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**“Distribuição geográfica, filogenia, morfologia e evolução da
dispersão de Bignonieae (Bignoniaceae)”**

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UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

ANDRÉ LUÍS CASARIN ROCHELLE

**“DISTRIBUIÇÃO GEOGRÁFICA, FILOGENIA, MORFOLOGIA E
EVOLUÇÃO DA DISPERSÃO DE BIGNONIEAE
(BIGNONIACEAE)”**

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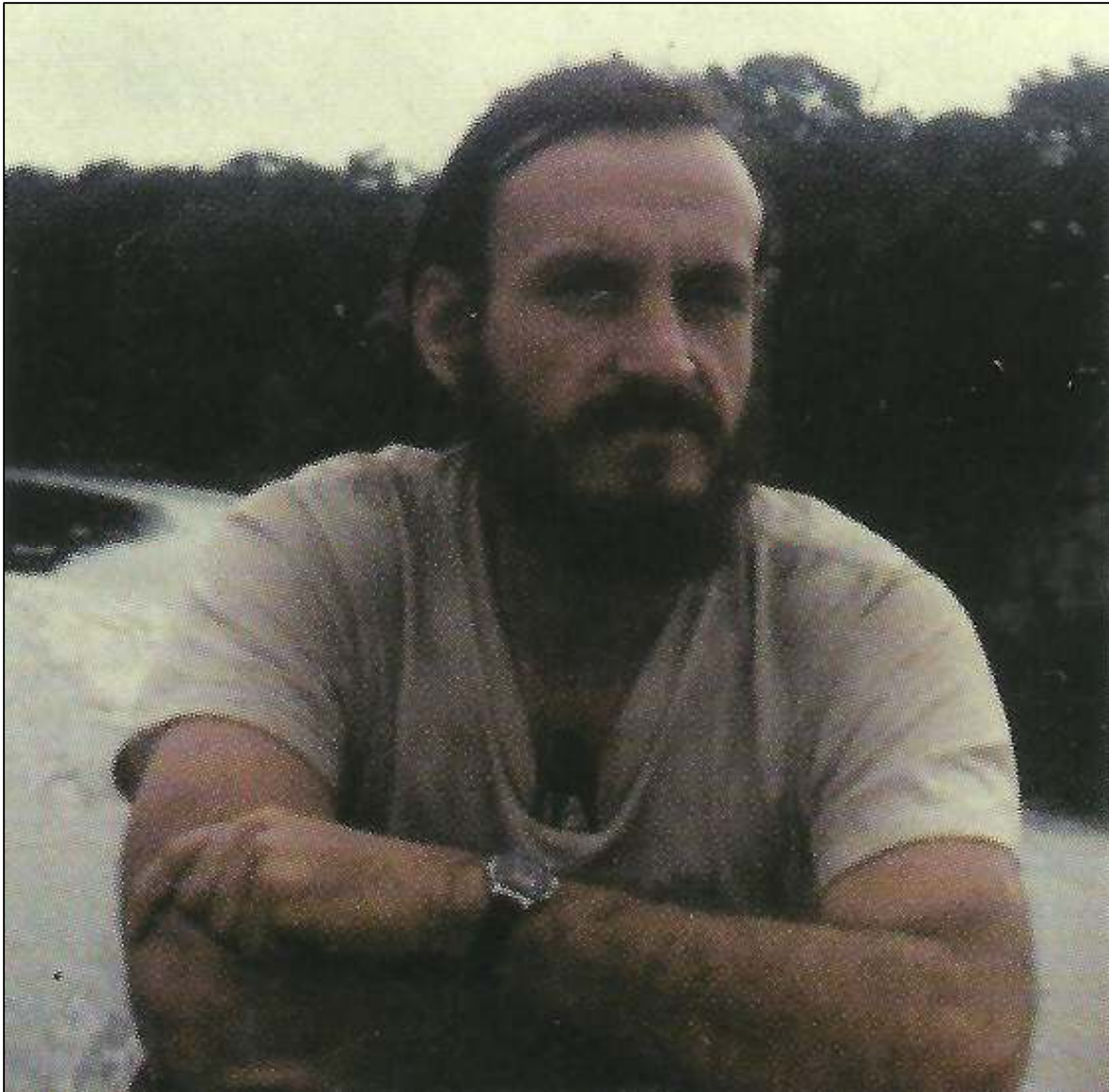
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em memória de Alwyn Howard Gentry (1945 - 1993)

Al Gentry foi uma incomparável autoridade em ecologia de florestas tropicais e um dos maiores exploradores botânicos de todos os tempos. Seus estudos sobre a família Bignoniaceae e seus estudos ecológicos sobre diversidade de florestas tropicais mudaram a maneira como biólogos pensam sobre florestas tropicais e sua conservação.

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**“Se pude enxergar mais longe,
foi porque estava sobre os ombros de gigantes”**

Sir Isaac Newton (1643-1727)

Dedico este trabalho a dois grandes cientistas e botânicos do século XX: John Christopher Willis (1868 - 1958) e Alwyn Howard Gentry (1945 - 1993).

RESUMO GERAL

Integramos biogeografia, ecologia, filogenia e evolução da tribo Bignonieae (Bignoniaceae) para testar as seguintes hipóteses: (1) a área de distribuição geográfica das espécies é positivamente relacionada com sua idade filogenética, conhecida como "hipótese da idade e área", formulada por J.C. Willis, em 1922 que prevê que espécies antigas ocupariam maiores áreas de distribuição enquanto espécies recentes ocupariam menores áreas (endêmicas); (2) área de distribuição geográfica das espécies é positivamente relacionada com o potencial de dispersão anemocórico das sementes; e (3) o potencial de dispersão anemocórico é negativamente relacionado com a idade filogenética das espécies. Realizamos experimentos em túnel de vento para mensurar o potencial de dispersão anemocórico das sementes medindo sua distância de voo (SFD) e investigamos sua relação com oito atributos morfológicos biomecânicos - tamanho total (STS), tamanho do núcleo seminal (SNS), tamanho das alas (SWS), massa (SM), área (SA), razão entre tamanho do núcleo seminal e tamanho da asa (SNS/SWS), razão entre massa e tamanho da asa (SM/SWS) e razão entre massa e área (SM/SA). Analisamos a relação entre as características biomecânicas das sementes responsáveis por um maior potencial de dispersão com a idade filogenética das espécies e sua distribuição geográfica para investigar a evolução dos caracteres relacionados a maior habilidade de dispersão. Realizamos experimentos para verificar diferenças na morfologia e no potencial de dispersão das sementes de herbário em comparação com sementes coletadas em campo, visando validar estudos com sementes herborizadas. Não encontramos relação entre idade filogenética e área de distribuição. Esta relação parece ser influenciada pela diferença na eficiência de dispersão das espécies, apontada como um importante fator na distribuição, especialmente em espécies anemocóricas. 83% das espécies apresentaram correlação entre variáveis morfológicas e SFD. A razão SM/SA apresentou a maior correlação com SFD (36 espécies). SWS e SA apresentaram correlação positiva com SFD. SNS/SWS e SM/SA apresentaram correlações negativas com SFD, demonstrando que características morfológicas das sementes influenciam seu potencial de dispersão, principalmente massa e área. SFD apresentou correlação positiva com área de distribuição e negativa com idade. SNS apresentou correlação positiva com idade. SM/SA apresentou correlação positiva com idade e negativa com área de distribuição. Os resultados mostraram que espécies com sementes de maiores capacidades de voo possuem maiores áreas de distribuição e são mais recentes, evidenciando uma possível seleção no sentido da redução do núcleo seminal que diminuiu a massa das sementes e consequentemente reduziu a razão massa/área, aumentando a capacidade de voo e o potencial de dispersão da espécie. Inferimos que características morfológicas biomecânicas podem ter sido selecionadas no sentido de aprimorar o potencial de dispersão das sementes, principalmente na combinação entre sua massa e área, favorecendo as espécies mais jovens, possibilitando uma dispersão mais eficiente e a expansão da sua distribuição. Complementarmente, demonstramos que o processo de herborização não afeta significativamente os caracteres morfológicos e a distância de voo das sementes, validando os dados gerados pelo nosso experimento. Conhecimentos sobre distribuição de espécies são

importantes para a conservação na região tropical onde a megadiversidade é composta majoritariamente por espécies endêmicas.

Palavras-chave: área de distribuição, biomecânica, características morfológicas, distância de dispersão, distância de voo de sementes, distribuição geográfica, idade filogenética, potencial de dispersão, semente anemocóricas, sementes aladas.

ABSTRACT

We integrated biogeography, ecology, phylogeny and evolution of the tribe Bignonieae (Bignoniaceae) to test the hypothesis that: (1) geographic range size is positively related with species phylogenetic age - the "Age and Area Hypothesis" - formulated by J.C. Willis (1922) and which states that older species would have larger geographic range sizes because they had more time to disperse while younger species would have smaller geographic range sizes; (2) range size is positively related with seed wind dispersal potential; and (3) wind dispersal potential is negatively correlated with species age. We used a wind tunnel to experimentally measure the seed wind dispersal potential measuring the seed flight distance (SFD). We analyzed the correlations of SFD with: seed total size (STS), seminal nucleus size (SNS), seed wing size (SWS), seed mass (SM), seed area (SA), ratio SNS/SWS, ratio SM/SWS, and ratio SM/SA. We analyzed the correlations between seed morphological traits related to wind dispersal potential with species phylogenetic age and their extant geographic range size to investigate a possible evolution of the traits related to an improved dispersal. We conducted an experiment to check if there are significant changes in morphology and flight potential in anemochoric seeds before and after herborization, aiming to validate experiments realized with herbarium seeds. We found no correlation between species phylogenetic age and their geographic distribution area. This relationship found for other taxonomic groups could have been affected here by species dispersal ability, which is an important driver of geographic distribution, especially in wind-dispersed species. 83% of the species had at least one variable correlating with SFD. Ratio SM/SA showed correlation with SFD in 36 species. Considering all the species together, SWS and SA showed positive correlation with SFD. Ratios SNS/SWS and SM/SA showed negative correlations with SFD. Results showed that seed morphological traits are correlated with wind dispersal potential, especially seed mass and area. Seed dispersal distance was positively correlated with the extant geographic range size, and negatively correlated with species phylogenetic age. SNS showed positive correlation with age, and ratio SM/SA showed positive correlation with age and negative correlation with geographic range size. Results indicate that species that have seeds with higher flight capacities are more recent phylogenetically and have larger geographic range sizes. It suggests a selection towards the reduction of the SNS, which reduced the seed mass and therefore their ratio SM/SA, increasing their flight ability and colonizing potential. We infer that some seed morphological traits may have been selected in order to improve seed dispersal potential, especially in the trade-off between seed mass and seed area. Therefore, it benefited younger species enabling them to disperse over larger areas in less time. Complementarily, we showed that herborization does not significantly affect seed morphological traits neither their flight distance, validating the data generated with experiments realized with Bignonieae herbarium seeds. Knowledge about the factors that shape species distribution is important for conservation, especially for the tropical region where the megadiversity is composed in most part by species with small distribution areas (endemics).

Keywords: anemochoric seeds, biomechanical traits, dispersal distance, dispersal potential, geographic distribution, morphological traits, phylogenetic age, range size, seed flight distance, seed traits, winged seeds.

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CONSIDERAÇÕES INICIAIS

Este é um estudo que integra Biogeografia, Ecologia, Filogenia e Evolução. Pode-se dizer que o assunto abordado nessa tese teve início em 1922, com a publicação da "Hipótese da Idade e Área" de John Christopher Willis (Willis, 1922), ou até mesmo antes disso, pois a questão principal que direciona as ideias desenvolvidas aqui trata-se de uma das questões mais antigas e fundamentais da Ecologia: Quais fatores controlam a distribuição das espécies no espaço e no tempo ?

A parte biogeográfica se apoia em um vasto banco de dados, resultado do trabalho de toda a vida de um dos maiores botânicos e cientistas que o mundo já teve, Alwyn Howard Gentry que ao longo de 28 anos de uma produtiva carreira científica coletou aproximadamente 80.000 espécimes nos 5 continentes, mas concentrou seus esforços nas impressionantes florestas da América do Sul. Além disso, sua especialidade era a família Bignoniaceae, a família que escolhemos para conduzir este estudo.

A parte ecológica refere-se aos experimentos conduzidos em um túnel de vento para mensurar o potencial de dispersão de espécies da tribo Bignonieae (Bignoniaceae) e suas correlações com os atributos morfológicos biomecânicos apresentados pelas suas sementes.

A parte filogenética se apoia no trabalho de pesquisa de uma renomada sistemata brasileira, a Dra. Lúcia G. Lohmann que evidenciou as relações filogenéticas de um dos grupos de plantas mais diversos e amplamente distribuídos da América Neotropical, a tribo Bignonieae (Bignoniaceae).

A parte evolutiva é representada pelas ideias apresentadas no capítulo 3 que relacionam as características seminais responsáveis por um maior potencial de dispersão com a distribuição geográfica atual e com a idade filogenética das espécies.

Mas não seria justo adentrarmos nos textos técnicos e científicos que compõem os capítulos adiante, sem ao menos mencionar parte da retrospectiva histórica que esta por trás tanto das ideias que nortearam a maior parte deste trabalho quanto de boa parte dos dados utilizados para testá-las.

A Hipótese da Idade e Área foi publicada originalmente em 1922, mas possui suas origens antes disso, em uma série de publicações do próprio Willis (Willis, 1918) e de outros grandes nomes da Biologia e Ecologia do início do século XX, como por exemplo Hugo De Vries (De Vries, 1918) e Olof Arrhenius (Arrhenius, 1921). Segundo essa hipótese, a área de distribuição geográfica ocupada por uma espécie seria uma função de sua idade, ou seja, espécies mais antigas ocupariam maiores áreas de distribuição, pois elas teriam tido mais tempo para se dispersar por grandes áreas enquanto espécies mais recentes, portanto mais jovens, ocupariam áreas menores (endêmicas), pois não teriam tido tempo suficiente para expandir sua distribuição por áreas maiores.

A hipótese causou grande polêmica e não foi muito bem aceita na época, gerando bastante repercussão em uma série de artigos subsequentes (Willis, 1923; Fernald, 1924; Yule, 1925), sendo inclusive ridicularizada por alguns autores (Gleason, 1924). Os opositores das ideias de Willis levantavam questões sobre regiões com antigas floras que ocupam áreas geograficamente restritas na América do Norte (Fernald, 1924).

Willis continuou a desenvolver suas teorias e anos mais tarde publicou a obra de onde veio grande parte de sua fama, o livro "The Course of Evolution by Differentiation or Divergent Mutation rather than by Selection" (Willis, 1940) que apresenta uma teoria da evolução antagônica a teoria da seleção natural de Darwin (Darwin, 1859) e nada mais é que uma extensão dos conceitos iniciados com a hipótese da idade e área (Wright, 1941).

Infelizmente, as ideias de Willis foram desenvolvidas em uma época em que ainda não haviam sido desenvolvidas as técnicas de datação de fósseis, iniciadas somente em 1947 pelo químico americano Willard Frank Libby (Arnold & Libby, 1949), nem as análises genéticas e moleculares que dispomos hoje. Portanto, a hipótese acabou caindo no esquecimento e até recentemente não havia sido testada diretamente com um grupo de plantas neotropicais. Até o momento, poucos estudos testaram formalmente a hipótese da idade e área com grupos de plantas neotropicais. Paul & Tonsor (2008) testaram a hipótese com espécies do gênero neotropical *Piper* (Piperaceae) e Paul *et al.* (2009) com espécies do gênero *Psychotria* (Rubiaceae).

Neste trabalho, utilizamos um vasto e importante grupo de plantas neotropicais, a tribo Bignonieae (Bignoniaceae) para testar algumas hipóteses biogeográficas e evolutivas relacionadas à idade filogenética das espécies, à sua área de distribuição geográfica e à morfologia das sementes no decorrer do surgimento e desenvolvimento das diferentes espécies do grupo, incorporando alguns elementos como dados sobre o potencial de dispersão anemocórica das sementes obtidos em um experimento realizado em túnel de vento.

INTRODUÇÃO GERAL

A distribuição atual de uma espécie sobre a superfície terrestre é frequentemente um fenômeno muito complexo, pois elas apresentam grande variação em suas distribuições geográficas, apresentando desde distribuições amplas até muito restritas (Lester *et al.* 2007). Mesmo espécies intimamente relacionadas podem apresentar áreas de distribuição muito distintas (Brown *et al.*, 1996).

As variáveis que controlam a distribuição das espécies sempre foram um dos temas centrais em Ecologia, especialmente na região neotropical que abriga aproximadamente 70% das espécies do planeta (MMA, 1999). Os fatores que determinam essa distribuição são resultantes da interação de muitas variáveis, algumas vezes inerentes à própria espécie, outras vezes relacionadas ao ambiente que a cerca e muitas vezes possuindo componentes de ambos (Willis, 1923).

Uma grande variedade de fatores ecológicos e evolutivos tem sido utilizada para explicar as variações nas amplitudes de distribuição geográfica de diferentes espécies (Willis, 1922; Brown & Kodric-Brown, 1977; Hansen, 1980; Brown, 1984; Stevens, 1989; Oakwood *et al.*, 1993; Edwards & Westoby, 1996; Gaston, 1996; Thompson *et al.*, 1999; Brandle *et al.*, 2002; Lloyd *et al.*, 2003; Lester *et al.*, 2007). No entanto, os fatores exatos que determinam essas variações ainda permanecem desconhecidos.

Estudos sobre o padrão de variação na distribuição das espécies em diferentes grupos taxonômicos e em diferentes regiões do planeta frequentemente relacionam as variações na distribuição das espécies com variáveis ambientais (Stevens, 1989; Brandle *et al.* 2002) ou com

variáveis biológicas das próprias espécies, como caracteres fisiológicos ou morfológicos (Edwards & Westoby, 1996; Lester *et al.*, 2007).

Entre os fatores propostos para explicar a variação na distribuição geográfica das espécies estão: a amplitude de nichos (Thompson *et al.*, 1999), variabilidade e tolerância ambiental (Gaston, 1996; 2003), tamanho corporal (Gutierrez & Menendez, 1997), tamanho populacional (Brown, 1984; Brown *et al.*, 1996), efeitos latitudinais (Stevens, 1989), dinâmica de colonização/extinção (Brown & Kodric-Brown, 1977; Hanski, 1999) e eficiência de dispersão (Lester *et al.*, 2007). Entretanto, nenhum desses fatores emergiu até o momento como um condicionante universal da extensão da distribuição geográfica das espécies.

A relação entre a amplitude da distribuição geográfica de um táxon com a sua idade foi inicialmente proposta pela hipótese da “idade e área” (Willis, 1922) que estabelece que espécies mais antigas teriam áreas de distribuição geográfica mais amplas, pois teriam tido mais tempo para se dispersar por grandes áreas, enquanto espécies mais recentes, teriam áreas de distribuição menores. No entanto, apesar de essa hipótese ter causado alvoroço científico na época (Matthews, 1922; Willis & Yule, 1922; Willis, 1923), a falta de grupos com filogenias robustas impossibilitou seu teste por muito tempo.

Paralelamente, teorias que relacionam a amplitude de distribuição geográfica dos táxons com caracteres morfológicos dos diásporos e a eficiência de sua dispersão sugerem que quanto maior a eficiência na dispersão do propágulo, maior será a amplitude de distribuição da espécie (Hanski *et al.*, 1993; Brown *et al.*, 1996; Gaston, 1996; 2003). Esta habilidade ou eficiência de dispersão é invocada como uma explicação para a variação na amplitude de distribuição das espécies tanto em sistemas terrestres quanto em sistemas marinhos e para uma grande variedade

de grupos taxonômicos, incluindo insetos (Gutierrez & Menendez, 1997; Malmqvist, 2000; Brandle *et al.*, 2002), plantas (Oakwood *et al.*, 1993; Edwards & Westoby, 1996; Thompson *et al.*, 1999; Clarke *et al.*, 2001; Lloyd *et al.*, 2003; Lowry & Lester, 2006) e moluscos (Hansen, 1980; Jablonski, 1986; Pfenninger 2004).

