystems (such as Sapotaceae in Amazonian forest, Lauraceae in the Cost-Rican moist forest), allowing a better understanding of evolutionary patterns and general trends in the reproductive phenology of high diverse ecosystems.

Acknowledgments

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Tables:

Table 1. Results of circular statistic analyses for the occurrence of seasonality on phenological behavior of the 34 Myrtaceae species. Rayleigh test was performed for significance of the mean vector (μ) or mean date (omitted when no significant).

	Floral bud		Flower (anthesis)		Immature fruit		Mature fruit	
	onset	peak	onset	peak	onset	peak	onset	peak
Mean Date	12 Dec	27 Dec	15 Jan	18 Jan	29 Jan			
Mean Vector (μ)	340.30°	355.72°	13.99°	17.68°	27.97°	45.58°	207.34°	223.77°
Length of Mean Vector (r)	0.46	0.42	0.35	0.35	0.37	0.20	0.09	0.11
Median	340.18°	351.97°	12.21°	24.72°	25.51°	64.32°	231.79°	231.79°
Circular Standard Deviation	71.26°	75.35°	82.88°	82.88°	80.80°	103.65°	126.40°	121.68°
Rayleigh Test (Z)	7.24	6.03	4.19	4.20	4.65	1.29	0.26	0.37
Rayleigh Test (p)	0.001	0.002	0.014	0.014	0.009	0.278	0.772	0.691

Table 2. Results of multiple regression analyses between climatic factors and species number active in each phenophase.

Dependent variables	Regression summary	P (independet variables)		
		Month rainfall	Month mean temperature	Day lenght
Floral Bud	R_{adj}=0.823; $F_{3;26}$=40,16**	0.667	0.054	0.000
Flower	R_{adj}=0.728; $F_{3;26}$=23,17**	0.190	0.028	0.003
Immature Fruit	R_{adj}=0.572; $F_{3;26}$=11,58**	0.695	0.000	0.000
Mature Fruit	R_{adj}=0.338; $F_{3;26}$=4.43*	0.149	0.802	0.052

Legend: * $p<0,05$; ** $p<0,001$

Table 3. Proportion variance explained through of methods that partitioned or not the variance explained by each component. Note that when no partitioned the variation the proportion shared between climate and phylogeny [b] is present in all the analyses. Variance proportions computed through adjusted coefficient of determination.

Method		Without Partition of Variation Independent variables			With Partition Variation Fractions individuals			
Phenophases		Phylogeny and Climate	Phylogeny	Climate	Purely Phylogeny	Phylogeny and Climate	Purely Climate	Unexplaied
		[a+b+c]	[a+b]	[b+c]	[a]	[b]	[c]	[d]
ONSET	Bud floral	93.46	49.40	92.63	0.82	48.58	44.06	6.54
	Flower	86.36	49.13	87.39	-1.03	50.16	37.23	13.64
	Immature fruit	85.28	64.50	78.08	7.20	57.30	20.78	14.72
	Mature fruit	91.85	29.80	92.45	-0.61	30.41	62.05	8.15
PEAK	Bud floral	96.40	67.80	91.73	4.67	63.14	28.60	3.60
	Flower	84.55	52.10	86.02	-1.48	53.58	32.45	15.45
	Immature fruit	88.06	42.30	83.51	4.55	37.75	45.76	11.94
	Mature fruit	95.45	34.60	95.56	-0.11	34.71	60.85	4.55

Table 4. Phylogenetic inertia existent in the reproductive morphological traits of Myrtaceae species.

	Morphological traits (log)	R adjusted	p
Flower	pistil length	0.42	0.00
	stamen length	0.54	0.00
	corolla diameter	0.66	0.00
	distance between opposes stamens	0.63	0.00
	pedicel length	0.70	0.00
Fruit	diameter	0.43	0.00
	lenght	0.51	0.00
	mass	0.62	0.00
	pulp mass	0.66	0.01
	number of seed	0.87	0.00
Seed	diameter	0.50	0.00
	lenght	0.50	0.00
	mass	0.77	0.00

Table 5. Phylogenetic inertia existent in the phenological traits of Myrtaceae species.

Phenological traits (log)	R adjusted	p
Duration (phenophase length)		
bud flower	0.64	0.00
flower	0.23	0.02
immature fruit	0.48	0.00
mature fruit	0.33	0.00
Developmental time		
flower	0.96	0.00
fruit mature	0.26	0.02

Table 6. Comparative analysis of relationships among flowers, fruits, seeds and phenology (considering star and hierarchical phylogeny), in accordance with Primack's hypotheses.

Adapted of Primack hypotheses (1-5)	Star phylogeny			Hierarchical phylogeny			Number of species
	β	R adjusted	p	β	R adjusted	p	
1) Size flower X size fruit							
1.1) corolla diameter X fruit diameter	0.58	0.31	0.02	0.09	0.00	0.65	25
1.2) distance between oppose stamens X fruit diameter	0.49	0.21	0.01	0.25	0.02	0.21	25
2) Number of seeds X diameter fruit	0.54	0.26	0.00	0.53	0.25	0.01	26
3) Size flower or fruit X developmental time (D.T.)							
3.1) corolla diameter X bud flower D.T.	0.00	0.00	0.98	0.13	0.00	0.53	26
3.2) fruit diameter X fruit mature D.T.	0.13	0.00	0.52	0.32	0.07	0.11	26
3.3) seed diameter X fruit mature D.T.	0.20	0.00	0.32	0.47	0.19	0.02	26
4) D.T. of flowers and fruits X sequence of onset reproduction (S.O.R.)							
4.1) bud flower D.T. X S.O.R.	0.22	0.00	0.34	0.14	0.00	0.54	21
4.2) fruit mature D.T. X S.O.R.	0.64	0.38	0.00	0.44	0.15	0.04	21
5) Size flower and fruit X sequence of onset reproduction (S.O.R.)							
5.1) corolla diameter X S.O.R.	-0.22	0.00	0.34	-0.21	0.00	0.38	20
5.2) fruit diameter X S.O.R.	-0.22	0.00	0.36	-0.04	0.00	0.87	19
5.3) seed diameter X S.O.R.	-0.07	0.00	0.78	0.01	0.00	0.96	19

Note: Morphological data and development time were log-transformed. Sequence of onset reproduction represents the date of onset bud flower in Julian days.

Figure legends:

Plate 1. (Left) An example of Myrtaceae flower, *Eugenia sulcata*: the stamens generally are the most conspicuous structures in the open flower. (Right) An example of seed disperser of Myrtaceae: *Tangara cyanocephala* consuming the fruit of *Myrcia ilheosensis*. Photo credits: (left) V. G. Staggemeier, (right) A. C. Guaraldo.

Figure 1. Ecological diagram of the climate elaborated in accordance with Walter (1973). The months of the year are represented along the horizontal axis from July to June. Left vertical axis represents temperature (˚C) and the right axis is the precipitation (mm). This diagram covers the period from 1856 to 1985 of Cananéia city, São Paulo state, Brazil. Black area represents super-humid period and the hachured area less-humid period.

Figure 2. Reproductive phenology of Myrtaceae and climatic data for the study period.

Figure 3. (A) Percentage of species in flowering: area hachured corresponds to hypothetical pattern where the flowering of species occur at random; the dotted line correspond to hypothetical pattern where species flowering in a segregated way; and dashed line represent the pattern observed in the present study where species flowering in a aggregated way. (B) Percentage of species in fruiting: area hachured corresponds to observed pattern in the present study where the fruiting species occur at random; the dotted line correspond to hypothetical pattern where species fruiting in a segregated way; and dashed line correspond to hypothetical pattern where species fruiting in a aggregated way. The hypothetical curves were elaborated based in values of overlap computed in the simulated matrices.

Plate 1

Fig. 1

Cananéia (3m)
Brasil
(25°00'S; 47°55'W)   1676 h   21.3°C   2248 mm
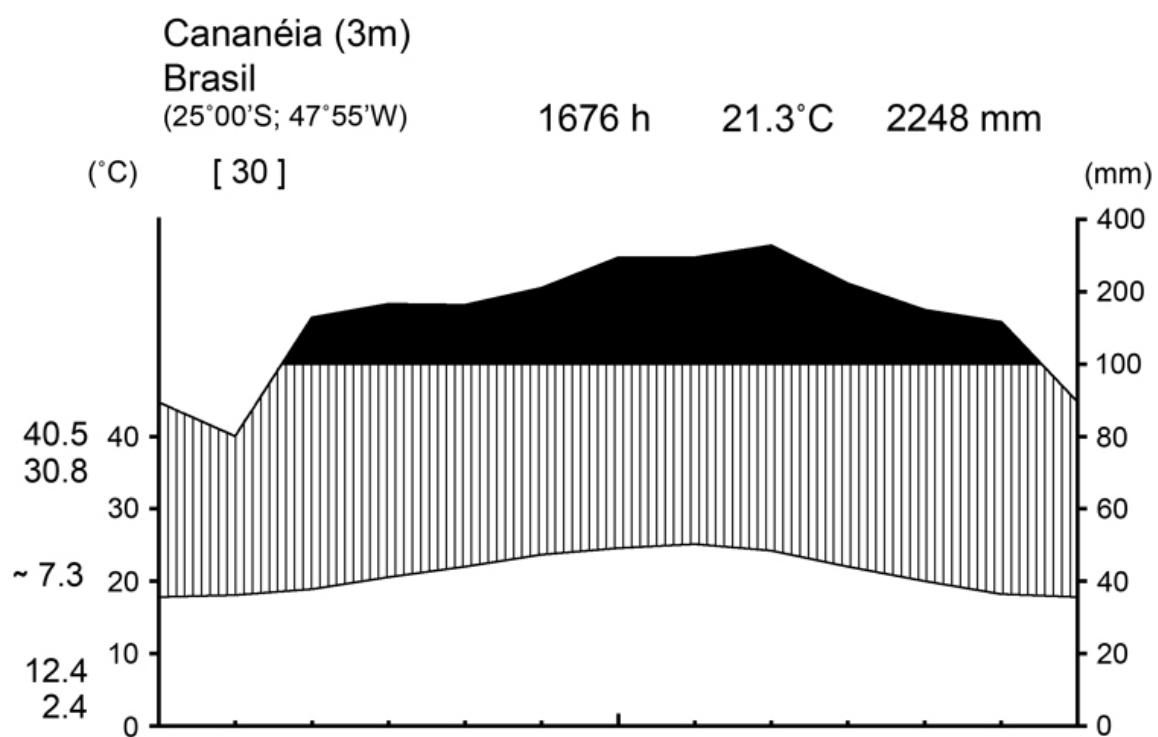
Fig 2.
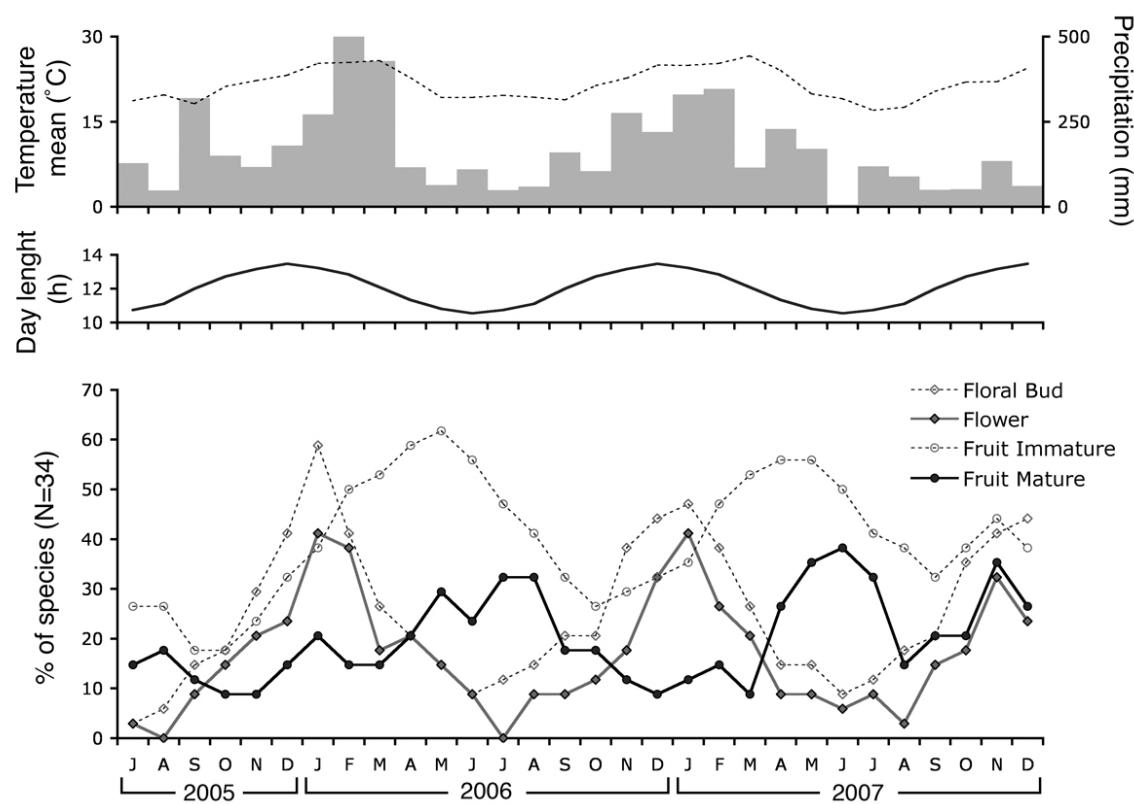
Fig 3.
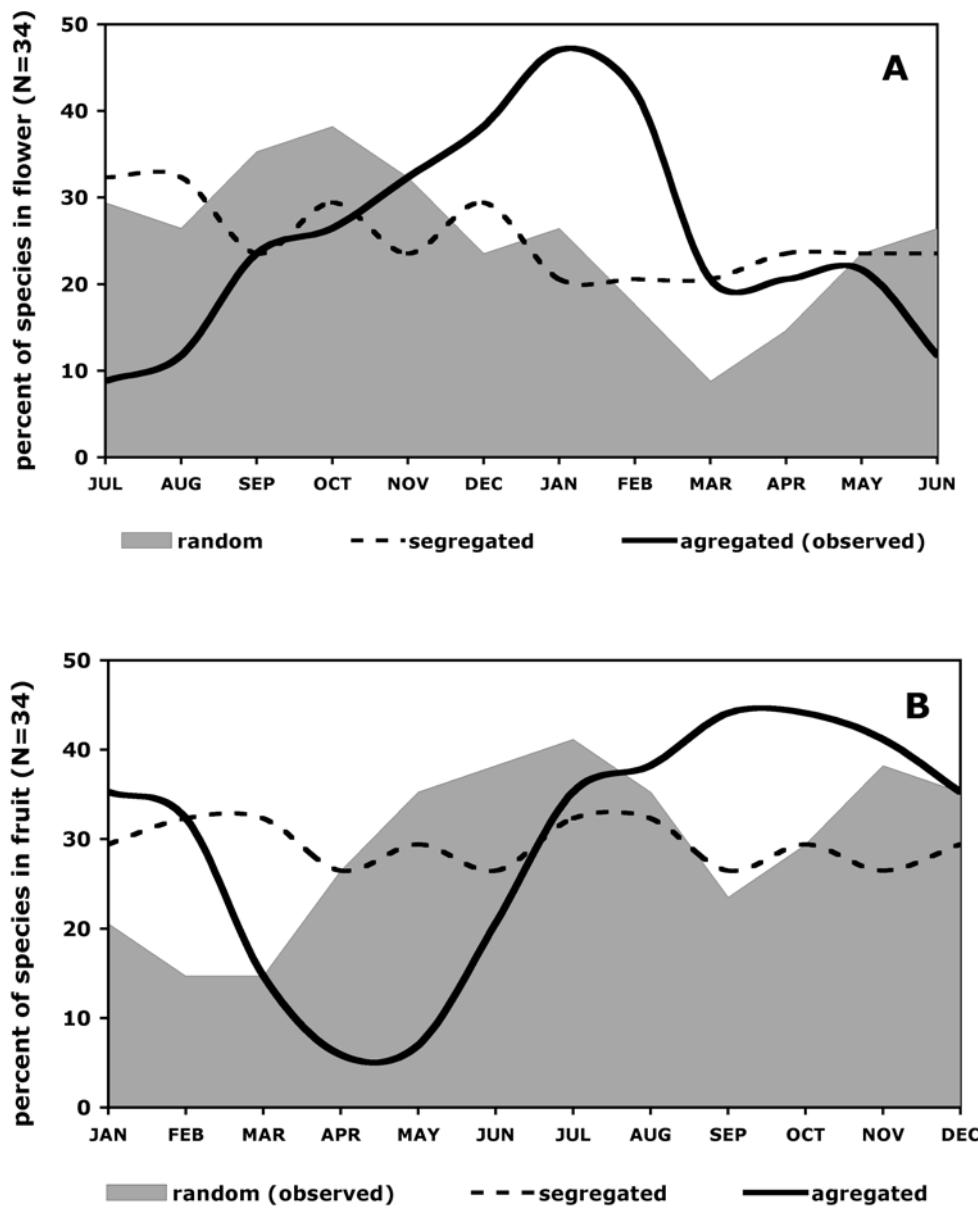
Appendix A. Geographic distribution of species studied from observations phenological. Peak dates for flowering and fruiting and individuals number observed.

Species	Distribution	Peak Flower	Peak Fruit Mature	N obs
Blepharocalyx salicifolius	Brazil to N. Argentina	15.Feb	4.May	11
Calyptranthes cf. *rubella*	Brazil (E. & SE. Santa Catarina, Rio Grande do Sul)	15.Feb	14.May	14
Campomanesia guaviroba	E. & S. Brazil to Argentina (Misiones)	11.Jan	19.May	5
Campomanesia xanthocarpa	SE. & S. Brazil to NE. Argentina	12.Sep	4.Nov	2
Eugenia cuprea	SE. Brazil (to Paraná)	22.Oct	20.Dec	58
Eugenia neoaustralis	SE. & S. Brazil	10.Oct	25.Dec	8
Eugenia neoglomerata	Brazil	13.May	13.Oct	7
Eugenia oblongata	SE. Brazil (to Paraná)	6.Jun	22.Aug	3
Eugenia stigmatosa	E. & S. Brazil	25.Jul	21.Nov	3
Eugenia sulcata	Brazil (Rio de Janeiro to Santa Catarina)	17.Nov	19.Jan	6
Eugenia umbelliflora	Brazil (São Paulo to Santa Catarina)	28.Mar	14.Aug	36
Eugenia verticillata	SE. & S. Brazil	9.Apr	19.Sep	1
Marlierea obscura	SE. & S. Brazil	14.Feb	22.May	14
Marlierea racemosa †	SE. & S. Brazil	16.Dec	2.Jul	12
Marlierea tomentosa †	E. & S. Brazil	21.May	3.Oct	52
Myrceugenia myrcioides	E. & S. Brazil	20.Mar	25.Aug	2
Myrcia amazonica †	Trop. America	23.Sep	12.Nov	11
Myrcia brasiliensis	SE. & S. Brazil	5.Jan	19.May	5
Myrcia hartwegiana	SE. & S. Brazil	13.Feb	8.May	10
Myrcia hebepetala	Brazil	10.Mar	8.Oct	9
Myrcia ilheosensis	S. Trop. America	13.Feb	20.Jun	23
Myrcia insularis †	SE. Brazil	20.Nov	21.Jan	11
Myrcia isaiana †	Brazil (Espírito Santo)	16.Sep	29.Nov	8
Myrcia multiflora	Trinidad to S. Trop. America	12.Jan	25.Mar	59
Myrcia palustris	SE. & S. Brazil to NE. Argentina	27.Jan	24.May	2
Myrcia pubipetala	Brazil to Bolivia	19.Feb	17.Jul	9
Myrcia pulchra †	SE. & S. Brazil	9.Jan	25.May	10
Myrcia racemosa	SE. & S. Brazil	5.Feb	12.Jul	16
Myrcia spectabilis	E. & S. Brazil	24.Jan	5.Aug	13
Myrcia splendens	Mexico to Trop. America	2.Dec	27.Jan	41
Myrcia tijucensis	SE. & S. Brazil	11.May	5.Oct	2
Pimenta pseudocaryophyllus	Bolivia to Brazil	20.Oct	30.Jan	4
Psidium cattleianum	E. & S. Brazil to NE. Uruguay	28.Dec	20.Mar	73
Siphoneugena guilfoyleiana	Brazil (São Paulo)	27.Aug	18.Nov	10

Note: † Species not included in phylogenetic analysis. Species name and distribution followed World Myrtaceae Checklist & Bibliography (Govaerts 2008).

CAPÍTULO 2

QUANTIFYING THE INTERACTIONS STRENGTH IN

THE SEED DISPERSAL NETWORK OF MYRTACEAE

Quantifying the interactions strength in the seed dispersal network of Myrtaceae

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Running title: Seed dispersal in Myrtaceae

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Abstract:

Given that the network structure has important implications for the coexistence and stability of species as well as for the coevolutionary process we seek through of network analysis, to study the immediate consequences of frugivore activity in quantitative effectiveness of seed dispersal in Myrtaceae at Atlantic rain forest. This family is a dominant component of this threatened ecosystem and presented a wide interspecific variation in fruit morphological traits which are intensity consumed by frugivores being an interesting model to evaluate how are structured the biotic interactions in this ecosystem. We investigated species composition and interaction structure of Myrteae network. A total of 11 Myrtaceae species and 42 frugivore species established 97 interactions. The mean number of interactions for plants was 9.7 and for animals 2.3. The number of interactions per bird species was positively correlated with its local abundance and for plants with its crop size. The network revealed a significantly nested structure, weak interactions and low asymmetry. The factor contributing more for the quantitative effectiveness of seed dispersal was the frequency of visit. Removal and visitation rates were affected by bird abundance and plant crop size. The seed dispersal probability was closely associated with the morphology of birds and seeds. The most important birds species for seed dispersal of Myrtaceae were the Turdidae species, with a high strength in the network. Of a total of 3296 handled fruits 73% were effectively dispersed by birds. Fringilidae, Thraupidae, Turdidae and Tyrannidae dispersed 84% of the fruits handled successfully. In the specific level, *Turdus rufiventris* dispersed 20.2% of the total of dispersed fruits of Myrtaceae and *Turdus albicollis* 14.6%, *Turdus flavipes* 12.3% and *Turdus amaurochalinus* 5.7%. To know what frugivores and plants species play an important role in a seed dispersal network is the base for its conservation. From the standpoint of conservation of tropical ecosystems, in special the Atlantic rain forest, this study

highlights the importance of small size birds in the maintenance of the dispersal process in this threatened ecosystems.

INTRODUCTION

More than 90% of the tropical plant species rely on animals for the dispersal of their seeds (Jordano 2000). This fact illustrates the importance of mutualism for biodiversity maintenance; if the seed dispersers disappear, their plant partners may follow (Bascompte & Jordano 2007). The lost of large seed dispersers due to hunting or habitat reduction have a strong negative consequence in seed dispersal by decreasing the frequency of visits and fruits removal rates (Staggemeier & Galetti 2007), which is an threat to biodiversity in the Earth (Wright 2003).