No Reino Vegetal, caracteres associados aos diásporos podem influenciar na distribuição das espécies por estarem relacionados com uma maior ou menor eficiência na dispersão, uma vez que diferentes estratégias podem levar a uma dispersão mais ou menos eficiente. Por exemplo, algumas espécies podem produzir uma grande quantidade de sementes pequenas e ampliar sua capacidade de colonização, enquanto outras podem produzir uma pequena quantidade de sementes grandes e apresentar menor taxa de mortalidade na fase de plântula, especialmente em ambientes com condições rigorosas (Jurado & Westoby, 1992; Milberg *et al.*, 1998; Coomes & Grubb, 2003; Khurana & Singh, 2004; Turnbull *et al.*, 2004; Baraloto *et al.*, 2005).

O conflito entre número e massa de sementes é um exemplo das muitas demandas conflitantes (“trade-offs”) descritas para diversas espécies de plantas (Westoby *et al.*, 1996; Leishman *et al.*, 2000; Moles & Westoby, 2004). Considerando um grupo de espécies filogeneticamente aparentadas, com o mesmo tipo de propágulo e o mesmo modo de dispersão, a variação espacial e temporal de atributos considerados biomecânicos, como a massa e o tamanho dos diásporos, pode estar relacionada com a habilidade de dispersão de cada espécie e com as pressões seletivas envolvidas na evolução da dispersão deste clado.

A família Bignoniaceae é uma família de plantas arbustivas, arbóreas e trepadeiras com distribuição pantropical (Lohmann, 2004). O centro de diversidade da família é na América tropical, onde possui aproximadamente 635 espécies distribuídas em 42 gêneros (Lohmann &

Ulloa, 2008). A família foi tradicionalmente dividida em oito tribos (Gentry, 1991), sendo quatro endêmicas da região Neotropical. Bignonieae representa uma das tribos endêmicas dos Neotrópicos, incluindo todas as lianas e arbustos neotropicais com cápsulas septicidas. Abrange cerca de 400 espécies distribuídas entre 21 gêneros (Lohmann & Taylor, 2013), sendo o maior clado de lianas dos Neotrópicos (Lohmann, 2006). Recentemente, a filogenia da tribo Bignonieae foi reconstruída com base em marcadores moleculares (Lohmann & Taylor, 2013), esclarecendo o parentesco entre as diversas linhagens do grupo. Além disso, registros fósseis foram incorporados à filogenia (Lohmann *et al.*, 2013), de forma que a idade de diversificação das diferentes linhagens dentro do grupo é conhecida.

Nesta tribo, além da robusta filogenia datada, calibrada por dados de registros fósseis, a maioria das espécies apresenta diásporos alados e dispersão primariamente anemocórica (Lohmann, 2004), o que a torna um modelo adequado para o presente estudo, pois nos permite quantificar experimentalmente a habilidade de voo das sementes e utilizar esse dado como um descritor do potencial de dispersão da espécie. Além da tribo ser monofilética, exclusivamente Neotropical, ela é amplamente distribuída do norte da Argentina e Chile ao sul dos Estados Unidos (Lohmann, 2006) e os seus membros ocorrem em uma grande variedade de habitats, desde ambientes muito secos (como o cerrado e a caatinga) até muito úmidos (como florestas atlânticas e amazônicas), exibindo uma grande variedade de padrões de distribuição (Lohmann *et al.*, 2013). Algumas espécies são localmente endêmicas enquanto outras são amplamente distribuídas nas 3 Américas. Algumas são restritas a um único habitat enquanto outras ocupam vários tipos de ambientes (Gentry, 1979). Estes fatores fazem de Bignonieae um excelente modelo para estudos biogeográficos neotropicais (Lohmann *et al.*, 2013).

Neste trabalho utilizamos uma filogenia datada da tribo Bignonieae (Bignoniaceae), junto com um vasto banco de dados contendo mais de 30.000 pontos georeferenciados de coleta das espécies e outro contendo as características morfológicas das sementes aliado a dados sobre o potencial de dispersão anemocórico das sementes gerados através de um experimento em túnel de vento para investigar as relações existentes entre a idade filogenética das espécies, sua área de distribuição geográfica e os atributos biomecânicos de suas sementes relacionados à eficiência de dispersão por anemocoria.

No capítulo 1, testamos formalmente a "Hipótese da Idade e Área" com a tribo Bignonieae (Bignoniaceae). Especificamente, testamos se as espécies filogeneticamente mais antigas, possuem uma maior área de distribuição geográfica em relação às espécies filogeneticamente mais recentes, como pressuposto pela teoria.

No capítulo 2, investigamos experimentalmente quais características morfológicas das sementes possuem relação com sua habilidade de dispersão por vento, através da mensuração da distância de voo das sementes em um experimento realizado em túnel de vento. Especificamente, testamos a relação entre o potencial de dispersão anemocórica das sementes aladas de 50 espécies com a variação de oito caracteres morfológicos considerados importantes na biomecânica da semente.

No capítulo 3, integramos os dados sobre a ecologia, a filogenia e a biogeografia das espécies analisadas em um contexto evolutivo e analisamos as relações entre as características morfológicas biomecânicas das sementes que estão relacionadas com um maior potencial de dispersão anemocórico com a idade filogenética e a área de distribuição geográfica das espécies para investigar uma possível evolução dos caracteres relacionados a uma maior habilidade de

dispersão. Especificamente, testamos as hipóteses que (i) a área de distribuição geográfica das espécies é positivamente correlacionada com a distância de voo das sementes, e (ii) a idade filogenética das espécies é negativamente correlacionada com a distância de voo das sementes.

No capítulo 4 realizamos um experimento para verificar se há diferenças na morfologia e no potencial de dispersão das sementes de herbário em comparação com sementes coletadas em campo, visando validar os resultados obtidos em nossos experimentos realizados com sementes herborizadas.

Os dados oriundos deste estudo fornecerão informações sobre os fatores que influenciam na distribuição das espécies em um dos grupos mais diversos e abundantes de plantas da região Neotropical. Além da importância ecológica da família Bignoniaceae, este grupo foi escolhido por constituir um modelo ideal e contar com grande parte dos dados necessários para testar as hipóteses de interesse.

A determinação das melhores maneiras para a manutenção e manejo da biodiversidade requer o conhecimento de como as espécies se distribuem no tempo e no espaço e dos fatores que influenciam na amplitude dessa distribuição (Gaston, 1994; IUCN, 1994). Além disso, a distribuição geográfica das espécies constitui uma das variáveis que descrevem seu grau de raridade (Rabinowitz *et al.*, 1986; Ricklefs, 2002), e sua susceptibilidade à extinção. Dessa forma, o conhecimento dos fatores que determinam a amplitude geográfica das espécies representa um passo imprescindível para fundamentar o planejamento de ações visando à conservação e o manejo sustentável das espécies.

Neste contexto, um melhor conhecimento das variáveis associadas à amplitude geográfica das espécies apresenta um grande potencial de ampla aplicação prática e teórica, pois pode

subsidiar o planejamento de ações para o manejo de recursos bióticos de modo sustentável, a conservação de espécies ameaçadas, o estabelecimento de unidades de conservação e a recuperação de áreas degradadas, bem como pode alimentar modelos para prever o impacto de mudanças climáticas sobre a distribuição das espécies. Por outro lado, um melhor conhecimento da distribuição geográfica das espécies e sua relação com a filogenia e habilidade de dispersão representa também uma aquisição teórica importante pois pode contribuir para o aprimoramento de algumas teorias ecológicas e biogeográficas.

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CAPÍTULO 1

The Age and Area Hypothesis revisited: Do older species have larger geographic range sizes?

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Abstract

Aim We tested the hypothesis that plant geographic range sizes are positively related to taxon age, known as the "Age and Area Hypothesis" originally proposed by J. C. Willis (1922). In this context, endemic species are expected to be younger than widely distributed taxa, which are thought to present broader range sizes.

Location Species ranged from northern Chile and Argentina to the south of United States.

Methods We used a time-calibrated phylogeny of the tribe Bignonieae (Bignoniaceae) to infer the age of individual taxa and a large occurrence dataset based on herbarium records to estimate the geographic range size. We used a simple linear regression to test for correlation between the selected variables.

Results No correlation was found between taxon age and geographic range size in Bignonieae.

Main conclusions The relationship between age and area found by other authors for other taxonomic groups could have been affected here by the dispersal mode of members of Bignonieae, most of which are wind dispersed. Wind dispersal is a very efficient mode of dispersal, which may have influenced current patterns of geographic distribution in the tribe. Further studies, with additional wind dispersed taxa are needed in order to test whether this pattern extends to other wind dispersed taxa. The knowledge about the factors that shape the species distribution is important for conservation, especially for the tropical region where the megadiversity is composed in most part by species with small distribution areas (endemics).

Keywords: Bignonieae, geographic distribution, phylogenetic age, phylogeny

INTRODUCTION

Plant species may greatly vary in their geographic distributions (Paul & Tonsor, 2008) even between closely related species (Brown *et al.*, 1996). For decades, natural scientists try to elucidate the drivers of species geographical distributions and a great number of ecological and evolutionary variables have been used to try to explain variations in species geographic range sizes (Willis, 1922; Brown & Kodric-Brown, 1977; Hansen, 1980; Brown, 1984; Stevens, 1989; Oakwood *et al.*, 1993; Edwards & Westoby, 1996; Gaston, 1996; Thompson *et al.*, 1999; Brändle *et al.*, 2002; Lloyd *et al.*, 2003; Lester *et al.*, 2007).

Among the variables proposed to explain species geographic range variations are: niche range (Thompson *et al.*, 1999), tolerance to environmental variability (Gaston, 1996, 2003), body size (Gutierrez & Menendez, 1997), population size (Brown, 1984; Brown *et al.*, 1996), latitudinal effects (Stevens, 1989), colonization and extinction dynamics (Brown & Kodric-Brown, 1977; Hanski, 1999) and dispersal efficiency (Lester *et al.*, 2007).

Studies on geographic distribution patterns for different taxonomic groups in different regions of the world often relate geographic range variations with environmental variables (Stevens 1989; Brändle *et al.* 2002) or with species morphological features (Edwards & Westoby, 1996; Lester *et al.*, 2007). However, none of these factors has emerged to date as a universal driver of species geographical distribution.

A nineteenth century renowned botanist, called John C. Willis proposed that the species geographic distribution area was correlated with their age (Willis, 1922). This theory, known as “age-and-area hypothesis” states that older taxa would have larger geographic distribution area because species in these groups would have had more time to disperse over larger areas, while

younger taxa would have smaller distribution areas. The hypothesis caused scientific uproar at the time (Matthews, 1922; Willis & Yule, 1922; Willis, 1923) and did not have much support (Stebbins & Major, 1965) been sometimes, even ridiculed (Fernald, 1924; Gleason, 1924).

It is worth to remember that there were not methods of molecular and phylogenetic analysis available at that time. Even many decades later, the lack of groups with concise phylogeny made impossible a definitive test of the hypothesis, so it remained forgotten for a long time. Recently, the increasing availability of biological molecular data and "Hubbell's neutral theory" publication (Hubbell, 2001a) gave new life to the subject. In his neutral model, Hubbell predicts that most rare and endemic species will be young while most widely distributed species will be older (Hubbell, 2001a, b).

Despite J.C. Willis having developed his hypothesis thinking about tropical floras, especially Ceylon (now Sri Lanka), up to now, there have been few studies explicitly testing the hypothesis with tropical plants. A study with the neotropical genus *Piper* found a positive relationship (Paul & Tonsor, 2008) and a study with the genus *Psychotria* found a weak but significant positive relationship (Paul *et al.*, 2009) between species age and area, corroborating Willis hypothesis. In contrast, studies with other organisms, like primates and carnivores found negative relationships (Jones *et al.*, 2005), while studies with birds gathered a mix of positive, negative and lacking of relationships (Gaston & Blackburn, 1997; Webb & Gaston, 2000). This conflicting results highlights the importance of deepening the studies integrating phylogenetic and biogeographic patterns.

The megabiodiversity that now are threatened in the tropical region is mostly composed of species with few individuals and small geographic ranges (Wallace, 1878; Dobzhansky, 1950;

Gaston, 1994; Hubbell, 2001a). This vast diversity is just beginning to receive adequate genetic treatment and improved estimates of range size (Pitman *et al.*, 2001). Thus, a better knowledge about the features that causes the variations in the species geographic distribution is an important tool for population and community studies and they can be used to analyze the factors that inhibit or facilitate certain species colonization (Guasp *et al.*, 1996), been important for the planning of conservation actions, especially for the tropical region where the megadiversity is composed in most part by species with small distribution areas (endemics). Additionally, the establishment of relationships between geographic distribution and phylogeny will generate new and relevant information that may serve as the basis to the development of new ecological and phytogeographical models.

In this study we tested the “age-and-area hypothesis” using a large and important neotropical species group, the tribe Bignonieae (Bignoniaceae). We specifically address if there is a positive relationship between species phylogenetic age and their geographic range size.

METHODS

Bignoniaceae and Bignonieae

Bignoniaceae is a plant family containing climbers, shrubs and trees with pantropical distribution (Lohmann, 2004). They are predominantly neotropical and constitute an important component of neotropical forests (Olmstead *et al.*, 2009). The family includes 82 genera and 827 species (Lohmann & Ulloa, 2008). Approximately half of species belong to the New World endemic tribe Bignonieae (Lohmann & Taylor, 2013), which comprises a major component of

the neotropical liana flora. The diversity center of the tribe is tropical America where there are about 42 genus and 635 species (Lohmann & Ulloa, 2008).

The family was traditionally divided in eight tribes, four of them being endemic to the Neotropics (Gentry, 1991). Bignoniaceae is one of the Neotropics endemic tribes including all the Neotropical shrubs and climbers with septicide capsules comprising c. 400 species and 21 genus (Lohmann & Taylor, 2013). It is the largest single clade of lianas in the Neotropics ranging from the northern Argentina and Chile to southern United States (Lohmann, 2006). Recently, a combined nuclear and chloroplast DNA (cpDNA) study of Bignoniaceae including nearly one-third of the species resolved many of the generic delimitation problems and clarified the relationships among several lineages of the group (Lohmann, 2006) resulting in a revised classification with a phylogenetic tree reconstructed based on molecular markers (Lohmann & Taylor, 2013). This study strongly supports the monophyly of the group. Additionally fossil records were incorporated to the phylogeny (Lohmann *et al.*, 2013) which make possible to assess the age of diversification of the different lineages within the group.

For this study we included 19 genera and 102 species of Bignoniaceae. This clade was chosen because it is monophyletic and has a good time-calibrated phylogenetic treatment, which make possible a reliable estimation of species age. The species are widely distributed and geographically widespread occurring in a wide array of habitat types, ranging from dry (e.g. caatinga and cerrado) to humid (e.g. Atlantic and Amazon forests) exhibiting a variety of distribution patterns (Lohmann *et al.*, 2013). Some of them are locally endemic or restricted to a single habitat while some are widely distributed in South and Central America in several habitat types (Gentry, 1979). All these features make Bignoniaceae an excellent model for Neotropical biogeographical studies (Lohmann *et al.*, 2013).

Phylogenetic Age (PA)

We used a time-calibrated phylogeny of the tribe Bignonieae (Lohmann *et al.*, 2013) to assess the species phylogenetic age (PA). The tree contains the time-calibrated phylogeny of the 102 Bignonieae species considered in this study. We used the software Mesquite v. 2.72 (Maddison & Maddison, 2010) to assess the species relative ages through the nodes divergence dates in the phylogenetic tree. PA was expressed in millions of years (mi.y^{-1}).

Geographic range size (GRS)

To assess the species geographic range size (GRS) we used a large dataset (L.G. Lohmann, unpublished data) containing about 30.000 georeferenced presence points of species of Bignonieae. The dataset contains the collections made by Alwyn H. Gentry during several years of research in the Neotropics.

Based on this dataset we used a GIS software (Arc-GIS v. 10) to construct geographic distribution maps for each of the 102 species included in the analysis. The known occurrence points of each species were plotted on a georeferenced shape of neotropical region, then, we used each individual map to estimate the GRS for each species by drawing the minimum polygon - MP (Southwood, 1966) around all the species occurrence points and calculating the polygon area. The GRS was expressed in square kilometers (km^2).

Data analysis

To test our hypothesis we submitted the log-transformed values of PA and GRS to a simple linear regression. The coefficient of determination (R^2) was used to evaluate the dependence degree of the dependent variable (y axis - GRS) in relation to the independent variable (x axis - PA). The analysis was performed in Bioestat v.5. (Ayres *et al.*, 2007)

RESULTS

The 102 species considered in our study are spread through an area of about 34,615,210 km² from northern Argentina and Chile to the south of United States, occurring in 20 continental countries plus all Caribbean islands (Fig. 1). Species GRS showed a continuous distribution (Fig. 2) ranging from 4,304.5 to 32,764,400 km².

The phylogenetic tree for the species considered in our analysis show 108 species belonging to 23 genera (Fig. 3), because it includes some species which do not belong to the tribe. PA also showed a relatively continuous distribution with species ranging from 4.2 to 49.8 mi.y⁻¹ (Fig.4).

We found no relationship ($y = 0.072x + 6.3461$, $R^2 = 0.0006$, $p = 0.80$, $n = 102$) between PA and GRS for the 102 Bignoniaceae species considered in our study (Fig. 5).

The species with the greatest GRS (*Dolichandra unguis-cati* (L.) L.G.Lohmann), which occurs in an area of about 32 millions km² (from Argentina to Mexico), and that according to our hypothesis was expected to be the oldest species had only about 12.2 mi.y⁻¹, while the oldest species (*Perianthomega vellozoi* Bureau), with more than 49 mi.y⁻¹, which was expected to be

the one with the greatest GRS occupied an area of only about 1 million km². On the other hand, the species with the smallest range (*Adenocalymma salmoneum* J.C.Gomes), which occurs in an area of about 4,304.5 km², and that was expected to be the youngest species, had about 5.8 mi.y⁻¹, while one of the youngest species (*Fridericia patellifera* (Schltdl.) L.G.Lohmann) with about 4.7 mi.y⁻¹, occupied an area of more than 14 million km² (from central South America to Mexico).

DISCUSSION

The extant distribution of a plant upon the earth surface is a very complex phenomenon. It is the result from the interaction of many variables, some of them inherent to the plant itself, some to its surrounding environment, and often it is due to a mixture from both. Theoretically, the species age would be an important variable included in this system, because the older the species, more time it had to spread to a greater area (Willis, 1922), but the influence of many deterministic and stochastic forces acting at different levels of biological organization and temporal duration make the understanding of this system a difficult task.

Our result did not support a positive age and area relationship as hypothesized by Willis (1922). It also contradicts the findings of Paul & Tonsor (2008) and Paul *et al.* (2009), which found positive correlations between the age and the geographic range for *Piper* and *Psychotria* species, respectively.

There are some important caveats to this results that should be better discussed because several features can potentially obscure a positive age and area relationship and the studies do not yet provide any clear pattern for the generality of this relationship.