The knowledge of how the mutualistic interactions are structured in the community is the first step to understand the functional dynamics of plant-frugivore mutualism and it is the only way to assess the magnitude of the effect of species loss in the natural ecosystems. Jordano (1987) was the first author exploring mutualisms between plant-animals through of the network perspective. In the actual decade there is a crescent the number of studies that confronts the plant-animals interactions utilizing the approach of complex networks (Memmott 1999; Memmott & Waser 2002; Jordano *et al.* 2003; Bascompte *et al.* 2003, 2006; Vázquez & Aizen 2004; Thompson 2006; Guimarães *et al.* 2006; Guimarães *et al.* 2007a). This technique allows visualizing the global structure of interactions between species and theirs interdependent relations (Rico-Gray 2006) more than simply describe what species participate of the interactions. The network analyses enlarge the understanding of how interactions are distributed among species pairs in nature (quantitative and qualitatively) embedded the evolution of mutualism in a community context (Jordano 1987; Bascompte & Jordano 2007).

Ecological relationships between organisms are rarely, if ever, random because they are constrained by multiple interacting factors, including, in its broadest sense, the coevolutionary

history of the interacting organisms (Ollerton *et al.* 2007). Recent work has led to the unambiguous conclusion that mutualistic networks are very heterogeneous (the bulk of the species have a few interactions, but a few species are much more connected than expected by chance), nested (specialists interact with subsets of the species with which generalists interact), and built on weak and asymmetric links among species (Bascompte & Jordano 2007). Both ecological variables (e.g., phenology, local abundance, and geographic range) and past evolutionary history may explain such network patterns (Bascompte & Jordano 2007), but few studies evaluated these factors (but see Ollerton *et al.* 2003; Vázquez & Aizen 2004; Rezende *et al.* 2007).

In a network the species are interpreted like a set of nodes connected through links (mutualistics interactions); these links can characterize the intensity or weight of the interactions between species (Bascompte & Jordano 2007). The quantitative component of seed dispersal effectiveness, resultant of the combination of visits frequency, fruit removal rates and seed dispersal probability (Schupp 1993), can be a good measure to represent the strength of mutualism between plants and their dispersers. When these three proportions are analyzed alone neither is an appropriate surrogate of effectiveness (Schupp 1993) given that different factors operate in each one. To identified which factors affect the plant-frugivore interaction constitute an important step to understand how the animals can affect the distribution, abundance, evolution and genetic of plants species (Schupp 1993; Wenny 2000; Jordano & Schupp 2000; Jordano & Godoy 2002; Wang & Smith 2002). For example, the frequency of visits and removal rate can be affect by the frugivory scale, size and abundance of birds (Schupp 1993; Jordano & Schupp 2000) or/and by the fruit number produced (crop size) and abundance of plants (Murray 1987; Foster 1990; Korine *et al.* 2000). In addition, the removal rate and probability of bird handled a fruit

with success can depend on plant and bird size (Jordano 1995). The fruit removal does not assure its dispersal, the probability of bird handled a fruit with success, swallowing or carrying it away from parental plant is directly associated with bird and fruit size (Wheelwright 1985; Cortes *et al.* 2008). Hence, the effectiveness of seeds dispersal depends on possible different proportions of these three components (visit frequency, removal rate and seed dispersal probability). To explore the quantitative effectiveness of seed dispersal like species strength and interactions strength within of the mutualistic network is of great relevance to understanding of the actual structure of plant-frugivore interactions and also can be used to understand constraints on plant-animal coevolution.

Given that the network structure has important implications for the coexistence and stability of species as well as for the coevolutionary process (Bascompte & Jordano 2007), we seek through of network analysis, to study the immediate consequences of frugivore activity in quantitative effectiveness of seed dispersal in Myrtaceae at Atlantic rain forest. This family represents an interesting model to evaluate how the biotic interactions are structured in this ecosystem because it have supreme importance in flora of this vegetation (Mori 1983, Oliveira-Filho & Fontes 2000), a wide variation of fruiting phenological patterns express in the great number of species accomplished to the wide interspecific variation in fruit morphological traits (fruit size, colour and number of seeds) (Lugdaha & Proença 1996), and it is an important resource for the maintenance of animals in Atlantic Forest (Pizo 2002). Birds and monkeys are the major Myrtaceae seed dispersers over all Neotropical region (Gressler *et al*. 2006). Besides the importance of Myrtaceae in the structure of endangered tropical ecosystems, studies about the reproductive biology of their species are scarce.

In this framework, we asked the following questions:

1) What characterizes the species compositions of the plants and animals constituting the seed dispersal network of Myrtaceae?

2) Are there any patterns of specialization and generalization of plant and animal species? And what determines the level of specificity in an interaction?

3) How different are the frugivores of Myrtaceae in relation to visitation patterns, fruits removal and seed dispersal probability?

4) Is there any characteristic that distinguishes the species more dominant or weaker in the Myrtaceae-frugivore network?

METHODS:

Study site

The study was carried out at the Parque Estadual da Ilha do Cardoso (PEIC, Fig. 1), São Paulo state, southeastern Brazil (47˚54'75''W, 25˚03'88''S, 3-15 m a.s.l.). The PEIC is a protect continental island of 15,100 ha, covered exclusively by Atlantic rain forest vegetation (Bernardi *et al.* 2005). The PEIC flora has been studied in detail (Barros *et al.* 1991; Mello & Mantovani 1994; Sugyama 1998). The climate is classified as subtropical humid (C*fa*) under the Köppen (1923) system, ever wet with no dry season and mean temperature is above 20˚C. The average annual rainfall is 2248 mm, with one rainy season from September to May, when monthly rainfall is over 100 mm, and a less rainy season from June to August, when rainfall is less frequent and may fall under 100 mm/month. The mean annual temperature is 21.3 ˚C. Meteorological data from 30-years period (1956-1985) are from the city of Cananéia station (5 km from the study area) and were obtained from the Oceanographic Institute of the University of São Paulo (USP).

Studied species

The Myrtaceae family comprises more than 130 genera and between 3800-5800 species (Wilson *et al.* 2001) and can be found all over the world, but especially in South America, Australia and Tropical Asia, the three centers of diversity for the family (World Checklist Myrtaceae 2008). Brazilian Myrtaceae belongs to tribe Myrteae, whose main distinctive feature is the production of fleshy indehiscent fruits (Wilson *et al.* 2001). Fruits have a wide interspecific variation in morphological traits, but the species are very similar in the fruit pulp composition, rich in carbohydrates and water (Pizo 2002; E. Cazetta *personal communication*). These fruits are an important resource for the maintenance of animals in the Atlantic Forest (Pizo 2002; Gressler *et al.* 2006). A deeper understanding of the reproductive biology of this group may represent an invaluable contribution toward their conservation. The identification of species was made by specialists in the family (see acknowledgements) and voucher specimens of studied plants are deposited in the Herbarium Rio Clarense (HRCB) of UNESP - São Paulo State University.

The fruiting of Myrtaceae in the study area occurs all over year (Fig. 2) (Staggemeier *et al.* 2007). Detailed phenological information of species will be presented in other paper but will be mentioned here when relevant. The frugivory registers were obtained from July 2005 to August 2007. We observed 11 species of Myrtaceae (84 individuals) during 609h25' (Table 1). The crop size of each individual was estimated by direct counting of fruits before the observation begins (Table 1). The plant species were ranked in accordance with its local abundance (Table 1) as: 1. Rare, few individuals scattered in the area; 2. Common, many individuals occurring clumped in the area; 3. Dominant, very common, numerically dominant and frequent in the area.

Focal observations

The events of fruit consumption by birds were registered in accordance with focal-tree method (see Galetti *et al.* 2004) during 609h25' of observations. The observations were conducted at varying periods from sunrise to 12h00 and from 13h00 to sunset. To assess the birds' feeding behavior and seed dispersal we recorded bird species, time of arrival in the plant, visit duration, and number of fruits handled according to avian feeding behavior. Birds were considered seed dispersers when they remove seeds by successfully swallowing the whole fruit or carrying it in the bill to distinct places, whereas seed thieves peck the fruit for pulp pieces, detach the fruit, and drop or regurgitate it beneath the tree, where the mortality rate is usually higher than in micro-sites far from the reproductive tree (Jordano & Schupp 2000). No animals were observed visiting the fruits of *Myrcia racemosa* during the focal observations (55 hours in 7 individuals) thus this species was not included in the network analyses that evaluate the strength of plant-animal interactions. The birds were ranked in abundance classes: (1) Occasional, few individuals observed only in one period of year; (2) Common, few individuals but observed all over the year; (3) Dominant, many individuals presented throughout all year. And the birds were also ranked in a frugivory scale based in the literature: (1) insectivore, consumes manly insects; (2) omnivore, consumes invertebrates, nectar, and fruits; (3) insectivore-frugivore, consume manly insects and secondarily fruits; (4) frugivore-insectivore, consume manly fruits and secondarily insects; (5) frugivore, consumes manly fruits. Others animals (mammals) can consume Myrtaceae fruits in the PEIC, such as *Cerdocyon thous*, *Dasyprocta leporina*, *Tayassu pecari* and *Allouata guariba*, but only birds were considered in this study.

Morphological constraints: birds and plants

Birds are able to select fruits based on their size and, usually, swallowing is constrained by fruit width (Wheelwright 1985; Cortes *et al.* 2008). Thus for better comprehension of avian feeding behavior, we collected approximately 20 fruits of at least 3 individuals and measured: length, diameter and mass of fruit and seed, number of seeds per fruit and pulp mass (Table 2) for all 11 species. We also measured the bill morphology of the birds observed from specimens of museum (MZUSP - Museu de Zoologia da Universidade de São Paulo). We measured 10 individuals for each species, generally 5 males and 5 females. The measurements registered were: maxilla height (mm); culmen length 1 (mm, from bill tip to mouth commisures); culmen length 2 (mm, from bill tip to feathers); gape width measured at the mouth commisures (mm); bill width at the culmen base (mm); bill height measured at the narines (mm); bill height at the culmen base (mm). Body mass (g) was obtained from the literature.

To minimize number of the morphological variables analyzed we utilize the PCA technique (Legendre & Legendre 1998). For fruit morphology the first axis accounted for 59.7% of fruit morphological variation and was related to fruits characteristics (length, diameter and mass of fruit, number of seeds and pulp mass); the second axis accounted for 38.1% and was related to seed characteristics (length, diameter and mass of seed). For the PCA of bird morphology only the scores of the first axis were retained for posterior analyses because this axis accounted for 85.5% of the morphological variability of birds and were related to seven bill measurements and the body mass. The scores of species ordination were utilized in the further analyses; from this point we referred only to fruit size (related to scores of the first axis of PCA for fruit morphology), seed size (related to scores of the second axis of PCA for fruit morphology) and bird size (related to scores of first axis of PCA for bird morphology).

Network analyses

The interactions network initially was represented as a binary interaction matrix (as described in Jordano 1987), with rows represented by frugivores species and columns represented by plant species. In these matrices, a cell *mn* containing ''1'' represents an interaction between the frugivores species *m* and plant species *n,* while a cell with ''0'' represents no interaction. The network size is equal to the sum of plant species number (P) and the frugivore species number (F) interacting. We consider all focal observations register of feeding (independent of effectiveness of seed dispersal) to describe the network topology. From this matrix we calculate the linkage level (L = total number of interactions per species) or generalization level (Jordano 1987), their conectance (proportion of all the *mn* possible interactions) (Jordano 1987) and system temperature (nestedness) (Bascompte *et al.* 2003).

Species with high linkage levels utilize many partner species, and thus are more generalized than species with low linkage levels. A possible relationship between generalization (linkage level), bird morphology, abundance and frugivory scale was tested using the non-parametric Spearman's correlation coefficient (Zar 1996) for birds. Plants linkage level was associated with crop size, fruit and seed morphology, length of fruiting (time in months that the specie produce mature fruits) and plant abundance, also through of Spearman's correlation coefficient.

We reorganized rows and columns of the matrix as a maximally packed matrix to assess level of nestedness (Bascompte *et al.* 2003): plant and animal species were arranged in order of linkage level, from the most generalized species (highest number of interactions) to the most specialized species (lowest number of interactions). In a perfectly nested matrix all present interactions will be concentrated in the perfectly positive triangle in the matrix, while absent

interactions will be found in the lower right part of matrix. The line separating the presences and absences in a perfectly nested matrix is called the boundary threshold. System temperature T is a measure of the deviation of such unexpected presences and absences from the boundary threshold (Atmar & Patterson 1993). The statistical significance was evaluated using Monte Carlo simulations. System temperature ranges from $0°$, indicating perfect nestedness, to $100°$ when system is completely anti-nested (Atmar & Patterson 1993).

In addition, matrix containing information of the quantitative effectiveness of seed dispersal (QSD) between pairs of species was elaborated using the focal observation registers. In this matrice the 1 in the binary matrix were replaced by quantitative effectiveness of seed dispersal. We represented the quantitative component of effectiveness seed dispersal (QSD) by the product of visit frequency, removal rate and seed dispersal probability (adapted from Schupp 1993). The mutual dependence represents the interaction strength in a network, and the sum of all dependences for a species represent the species strength in network (see more detailed in Bascompte & Jordano 2007). To determine what are the characteristics of the species (plants and birds) more important in the network, we associated the species strength with the following factors: size and abundance of birds, frugivory scale, fruit and seed size, crop size and plant abundance.

Quantitative effectiveness of seed dispersal

To determine if some of the three elements of QSD (frequency of visits, removal rate and seed dispersal probability) contributed more to the final result of dispersal we regressed QSD against the frequency of visits, removal rate and dispersal probability. And to determine what factors affect each level of the quantitative component we related the three elements of the QSD

to the possible factors acting in each one: size and abundance of birds, frugivory scale, fruit and seed size, crop size and plant abundance.

When the assumptions for parametric statistical analyses were fulfilled, we used multiple linear regression or ANCOVA (Zar 1996); when not, we carried out Spearman correlations (Zar 1996). Transformations were employed when needed: log for values of frequency (handled fruits per hour, handled fruits per visit and QSD), square root for counting (crop size, linkage level) and arc sine of square root for proportions (seed dispersal probability, dependence values).

RESULTS

A total of 42 bird species (belonged to 17 families) consumed fruits of 10 Myrtaceae species in PEIC, and established a total of 97 interactions (Fig. 3), 23% of the total possible interactions. Of the 42 bird species, only one is a migratory species while all the others are residents in the study area. Approximately 12% of the species interacting with the studied plants are endangered or near threatened: *Cyanocorax caeruleus*, *Procnias nudicollis*, *Phylloscartes kronei*, *Tangara peruviana* and *Thraupis cyanoptera* (IUCN 2006). Of the 42 species consuming fruits only two did not act as seed dispersers of any Myrtaceae species, *Thamnophilus caerulescens* and *Philydor atricapillus,* because they dropped or consumed only the pulp of the six fruits handled.

Linkage level for animal species (Lm) ranged from 1 to 5 plant species (mean ± SD = 2.31 ± 1.46) and for plants (Ln) from 3 to 16 animal species (mean ± SD = 9.70 ± 5.60) (Fig. 4). A positive correlation was found between abundance and generalization level (linkage) for the animals species (N = 42, r_s = 0.38, P < 0.014) (Table 3). The generalization level for plants was positively correlated with crop size (mean fruit number produce per specie) (N = 10, r_s = 0.79, P =

0.004, Table 3). Hence, bird species interacting with many Myrtaceae species tended to be the most abundant in the community and the most productive Myrtaceae species (in fruit numbers) in the community tended to interact with more bird species.

System temperature (T) was 30.89°, which is significantly lower than expected by chance [T in 1000 Monte Carlo simulations, mean ± SD = 45.54° ± 6.24°, P (T < 30.89°) = 0.0009]. Thus, the network is characterized by a nested structure, which is significantly more ordered than if plant species were visited randomly by birds, or bird species were feeding randomly on plants.

The majority of interactions (69%) were approximately symmetric (Fig. 5), distributed between 0 and 0.5 in the asymmetry scale (where 0 is perfectly symmetric and 1 is asymmetric). When we looked at the asymmetry from the standpoint of the interaction strength we found that the combined interaction strength (dependence *mn* multiply by dependence *nm*) increased with the asymmetry of the interactions (log-transformed data: R^2: 0.43; $F_{1,82}$: 62.36; P = 0.000; t: 7.897, P = 0.000) (Fig 6). Thus, the more symmetric interactions will be weaker in the Myrtaceae network. There was a significant positive relationship between species strength and its degree, the species strength grew faster than the species degree (Fig 7). When we included in the comparison the mean dependence value we found that only the generalization level accounted for the species strength (linear regression with log-transformed data for animals strength: R^2: 0.49, $F_{2,37}$: 18.03, P = 0.000 and generalization level: t = 2.0, P = 0.05; for plants: R^2: 0.85, $F_{2,7}$: 19.39, P = 0.001 and generalization level: t = 2.5, P = 0.04). Hence, animal species interacting with many species of Myrtaceae were the most important in terms of effectiveness of seed dispersal visualized globally in the network. However when we looked at each interaction alone the contribution of these species was usually weak. Concluding, the symmetric pattern was a consequence of weak interactions, established between the more generalist species, which are the strongest in the

network.

In addition, there was not a relation between bird size and linkage level (F$_{1,37}$: 1.06, P = 0.31) or between bird size and strength in the network (F$_{1,37}$: 1.17, P = 0.29). We found positive association between linkage level and species strength with bird abundance (r$_s$: 0.33, P = 0.03 and r$_s$: 0.35 and P = 0.02, respectively). The frugivory scale was not associated with the importance of the species in the network (r$_s$: 0.21, P = 0.19).

The Myrtaceae species with greater seed dispersal success, were the more generalist species, and also the ones offering a large number of fruits (F$_{1,8}$: 9.73, P = 0.01). The plant abundance (r$_s$: 0.18, P = 0.61) as well as fruit and seed size did not affect the effectiveness of seed dispersal (fruit and seed size *versus* species strength: F$_{2,7}$: 0.73; P = 0.52).

Seed dispersal effectiveness

Of the 3296 handled fruits, 73% were effectively dispersed and the families Fringilidae, Thraupidae, Turdidae and Tyrannidae were responsible for 84% of the dispersal of the fruits handled with success (2.8%, 13.7%, 52.8% and 14.9%, respectively). In a more specific level, *Turdus rufiventris* dispersed 20.2% of the Myrtaceae fruits and *Turdus albicollis* 14.6%, *Turdus flavipes* 12.3% and *Turdus amaurochalinus* 5.7%.

When we study in detail each plant-frugivore pair, we found that the quantitative effectiveness of seed dispersal was better explained by frequency of visit (ß=0.573) than by removal rate (ß=0.388) or seed dispersal probability (ß=0.467). Those three elements accounted for 69.2% of the variability in the seed dispersal effectiveness (Table 4).

The seed dispersal probability was affected by bird and seed size (Table 4). Fruits with smaller seeds had better chances of be effectively dispersed, and larger birds had greater

probability of handle a fruit with success (Table 4). The fruit size did not affect the success of seed dispersal; large fruits that contain little seeds (e.g. *Psidium cattleianum*) presented higher success rates than small fruits containing larger seeds (Fig 8). The species containing the largest seeds among the studied species were *Myrcia spectabilis* and *Eugenia umbelliflora,* and less than 30% of handled seeds were effectively dispersed. The birds with greater potential as seeds dispersers of Myrtaceae were the larger frugivores (Ramphastidae, Cracidae, Trogonidae, Corvidae and Cotingidae) because the bill width is greater than the maximal diameter of fruits of at least 8 of the 11 species studied (Fig 9). In the other extreme, Parulidae, Vireonidae, Columbidae, Fringilidae, Pipridae and Thraupidae, are the families with smaller bill width and consequentially with small chances of handle one fruit with success (Fig 9).

The frequency of visits was positively affected by crop size and bird abundance (Table 4). Thus, the more abundant birds were frequent visitors of Myrtaceae fruits, and the more consumed species were offering more fruits. The removal rate was positively affected by bird and crop size (Table 4).

Birds with the highest seed dispersal effectiveness values belong to the family Turdidae (*Turdus albicollis*, *T. rufiventris*, *T. flavipes* and *T. amaraurochalinus*), these birds interacted with 4-5 Myrtaceae species. *Turdus albicollis* dispersed more than 50 % of the total seeds handled successfully for three Myrtaceae species: *Calyptranthes* cf. *rubella* (81%), *Myrcia brasiliensis* (47.5%) and *Myrcia spectabilis* (50%), and present the highest strength of the network (Fig 3). *Turdus rufiventris* was responsible for 45% of effective dispersal of *Myrcia splendens* and 71% of *Myrcia pulchra*, and was the second bird species in importance for Myrtaceae family. *Elaenia obscura* (Tyrannidae) was the third strongest effective disperser in the network, however its importance was not accounted by high linkage level, but by the strong interaction with one

species, *Myrcia hartwegiana*, which depended widely on this bird species for seed dispersal (Fig. 3). Other two strong interactions with this same characteristic were: *Euphonia violacea - Blepharocalyx salicifolius* (44.36% of fruits handled successful were dispersed by this bird) and *Ramphastos vitellinus - Myrcia brasiliensis* (35%). *Psidium catleianum* depended widely on two species of birds *Cyanocorax caeruleus* (53%) and *Ramphocellus bresilius* (42%).

DISCUSSION

Myrtaceae plant-frugivore network

The Myrtaceae plant-frugivore network was significantly nested. Nestedness implies that Myrtaceae species specialized attracted a smaller subset of frugivore visiting more generalized Myrtaceae species, and that specialized birds fed on a subset of the Myrtaceae species consumed by more generalists frugivores. Bascompte *et al.* (2003) and Thompson (2005) have hypothesized that those mutualistic relationships are generally characterized by nested interactions, as opposed to random or compartmentalized patterns, because the relatively stable set of resources provided by the core of generalist–generalist associations can allow a larger number of specialized interactions to persist. Support for this hypothesis has been provided for the following mutualisms: plant–pollinator; animal–seed dispersal; ant–plant relationships; anemonefish and their host sea anemones; marine cleaning (Dupont *et al.* 2003; Ollerton *et al.* 2003; Bascompte *et al.* 2003, 2006; Jordano *et al.* 2006; Guimarães *et al.* 2006, 2007b; Ollerton *et al.* 2007).

The generalization level of birds consuming Myrtaceae was related to its abundance at the study area and the most productive Myrtaceae species in the community were the more generalist ones. Then, the pattern of nestedness we observed may imply in a network structured by the abundance of birds and the productivity of Myrtaceae species. The effect of relative abundance

has been rarely examined in mutualistic networks, but Dupont *et al.* (2003) in a nested plant flower-visitor network of the sub-alpine zone of Tenerife found that the pollinator species that visit a wide range of plant species are also the most abundant. Similar results are noted by Ollerton *et al.* (2003) and Vázquez & Aizen (2004).

Jordano *et al.* (2003, 2006), Medan *et al.* (2006) and Ollerton *et al.* (2007) used the term 'forbidden interactions' to describe interspecific relationships within a network which cannot occur owing to physical, biochemical or phenological mismatch between species, and could account for part of the nested pattern. In the Myrtaceae species studied the fruits were available all over the year (Fig. 2) and were dispersed only by resident birds (the exception is *Tyrannus melancholicus*, but it was a rare visitant interacting just with two plant species). Less than 8% of the zero interactions recorded between Myrtaceae and frugivores were due to morphologically forbidden interactions, in which the bill width was smaller than the seed diameter. Besides the wide morphological association between bill and seed width, the remaining 92% of the zero interactions where possibly caused by local factors (e.g. bird habitat preferences; fruits accessibility) that prevent these interactions even when there was overlap in the morphological combinations.

Most of the interactions in the Myrtaceae network were approximately symmetric and weak, and these weak relationships were established between the strongest species of the network. Thus, the strength of the important species in the Myrtaceae network was linked to the many interactions with low dependency. The birds depend more on Myrtaceae plants than otherwise, meaning that each animal has a small contribution for the plant dispersal.