Our analysis encompassed only a fraction (about 26%) of Bignoniaceae total number of species, as did the *Piper* (Paul & Tonsor, 2008) and the *Psychotria* study (Paul *et al.*, 2009), but in their case the fraction was even smaller (about 5-10%). Taxon sampling can affect the age estimates because missing taxa would influence the estimated divergence times of species if they were included in the analysis (Linder *et al.*, 2005) leading to an overestimation of ages (Chown & Gaston, 2000; Webb & Gaston, 2000; Jones *et al.*, 2005). It is also important to remember that when Willis proposed its hypothesis he said that it would be evident only in relatedness groups of species (Willis, 1922), premeditating the problem of the taxa gaps in the group phylogeny.

In order to effectively integrate species age information derived from molecular data into our understanding of ecology and phytogeography, we need to recognize all the potential sources of error in the data used to test the hypothesis as well as take a broader perspective on the simple age and area hypothesis proposed by Willis (1922).

The main shortcoming of the traditional age and area hypothesis (Willis, 1922) is its failure to account for old species with small geographic ranges and young species with large ranges. The relationship between species age and geographic distribution may take different forms and Willis "age and area" hypothesis is only one of the possible outcomes. Other researchers (Chown 1997, Gaston 1998, 2003, Chown & Gaston 2000) have summarized several alternative models of post-speciation range-size transformations (e.g., cyclical, random, stasis, etc.) that could better explain the age and area relationships of some species. For example, some empirical evidence suggests that in some cases the relationship between species age and geographic range may be a hump-shaped curve (Webb & Gaston, 2000), where both old and young species have small ranges and intermediate age species have the largest ranges (Foote *et al.*, 2007), because younger species start with small geographic range sizes, and at an

intermediate age they reach their maximum range size, and then, as they become older, their populations gradually decline experiencing an extinction process that causes a gradual geographic range size reduction until they eventually become extinct. Such a pattern was already found for fossil assemblages of Cenozoic molluscs (Foote *et al.* 2007).

Since its origin, each individual species pass through a series of events during its spreading and evolution and has its own unique life history, and there are a variety of processes that can expand or reduce species ranges, so each individual clade may also have its own unique age-area relationship. Bignoniaceae is a speciose clade and an old plant lineage (~40 Ma). Species-rich tribes like Bignoniaceae have a wide range of ages and geographic distribution areas and, as a consequence, species occur in a wide range of habitats (Lohmann *et al.*, 2013) and under many different environmental and ecological situations (Olmstead *et al.*, 2009). Therefore, these species may have experienced stochastic area retractions caused by local extinctions driven by the climatic oscillations throughout the last thousands of years, especially by the Holocene environmental change (Lohmann *et al.*, 2013).

A similar perspective was given by Wilson (1959, 1961), although developed in the context of island biogeography. He termed "the taxon cycle" the sequential phases of expansions and contractions of a species range after the colonization of a new area. According to Wilson, insular species would evolve through a series of stages from newly arrived and broadly distributed colonist (indistinguishable from their mainland relatives) to highly differentiated and ecologically specialized endemics, which ultimately become extinct (Wilson, 1959; 1961; Lomolino *et al.*, 2006). According to him, species would pass through a stage of "initial expansion", where it colonizes and establishes populations in a broad area without differentiation from the source population, followed by a stage of "ecological and evolutionary specialization",

where populations differentiate to the point they represent endemic subspecies or even species and become adapted to new habitats often exhibiting associated changes such as reduced dispersal ability, shifts in body size, and increased specialization. However, at this point, some populations have become extinct, so that the taxon range has contracted and its distribution is smaller, beginning the stage of "initial contraction", where differentiation and range contraction have continued to the point that the taxon comprises just a few relictual, endemic species with highly specialized populations restricted to specific habitats, finally reaching the "endemic stage", where the ranges of relictual populations have contracted further as a result of their extreme specialization (Wilson, 1959, 1961).

Wilson found this pattern studying insular ants in the islands of Melanesia (New Guinea, Western Pacific). Analyzing differences in distributions and ecological associations of insular ants in a snapshot of time, he inferred what appeared to be stages in the expansion and taxonomic differentiation of ants (Wilson, 1959). Later, Ricklefs & Cox (1972, 1978) reported ecological and evolutionary shifts in West Indian birds that showed successive stages of what they interpreted as a taxon cycle. Similarly, Roughgarden and colleagues used the taxon cycle theory to explain the evolution of body size in West indian lizards (Roughgarden, 1974; Roughgarden & Fuentes, 1977; Roughgarden *et al.*, 1987; Roughgarden & Pacala, 1989; Roughgarden, 1992).

More recently, Ricklefs & Bermingham (2002) have reviewed the subject and provided a much more explicit, causal explanation for taxon cycles. Immigration and the many factors influencing this fundamental process explain the expansion phase and subsequent environmental selective pressures, including interspecific interactions, explain the contraction phase. While new colonists enter the expansion phase because they have escaped from the mainland enemies, new competitors begin to expand their ranges too, and predators and parasites subsequently learn to

exploit these new prey and hosts, eventually triggering a contraction phase. Surprisingly, Wilson's theory has attracted little attention from most biogeographers and ecologists in the last decades, and a series of more recent studies by Ricklefs and colleagues using phylogenetic analysis coupled with detailed information on the ecology and distributions of Lesser Antillean birds have confirmed most of the ideas of the theory at least for this specific insular fauna (Ricklefs & Bermingham, 2002). They asserted that "alternating phases of expansion and contraction are nearly universal and it is possible to study taxon cycles analytically in a wide variety of groups and regions". In fact, recent researches (Briggs, 2003; 2004) revealed that expansions and contractions of geographic ranges, at least in the marine realm, are correlated.

The taxon cycle represents an idea in an opposite direction from the hypothesis formulated by Willis (1922) and the existence and performance of this cycle would explain why ancient species, which in the past were broadly distributed, are now highly specialized and restricted to small geographic areas (endemics). That is the case of *Pachyptera aromatica* (Barb.Rodr.) L.G.Lohmann, one of the oldest species in the phylogeny (about 36 mi.y⁻¹) with a relatively small geographic range (about 448 000 km²) restricted to Western Amazon, and *Fridericia patellifera* (Schltdl.) L.G. Lohmann, one of the youngest species (about 3.5 mi.y⁻¹) with a vast geographic range (about 14 millions km² - from Central South America to Mexico).

Another possibility for this result is the possible existence of an improvement of the species dispersal efficiency along the evolution of the derived taxa, so that older species, despite having more time to disperse over larger areas, are overcome by the dispersal of the newer and more dispersal efficient species. This possibility is now under testing by the authors and will be further discussed in another article (Chapter 3, in this thesis).

We have other evidences indicating that simply age, as stated in Willis hypothesis, often it is not a major factor in shaping plant species distribution. For example, rain forests exist from the late or mid-Cretaceous, about ~100 millions of years ago (Morley, 2000; Davis *et al.*, 2005), but the analysis of the diverse legume genus *Inga* suggests that it is a young genus and many species originated on the scale of 2-10 millions of years ago (Richardson *et al.*, 2001), therefore *Inga* species must be considered quite young (Bermingham & Dick, 2001), but despite its relatively recent origin, this clade has spread throughout the forests of the South and Central America, and at many sites *Inga* species are important forest components in terms of both number and biomass (Richardson *et al.*, 2001). In fact, legume clades in general may be remarkably young given their widespread distribution and numerical importance in tropical forests, about 4-16 millions of years ago (Lavin *et al.*, 2004).

Other speciose tropical clades are considerably older, such as those in the Annonaceae (e.g., *Xylopia*, *Annona*) which appear to be on the scale of approximately 15-25 Ma (Richardson *et al.*, 2004; Pirie *et al.*, 2006). Like Bignoniaceae, many of these clades have pantropical or even cosmopolitan distributions; in fact, one of the most widespread tropical plant species, *Symphonia globulifera* (Clusiaceae), also ages to the mid-Tertiary, about 28 millions of years ago (Dick *et al.*, 2003). In Africa, the origin of the herbaceous begonias (Begoniaceae) is also on the scale of approximately 30 Ma, but many of the species in this group diverged relatively recently, from about 1 to 10 millions of years ago (Plana *et al.*, 2004). In another widespread herbaceous genus, *Costus* (Costaceae), the neotropical species appear to have diversified rapidly and recently (Kay *et al.*, 2005).

In the case of very recent diversification of clades like *Inga* and *Costus*, widespread species within these genera provide evidence that common members of these clades are not

particularly old. However, the relationships of age and area within these and other genera have not been directly assessed. In a rapidly diversifying genus, if more widespread species were found to be older, the expected slope of the age and area relationship would simply be very steep. However, finding young but common species would certainly not be surprising in the light of recent evidence confirming a rare species advantage in many tropical forests, probably resulting from lower density-dependent or frequency-dependent mortality (Harms *et al.*, 2000; Volkov *et al.*, 2005; Wills *et al.*, 2006). Rare species that have a fitness advantage are expected to increase in abundance much more rapidly than predicted under neutral drift, for example, resulting in younger species that have large range and population size. Thus, if new species do indeed start with small population and range sizes, some of these species may be expected to increase their population and range sizes rapidly. Overall, the generality of a positive age and area relationship in tropical plant species awaits future analysis, particularly of densely sampled and speciose clades (Paul & Tonsor, 2008).

Fortunately, there is considerable promise that in the near future we can gain a broader perspective on age and area relationships in tropical plants. For example, work on the diverse tropical herbaceous genus *Begonia* (Begoniaceae) has provided insight into the phylogenetics and timing of diversification in this pantropical genus (Forrest & Hollingsworth, 2003; Plana *et al.*, 2004). Likewise, phylogenetic work on the diverse pantropical genus *Psychotria* (Rubiaceae) (Nepokroeff *et al.*, 1999) promises to provide evidence from a genus that in many ways mirrors *Piper* in its species ecology, abundance and distribution (e.g., high local and regional species richness, numerical abundance, understory and gap habitat), although it is phylogenetically distantly related .

Interestingly, Hamilton (1989) suggested that within the Mesoamerican members of *Psychotria* subgenus *Psychotria*, species groups often contained one basal member with a large geographic range, and putatively derived members with narrow ranges, which would be a more direct validation of the age and area hypothesis.

Up to now, there have been few studies that explicitly test the age-and-area hypothesis, especially with Neotropical plant clades, but comparing our results with studies made with other organisms reveals the difficulty to generalize this hypothesis.

Studies made with birds show conflicting results. Gaston & Blackburn (1997) found no relationship between mean range size of a clade and the clade age in a study with the entire New World avifauna, but they found a weak positive relationship between evolutionary age and the total clade range size. In another study, Webb & Gaston (2000) examined six clades of birds and they found many forms of age and range size relationship. Overall, approximately 20-50% of the variance in range size could be accounted for by species age (inferred from standard mitochondrial DNA molecular clock divergence estimates of 2% divergence per million years) but only one clade showed a positive age-and-area relationship; three clades showed a negative relationship and two clades showed a hump-shaped relationship. A study made with *Sylvia* warblers found a weak but significant positive relationship between the breeding range size of the species and the species age, but the relationship could be better explained by older species generally having better dispersal abilities than younger species (Böhning-Gaese *et al.*, 2006), which indicates the importance of the species intrinsic features in the dispersal process, including morphological features that influence their dispersal efficiency. And analyzing large molecular datasets of primates and carnivores, Jones *et al.* (2005) found evidence of a weakly negative age and area relationship.

Although, dispersion in a fluid environment can be considered a different mechanism when compared with the terrestrial environment. Two studies made with marine fossil fauna found indirect evidence supporting a positive relationship between species age and their geographic area. Miller (1997), in a study made with Ordovician marine genera found that older genera had larger ranges than young genera. Jablonski (1987) related a positive relationship between species duration (age) and geographic range size in the beginning of fossil molluscs species lifetimes, followed by long periods of stasis, however, the focus of these studies was not specifically testing age-and-area relationships, but on the possibility of species level selection.

The positive and significant age and area relationship as predicted by Willis seems not to be supported by the results of most part of the studies, but the data shows that the studies that used fossil data and species duration as a measure for age found some evidence for a significant age and area relationship (see Jablonski, 1987; and Miller, 1997) while studies using extant species and molecular divergence dates as a measure for age generally found no significant relationship between species age and their geographic range size (for example, this study), or a mixture of positive and negative relationships (Webb & Gaston, 2000; Jones *et al.*, 2005).

These different results may be related to the different sampling methods used by the different authors. A fossil record sampling allows the range size estimation at multiple ages and the assessment of the species range size variation over the species complete evolutionary history, while the molecular dating methods permits only a snapshot of the species extant range size at a specific point in time and the inference of the general trend of the age and area relationship for a group of organisms. Analyzing only snapshots of species ages and range sizes relationship can introduce considerable variance into this relationship, especially if the species follow varying

post-speciation range size transformation over time, even if the general shape of the relationship is similar, i.e. hump-shaped (Paul & Tonsor, 2008).

In addition to the differences between fossil versus molecular analysis of age and area, studies with extant species suggest that the phylogenetic level of the analysis is important. The results of studies made with large clades, which generally contains many well-defined and potentially divergent subgroups (e.g., mammals, carnivores, or birds) tend to find no or weak relationships (Jones *et al.*, 2005). Studies of specific clades within these broad groups find significant, but inconsistent, relationships (e.g., the six clades of birds studied by Webb & Gaston, 2000). This discrepancy suggests that the signal of an age and area relationship may be obscured when clades with distinct evolutionary histories are combined (Paul & Tonsor, 2008).

The contradicting results found for the age and area relationship in this and other studies highlights the importance of deepening the studies integrating phylogeny, biogeography and conservation and calls for further investigation into the generality of this relationship using neotropical plant groups. If, in general, many rare species are found to be young species, this information may be crucial to incorporate into our understanding of the variation in range size among species and, at the local scale, variation in abundance, which often shows a positive relationship with range size (Gaston, 1994).

Unfortunately, there are very few molecular datasets available for specific clades of tropical plants that can be effectively used to assess age and area relationships (Paul & Tonsor, 2008). Most of these data examine higher phylogenetic levels like families or even higher (Renner *et al.*, 2001; Davis *et al.*, 2005; Lavin *et al.*, 2004) and they focused on the origin and age of the clades and species that make up current tropical communities. For this reason, any

possibility of deepening the tests about "age and area" hypothesis represents an opportunity that cannot be wasted.

We showed here that the relationship between species age and geographic range size does not occur in Bignoniaceae in contrast with results from other clade studies. It suggests that this relationship should be viewed more broadly than the simple hypothesis presented by Willis (1922) and further studies should incorporate more elements in the analysis, like environmental variables or species intrinsic features, especially those linked to dispersal ability. Investigations in this way can lead to new understandings and theories about the role of phylogenetic and historical features on the current distribution of species.

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FIGURES LEGENDS

Figure 1. Geographic distribution of the Bignonieae genera considered in the analysis of "age and area hypothesis".

Figure 2. Distribution of the geographic range sizes in square kilometers (GRS - km²) of the 102 Bignonieae species considered in the analysis of "age and area" hypothesis.

Figure 3. Time-calibrated phylogeny of the tribe Bignonieae (from Lohmann *et al.*, 2013).

Figure 4. Distribution of the phylogenetic ages in millions of years (PA - m.y.) of the 102 Bignonieae species considered in the analysis of "age and area" hypothesis.

Figure 5. Linear regression of species log-transformed phylogenetic age (log PA - m.y.) and geographic range size (log GRS - km²) of the 102 Bignonieae species considered in the analysis of "age and area" hypothesis; $y = 0.072x + 6.3461$, $R^2 = 0.0006$, $p = 0.80$, $n = 102$.