The continuous fruit availability is a necessary part of the mutualism between plant and disseminator (Fenner 1998). Fruiting peaks of the Myrtaceae species studied were relatively short

with uniform distribution throughout the year without a clear seasonality at the community level (Staggemeier *et al.* 2007; see Fig. 2). The global effect of this fruiting patterns was to assure a continuous food resource to vectors, favoring their disperser local fidelity and potentially increasing their reliability as dispersers agents of Myrtaceae.

Effectiveness of seed dispersal

No factor influencing the quantity component of effectiveness can be adequately estimated alone (Schupp 1993), but some variables have a larger effect in the prediction of the final product. In the PEIC, the frequency of visit was the factor that better predicted the quantitative component, this pattern was observed in other studies (Schupp 1993; Jordano & Schupp 2000).

The abundance of frugivores has been the major factor affecting the composition and visitation patterns of birds on plants at different systems (Schupp 1993; Jordano & Schupp 2000). The significant relationships between abundance, linkage level and frequency of visits in PEIC corroborated this prediction. At PEIC, the frugivory variations were initially attributed to the variation in the birds abundance, but crop size also had a large importance in the variation of frugivore activity among Myrtaceae species. In general, the frugivores were attracted by larger crop sizes, and the frequency of visits and removal rates of Myrtaceae fruits were positively associated to the quantity of fruits produced. This probably occurred because fruits become more conspicuous in higher density and feeding only in plants with greater crops may decrease the cost of foraging over many plants (Foster 1990). In the PEIC, larger bird species consumed more fruits per visit corroborated with other studies (Jordano & Schupp 2000). Crop size has been investigated in several studies of fruits selection by frugivores, and in general they found a positive relation between crop size and fruit removal (Davidar & Morton 1986; Foster 1990;

Izhaki 2002; Saracco *et al.* 2005). Frugivores visiting plants typically widely differ in feeding rates (e.g., McDiarmid *et al.* 1977, Howe & Vande Kerkchove 1981; Jordano 1983; Snow & Snow 1988; see Schupp 1993 for review), and usually the larger removal rates are associated with bird size.

The success of Myrtaceae seed dispersal was closely dependent of birds and fruits morphology. The ability to handle, swallow and process a given fruit efficiently depends on fruit size relative to body size of the frugivorous, particularly the gape width and mouth size; but the main effect of fruit size on handling success, especially in single-seeded fruits is due to seed size and not to fruit size (Jordano 1995). Allocating many small seeds within a given fruit increases the diversity of dispersers by allowing small frugivores to ingest pulp pieces and seeds (Jordano 1995). This strategy was observed for *Psidium cattleianum* at the study site, which has the greater fruit among the studied species but the smaller seeds, allowing both *Ramphocelus bresilius* and *Turdus flavipes* to ingest peaces of fruits containing seeds and them act as dispersers; only *Cyanocorax caeruleus* was able to carried out whole fruits away from parental plant.

In our study 64% of fruits handled by Thraupidae and Fringilidae were "thieve" (dropped or pulp consumed). Levey (1987) found that the percentage of dropped seeds during feeding trials with several tanagers species (Thraupidae) in captivity increased as a function of seed size; these birds consistently dropped more than 60% of seeds which were greater than 2.0 mm in length.

Considering the variation in frugivory patterns in Myrtaceae, the effectiveness of seed dispersal can be defined as context-dependent because the importance of the dispersers was dependent of the characteristics plant species in question, and it does not exist a unique species identified like "key" for the Myrtaceae seeds dispersal. However, the Turdidae family was very important in dispersal effectiveness of Myrtaceae. This importance was closely associated with

the high frequency of visits, abundance and generalization level of *Turdus* species. The Turdidae species presented a very flexible behavior and can carried out movements in the superior strata (*Turdus flavipes*) and middle strata and even forage on the ground (*Turdus albicollis* and *Turdus rufiventris* (Stotz 1996); have large agility to fly (Sick 1997) and present variables techniques of fruit capture (reaching, perched, hanging, hovering, sally-stall). Because of this behavioral plasticity the feeding activity of these birds was not affect by differences among Myrtaceae plant species (such as fruits accessibility and strata occupied by plant). Only two Myrtaceae species were not consumed by *Turdus*: *Psidium cattleianum* and *Myrcia hartwegiana*.

In other studies of Myrtaceae, the same bird species or genera noted in the PEIC were registred: *Elaenia* sp, *Tyrannus melancholicus*, *Myiarchus swainsoni* (Proença 1990; M. M. N. Paes *unpublished dates*). In Trindad and Tobago the major dispersers of *Myrcia fallax* (denominated *Myrcia splendens* in our study) were three species of *Turdus* (*Turdus albicollis*, *Turdus fumigatus* and *Turdus flavipes* (Keller-Wolf 1988). These similarities indicate that it may exist one general pattern of seed dispersal for the family.

Rezende *et al.* (2007) demonstrated that one-half of the mutualistic networks have a phylogenetic signal for the number of interactions per species and that the species phylogenetically related tend to have a similar role in the network. The fact of more important species of the Myrtaceae network belonged the same bird family can be an indicative of the existence of a phylogenetic signal. To include the phylogenetic perspective in the approach of complex networks is essential to interpret the effects on extinction of species. The extinctions are not limited to eliminate species, loss complete picture of the evolutionary history of the seed dispersal mutualism.

We conclude that assessing the overall consequence of seed dispersal within the framework

of disperser effectiveness can provide a more comprehensive and realistic evaluation of the importance of the different seed dispersers. To know what frugivores and plants species play an important role in a seed dispersal network is the base for its conservation. From the standpoint of conservation of tropical ecosystems, in special of Atlantic rain forest, this study highlights the importance of birds of small size in the maintenance of the dispersal process in the threatened ecosystems. The more generalists bird species (McKey 1975), in function of the elevated rates of deforestation and fragmentation resultant of human pressures, have increasing importance in the seed dispersal and recuperation of degraded areas. The birds genus *Turdus* are one of the most speciose and widespread of passerine genera (Woelker *et al.* 2007) and will be interesting to investigate its effectiveness as seed disperser in other systems.

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Tables

Table 1. Myrtaceae studied species, number of individuals, sampling effort and crop size registered during the focal-tree observations.

Species	N individuals	Hours observation	Crop size (number of mature fruits)	Abundance
Myrcia splendens	9	57h00'	614	3
Blepharocalyx salicifolius	3	22h50'	203	1
Myrcia ilheosensis	16	114h15'	2317	3
Eugenia umbelliflora	9	55h00'	673	3
Myrcia pulchra	11	73h00'	333	2
Calyptranthes cf. *rubella*	7	71h10'	132	2
Myrcia brasiliensis	4	39h00'	100	1
Myrcia spectabilis	6	33h00'	32	2
Psidium cattleianum	5	34h00'	32	3
Myrcia hartwegiana	7	55h10'	42	2
Myrcia racemosa	7	55h00'	56	1

Note: The plant species were ranked in accordance with its local abundance as: 1. Rare, few individuals scattered in the area; 2. Common, many individuals occurring in clumped in the area; 3. Dominant, very common, numerically dominant and frequent in the area.

Table 2. Morphological characteristics of fruits and seeds of Myrtaceae. N*: number of fruits – number of seeds measured. When have one unique value signify that was measured the same quantity for fruits and seeds.

| Species | N* | colour | Fruit characteristics | | | | Seed characteristics | | | total mass | |
			diameter (mm)	length (mm)	mass (g)	number of seeds	diameter (mm)	length (mm)	mass (g)	seed per fruit (g)	Pulp mass (g)
Blepharocalix salicifolius	68	red	6.70 ± 0.82	5.67 ± 0.58	0.17 ± 0.06	1.34 ± 0.77	4.13 ± 0.51	3.38 ± 0.71	0.03 ± 0.01	0.04 ± 0.02	0.12 ± 0.05
Calyptranthes cf. *rubella*	16-14	black	6.77 ± 0.61	5.48 ± 0.64	0.18 ± 0.06	1.07 ± 0.27	3.38 ± 0.72	3.02 ± 0.67	0.03 ± 0.01	0.03 ± 0.01	0.14 ± 0.02
Eugenia umbelliflora	165	black	11.53 ± 0.88	13.96 ± 2.35	1.19 ± 0.35	1.03 ± 0.17	8.96 ± 0.97	11.41 ± 1.94	0.54 ± 0.16	0.55 ± 0.17	0.64 ± 0.24
Myrcia brasiliensis	22	red to black	10.89 ± 1.57	9.50 ± 1.40	0.72 ± 0.26	1.60 ± 0.88	5.61 ± 0.73	5.03 ± 0.73	0.11 ± 0.02	0.15 ± 0.06	0.71 ± 0.23
Myrcia hartwegiana	71	red	6.80 ± 0.75	5.75 ± 0.59	0.18 ± 0.07	1.54 ± 0.83	3.67 ± 0.45	3.46 ± 0.44	0.03 ± 0.01	0.04 ± 0.02	0.14 ± 0.05
Myrcia ilheosensis	193	dark purple	8.01 ± 0.88	6.00 ± 0.73	0.28 ± 0.09	1.44 ± 0.73	3.73 ± 0.47	3.33 ± 0.56	0.03 ± 0.01	0.04 ± 0.02	0.24 ± 0.07
Myrcia pulchra	90	black	7.42 ± 0.59	7.06 ± 0.55	0.27 ± 0.07	1.17 ± 0.38	4.16 ± 0.31	4.00 ± 0.33	0.04 ± 0.01	0.05 ± 0.01	0.22 ± 0.06
Myrcia racemosa	30	gray	8.45 ± 1.19	7.42 ± 0.71	0.37 ± 0.15	1.20 ± 0.48	6.70 ± 0.47	5.35 ± 0.43	0.12 ± 0.04	0.13 ± 0.05	0.24 ± 0.13
Myrcia spectabilis	79	gray	15.17 ± 1.56	14.98 ± 1.31	2.30 ± 0.72	1.04 ± 0.19	9.84 ± 1.03	9.99 ± 0.95	0.57 ± 0.13	0.59 ± 0.17	1.71 ± 0.64
Myrcia splendens	140	black	6.96 ± 0.74	9.85 ± 1.54	0.34 ± 0.10	1.15 ± 0.36	4.45 ± 0.47	7.47 ± 1.14	0.10 ± 0.03	0.11 ± 0.04	0.23 ± 0.08
Psidium cattleianum	20-174	yellow	24.49 ± 5.11	25.29 ± 5.70	9.37 ± 5.79	85.56 ± 48.18	2.37 ± 0.43	2.85 ± 0.37	0.01 ± 0.00	0.62 ± 0.40	8.89 ± 5.79

Table 3. Association between the generalization levels of the potential dispersers and of the Myrtaceae species with the studied factors calculate across of Spearman correlation coefficient (r_s). Correlations statistically significant are hachured.

	r_s	P	N species
Potential dispersers			
Bird morphology	-0.16	0.331	43
Frugivory scale	0.10	0.529	44
Abundance	0.38	0.014	44
Myrtaceae species			
Fruit size	-0.05	0.894	10
Seed size	0.03	0.937	10
Crop size	0.79	0.004	10
Abundance	0.30	0.373	10
Fruiting lenght	-0.14	0.941	10

Table 4. Association between the quantitative effectiveness component of seed dispersal and its three elements: frequency of visit, removal rate and seed dispersal probability, and factors affecting each element. Associations statistically significant are hachured.

Quantitative effectiveness of seed dispersal

	R Square	F	Sig.
	0.692	69.804	0

independent variables	Beta	t	Sig.
Frequency of visits	0.573	9.927	0
Removal rate	0.388	6.667	0
Probability of seed dispersal	0.467	8.018	0

Frequency of visits

	R Square	F	Sig.
	0.242	2.53	0.011

independent variables			
Bird size		0.433	0.512
Crop size		3.974	0.05
Bird abundance		3.329	0.041
Plant abundance		2.6	0.081
Bird abundance x Plant abundance		0.25	0.909

Removal rate

	R Square	F	Sig.
	0.202	5.388	0.001

independent variables	Beta	t	Sig.
Bird size	0.19	1.941	0.056
Fruit size	-0.161	-1.553	0.124
Seed size	-0.082	-0.821	0.414
Crop size	0.307	3.003	0.004

Probability of seed dispersal

	R Square	F	Sig.
	0.303	12.73	0

independent variables	Beta	t	Sig.
Bird size	0.234	2.598	0.011
Fruit size	0.057	0.622	0.536
Seed size	-0.498	-5.466	0

Figure Legends

Fig 1. Panoramic view of the Atlantic rain forest studied in the Parque Estadual da Ilha do Cardoso, southeastern Brazil.

Fig 2. Distribution fruiting phenology: (A) percentage of 34 Myrtaceae species found in the area of study; (B) percentage of fruiting individuals for 11 Myrtaceae studied species in the focal observations. The percentages represent the species mean activity for the period of July 2005 to December 2007.

Fig 3. Plant-frugivore matrix of the Myrtaceae in Atlantic rain forest. Actual interactions obtained of registers focal, species strength and percentage of fruits disperse for each species of plant by each bird specie.

Fig 4. Cumulative distribution degree (k) describing the probability of finding a bird species interacting with at least k plants (open circles) and the probability of finding a plant species interacting with at least k animals (closed circles) in the network.

Fig 5. Asymmetry values distribution of interactions among frugivores and plants. Zero indicates perfectly symmetry and 1 asymmetry.

Fig 6. Regression between asymmetry (log transformed) and combined strength of the interaction (log transformed)

Fig 7. Relation between the species degree and its strength. The species strength grows faster than species degree.

Fig 8. Box-plot of seed diameter of Myrtaceae species (A) and treatment given to fruits by frugivorous in Ilha do Cardoso, Brazil (B).

Fig 9. Cumulative frequency of Myrtaceae fruit width sampled at Ilha do Cardoso, Brazil, as follow: a- *Myrcia hartwegiana*; b- *Calyptranthes* cf. *rubella*; c- *Blepharocalyx salicifolius*; d- Myrcia splendens; e- *Myrcia ilheosensis*; f- *Myrcia pulchra*; g- *Myrcia racemosa*; h- *Myrcia brasiliensis*; i- *Eugenia umbelliflora*; j- *Myrcia spectabilis*; k- *Psidium cattleianum*. Mean gape sizes of frugivorous birds are indicated with arrows, the hachured area represented the range of gape size for bird families with more than four species of visitants.

Fig 1.

Fig 2.
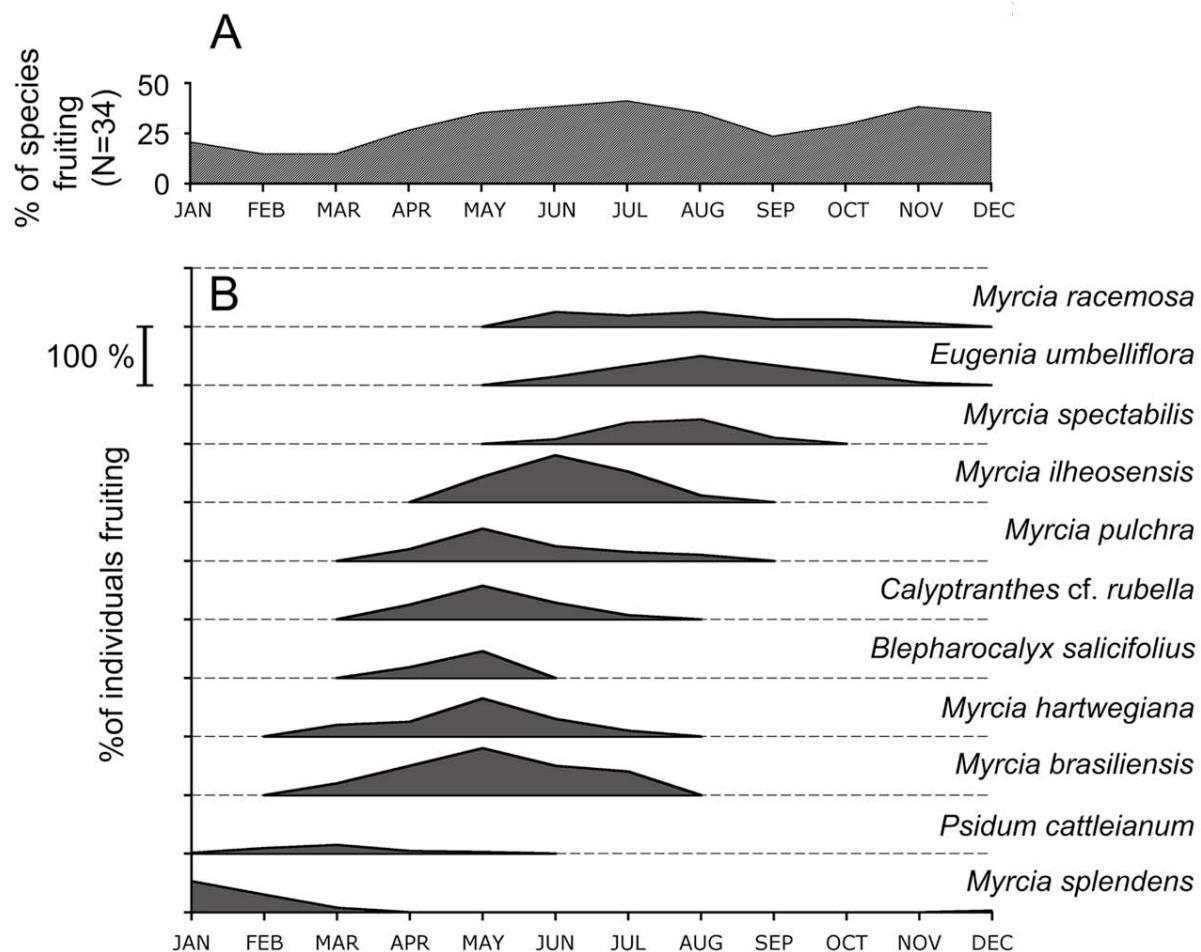
Fig 3.

|	Myrcia splendens	Blepharocalyx salicifolius	Myrcia ilheosensis	Eugenia umbelliflora	Myrcia pulchra	Calyptranthes cf. rubella	Myrcia brasiliensis	Myrcia spectabilis	Psidium cattleianum	Myrcia hartwegiana	Species Strength
Turdus albicollis			19.5	16.6		81.4	47.5	50.0			2.150
Turdus rufiventris	45.0	5.3	0.4	16.6	71.1						1.383
Elaenia obscura				11.3						78.9	0.902
Turdus flavipes		2.3	27.3	11.3				8.3	5.3		0.544
Cyanocorax caeruleus									52.6		0.526
Turdus amaurochalinus	4.6		3.4	25.8	18.5						0.523
Euphonia violacea		44.4			0.6					5.3	0.502
Ramphocelus bresilius	3.7				0.6				42.1		0.464
Ramphastos vitellinus							35.0				0.350
Patagioenas plumbea			26.1								0.261
Chiroxiphia caudata			0.4		0.6			25.0			0.260
Thraupis sayaca	4.7	15.8		0.7			2.5				0.236
Tangara seledon		2.3	0.1			12.4		8.3			0.231
Tangara cyanocephala		10.5	6.1			5.4					0.220
Tangara peruviana				1.3	0.6					15.8	0.177
Myiarchus ferox	12.3	3.8									0.160
Procnias nudicollis				5.3			10.0				0.153
Pitangus sulphuratus	2.6		2.5	7.3							0.124
Myiarchus swainsoni	11.4										0.114
Thraupis cyanoptera			7.4	1.3	2.3						0.110
Myiarchus tyrannulus	9.1		0.8								0.099
Thraupis palmarum	3.7	6.0									0.097
Habia rubica								8.3			0.083
Tachyphonus cristatus	0.6						5.0				0.056
Penelope superciliaris			5.0								0.050
Manacus manacus			0.2		4.6						0.048
Euphonia pectoralis		4.5									0.045
Parula pitiayumi		2.3									0.023
Tyrannus melancholicus	1.2	0.8									0.020
Dacnis cayana		1.5	0.3								0.018
Myiozetetes similis				1.3							0.013
Vireo olivaceus	1.0										0.010
Trogon viridis						0.8					0.008
Celeus flavescens		0.8									0.008
Megarynchus pitangua			0.7								0.007
Rhytipterna simplex				0.7							0.007
Tachyphonus coronatus				0.7							0.007
Euphonia cyanocephala					0.6						0.006
Phylloscartes kronei					0.6						0.006
Zonotrichia capensis	0.1										0.001
Species Strength	9.22	7.02	6.67	5.41	3.61	1.99	1.97	1.78	1.34	1.00	