FIGURES

Figure 1

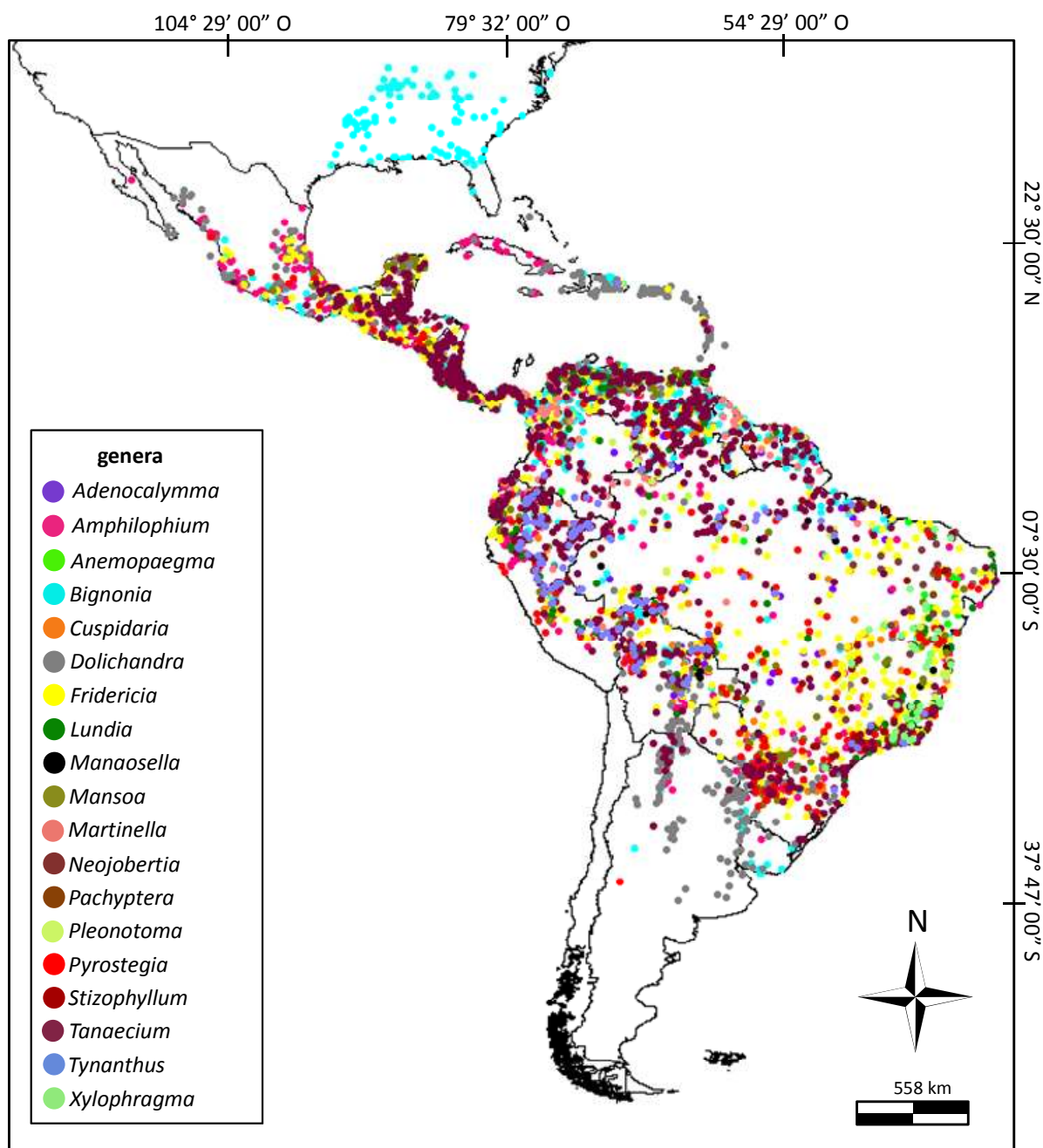


Figure 2

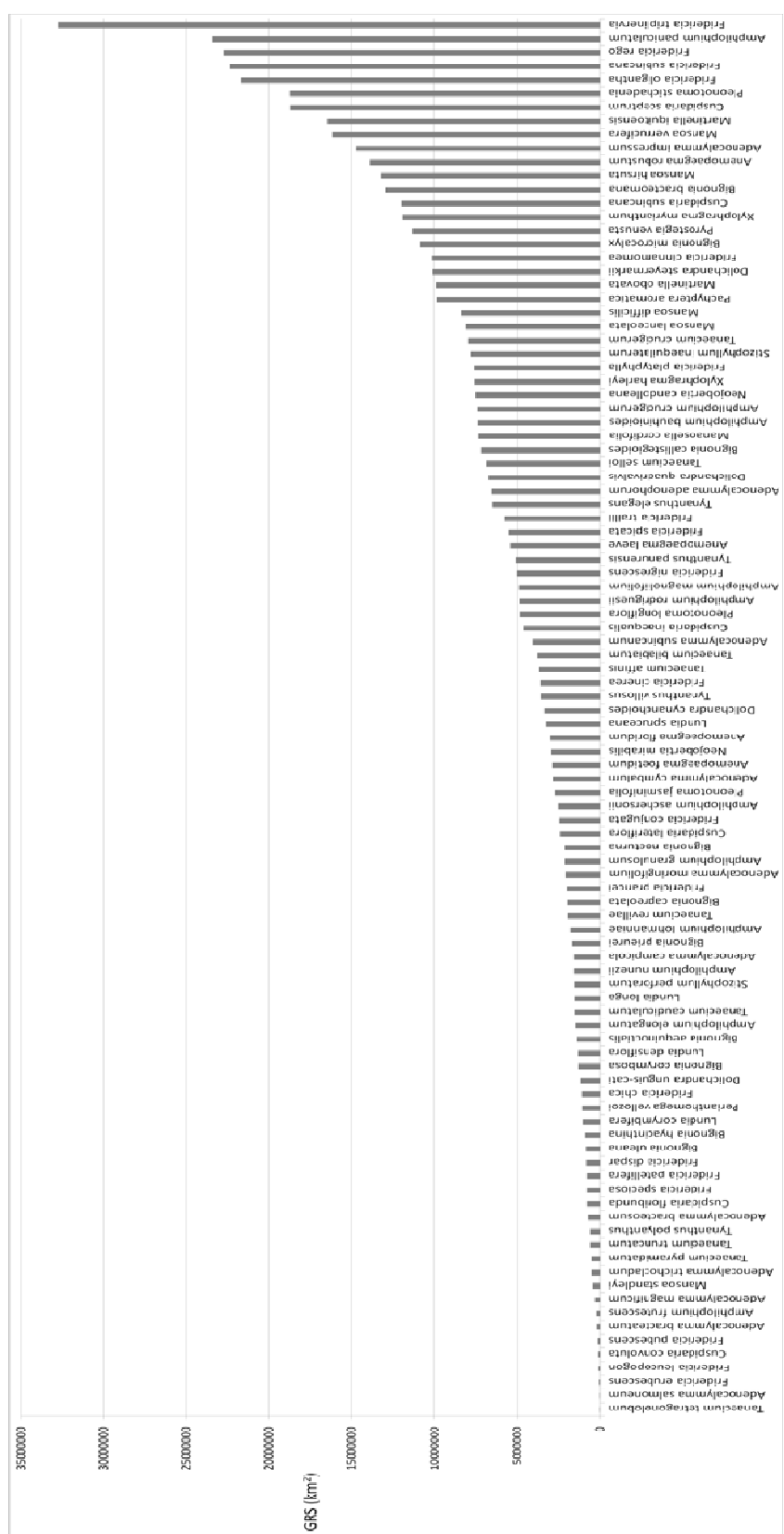


Figure 3

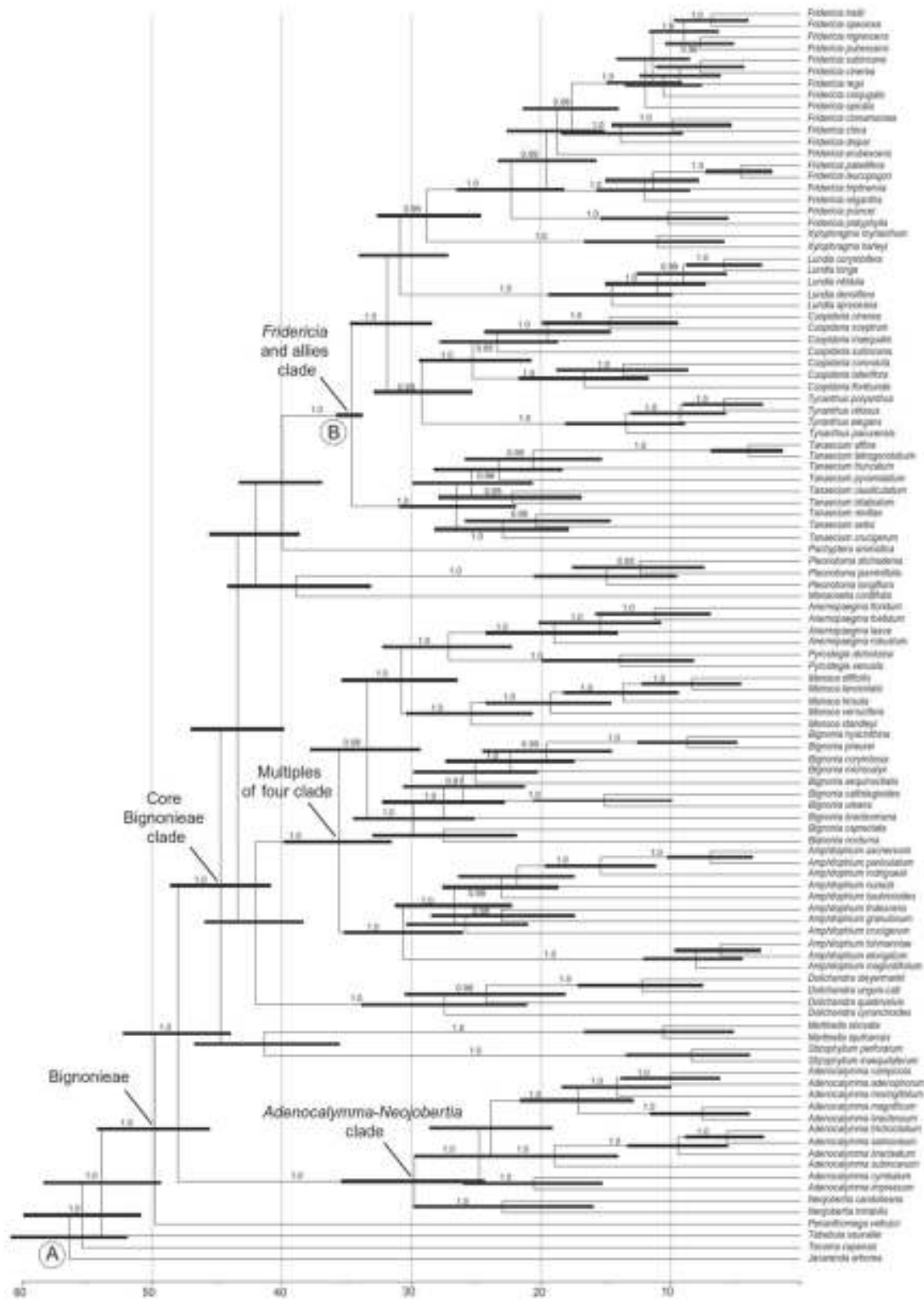


Figure 4

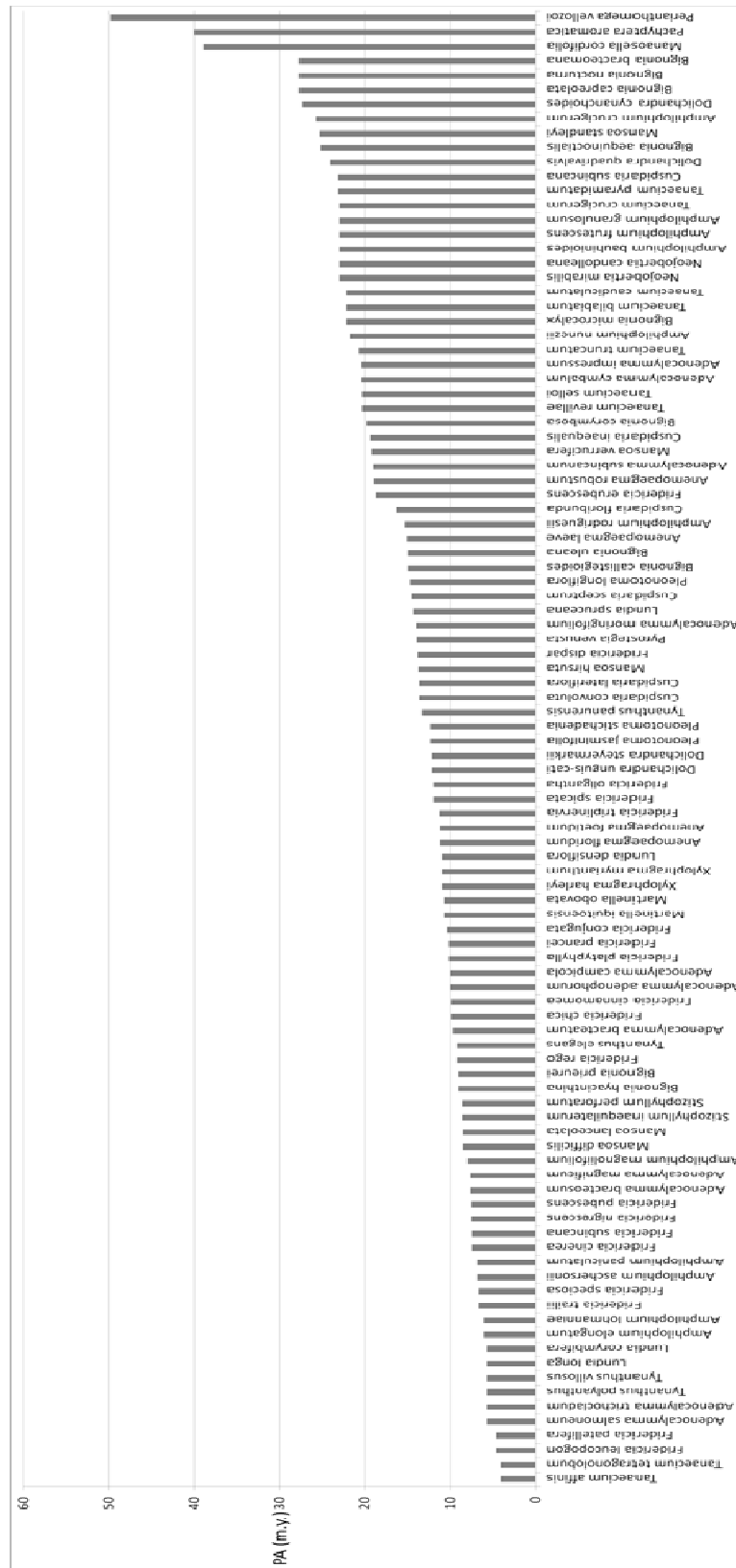
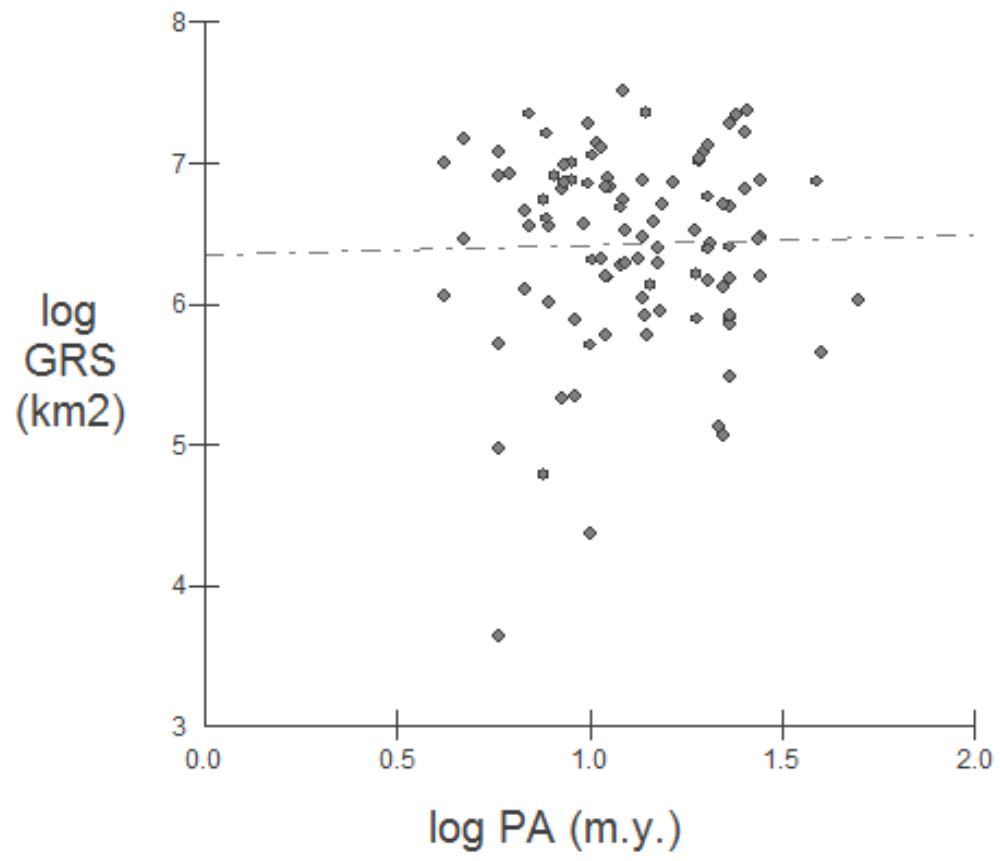


Figure 5



CAPÍTULO 2

Size matters? an experimental study on wind dispersal potential and seed morphological traits

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Running head: Wind dispersal efficiency and seed morphology

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Abstract

We investigated the relationship between seed morphological traits and dispersal potential of 50 Bignoniaceae species. Specifically, we tested whether eight morphological features were related to the potential of dispersal by wind. We aimed to test the hypotheses that anemochoric seed dispersal potential is related to specific morphological biomechanical traits. We expected that: (i) smaller seminal nucleus size, (ii) greater seed total size (iii) greater seed wing size, (iv) smaller seed mass, (v) greater seed area, (vi) smaller proportion between seminal nucleus size and seed wing size, (vii) smaller proportion between seed mass and seed wing size, and (viii) smaller proportion between seed mass and seed area, were associated with a greater flight distance, and therefore, an improved dispersal efficiency. We collected seeds from herborized specimens and measured the following seed morphological traits: (1) seed total size (STS), (2) seminal nucleus size (SNS), (3) seed wing size (SWS), (4) seed mass (SM), (5) seed area (SA), (6) the ratio between seminal nucleus size and seed wing size (SNS/SWS), (7) the ratio between seed mass and seed wing size (SM/SWS), and (8) the ratio between seed mass and seed area (SM/SA). Then, we used a wind tunnel to assess seed flight potential under controlled conditions. We measured the distance that the seed flew inside the tunnel (seed flight distance - SFD) and used it as a proxy for wind dispersal potential. We analyzed the data under two different approaches. First, considering the data of each species individually. Second, considering the data of all species together. Most species (43 species - 83%) had at least one of the variables with significant correlation with the SFD. Four species showed correlation between all the variables analyzed and SFD, and seven species showed correlation between seven of the eight variables analyzed and SFD. Negative correlations between SNS and SFD were found in 16 species. Positive correlations between STS and SFD were found in 17 species. Positive correlations between SWS and SFD were found in 15 species. Negative correlations between SM and SFD were found in 23 species. Positive correlations between SA and SFD were found in 17 species. Negative correlations between the ratio SNS/SWS and SFD were found in 13 species. Negative correlations between the ratio SM/SWS and SFD were found in 25 species. The ratio SM/SA was the variable which showed more correlation with SFD with 36 species showing this negative correlation. In the second approach, considering all the species together, the variables SWS ($R^2 = 0.21$; $p=0.005$), and SA ($R^2 = 0.28$; $p=0.002$) showed positive and significant correlation with SFD. The ratio variables, SNS/SWS ($R^2 = 0.29$; $p=0.0007$), and SM/SA ($R^2=0.42$; $p=0.0001$) showed negative and significant correlations with SFD. Our results showed that some seed morphological variables are correlated with wind dispersal efficiency, especially regarding to the seed mass and area. The knowledge about the factors that shape the species distribution is important for conservation, especially for the tropical region where the megadiversity is composed in most part by species with small distribution areas (endemic).

INTRODUCTION

Dispersal can be defined as the movement of individuals from where they were born to where they reproduce (Darling et al. 2008), but this apparently simple definition represents a central life history trait that carries a wide variety of fundamental and significant ecological and evolutionary consequences (Clobert et al. 2001, Levin et al. 2003, Kokko & López-Sepulcre 2006). According to Dieckmann et al. (1999), it is difficult to imagine any ecological or evolutionary problem that would not be affected by dispersal.

Over the last two decades, scientific literature has received an increased growth in seed dispersal publications (Augspurger & Franson 1987, Hensen & Müller 1997, Levey et al. 2002, Forget et al. 2005, Dennis et al., 2007, Bullock & Nathan, 2008, and others) largely driven by the increasing appreciation that seed dispersal is critical to many ecological questions.

Seed dispersal has a prominent role in recent studies on recruitment limitation (Clark et al. 2007), plant migration in response to historic and future climate change (Ibáñez et al. 2006), evolutionary trade-offs (Clark et al. 2004), structure of interaction networks (Bascompte & Jordano 2007), scale dependence of ecological processes (Burns 2004), maintenance of biodiversity (Bascompte & Jordano 2007), structuring of species–area curves (Rosindell & Cornell 2009), ecological consequences of habitat fragmentation (Cordeiro & Howe 2003), weed invasions (Buckley et al. 2006), and the effectiveness of corridors for conservation (Levey et al. 2005).

Seed dispersal also affects the level of gene flow (Govindaraju 1988, Young et al. 1996, Jordano et al. 2007) influencing in processes as local adaptation and speciation (Barton & Hewitt 1989; Harrison & Hastings 1996). It may rule the dynamics and long-term survival of metapopulations

(Saunders et al. 1991; Husband & Barrett 1996; Poschlod et al. 1996, Menges 2000, Spiegel & Nathan 2007) and, consequently, is linked to population survival (Opdam 1990).

Additionally, dispersal has profound effects on the genetic structure of populations (Wright 1943, 1969), and this can be used to infer the phylogeographic structure of plants (Petit & Grivet 2002). Recently, dispersal has been considered incremental in the context of conservation biology and restoration ecology (Nuttall & Haefner 2007) because it often constrains vegetation recovery and community assembly (Zobel et al. 1998, Bakker & Berendse 1999).

Despite its importance, it has been only in the recent decades that the ecology of dispersal has received more rigorous scientific attention (Willson & Traveset 2000). Many empirical and theoretical advances have recently been made, but there are still important gaps that need to be complemented with more research to integrate the knowledge of dispersal studies with other fields, as phylogenetics, biogeography and functional ecology.

Many studies have described differences in the dispersal potential of plant species (e.g., Bullock & Primack 1977; Andersen 1991; Fischer et al. 1996), especially studies about evolutionary aspects of dispersal (Comins et al. 1980, Olivieri et al. 1995, Cody & Overton 1996, Dieckmann et al. 1999). These studies show that different dispersal strategies can lead to different efficiency in the dispersal process. For instance, some species produce a great amount of small seeds and improve their colonization capability, while others produce a small amount of big seeds, which reduces their colonization capability, but on the other hand, gives them smaller mortality rates at the seedling stage, especially in extreme environments (Jurado & Westoby 1992, Milberg et al. 1998, Coomes & Grubb 2003, Khurana & Singh 2004, Turnbull et al. 2004, Baraloto et al. 2005). This conflict between seed number and seed mass is only one example of the many

"trade-offs" described for different plant species (Westoby et al. 1996, Leishman et al. 2000, Moles & Westoby 2004) and represents just one of the many strategies acquired by plants to cope with the constraining forces of the environmental and evolutionary pressures they have to face during their life history.