Fig 4.
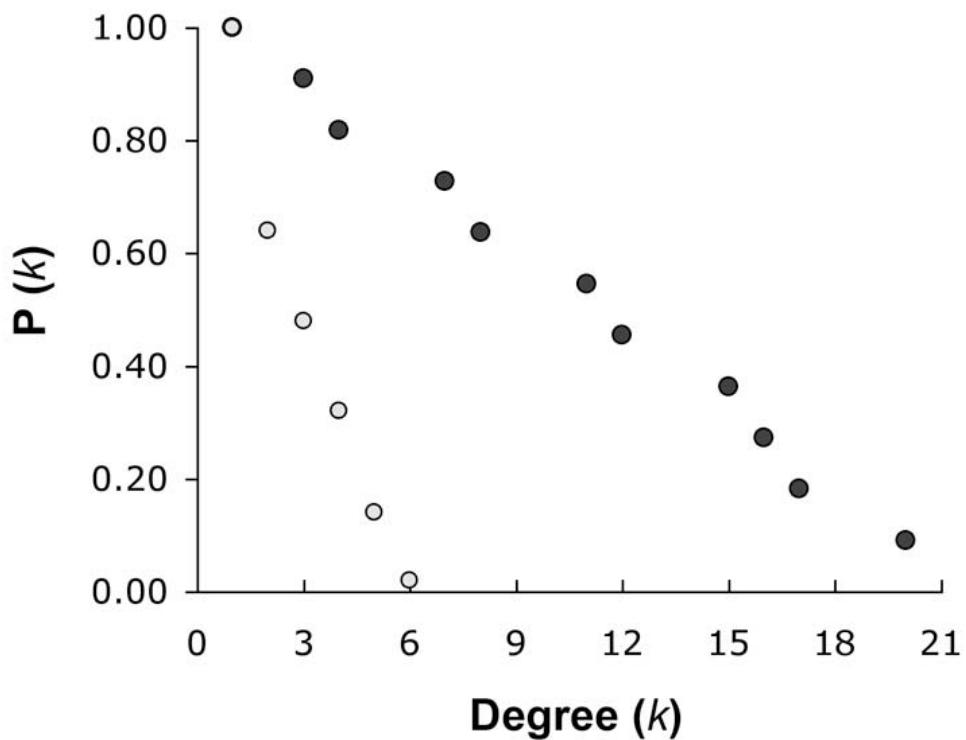
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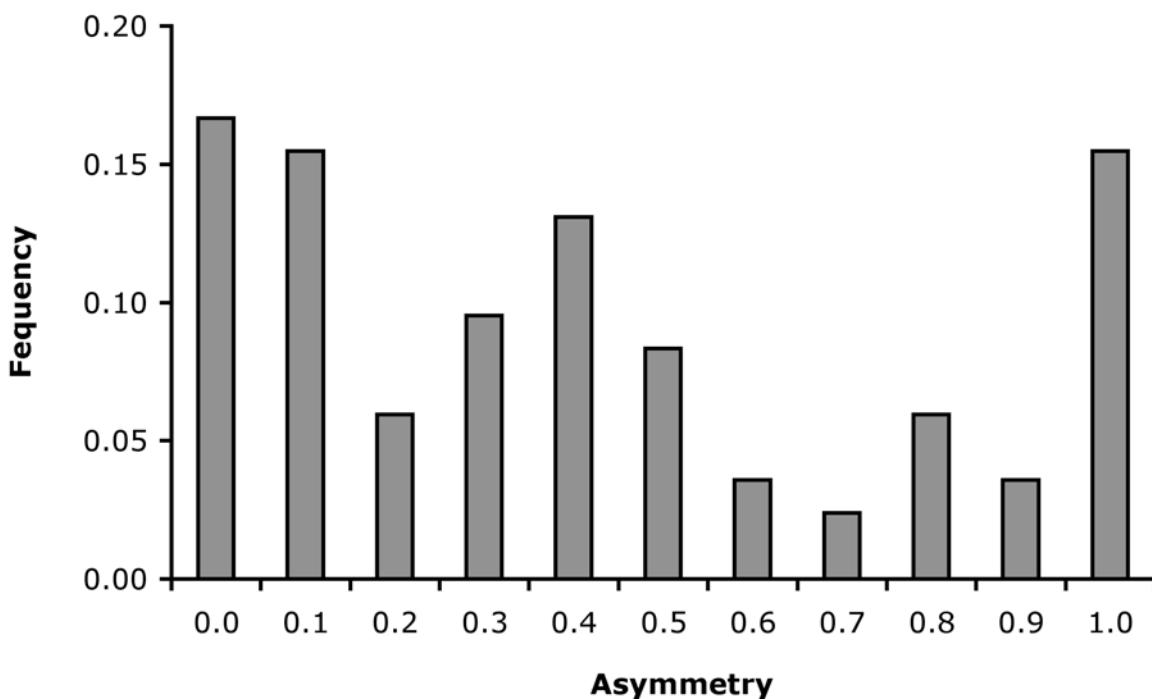
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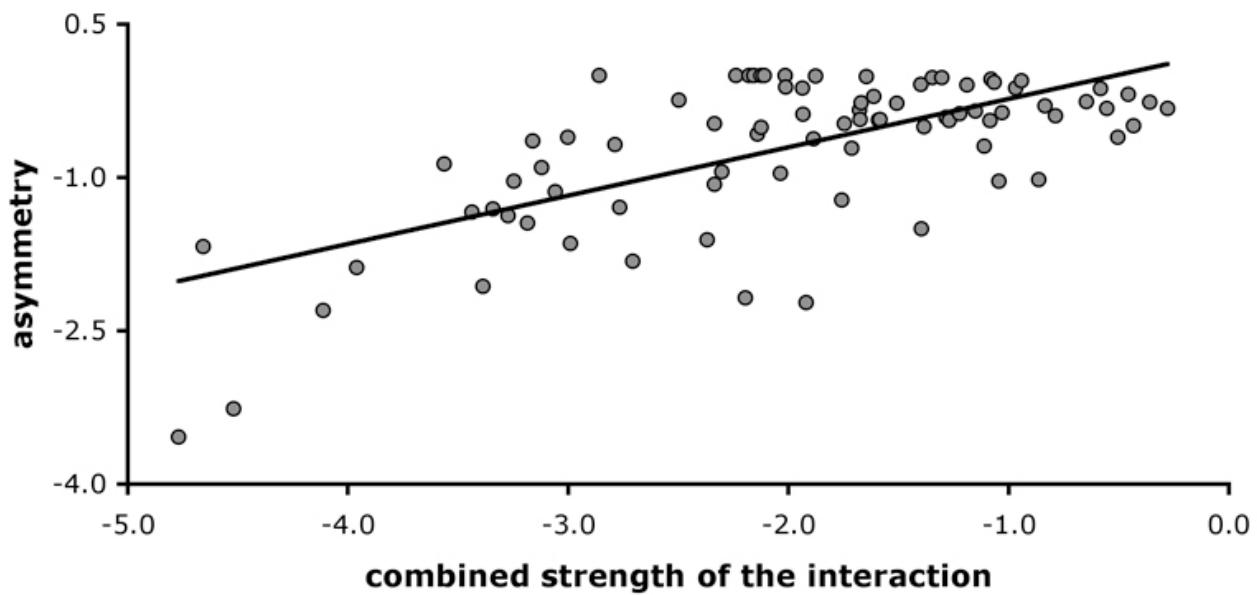
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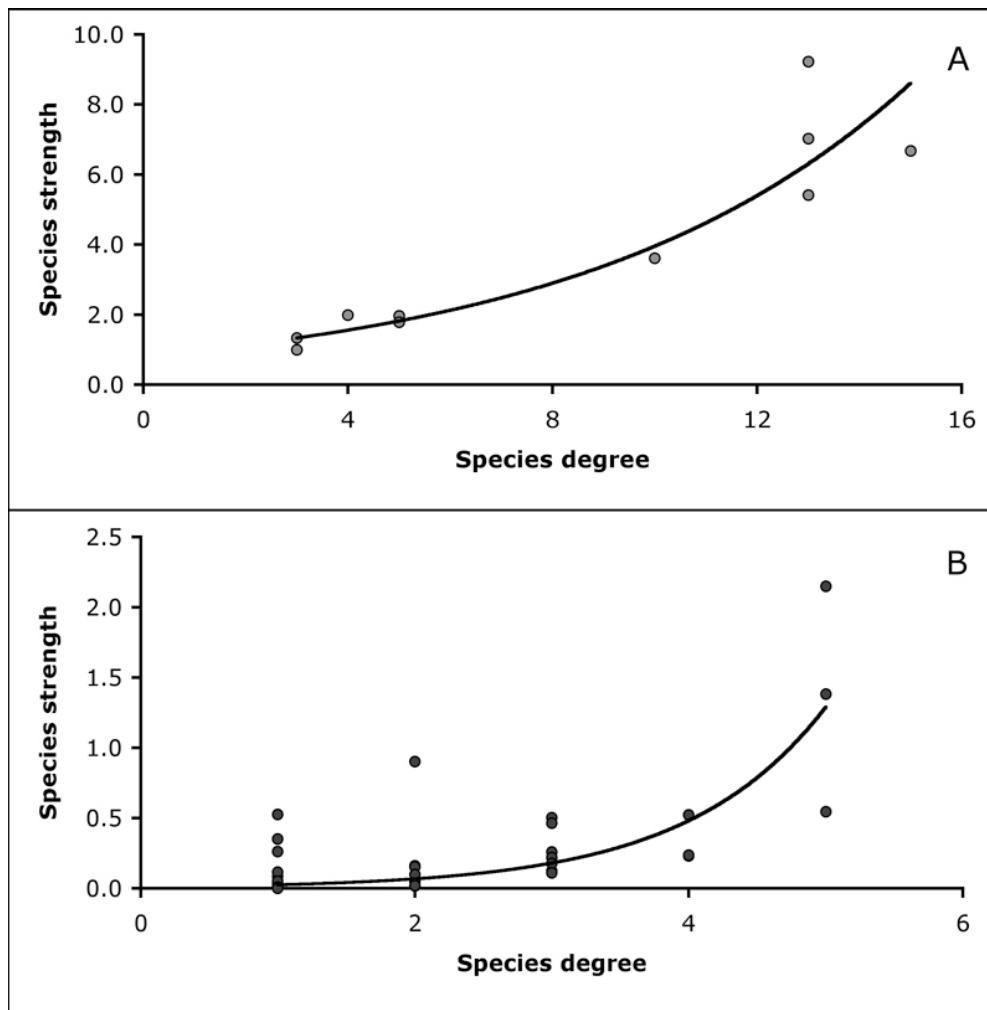
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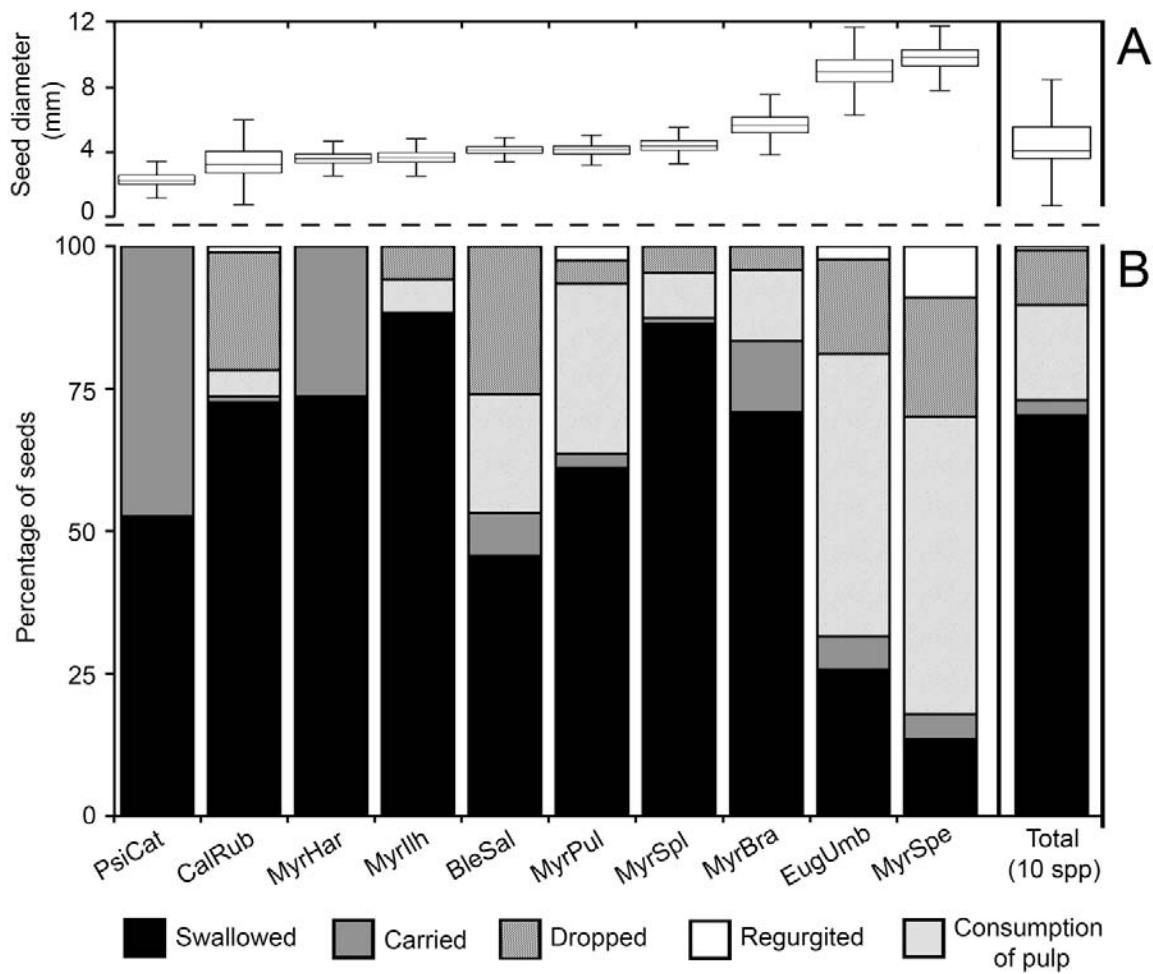
Fig 9.
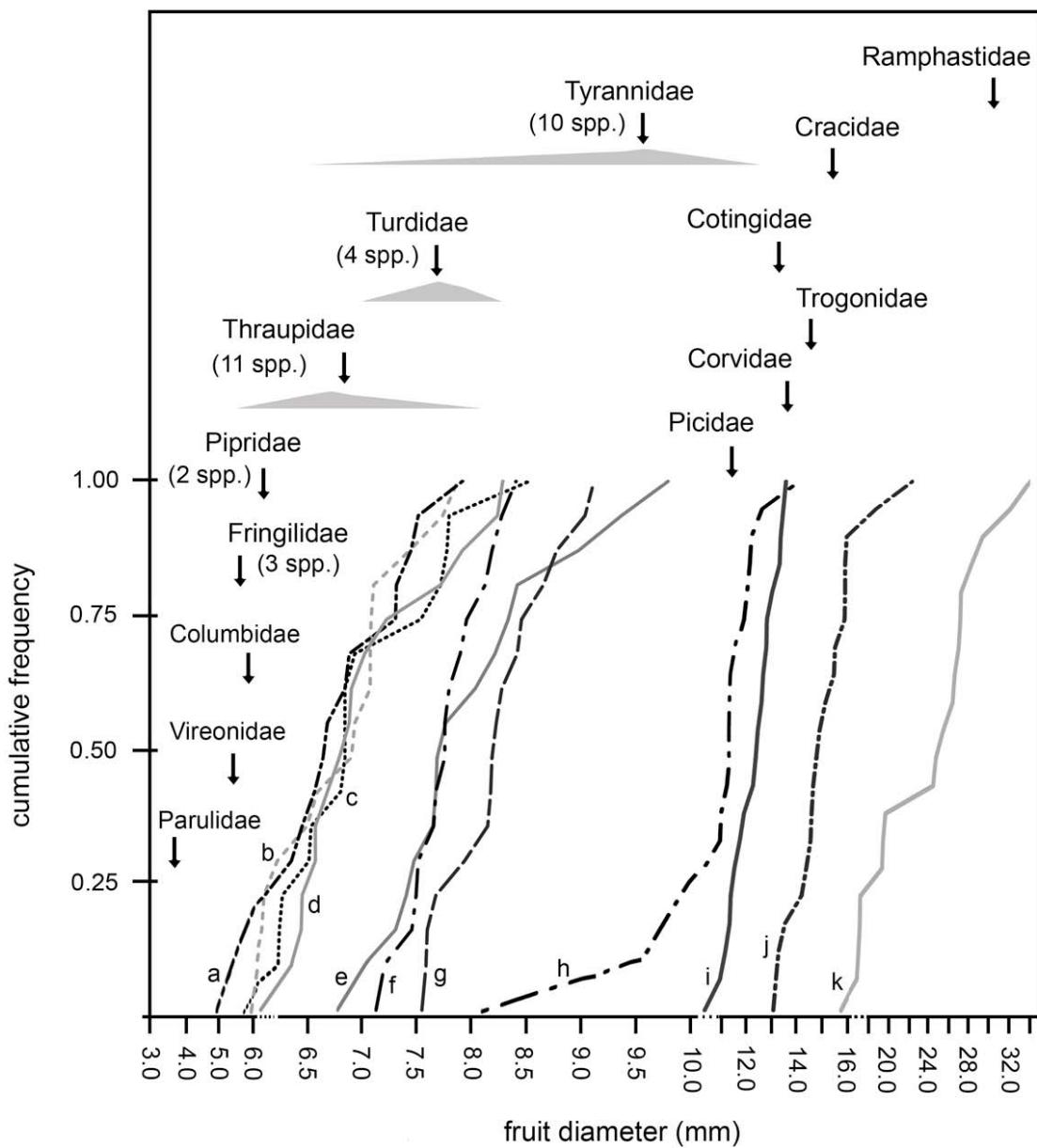
CONCLUSÕES E CONSIDERAÇÕES FINAIS