According to some studies, the distances traveled by the diaspores from its source vary depending upon environmental factors (as wind speed, for example) and biological factors, as species specific traits (Okubo & Levin 1989) that could improve the dispersal process. In this context, there are theories that relate propagules specific morphological traits with species dispersal potential (Augspurger & Franson 1987). Studies with different taxonomic groups in different regions throughout the world often relate the variations in species geographic distribution patterns with species morphological features and adaptations (Edwards & Westoby 1996, Lester et al. 2007).

Although seed dispersal has already been the subject of sophisticated modeling studies (Bullock & Clarke 2000), including seed dispersal potential measurements (Tackenberg et al. 2003), and mechanistic models development attempts (Greene & Johnson 1989, 1996, Okubo & Levin 1989), the efficiency of the dispersal process is a phenomenon hard to measure (Bullock & Clarke 2000) and rarely it has been tested experimentally. According to Kokko & López-Sepulcre (2006), only experiments will provide the most solid answers to clearly identify the causal mechanisms behind dispersal.

As frequently reported, the dispersal distance of varying anemochorous diaspores can be derived from their fall velocity (e.g., Green 1980, Ernst et al. 1992, Cody & Overton 1996) and the existent investigations presenting experimentally recorded dispersal distances employ different

methods (e.g., Sheldon & Burrows 1973, Levin & Kerster 1974, Rabinowitz & Rapp 1981, Matlack 1987, Kadereit & Leins 1988, Ernst et al. 1992, Andersen 1992, 1993, van Dorp et al. 1996, Hensen & Müller 1997).

Considering a group of phylogenetically closely related species with the same type of dispersion and the same type of diaspore (a flattened two-winged seed); the variation in the size and shape of some seed biomechanical traits could be linked to the species dispersal efficiency. For example, in the tribe Bignonieae, the vast majority of species have winged seeds and the dispersion is primarily by wind (Lohmann 2004). In this case, dispersal potential could be represented by the seed flight potential, because the greater the species seed flight ability, the greater its dispersal potential. This feature makes this group an appropriate model for the present study.

In this study, we used a wind tunnel to develop a new method to experimentally measure anemochorous winged seeds potential dispersal distances and test the relationship between seed morphological traits and wind dispersal potential for 50 species of a large and important Neotropical species group, the tribe Bignonieae (Bignoniaceae).

We specifically addressed if the seed flight potential is positively correlated with: (i) seed total size, (ii) seed wing size, (iii) seed area; and negatively correlated with: (iv) seminal nucleus size, (v) seed mass, (vi) ratio between seminal nucleus size and seed wing size, (vii) ratio between seed mass and seed wing size, and (viii) ratio between seed mass and seed area. We expected that variations in these traits were correlated with variations in seed potential dispersal distances.

METHODS

The plant family Bignoniaceae and the tribe Bignonieae

Bignoniaceae is a plant family with 82 genera and 827 species (Lohmann & Ulloa 2012). The diversity center is tropical America where there are about 42 genus and 635 species (Lohmann & Ulloa 2012). They are predominantly neotropical and constitute an important component of neotropical forests (Olmstead et al. 2009). The family includes climbers, shrubs and trees with pantropical distribution (Lohmann 2004). Approximately half of both genera and species belong to the New World endemic tribe Bignonieae (Lohmann & Taylor, 2013), which represents the largest single clade of lianas in the Neotropics (Lohmann, 2006).

This study considered 50 species currently recognized in the group (Table 1). The species were chosen in a way to represent the greatest possible number of genera covered by the phylogeny (16 out of 20) (Lohmann et al. 2013) and according to the number of available exsiccates containing viable seeds for each species. We choose this group because it is monophyletic (Lohmann 2006), geographically widespread and widely distributed ranging from northern Argentina and Chile to the south of United States. Additionally, species have the same type of seed (a typically flattened two winged seed - Figure 1) and the seeds have absent or reduced endosperm (Manning 2000, Judd et al. 2002, Datta 2003, Lohmann 2004; Olmstead et al. 2009), therefore they do not present any attractive for the fauna and do not have secondary dispersion. Also, the vast majority of Bignonieae species show winged seeds having their dispersion primarily made by wind (Lohmann 2004), making them an appropriate model for the issues under investigation here, because the results are not biased by the existence of secondary dispersion.

Seeds morphological traits (SMT)

We collected the seeds in vouchers from several herbaria in Brazil (ESA, HRCB, IBGE, SP, SPF, R, RB, UB). We used 20 seeds from each individual and at least three individuals from each species and from different regions of the species entire distribution. In laboratory we selected the more intact viable seeds to use in the study; i.e. seeds without defects like broken wings and with the seminal nucleus fully developed.

We then measured the following seed morphological traits with a digital caliper (Digimatic Caliper, Mitutoyo, Japan): (1) seed total size - STS, (2) seminal nucleus size - SNS, and (3) seed wings size - SWS (Figure 1). The dimensions were taken with the seed longitudinally oriented (Figure 1).

With a high precision analytical balance (METTLER AE240(s), Instrument Corporation, Hightstown, New Jersey, USA) we measured the (4) seed mass (SM), and with a Area Meter (LI-2100C Area Meter, LI-COR Biosciences, Lincoln, Nebraska, USA) we measured the (5) seed area (SA).

With this variables we calculated other three variables that may be related with seed flight potential: (6) seminal nucleus size/seed wing size ratio (SNS/SWS), (7) seed mass/seed wing size ratio (SM/SWS), and (8) seed mass/seed area ratio (SM/SA).

Wind dispersal potential measurements

Several environmental features can affect the wind dispersal potential of a seed, especially in the natural environment. For this reason, we proposed an experimental study in a wind tunnel with

controlled conditions to assess the relations between seed morphology and dispersal potential by wind, minimizing the effects of other varying environmental features. Dispersal potential here refers specifically to the potential mean dispersal distance traveled by a winged seed inside the tunnel with a constant wind speed, in this case 1 m/s.

The wind tunnel consisted of a semi-cylindrical structure made of polycarbonate coupled with a fan with speed regulation (dimmer). The tunnel dimensions were 70 x 70 x 240 cm, in height, width and length, respectively. The wind tunnel was constructed within the dependences of herbarium UEC (Campinas State University, Campinas, São Paulo, Brazil), because this way we could also have control on air humidity and temperature, which were set to $65 \pm 5\%$ and $18 \pm 1^\circ\text{C}$, respectively.

This way, we could assess the 'seed flight distance' (SFD) in controlled conditions for different seeds of different species and use it as proxies of wind dispersal potential, because for a seed that is carried by the wind, the greater its SFD, the greater its dispersal potential.

The SFD was measured by setting the fan speed at a fixed value (1 m/s) and exposing the seeds from different species to an artificially-produced, regularly, and horizontally blowing air stream of constant speed, and measuring the distance traveled by the seed inside the tunnel after it had been released from an opening at the top of the tunnel (0.7 m of height). All the seeds were released under the same conditions and in the same orientation. This a manner of directly assess the seed dispersal distance potential, instead of indirect measures (like seed fall velocities, or flight angles, for example).

Data analysis

We used simple linear regression to assess the correlation among the eight seed variables we measured with their SFD. The analysis were performed in Bioestat v.5. (Ayres et al. 2007) and were considered significant at Bonferroni corrected level. We used Bonferroni corrected level of significance because we performed several comparisons from the same dataset.

The measurements were made considering each seed as an individual, and we used two different approaches to analyze the data. First, we measured and calculated the variables for 20 seeds of each species and analyzed the data considering each species individually.

In the second approach, we gathered the data for each species and analyzed the data for the 50 species considered together. Here, we calculated the average measures of each variable for each species and confronted these values against the average values of SFD of each species.

RESULTS

Table 1 shows the results (R^2) of the linear regressions performed between the 8 seed morphological variables and their flight potential for each of the 50 species we analyzed. Only 7 species had no variables correlating with SFD. Most part of the species (43 species - 83%) had at least one of the variables with significant correlation with the SFD. 4 species showed correlation between all the variables analyzed and their SFD, and 7 species showed correlation between 7 of the 8 variables analyzed and their SFD.

SM had a wide variation of 60 fold in its values, varying from 0.004 g to 0.242 g. SA had a 18 fold variation, ranging from 1.17 to 21.13 cm², while the ratio SM/SA showed a substantially smaller variation of only 6 fold, ranging from 0.003 to 0.02 g/cm².

The relationship between SNS and SFD was found for 20 species. 16 species showed negative relationship, as hypothesized, but 4 species showed an unexpected positive relationship between SNS and SFD (Table 2).

23 species showed correlation between STS and SFD, been positive, in 17 cases, as we expected, and negative in 6 cases. 19 species showed correlation between SWS and SFD, been positive in 15 cases, as expected, and negative in 4 cases (Table 2).

26 species showed correlation between SM and SFD, been negative in 23 cases, as hypothesized and positive in only 3 cases. 22 species showed correlation between SA and SFD, been 17 positives, as we expected, and 5 negatives (Table 2).

The correlation between the ratio SNS/SWS was found in 16 species. In 13 cases the correlation was negative, as expected and in 3 cases the correlation was positive. 26 species showed correlation between the ratio SM/SWS and SFD, been negative, as hypothesized in 25 cases. In only 1 case this relationship was positive (Table 2).

The ratio SM/SA was the variable which showed more correlation with SFD. 36 species showed correlation between SM/SA and SFD, been negative, as we expected, in all the cases (Table 2).

In the second approach, considering all the species together, the variables SWS (Figure 2 - $R^2 = 0.26$; $p=0.003$), and SA (Figure 3 - $R^2 = 0.28$; $p=0.002$) showed positives and significant correlations with SFD. Analyzing the ratio variables, SNS/SWS (Figure 4 - $R^2 = 0.29$;

$p=0.0002$), and SM/SA (Figure 5 - $R^2=0.42$; $p=0.0001$) showed negatives and significant correlations with SFD.

DISCUSSION

Our results demonstrate that variations in some seed morphological traits are correlated with variations in seed flight distance. Apparently, the reduction of the seminal nucleus promotes greater dispersal distances, probably because most of the seed mass is represented by the seminal nucleus. This idea is supported by the fact that the correlation between SM and SFD was negative and significant for almost half of the species analyzed. On the other hand, an increase in the seed total size and seed wing size also leads to greater dispersal distances, and this is supported by the fact that seeds with a greater area also have greater flight distances.

When some of this relations are considered together, as in the case of the variables calculated as ratios, this pattern become even more evident. The variable which presented correlation with SFD in 72% of the species was the ratio SM/SA, which was negative in all cases and highly significant. In other words, the SM reduction (caused by a SNS reduction or by an overall mass reduction due to thinner seed tissues) coupled with an increase in the seed size and area promotes an improved wind dispersal potential for the species of this group.

This pattern is also supported by the correlation of SFD with the ratio SNS/SWS, which was significantly negative for 13 species, demonstrating that the less unit of seminal nucleus per unit of seed wing, the better the seed flight potential. It is reaffirmed by the correlations of SFD with the ratio SM/SWS, which was significantly negative in half the species analyzed, and with the

ratio SM/SA, which was significantly negative for 36 species, demonstrating that the less unit of mass per unit of seed wing and seed area, the better the seed flight potential.

The results of the analysis considering all species together corroborate this interpretation, because the positive and significant correlations of SA ($R^2 = 0.28$; $p=0.002$) (Figure 3) and SWS ($R^2 = 0.26$; $p=0.0003$) (Figure 2) with SFD and the negative and significant correlations of ratio SNS/SWS ($R^2 = 0.29$; $p=0.0002$) (Figure 4), and ratio SM/SA ($R^2=0.42$; $p=0.0001$) (Figure 5) with SFD, proves that this pattern is intra and interspecific, with significant improvement in wind dispersal potential been correlated with increases in the seed size and area and with reduction of seed mass. In other words, the same correlations were found either by analyzing the data for each species individually and analyzing the data of all species together.

According to Fenner (1985), any feature of the structure of a wind-dispersed seed which reduces the speed with which it falls to the ground after release will increase its chances of being transported laterally by wind currents. Our results give support to the idea that the morphological designs of wind-dispersed diaspores appear to have been shaped to slow their rates of descent and increase their chances of exposure to horizontal winds (Augsburger 1986).

Other authors have found similar patterns. Augspurger & Franson (1987), for example, conducted an experiment using artificial fruits varying in mass, area and morphology to show that wind-dispersed fruits (samaras) with smaller mass/area ratios had greater mean dispersal distances. When the artificial samaras varied in area and mass, but maintained the same mass/area ratio, no consistent pattern in the mean dispersal distance variation was detected.

It has been demonstrated that some morphological changes brings more dramatic increase in dispersal than others probably due to limitations imposed by evolutionary constraints. As

reported by Augspurger & Franson (1987), independent changes in seed mass or fruit area significantly affect dispersal, but the joint changes in these two parameters seems to have even more influence on the dispersal potential, because either a decrease in seed mass or an increase in fruit area decreases wing-loading (a measure of seed mass/seed surface area) which, in turn, promotes dispersal. Dispersal is not affected in any consistent or significant manner by simultaneous changes in mass and area, provided wing-loading and general morphology remain constant. Their experiment demonstrates that the types of the evolutionary adjustments in morphology that can be made are restricted, unless accompanied by appropriate changes in wing-loading (see also Augspurger 1986).

Our results strongly agrees with results from other experiments of anemochorous seed dispersal potentials in wind tunnels. Hensen & Müller (1997) used a wind channel to study the dispersal flight potential of 11 anemochoric species from Germany grasslands, and they attribute the flight behavior or potential dispersal distance of anemochorous diaspores to mass as well as to their distinct surface structures influencing air resistance, including seed surface area.

The variation presented by these two traits work in a manner that the increasing or reduction in mass is accompanied by increasing or reduction in area, probably in an attempt to avoid significant changes in wing-loading (i.e., seed mass/seed area) diminishing any loss of dispersal potential. This idea is evidenced by the narrow range of the values in the ratio SM/SA among the 50 species, relative to the wide ranges in SM and SA, which indicates a constraint on selection acting on the relationship between seed mass and area. Augspurger (1986) reported the same pattern in a study with 34 anemochoric neotropical species in Barro Colorado, Panama.

Dispersion in a fluid environment can be considered a similar mechanism compared with the terrestrial environment. These results, obtained with seeds dispersing under experimental controlled conditions, are consistent with expectations based on standard equations in fluid dynamics (Vogel 1981, Augspurger & Franson 1987), which says that the terminal velocity of any object is a function of its size and density. Large but light objects fall more slowly than large but dense objects (Vogel 1981).

The mechanical design of a plant and its parts, especially the reproductive organs, is fundamental to its fitness and reproductive performance. Many plant traits appear to have evolved in response to abiotic and biotic mechanical forces (Read & Stokes 2006), and the wind is one of the most evident of them (Ennos 1997). Venable et al. (1998) has already documented the existence of adaptive geographic variation for anemochoric seed morphology of an Asteraceae in Mexico highlands, where variation in achenes morphology of 36 populations were related with climate and different vegetation types.

The ecological implications for altering seed mass and area may be quite different. Lowering seed mass may reduce the probability of success in seedling establishment, but may be accompanied by an increase in crop size. Increasing seed area does not alter seedling establishment, but may be accompanied by a decrease in crop size (Augspurger & Franson 1993). Added mass increases wing-loading (mass/area), thereby decreasing dispersal capacity; hence there is a potential trade-off between dispersal distance (by wind) and the nutritional reserves and protective seed coverings and tissues that might confer an advantage during dispersal, any dormancy period, and establishment (Augspurger 1988).

Smaller seeds may have lower probability of survival, but they may be better able to utilize a new subset of habitats. Larger seeds presumably have higher probabilities of survival. In contrast, variation in fruit area has no effect on seed mass and it is difficult to think how it would affect seedling establishment. Therefore, whether it is advantageous to alter wing-loading by changes in seed mass or fruit area depends upon relative construction costs of seeds, plasticity of size, and overall seedling ecology (Augspurger & Franson 1993).

Studies on population biology created some hypothesis to explain the features responsible for diaspores selection towards greater dispersal distances, which are usually related to density-dependent effects. The ‘colonization-hypothesis’ links the dispersal of diaspores to the condition of reaching new habitats, while the ‘escape-hypothesis’ attributes it to the possibility of reduce intraspecific competition (Howe & Smallwood 1982). Many studies indicate that an increase in dispersal distance reduces seed and seedling mortality by reducing the species density near the parent tree (Augspurger 1984, Clark & Clark 1984). A high concentration of seeds on the ground often attracts predators reducing the survival chances (Fenner 1985). It is exemplified by Janzen (1972) with the predation of a Costa Rican tree seeds by the bug *Dysdercus fasciatus*.

Millimeter by millimeter, generation to generation, nature has been selecting and shaping the more adapted individuals. The different seed dispersal patterns exhibited by the different species presumably reflects the natural selection for features which increase the chances of each individual seed being effectively transported and placed on favorable sites. But, it does not always necessarily involve maximizing the dispersal distance, because seed dispersal distance is just one of the steps involved in the complex wind dispersal process, and not always a greater dispersal potential is automatically and positively correlated with a better fitness because a

favorable site not always is located far away from the parental plant (Fenner 1985), as is often the case with desert plants (Ellner & Shmida 1981).

It can be exemplified with examples of reduced dispersal abilities found in insular organisms (Cody & Overton 1996) and fragmented landscapes (Soons & Heil 2002). When the effective area that permits a species to exist is reduced, there are no reasons to invest in greater dispersal abilities because the long-dispersing individuals would be negatively selected, and in this case, the features related to better dispersal would not be selected in this way (Carlquist 1966).

The mechanical design of winged seeds seems to have been finely shaped in order to achieve a better motility and consequently greater dispersal distances. A certain amount of data has been discovered about the importance of mechanical properties of the plant organs, and about how they interact with the environment (Niklas 1992, 1999, Rowe & Speck 2005, Fournier et al. 2006; Reith et al. 2006), but the understanding about how these properties interact with each other spatially and temporally is much less evident, especially in terms of plant fitness and distribution (Read & Stokes 2006). Our results intend to provide more subsidies to this understanding.

The identification of the better ways to manage and maintain biodiversity requires the knowledge about how species are distributed and which features influence the extent of their distribution (Gaston 1994, IUCN 1994). Currently, human activities like habitat fragmentation, transport of invasive species, and climate change are creating new processes that isolate, connect, and shift landscapes at a much higher speed. All of this current anthropogenic environmental changes make the study of the dispersal a requirement for predictive ecology (Sutherland et al. 2004).

Therefore, dispersal distance data are also needed in nature conservation connected with landscape planning or concepts of creating ecological corridors (Verkaar 1990).

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FIGURE LEGENDS

Figure 1. Seed schematic figure showing the measured variables. SNS = seminal nucleus size; STS = seed total size; SWS = seed wing size. $SWS = SWS1 + SWS2$.

Figure 2. Linear regression of species seed flight distance (SFD - cm) and seed wing size (SWS - cm) values of 50 Bignoniaceae species; $y = 25.757x + 118.09$, $R^2 = 0.26$, $p = 0.0003$.

Figure 3. Linear regression of species seed flight distance (SFD - cm) and seed area (SA - cm^2) values of 50 Bignoniaceae species; $y = 7.627x + 154.03$, $R^2 = 0.28$, $p = 0.0002$.

Figure 4. Linear regression of species seed flight distance (SFD - cm) and the ratio seminal nucleus size/seed wing size (SNS/SWS) of 50 Bignoniaceae species; $y = -228.61x + 278.63$, $R^2 = 0.29$, $p = 0.0002$.

Figure 5. Linear regression of species seed flight distance (SFD - cm) values and the ratio seed mass/seed area (SM/SA - g/cm^2) of 50 Bignoniaceae species; $y = -1671.6x + 54.41$, $R^2 = 0.47$, $p < 0.0001$.

FIGURES

Figure 1.

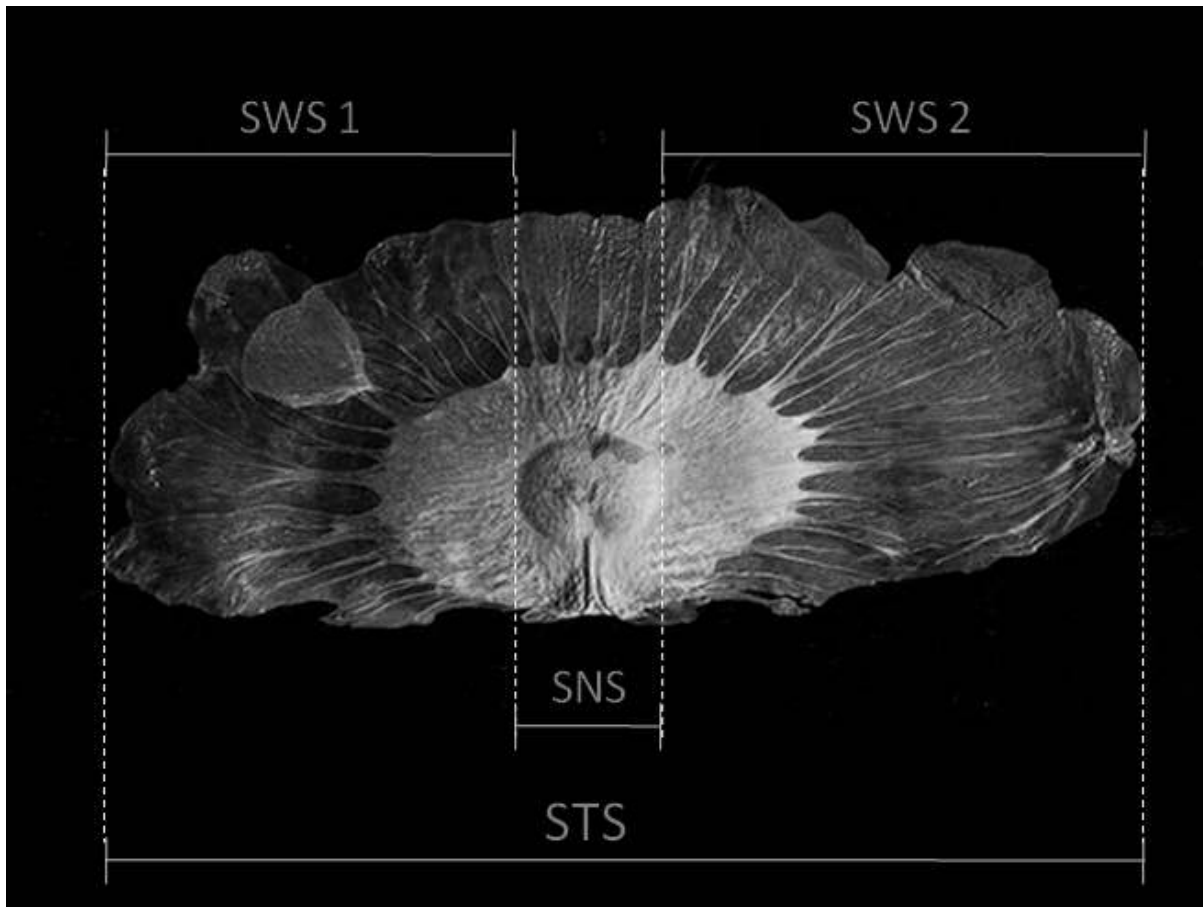


Figure 2.

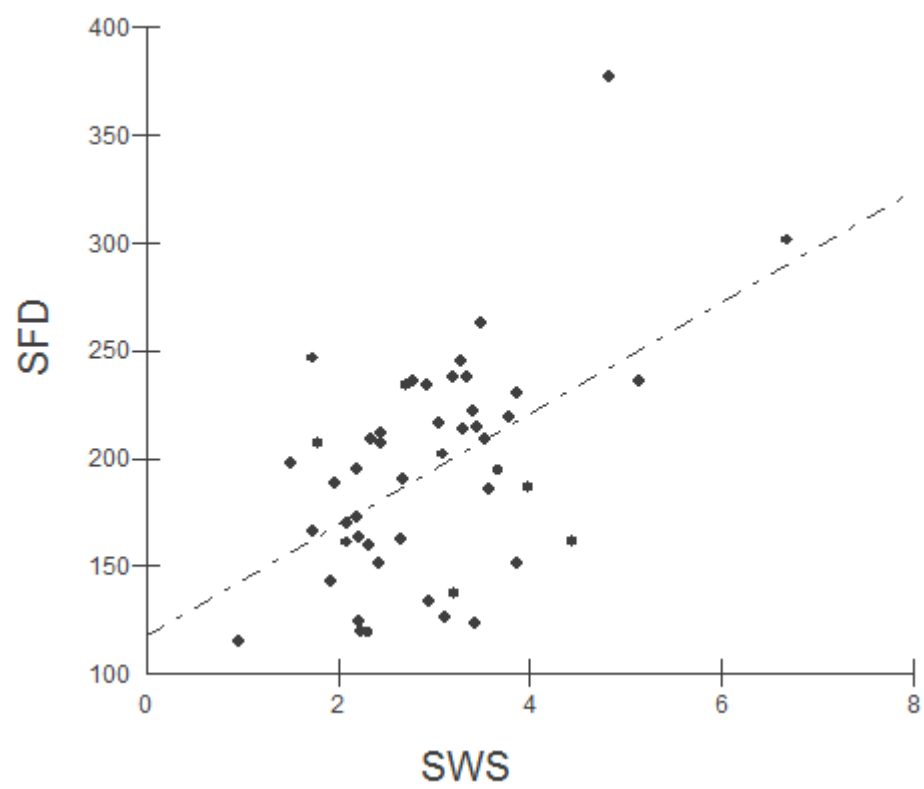


Figure 3

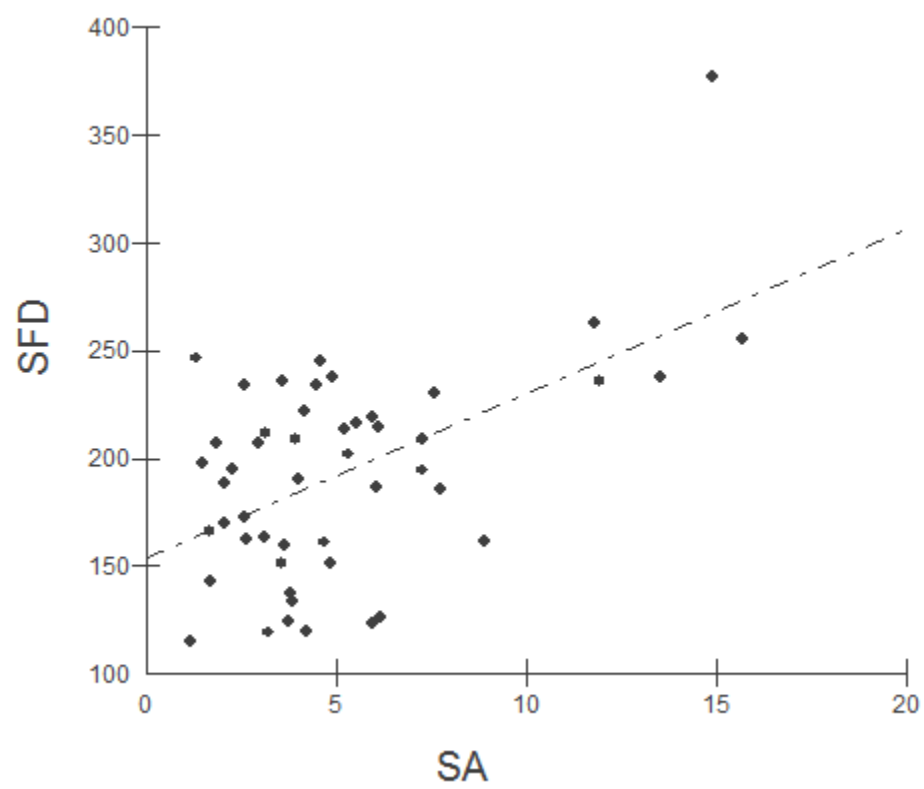


Figure 4.

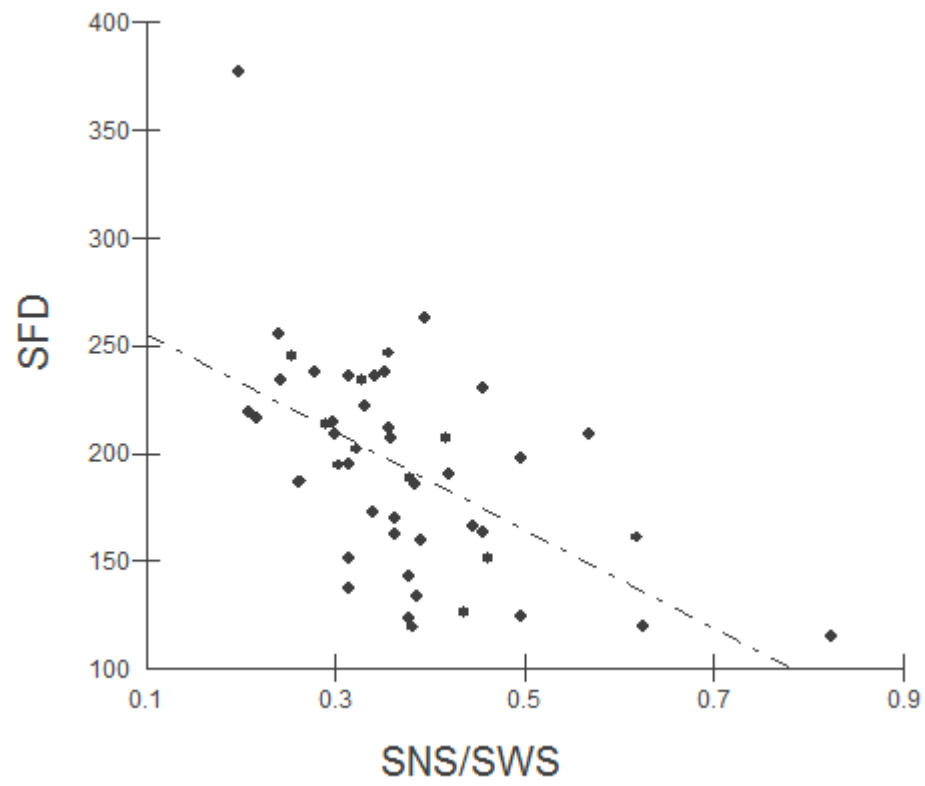


Figure 5.

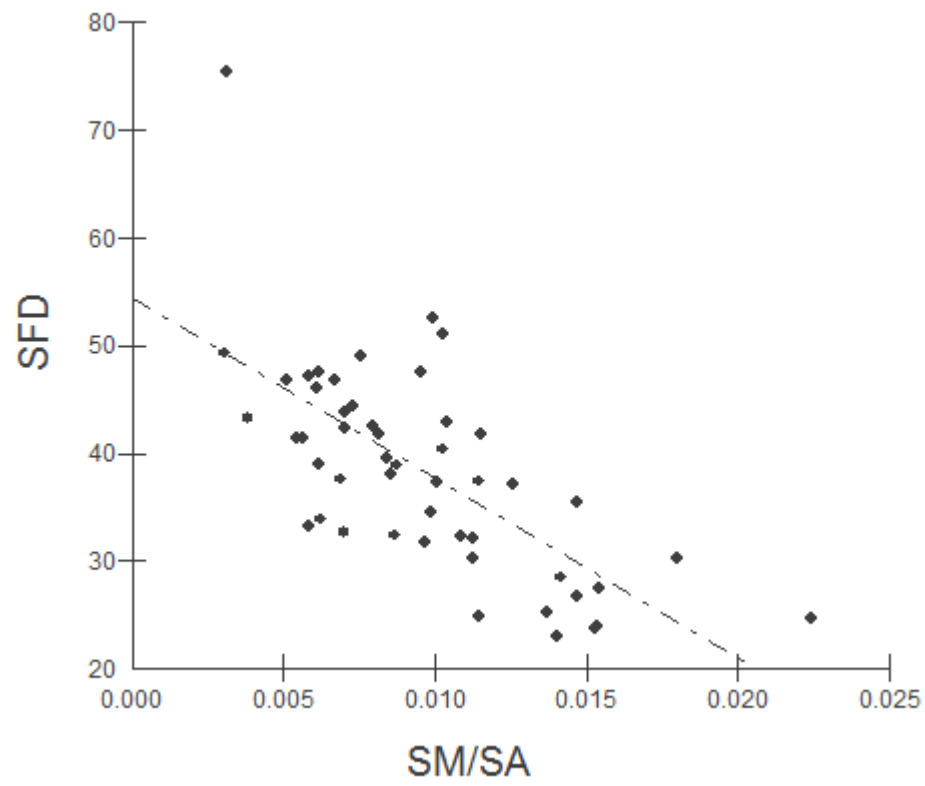


TABLE 1. Coefficients of determination of seed morphological variables (SNS = seminal nucleus size; STS = seed total size; SWS = seed wing size; SM = seed mass; SA = seed area) with seed flight distance (SFD) for 50 Bignoniaceae species. Significant coefficients are in bold. Significance at the Bonferroni corrected level is $p < 0.00625$. Species in bold have six or more variables significantly correlated with SFD.

SFD versus	SNS	STS	SWS	SM	SA	SNS/ SWS	SM/ SWS	SM/ SA
species								
<i>Adenocalymma cymbalum</i>	0.02	0.17	0.13	0.02	0.09	0.12	0.31	0.22
<i>Amphilophium aschersonii</i>	0.18	0.37	0.28	0.01	0.12	0.47	0.02	0.59
<i>Amphilophium bauhinioides</i>	0.47	0.005	0.004	0.59	0.03	0.47	0.57	0.52
<i>Amphilophium crucigerum</i>	0.55	0.57	0.65	0.42	0.50	0.03	0.16	0.13
<i>Amphilophium elongatum</i>	0.47	0.17	0.07	0.72	0.09	0.3	0.74	0.74
<i>Amphilophium magnoliifolium</i>	0.61	0.34	0.18	0.59	0.4	0.35	0.58	0.55
<i>Amphilophium paniculatum</i>	0.01	0.33	0.41	0.001	0.02	0.23	0.18	0.04
<i>Amphilophium parkerii</i>	0.34	0.04	0.01	0.04	0.2	0.001	0.01	0.44
<i>Anemopaegma floridum</i>	0.004	0.02	0.002	0.06	0.51	0.008	0.02	0.02
<i>Anemopaegma laeve</i>	0.12	0.3	0.39	0.4	0.41	0.1	0.02	0.53
<i>Bignonia aequinoctialis</i>	0.25	0.06	0.07	0.008	0.07	0.29	0.01	0.08
<i>Bignonia corymbosa</i>	0.01	0.03	0.11	0.17	0.6	0.002	0.17	0.43
<i>Bignonia nocturna</i>	0.57	0.13	0.52	0.07	0.45	0.37	0.72	0.52
<i>Cuspidaria cinerea</i>	0.01	0.66	0.7	0.66	0.76	0.28	0.56	0.8
<i>Cuspidaria convoluta</i>	0.54	0.1	0.14	0.49	0.25	0.17	0.59	0.62
<i>Cuspidaria lateriflora</i>	0.62	0.1	0.007	0.54	0.02	0.54	0.73	0.63
<i>Cuspidaria sceptrum</i>	0.01	0.006	0.01	0.001	0.001	0.03	0.002	0.03
<i>Dolichandra quadrivalvis</i>	0.22	0.12	0.16	0.23	0.17	0.22	0.3	0.31
<i>Dolichandra unguis-cattii</i>	0.02	0.25	0.42	0.03	0.24	0.23	0.002	0.36
<i>Fridericia chica</i>	0.56	0.51	0.51	0.53	0.56	0.68	0.73	0.77
<i>Fridericia cinerea</i>	0.42	0.05	0.02	0.58	0.02	0.47	0.61	0.44
<i>Fridericia cinnamomea</i>	0.1	0.26	0.22	0.11	0.15	0.06	0.13	0.09
<i>Fridericia conjugata</i>	0.06	0.23	0.03	0.32	0.09	0.01	0.08	0.05
<i>Fridericia erubescens</i>	0.73	0.3	0.09	0.42	0.48	0.70	0.33	0.57
<i>Fridericia leucopogon</i>	0.24	0.44	0.52	0.06	0.49	0.04	0.09	0.46
<i>Fridericia platyphylla</i>	0.39	0.35	0.33	0.39	0.33	0.05	0.4	0.44
<i>Fridericia pubescens</i>	0.06	0.07	0.07	0.03	0.15	0.03	0.03	0.38
<i>Fridericia rego</i>	0.01	0.02	0.04	0.14	0.05	0.02	0.09	0.40
<i>Fridericia speciosa</i>	0.3	0.24	0.52	0.02	0.37	0.51	0.24	0.29
<i>Fridericia spicata</i>	0.01	0.22	0.19	0.25	0.14	0.13	0.11	0.06
<i>Fridericia subincana</i>	0.13	0.12	0.01	0.02	0.09	0.17	0.04	0.23
<i>Fridericia triplinervia</i>	0.03	0.001	0.008	0.02	0.03	0.01	0.1	0.003
<i>Lundia corymbifera</i>	0.001	0.16	0.07	0.55	0.12	0.02	0.16	0.08
<i>Lundia densiflora</i>	0.01	0.25	0.14	0.006	0.22	0.17	0.21	0.52
<i>Lundia longa</i>	0.1	0.11	0.09	0.04	0.11	0.006	0.58	0.44
<i>Mansoa difficilis</i>	0.28	0.7	0.72	0.004	0.71	0.7	0.47	0.68

<i>Mansoa hirsuta</i>	0.45	0.01	0.01	0.48	0.08	0.31	0.43	0.43
<i>Mansoa lanceolata</i>	0.47	0.4	0.28	0.55	0.48	0.30	0.54	0.63
<i>Martinella obovata</i>	0.01	0.04	0.02	0.01	0.005	0.007	0.001	0.01
<i>Neojobertia candolleana</i>	0.3	0.37	0.32	0.71	0.25	0.04	0.65	0.77
<i>Neojobertia mirabilis</i>	0.07	0.005	0.01	0.33	0.008	0.1	0.001	0.48
<i>Pleonotoma jasminifolia</i>	0.07	0.004	0.005	0.52	0.001	0.01	0.43	0.52
<i>Pleonotoma longiflora</i>	0.4	0.39	0.52	0.54	0.44	0.58	0.60	0.60
<i>Pleonotoma stichadenia</i>	0.01	0.05	0.1	0.13	0.07	0.26	0.003	0.01
<i>Pyrostegia dichotoma</i>	0.01	0.27	0.37	0.25	0.50	0.14	0.27	0.27
<i>Pyrostegia venusta</i>	0.58	0.19	0.17	0.48	0.15	0.007	0.48	0.55
<i>Stizophyllum perforatum</i>	0.002	0.002	0.002	0.04	0.64	0.01	0.02	0.69
<i>Tanaecium pyramidatum</i>	0.36	0.001	0.35	0.43	0.32	0.41	0.58	0.41
<i>Tanaecium selloii</i>	0.41	0.32	0.16	0.43	0.38	0.35	0.39	0.4
<i>Xylophragma myrianthum</i>	0.002	0.58	0.61	0.47	0.55	0.52	0.73	0.66

TABLE 2. Number of significant correlations among seed morphological variables (SNS = seminal nucleus size; STS = seed total size; SWS = seed wing size; SM = seed mass; SA = seed area) and seed flight distance (SFD) for 50 Bignoniaceae species.