Essa dissertação esclareceu aspectos desencadeadores e restritivos dos padrões reprodutivos em Myrtaceae, contribuindo, desse modo, para o entendimento dos aspectos que regulam a reprodução das espécies em ambientes sem sazonalidade climática. Mais especificamente contribuiu para o entendimento estrutural das interações bióticas entre Myrtaceae e aves, apontando aspectos relevantes para a conservação das espécies. As conclusões deste trabalho e direções para estudos futuros podem ser assim resumidas:

1.   *A fenologia de Myrtaceae foi sazonal? Os padrões de floração e frutificação são relacionados à mudanças nos fatores abióticos (precipitação, temperatura e comprimento do dia?*

A floração em Myrtaceae foi sazonal, com pico de espécies em botões e flores entre os meses de dezembro e janeiro. O fator desencadeador da floração foi o aumento no comprimento do dia, relações com a temperatura foram de um modo geral, fracas e não houve relações entre a reprodução das espécies e as variações mensais de precipitação.

A frutificação de Myrtaceae não apresentou sazonalidade. Não houve evidências que apontassem para a influência do clima no padrão de frutificação. Frutos foram encontrados durante todo o período de estudo em diferentes intensidades ao longo do ano e sem um padrão definido.

Em ambientes sem sazonalidade climática com relação à temperatura e sem restrição hídrica ao longo do ano é esperado que outros fatores sejam relacionados à

reprodução das espécies. Quanto maior a distância em relação à linha do Equador, maior é a variação no comprimento do dia (Borchert *et al.* 2005). Desse modo o comprimento do dia seria o único mecanismo confiável para induzir maior sincronia na floração das espécies em ambientes sem estações climáticas definidas (Bollen e Donati 2005, Borchert *et al.* 2005).

2. *Qual a importância dos fatores ambientais (relacionados ao clima) e filogenéticos na determinação dos padrões reprodutivos desta família?*

A variação do padrão fenológico da família está associada às condições ambientais (de comprimento do dia, precipitação e temperatura) que caracterizam o momento do ano no qual elas se reproduzem, e este nicho reprodutivo está filogeneticamente estruturado devido à história compartilhada de origem e evolução dessas espécies no mesmo ambiente (Floresta Atlântica) (Lucas *et al*. 2007). Espécies aparentadas vivendo num mesmo ambiente tendem a responder do mesmo modo na presença de pressões seletivas (Harvey e Pagel 1991), então não é possível separar se uma adaptação similar a uma determinada pressão seletiva é similar devido ao compartilhamento do mesmo nicho ecológico ou a uma limitação filogenética que atua na resposta das espécies.

Esse foi o primeiro estudo a abordar a partição da resposta fenológica em um componente filogenético, outro ambiental e o compartilhamento de ambos. Demonstramos a importância de considerar essa partição de variação em estudos fenológicos, pois quando esta não é considerada, os resultados obtidos podem guiar a

conclusões biologicamente equivocadas de que, por exemplo, a filogenia tem um papel importante na reprodução das espécies, quando de fato não é possível distingui-lo. Esse resultado abre novas avenidas para o estudo da resposta fenológica de mesmas espécies que evoluíram sob pressões seletivas distintas (mesmas espécies ocorrendo em diferentes habitats), pois esse contexto de estudo permitirá separar a maior explicação devido à um conservantismo filogenético, caso de fato ele exista.

3. *Padrões coincidentes ou divergentes ocorrem na floração e frutificação de espécies que compartilham o mesmo grupo de polinizadores ou dispersores? Esse padrão pode ser resultante de processos como competição ou facilitação?*

A floração das espécies foi agrupada e esse padrão pode ser decorrente da existência de uma época mais favorável à polinização das espécies (Morellato e Leitão-Filho 1996, Sakai 2001). Não é possível distinguir entre competição e facilitação, são necessários estudos futuros detalhados sobre os polinizadores, a polinização e o sucesso reprodutivo das espécies nesse período de elevada sobreposição fenológica.

O padrão de frutificação não diferiu do acaso. A constância da frutificação (no sentido de sempre haver espécies ofertando frutos maduros durante o ano) pode estar associada à manutenção dos frugívoros na área de estudo, aumentando a confiabilidade da interação planta-dispersor, sendo uma estratégia da planta para sustentar animais dispersores residentes (Wheelwright 1985).

*4.	Há alguma evidência de qualquer influência das características morfológicas reprodutivas (de flores e frutos) na fenologia das espécies?*

Sim, o tempo de desenvolvimento dos frutos é afetado pelo tamanho das sementes. Sementes maiores necessitam de mais tempo para completar sua formação. E o tempo de desenvolvimento dos frutos está relacionado à fenologia de floração, de modo que espécies que investem mais tempo na maturação de seus frutos florescem no fim da estação de floração propícia. Apesar das espécies florescerem em maior intensidade numa determinada época do ano, essa diferença na seqüência de floração esclarece o padrão da constância de frutificação das espécies ao longo do ano.

*5.	O que caracteriza a composição das espécies de plantas e animais envolvidos na rede de dispersão de sementes de Myrtaceae?*

As espécies de plantas e aves variaram bastante com relação às suas características morfológicas e aos seus "ranks" de abundância. 12% das espécies de aves que interagiram com Myrtaceae estão ameaçadas ou vulneráveis à extinção. Sendo necessário portanto em um estudo futuro para avaliar as conseqüências da perda dessas espécies na efetiva dispersão de sementes de Myrtaceae. As aves que interagiram com as Myrtaceae são, em geral, generalistas quanto à sua dieta, utilizando invertebrados ou néctar como parte da sua alimentação.

6.   *Há qualquer padrão de especialização ou generalização nas espécies estudadas em relação ao número de espécies com as quais elas podem interagir? O que determina o nível de especificidade dessas interações?*

Sim, a rede apresentou uma estrutura aninhada, com fracas interações e baixa assimetria. A implicação do aninhamento é a de que as espécies especialistas da rede (aquelas que interagem com menos espécies) interagem com um subconjunto das espécies mais generalistas (aquelas que interagem com muitas outras espécies), interações especialista-especialista são raras. Segundo Bascompte *et al.* (2003) e Thompson (2005) essa estrutura confere robustez à rede, onde um conjunto de interações generalistas-generalistas pode permitir que as interações especializadas persistam. Na rede Myrtaceae-frugívoros as espécies de aves mais generalistas foram as mais abundantes, esse parece ser um padrão geral encontrado em outros estudos (e.g. Dupont *et al.* 2003). Sob o ponto de vista das Myrtaceae, encontramos que as espécies mais generalistas são aquelas que ofertam um número maior de frutos. Portanto, nossos níveis de generalização e especialização estão sendo moldados pela abundância de aves e pela safra das espécies de Myrtaceae.

7.   *Como são diferenciados os frugívoros em relação aos seus padrões de visitação, remoção de frutos e probabilidade de dispersão de sementes?*

As maiores taxas de visitação e remoção de frutos foram explicadas pela abundância das espécies de aves e pela safra das plantas. A probabilidade de remoção

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com sucesso está intimamente associada à morfologia das aves e das sementes (Wheelwright 1985; Cortes *et al.* 2008). Frutos que portam sementes menores tiveram maior chance de serem manipulados com sucesso e aves com maiores tamanho de bico e peso corpóreo tiveram maior chance de engolir ou carregar os frutos para longe da planta mãe onde as taxas de germinação e estabelecimento podem ser mais altas.

8. *Quais características distinguem os frugívoros mais fortes dos mais fracos na rede estudada?*

A relativa importância de cada frugívoro para a dispersão de sementes das plantas varia grandemente entre as espécies de aves (Jordano e Schupp 2000, Godínez-Alvarez *et al.* 2002, Jordano *et al.* 2007). Os frugívoros mais fortes foram aqueles que interagiram com muitas espécies de Myrtaceae, mas interagiram de modo fraco com estas plantas. As espécies mais fortes foram as aves da família Turdidade e as plantas com maior taxa de efetiva dispersão foram *Myrcia splendens*, *Myrcia ilheosensis* e *Blepharocalix salicifolius*. As espécies de *Turdus* mostraram ser os melhores agentes da dispersão, tornando essas aves fundamentais para a manutenção de Myrtaceae em Floresta Atlântica, especialmente na vegetação de restinga, a qual historicamente tem sido a primeira área desse bioma a sofrer as consequências da expansão humana (Souza e Capellari-Jr 2004). Do ponto de vista da conservação de ecossitemas tropicais, em especial da Floresta Atlântica, este estudo evidência a importância das aves de pequeno porte na manutenção do processo de dispersão de sementes em ecossistemas ameaçados. Avaliar as consequências globais dentro do contexto de efetividade de dispersão pode prover maior compreensão e uma avaliação mais realística dos diferentes dispersores.

Essa aproximação representa um melhor entendimento das interações ave-planta e seus fundamentais processos ecológicos e evolutivos. Portanto essas perspectivas devem ser consideradas em estudos futuros, especialmente aliadas à abordagem de redes complexas.

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