Variable 1	Variable 2	Number of significant correlation			Expected correlation
		TOTAL	negative	positive	
SNS	SFD	20	16	4	negative
STS	SFD	23	6	17	positive
SWS	SFD	19	4	15	positive
SM	SFD	26	23	3	negative
SA	SFD	22	5	17	positive
SNS/SWS	SFD	16	13	3	negative
SM/SWS	SFD	26	25	1	negative
SM/SA	SFD	36	36	0	negative

CAPÍTULO 3

The younger, the better: geographic range size and evolution of dispersal in Bignonieae (Bignoniaceae)

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Running head: Dispersal efficiency evolution in Bignonieae (8 words)

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Abstract

This study integrates the ecology, phylogeny and biogeography of a vast Neotropical plant group treated under an evolutionary approach. We analyzed the relationships between seed morphological traits related to wind dispersal potential with the phylogenetic age and the extant geographic range size of Bignoniaceae species to investigate a possible evolution of the traits related to an improved dispersal. Specifically, we tested the hypotheses that (i) species geographic range sizes are positively correlated with their seed dispersal potential by wind, and (ii) dispersal potential is negatively correlated with the species phylogenetic age, and additionally, we analyzed if variables that are related with improved wind dispersal potential have been selected along the species radiation and evolution. The study includes 48 species with their distribution ranging from the south of South America to south of North America. We analyzed the following seed morphological traits: (1) seed total size (STS), (2) seminal nucleus size (SNS), (3) seed wing size (SWS), (4) seed mass (SM), (5) seed area (SA), (6) the ratio between the seminal nucleus size and the seed wing size (SNS/SWS), (7) the ratio between the seed mass and the seed wing size (SM/SWS), and (8) the ratio between the seed mass and the seed area (SM/SA), which were tested and proved to be related with an improved wind dispersal potential in a previous wind tunnel experiment from the same authors. The geographic range sizes were calculated with a large dataset complemented with herbarium records and the phylogenetic ages were obtained from the dated molecular phylogeny of the group. We showed that seed dispersal distance is positively correlated with the extant geographic range size, and negatively correlated with species phylogenetic age. SNS showed a positive correlation with age, and the ratio SM/SA showed a positive correlation with age and a negative correlation with the extant geographic range size. The results indicate that species that have seeds with higher flight capacities are more recent phylogenetically and have larger geographic range sizes. We infer that species have been selected in order to favor their dispersal efficiency, especially in the SM/SA ratio, and this have benefited the younger species enabling them to disperse over larger areas. They may have passed through a SNS reduction during the evolution of the group, which reduced their mass and therefore reduced their SM/SA ratio increasing their flight ability and colonizing potential. It provides evidence that some seed morphological biomechanical traits may have been selected throughout this group evolution in order to benefit the dispersal efficiency, and therefore, this have enabled the increase of their geographic range sizes. The results highlight the importance of deepening the studies integrating dispersal ecology with phylogeny and biogeography.

Keywords: Bignoniaceae, anemochoric seeds, winged seeds, seed traits, morphological traits, biomechanical traits, dispersal distance.

Introduction

The phylogenetic diversification and ecological radiation of angiosperms that took place between 135 and 65 million years ago, was one of the major biotic upheavals in the history of life (Friis et al. 2011). In their way to ecological dominance, angiosperms have exhibited extraordinary developmental and evolutionary plasticity, and it has resulted in overwhelming morphological diversity and a great variety of adaptive types (Friis et al. 2011), scattered throughout virtually all locations on the planet.

Over the past decades the development of phylogenetic systematics has stimulated intense research on the reconstruction of evolutionary phylogenetic patterns, and many of the theoretical and methodological issues that formerly blocked the progress in phylogenetics have now been at least partly resolved, clearing the way for new research that has made rapid progress (Friis et al. 2011). Genetics, behavior, epidemiology, ecology, conservation and evolution are examples of fields that were illuminated by such information (Harvey & Nee 1996).

Almost every place on the planet harbors some kind of life, but no kind of life is able to live everywhere. Species show great variations in their geographic distributions (Paul & Tonsor 2008) even between closely related species (Brown et al. 1996), and elucidate the drivers of this variations has been a challenge to natural scientists for centuries.

Studies on geographic distribution patterns for different taxonomic groups in different regions of the world often relate the causes of variations in species geographic ranges with environmental variables (Stevens 1989; Brandle et al. 2002) or with species morphological features (Edwards and Westoby, 1996; Lester et al. 2007).

For plants, morphological traits associated with their diaspores may have influence on the species distribution because they are related with the species dispersal efficiency (Augspurger 1986; Augspurger and Franson 1987).

Among the several ecological and evolutionary features that have been used to explain the variations in species geographic ranges, the organism's ability to disperse is one of the more commonly cited potential determinants (Hanski et al. 1993; Gaston 2003; Lester et al. 2007). Some studies suggest that the greater the species dispersal efficiency, the greater their geographic range sizes (Brown et al. 1996; Gaston 1996). Dispersal ability is claimed as an explanation for geographic range size variation both in aquatic and terrestrial systems and for a great variety of taxonomic groups, including insects (Gutierrez & Menendez 1997; Malmqvist 2000; Brandle et al. 2002), plants (Oakwood et al. 1993; Edwards and Westoby 1996; Thompson et al. 1999; Clarke et al. 2001; Lloyd et al. 2003; Lowry & Lester 2006), fishes (Wellington & Victor 1989; Goodwin et al. 2005; Lester & Ruttenberg 2005; Mora & Robertson 2005), and molluscs (Hansen 1980; Jablonski 1986; Pfenninger 2004).

However, dispersal ability does not act alone, because dispersal, especially when it expands a species' range, is not an instantaneous process, so the time available for dispersal can also play a central role in explaining range size variation (Paul et al. 2009). Species with lower dispersal abilities may have large ranges if sufficient time is provided and species with similar dispersal abilities may have considerably different range sizes because they had different time intervals available for their dispersal (Paul et al. 2009).

Dispersal is considered a key feature to species survival, because a great variety of living organisms need to disperse to perpetuate the species. Especially for sessile organisms, the

dispersal process is the mechanism by which the species define their ranges and therefore maintain their existence.

Dispersal in plants, specifically, have been a topic of great interest to natural scientists for a long time (e.g., Ridley 1930; van der Pijl 1982) because it is related to several aspects of population and community structure and dynamics (Levin et al. 2003) and it is involved in many ecological or evolutionary problems (Dieckmann et al. 1999).

One of the primary motivations for studying dispersal is to understand the rates of spread of species (e.g., Okubo and Levin 2001, Turchin 1998) and the establishment of relations between species geographic ranges and biotic variables can generate new and relevant information that may serve as the basis to the development of new ecological and phytogeographical models.

The knowledge about the features that cause variation in the species geographic ranges is an important tool for population and community studies, because it can be used to analyze the factors that inhibit or facilitate certain species colonization (Guasp et al. 1996). It also has important practical applications in the planning of conservation actions, especially in the tropical region, where the megadiversity is composed in most part by species with small distribution areas (endemic).

In this study we integrate the ecology, the phylogeny and the biogeography of a vast Neotropical plant group treated under an evolutionary approach. Considering a group of phylogenetically closely related species and with the same type of dispersion and the same type of diaspore, the variation in the size and shape of seed biomechanical traits linked to the dispersal ability may have a relationship with the species geographic range size, especially in Bignoniaceae, which all

species have winged seeds and the dispersion primarily by wind (Lohmann 2004) making it an appropriate model for the present study.

We used a large neotropical species group, the tribe Bignonieae (Bignoniaceae), to analyze the existence of relationships between seed morphological traits associated to wind dispersal potential with the species phylogenetic age and the extant geographic range size to investigate a possible evolution of the traits related to improved anemochoric dispersal.

We specifically tested the hypotheses that (i) species geographic range sizes are positively correlated with their seed dispersal potential by wind, and (ii) dispersal potential is negatively correlated with the species phylogenetic age. Additionally, we analyzed if seed traits that were proved to be related with improved wind dispersal potential may have been selected along the species radiation and evolution.

We expected that some specific seed morphological traits that are associated with a greater dispersal potential were correlated with the species age and geographic range size. Seminal nucleus size, seed mass, ratio seminal nucleus size/seed wing size, ratio seed mass/seed wing size, and ratio seed mass/seed area were expected to be positively correlated with species phylogenetic age and negatively correlated with geographic range size. Seed wing size, and seed area were expected to be negatively correlated with species phylogenetic age and positively correlated with geographic range size.

Methods

The family Bignoniaceae and the tribe Bignonieae

Bignoniaceae is a plant family containing climbers, shrubs and trees with pantropical distribution (Lohmann 2004). They are predominantly neotropical and constitute an important component of neotropical forests (Olmstead et al. 2009). The family includes 82 genera and 827 species (Lohmann and Ulloa 2008). Approximately half of both genera and species belong to the New World endemic tribe Bignonieae (Lohmann and Taylor 2013), which represents the largest single clade of lianas in the Neotropics (Lohmann 2006). The diversity center is tropical America where there are about 42 genus and 635 species (Lohmann and Ulloa 2008).

The group is monophyletic, geographically widespread and widely distributed ranging from northern Argentina and Chile to southern United States (Lohmann 2006). The vast majority of species show the same type of seed (a flattened two-winged seed) and have their dispersion primarily made by wind (Lohmann 2004). Additionally, the seeds have absent or reduced endosperm (Manning 2000; Judd et al. 2002; Datta 2003, Olmstead et al. 2009), therefore, they do not present any attractive for the fauna and do not have secondary dispersion by frugivory, which makes them an appropriate model for our investigation.

For this study we considered 48 species currently recognized in the group (Lohmann and Taylor 2013). The species were chosen in a way to represent the greatest possible number of genera (16 out of 20) presented by the time-calibrated phylogenetic tree of the tribe (Lohmann et al. 2013), to include a wide range of ages (4.7 to 27.7 m.y.) and geographic range sizes (61,419.8 to 32,764,400 km²), and according to the number of available exsiccates containing viable seeds for each species.

Seed morphological traits (SMT) and dispersal potential

The seed morphological traits used in this study were taken from a previous study of the same authors (Chapter 2 in this thesis), in which we analyzed several seed biomechanical traits in relation to the seed dispersal potential by wind. Dispersal potential here refers to the potential seed dispersal distance measured in a wind tunnel experiment.

The variables were obtained from seeds collected from herborized materials from several herbaria in Brazil (ESA, HRCB, IBGE, SP, SPF, R, RB, UB). We selected 20 seeds from each species from at least three different specimens. We used a digital calliper rule (Digimatic Caliper, Mitutoyo, Japan) and a high precision analytical balance (METTLER AE240(s), Instrument Corporation) to measure the following seed morphological traits: (1) seed total size (TS), (2) seminal nucleus size (SNS), (3) seed wing size (SWS), (4) seed mass (SM), (5) seed area (SA), (6) seminal nucleus size/seed wing size ratio (SNS/SWS), and (6) seed mass/seed area (SM/SA). The dimensions were taken with the seed longitudinally oriented and all the seeds were released under the same conditions and in the same orientation. Then, we used an experiment in a small wind tunnel to assess the relation between these seed morphological traits and their dispersal potential by wind. The experiment consisted in inserting the seeds from different individuals and species in the tunnel with the wind set in fixed velocity (1 m/s). Then, we measured the distance that the seed flew inside the tunnel (SFD - seed flight distance) and used it as a proxy for wind dispersal potential, because for a seed that is carried by the wind, the greater the SFD, the better its dispersal. For the experiment details see Chapter 2 in this thesis.

Species Phylogenetic Age (PA)

A study combining nuclear and chloroplast DNA (cpDNA) of about one-third of the species in the tribe resolved many of the generic delimitation problems and clarified the relationships among several lineages of the group (Lohmann 2006) resulting in a revised classification with a phylogenetic tree reconstructed based on molecular markers (Lohmann & Taylor 2013). Additionally fossil records were incorporated to the phylogeny (Lohmann et al. 2013) which make possible to assess the age of diversification of the different lineages within the group.

To assess the species phylogenetic age (PA) we used the time-calibrated phylogenetic tree of the tribe Bignoniaceae (Lohmann et al. 2013), which contains the age estimation of the 48 species considered in this study.

We used the software Mesquite v. 2.72 (Maddison & Maddison 2010) to assess the species relative divergence dates in the phylogenetic tree. The PA was expressed in millions of years (mi.y^{-1}).

Geographic range size (GRS)

The species geographic range size (GRS) were calculated through the dataset compiled by L.G. Lohmann (unpublished data). It includes about 30.000 georeferenced presence points of the 382 species recognized in the tribe Bignoniaceae. The dataset comprises the collections made by Alwyn H. Gentry during several years of research in the Neotropics complemented with other personal and herbarium records.

We constructed geographic distribution maps of each species in a GIS software (Arc-GIS v. 10) plotting the known occurrence points of each species on a georeferenced shape. Then, we used each map to estimate the GRS for each species considering the polygon area of the minimum polygon around all the species occurrence points (Southwood 1966). The GRS was expressed in square kilometers (km²).

Data analysis

We tested our hypothesis using simple linear regression between species seed morphological traits with their geographic range size and phylogenetic age. The coefficient of determination (R²) was used to evaluate the dependence degree among the variables. The regression were considered significant at the Bonferroni corrected level because several comparisons were made within the same dataset. The analysis were performed in Bioestat v.5. (Ayres et al. 2007).

Results

PA showed a continuous distribution ranging from 4.7 to 27.7 mi.y⁻¹ and GRS also showed a continuous distribution ranging from 61419.8 to 32764400 km². SFD ranged from 65 to 377 cm.

SM showed a wide variation of 60 fold, ranging from 0.004 g to 0.242 g. SA showed a 18 fold variation, ranging from 1.17 to 21.13 cm². The ratio SM/SA showed a substantially smaller variation of only 6 fold, ranging from 0.003 to 0.02 g/cm².

Seed traits and geographic range size

Our measure of dispersal potential (SFD) showed a positive and significant correlation ($R^2 = 0.40$; $p < 0.0001$) with the extant geographic range size (Fig. 1), indicating that the greater the seed flight potential of a species, the larger its geographic range size.

The SM/SA ratio was the only variable that showed significant correlation ($R^2 = 0.34$; $p < 0.0001$) with the species extant geographic range size (Fig. 2). This result show that this trait is negatively correlated with the extant geographic range size of a species in a manner that the smaller the SM/SA ratio, the larger the geographic range size of the species.

Seed traits and phylogenetic age

SFD showed a negative and significant correlation ($R^2 = 0.43$; $p < 0.0001$) with species phylogenetic age (Fig. 3), indicating that seeds from younger species have greater flight potential compared with seeds from older species.

SNS showed a positive and significant correlation ($R^2 = 0.34$; $p < 0.0001$) with the species phylogenetic age (Fig. 4), indicating that younger species have smaller nucleus than older species. We infer that this pattern may have arisen because the species may have passed through a reduction of the size of their seminal nucleus during the evolution of the group.

The SM/SA ratio also showed a positive and significant correlation ($R^2 = 0.40$; $p < 0.0001$) with the species phylogenetic age (Fig. 5), indicating that younger species have lower units of mass per unit of area.

Discussion

Dispersal has important ecological and evolutionary consequences (Clobert et al. 2001; Bowler and Benton 2005), including the ability of species to change or expand their ranges (Holt 2003). The evolution of dispersal has already received some scientific attention, mainly through the development of different theoretical models (Hamilton and May 1977; Comins 1982; Levin et al. 1984; Olivieri et al. 1995; Travis and Dytham 1998) and the potential dispersal of plants have been already documented for temperate herbaceous species (Sheldon and Burrows 1973; Werner and Platt 1976; Platt and Weis 1977; Rabinowitz and Rapp 1981), for temperate trees of North America (Green 1980; Guries and Nordheim 1984), and *Eucalyptus* trees of Australia (Cremer 1977 *apud* Augspurger 1986), but it has been rarely studied using experimental data from Neotropical plants.

Fundamental plant traits depend substantially on their biomechanical design. The mechanical design, especially of the reproductive organs, is linked to its fitness and reproductive performance (Read and Stokes 2006). Although the costs, effects and subsequent trade-offs of this mechanical traits are not completely understood, they are intrinsically linked to survival and reproduction, so they are likely to be under strong selective pressures.

It has been shown that some species have evolved certain changes in some traits in organs like leaves, roots, and reproductive parts, in response to certain biotic and abiotic selective pressures in order to keep or improve their fitness (Ennos 1993; Berthier et al. 2001; Bobich and Nobel 2001; Ackerly 2004; Balsamo et al. 2004; Berthier and Stokes 2005; 2006; Danjon et al. 2005). It appears that many traits have evolved in response to abiotic and biotic mechanical forces

(Read and Stokes 2006), the wind being one of the most evident of these abiotic forces (Ennos 1997).

Despite the attention that the evolution of dispersal strategies has received, only recently it has become clear that dispersal can evolve relatively fast and become spatially heterogeneous in a spatially structured environment (Thomas et al. 2001; Hanski et al. 2004; Haag et al. 2005; Cheptou et al. 2008; Phillips et al. 2008).

Our results showed that the flight potential of anemochoric seeds from species of Bignoniaceae is positively correlated with their extant geographic range size, which means that species having seeds with greater flight abilities have larger geographic ranges. Additionally, this flight potential is negatively correlated with the species phylogenetic age, which means that the seeds with the greatest flight potential belong to the younger species, while seeds from older species have lower flight abilities. In other words, species that have seeds with greater flight abilities are phylogenetically more recent and have larger geographic range sizes.

The ratio SM/SA showed a positive correlation with age and a negative correlation with the extant geographic range size, which means that the seeds of younger species have smaller units of mass per unit of area and that this species also have larger geographic range sizes. Additionally, the size of the seminal nucleus showed a positive correlation with the species phylogenetic age, meaning that younger species have smaller seminal nucleus than older species.

Adaptations to the selective pressure exerted by wind have already been showed for some plant parts (Vogel 1989; 1992). Based in our results we infer that, in the cases where it meant an improvement of the fitness, some seed biomechanical morphological traits linked to improved dispersal may have been selected during the evolution of the group in order to favor their

dispersal potential, and therefore, this have enabled the increase of their geographic range sizes. Species may have experienced a selection towards reduction in seminal nucleus size, which reduced their mass and therefore reduced their SM/SA ratio increasing their flight abilities. This process may have benefited the younger species, allowing them to disperse over larger areas in a shorter time.

The importance of this two traits (seed mass and seed area), especially regarding to the seed dispersal process, have been also demonstrated in other studies with wind-dispersed tropical tree species (Augspurger 1986) and with artificial seeds (Augspurger and Franson 1987), so it is expected that this traits undergo selective pressures towards the improvement of their efficiency, and this would be reflected in their seed morphology.

This result is similar with the findings of the dispersal experiment of Augspurger and Franson (1987), using artificial fruits varying in mass, area and morphology. They showed that propagules (in this case, wind-dispersed samaras) with smaller wing-loading, which is a measure equivalent to our ratio SM/SA, have greater mean dispersal distances. When the artificial samaras varied in area and mass, but maintained the same wing-loading, they detected no consistent pattern in the mean dispersal distance variation.

The narrow range of the values in the ratio SM/SA among the 48 species, relative to the wide ranges in SM and SA, may indicate a constraint on selection acting on the relationship between seed mass and seed area. The pressures acting on this two parameters seems to work in order to maintain this trait constant, in a manner that any increasing or reduction in mass is accompanied by a parallel increasing or reduction in area, probably in an attempt to diminish any loss of

dispersal potential or keep some kind of allometric relationship. This same pattern was related by Augspurger (1986) in a study of 34 anemochoric neotropical species in Barro Colorado, Panama.

Evolution seems to have finely shaped the mechanical design of winged seeds in order to acquire better motility and, therefore greater dispersal distances, and adaptations to the selective pressure exerted by wind has already been showed for other plant parts (Vogel 1989; 1992; 2003). The morphological design of wind-dispersed diaspores apparently are shaped to slow their rates of descent and increase their chances of exposure to horizontal winds, which in turn can carry the seeds for greater dispersal distances (Augspurger 1986). But whether it is a benefit to alter the mass/area relationship by changes in seed mass or fruit area depends upon the relative costs of construction of the seeds and overall seedling ecology (Augspurger and Franson 1993). Any addition in mass will increase the wing-loading, thereby decreasing dispersal capacity (Read and Stokes 2006). Larger seeds presumably have higher probabilities of survival. Smaller seeds may have lower probability of survival, but they may be better able to utilize a new subset of habitats (Westoby et al. 1996; Coomes and Grubb 2003; Turnbull et al. 2004; Baraloto et al. 2005). In contrast, variation in fruit area has no effect on seed mass and it is difficult to think how it would affect seedling establishment, hence there is a potential trade-off between dispersal distance by wind and the nutritional reserves and protective seed coverings and tissues that might confer an advantage during seed dispersal and establishment (Augspurger 1988).

Despite having a completely different design, a similar pattern was reported for the wind-dispersed fruits (achenes) from Asteraceae by Sheldon and Burrows (1973). Measurements of dispersal potential for several species indicate that the effectiveness of dispersal is related to the ratio of the sizes of the pappus and the achene.

Dispersing individuals unavoidably will carry their genes with them. Thus, any genetic trait that influences the ability to disperse can cause spatial differentiation in the gene pool. Finding new habitats is an essential prerequisite for reproduce in them and an improved dispersal ability can make a seed arrive in new locations. When these new sites are suitable, this "good flying" seed (and all its genotypic and phenotypic attributes) can start a new population, expanding the species geographic range size. Thus, dispersal is a good example of a trait that can experience strong selection, especially at the range margins (Kokko and López-Sepulcre 2006). In particular, the leading edge of a moving population front can be composed of individuals whose dispersal-related genotypes differ from others (Travis and Dytham 2002; Hughes et al. 2007; Darling et al. 2008; Phillips et al. 2008).

Adaptive geographic variation for anemochoric seed morphology has already been documented for an Asteraceae in Mexico highlands (Venable et al. 1998). In addition, several examples suggest that evolution can be both fast and significant for the ability of a species to colonize new areas (Simmons and Thomas 2004; Phillips et al. 2006). The evolution of individuals with greater dispersive abilities near species range borders creates a positive feedback with potential to accelerate the expansion of a species (Kokko and López-Sepulcre 2006).

The generality of this trend can also be exemplified with studies made with other organisms. For example, recently colonized patches of the european butterfly *Melitaea cinxia* are mainly composed of individuals with higher flight ability than those found in old patches (Hanski et al. 2004) and allelic variation in a single gene can contribute significantly to this variation (Haag et al. 2005). In another example, marginal populations of crickets (*Conocephalus* and *Metrioptera* spp.) expanding their ranges in the United Kingdom showed increased frequencies of long-winged dispersive individuals, which indicates evolutionary change (Simmons and Thomas

2004). And in an unfortunately example, cane toads (*Bufo marinus*) introduced into Australia are rapidly invading the continent, helped by fast adaptation that produces longer-legged individuals and enhances dispersal at the invasion front (Phillips et al. 2006). Recent theoretical work shows that such differences can determine the stability of the species' range boundary and, consequently, play a decisive role in whether the species will expand its range (Guo et al. 2005).

Dispersal evolution may arise from conflicts between parent and offspring (Starrfelt and Kokko 2010), and the causal effects for the evolution of the dispersal process towards increased dispersal distances could be related to density-dependent effects. Many studies indicate that an increase in dispersal distance reduces seed and seedling mortality by lowering density near the parent tree (Janzen 1970; Augspurger 1984; Clark and Clark 1984). Moving to unknown territories entails mortality risks, and individuals can thus be selected to avoid it, unless sufficiently counterbalanced by dispersal-favoring mechanisms such as kin competition (Hamilton and May 1977), inbreeding avoidance (Bengtsson 1978), or spatiotemporal variability in resources (Van Valen 1971).

Populations, on the other hand, depend on dispersal, without which full utilization of resources in the environment would be impossible. Depending on how strongly each of the individual-level mechanisms favors dispersal, we may thus end up with species with very different potentials for expanding their ranges (e.g., Bohning-Gaese et al. 2006) or for maintaining their populations (Ozinga et al. 2009).

The pattern we found here goes against one of the oldest hypothesis formulated to explain geographic range size variations. The eighteenth century renowned botanist John C. Willis hypothesized that species age was the main responsible for species geographic range size

variations (Willis 1922). Theoretically, the species age would be an important variable, because the older the species, more time it had to spread to a greater area (Willis 1922), although it is not the case for the tribe Bignonieae (Chapter 1 in this thesis).

One of the main caveats of Willis's hypothesis is that he considers all the species having equal dispersal abilities. What we could demonstrate here is that even in a phylogenetically related group of species with all the species following the same seed morphological pattern, there are significant differences in the species dispersal potential and it could be influencing the species colonization rates and therefore, their geographic range sizes.

There are evidences of the existence of rain forests from about 100 millions of years ago (Morley 2000; Davis et al. 2005), but the analysis of some clades, like the diverse legume genus *Inga*, suggests that *Inga* species can be considered quite young (Bermingham and Dick 2001), with many species dating from 2 to 10 millions of years ago (Richardson et al. 2001). Despite this relative origin, this clade has spread throughout South and Central American forests, being important components in terms of both number and biomass at many sites (Richardson et al. 2001). In fact, legume clades in general may be remarkably young given their widespread distribution and numerical importance in tropical forests, about 4-16 millions of years ago (Lavin et al. 2004).

The distribution of species we observe today reflects a long history of alternating episodes of dispersal and isolation. The sea level fluctuations which opened and closed land corridors, the splitting of continents, and the rising of mountain ranges and islands, have all left their mark on the distribution of extant species (Kokko and López-Sepulcre 2006).

Bignoniaceae is a speciose clade and an old plant lineage (~40 Ma). Species rich tribes like Bignoniaceae have a wide range of ages and geographic distribution areas and as a consequence they occur in a wide range of habitats and under many different environmental and ecological situations. Therefore, they may experience drastic area retractions caused by local extinctions caused by the climatic oscillations throughout the last millions of years.

Other researchers (Chown 1997; Gaston 1998; 2003; Chown and Gaston 2000) have summarized several models of post-speciation range-size transformations (e.g., cyclical, random, stasis, etc.) that could potentially explain the pattern found here. For example, the age and area relationship may be explained by a hump-shaped curve, where species start with small range sizes, reach their maximum range size at an intermediate age, and then decline towards extinction when they are old. Bignoniaceae is a tribe with about 50 millions of years (Lohmann et al. 2013). Since the most part of the species we analyzed can be considered recent (about 4 to 8 mi.y^{-1}) or with intermediate ages (about 9 to 20 mi.y^{-1}), they would be in their expansion or maximum range size phase according to the hump-shaped post-speciation model, and therefore such species would have relatively greater range sizes. Such a pattern was already documented for fossil assemblages of Cenozoic mollusks (Foote et al. 2007).

Evolution by natural selection acting either on dispersal or on adaptive characters can lead to 'range collapse', where a species that originally occupied a variety of habitats becomes increasingly specialized over time and thus shrunken in its range, relative to its ancestral state (Holt 2003). The phenomenon of habitat loss may also occur due to evolutionary processes not involving adaptive trade-offs between habitats, as for instance, habitat specific accumulation of deleterious mutations that can lead to loss of marginal habitats (Kawecki et al. 1997).

Several potential factors can have direct and indirect influence on the geographic range size of a species and the extant distribution of a plant is a complex phenomenon resulting from many interacting variables, from the plant itself, from its surrounding environment, and often due to both. We are aware that seed dispersal distance is just one of the steps involved in the complex dispersal process, which also includes post dispersal phases, like an effective germination and a successful establishment. The different seed dispersal patterns exhibited by the different species presumably reflects the natural selection for features which increase the chances of each individual seed being successful in all the steps involved in the dispersal process. This does not necessarily involve maximizing the dispersal distance because not always a favorable site is located far away from the parental plant (Fenner 1985), as is often the case with desert plants (Ellner and Shmida 1981). It could be the reason why some species do not show such relationships. Some designs may be far from optimal due to constraints imposed by phylogenetic and evolutionary history (Read and Stokes 2006).

Even if environmental change is the primary determinant of range dynamics, the evolutionary responses by a species can modulate the magnitude, direction and pattern of its range shift (Holt 2003). Recent theory suggests that evolutionary dynamics within a species can also lead to range expansions or contractions, even with no contemporaneous directional trends in the environment (Kirkpatrick and Barton 1997). Over long temporal scales, changes in species' ranges almost surely reflect the impact of evolution in heterogeneous environments (Hoffmann and Blows 1994; Kirkpatrick and Barton 1997), but empirical evidence is increasingly showing that dynamism in range boundaries involves evolution in species' traits (Enquist et al. 1995; Davis and Shaw 2001; Thomas et al. 2001).

According to Read and Stokes (2006), although there have been an increasing amount about the importance of mechanical properties of the plant organs, and about how they interact with the environment (Niklas 1992; 1999; Rowe and Speck 2005; Fournier et al. 2006; Reith et al. 2006), the understanding about how some of these properties interact with each other spatially and temporally is not much evident, especially in terms of plant fitness and distribution. Our results intend to provide insights about how some plant biomechanical traits linked to reproduction may interact with the environment and respond to the surrounding selective pressures over time and space.

The advancement of knowledge about factors that shape species distribution is important for conservation, especially for the tropical region, where the megabiodiversity that now are highly threatened is mostly composed of endemic species with small geographic ranges (Wallace 1878; Dobzhansky 1950; Gaston 1994; Hubbell 2001), which is just beginning to receive adequate ecological and genetic treatment and improved estimates of range size (Pitman et al. 2001).

Species geographic range size is one of the variables that describes the species rarity degree (Rabinowitz et al. 1986, Ricklefs 2002) and therefore their extinction susceptibility. Additionally, it has been showed that dispersal can significantly decreases the probability of extinction (Roff 1974a; 1974b), and there exists evidence that indicates that genotype is important in this regard (Sakai et al. 1958; Krebs et al. 1973).

The identification of the better ways to manage and maintain biodiversity requires the knowledge about how species are distributed and which features influence the extent of their distribution (Gaston 1994; IUCN 1994). Thus, the knowledge about the factors that determine species geographic distribution represents an important acquisition for sustainable management

development and biodiversity conservation planning. The results highlight the importance of deepening the studies integrating phylogeny, ecology and biogeography in an evolutionary context.

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FIGURES

Figure 1. Linear regression between geographic range size (GRS - km²) and seed flight distance (SFD - cm) for 48 Bignoniaceae species ($R^2 = 0.40$; $p < 0.0001$; $y = 81680x - 5967135.9$; $n = 48$).

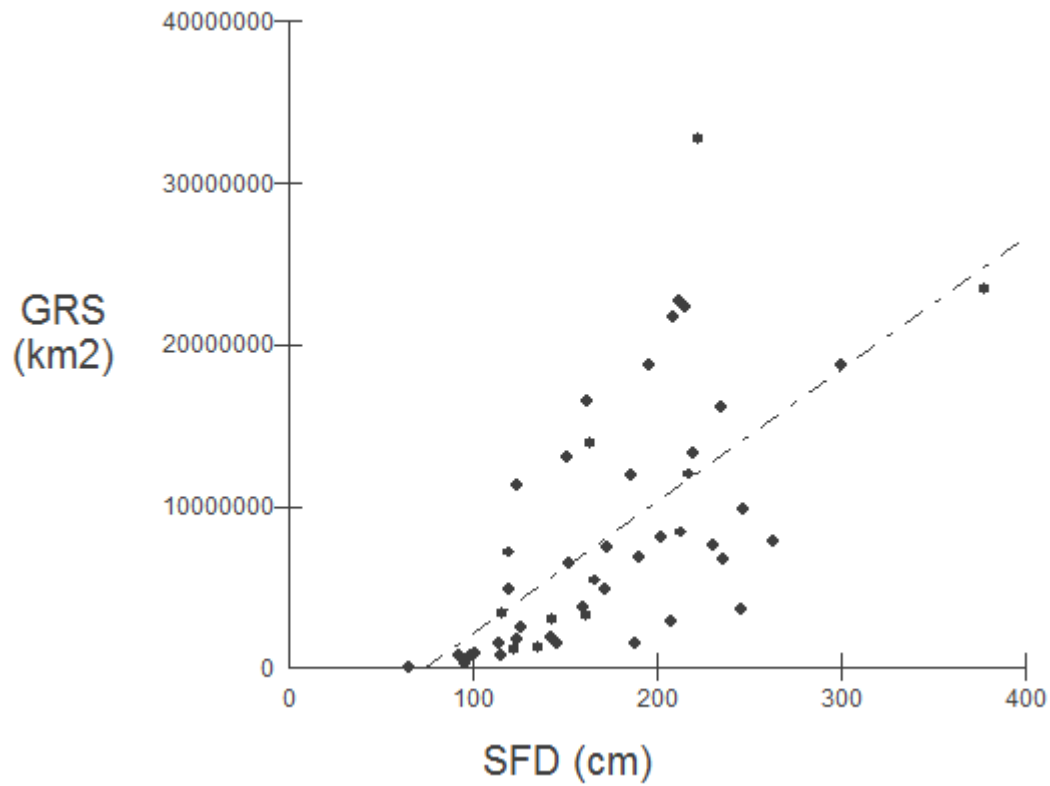


Figure 2. Linear regression between geographic range size (GRS - km²) and ratio seed mass/seed area (SM/SA - g/cm²) for 48 Bignoniaceae species ($R^2 = 0.34$; $p < 0.0001$; $y = -1119.8^6x + 20329248.2$; $n = 48$).

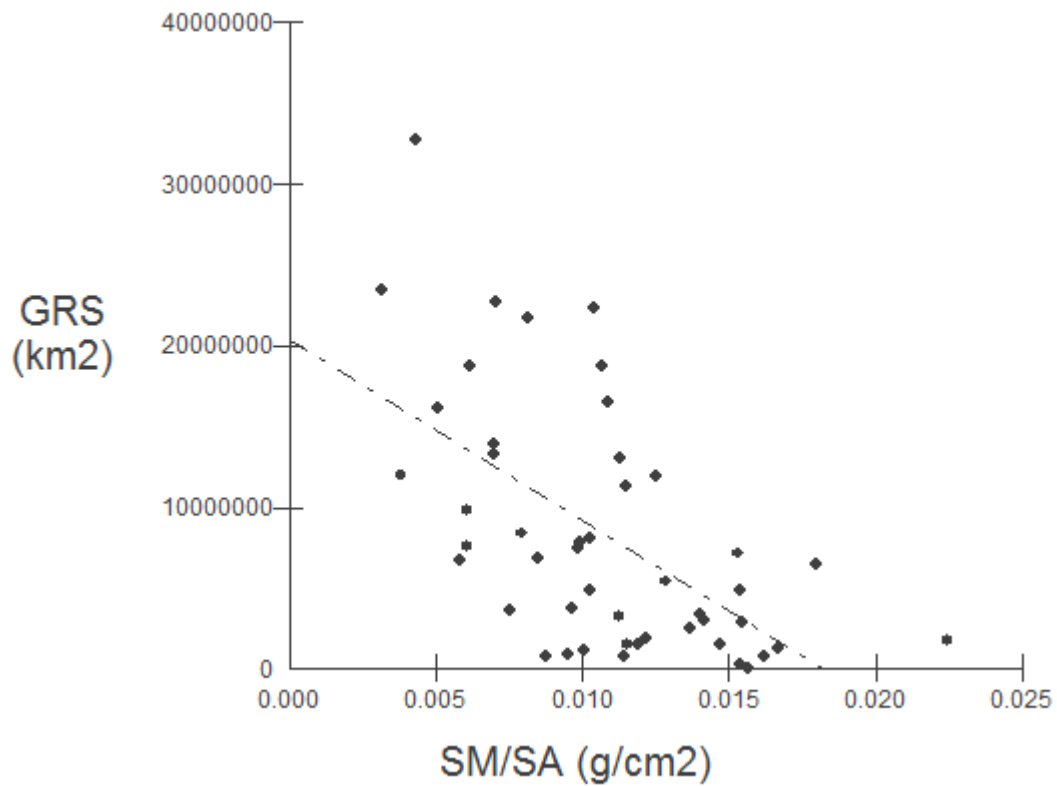


Figure 3. Linear regression between species phylogenetic age (PA - m.y.) and seed dispersal potential (SFD - cm) for 48 Bignoniaceae species ($R^2 = 0.43$; $p < 0.0001$; $y = -4.93x + 235.29$; $n = 48$).

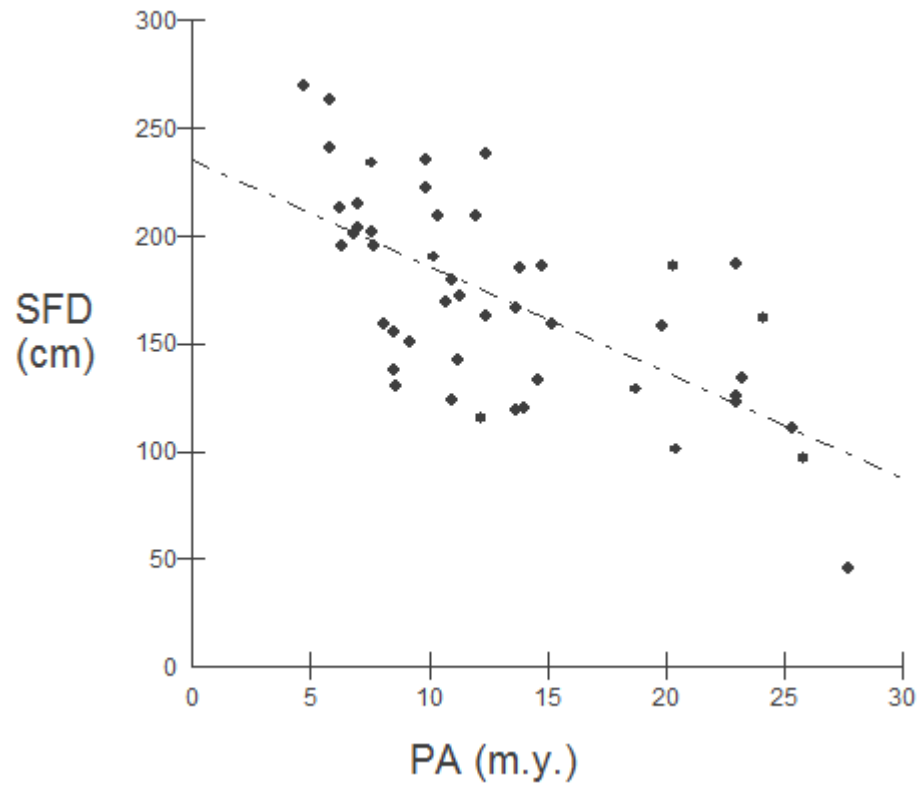


Figure 4. Linear regression between phylogenetic age (PA - m.y.) and seminal nucleus size (SNS - cm) for 48 Bignoniaceae species ($R^2 = 0.34$; $p < 0.0001$; $y = 0.027x + 0.6782$; $n = 48$).

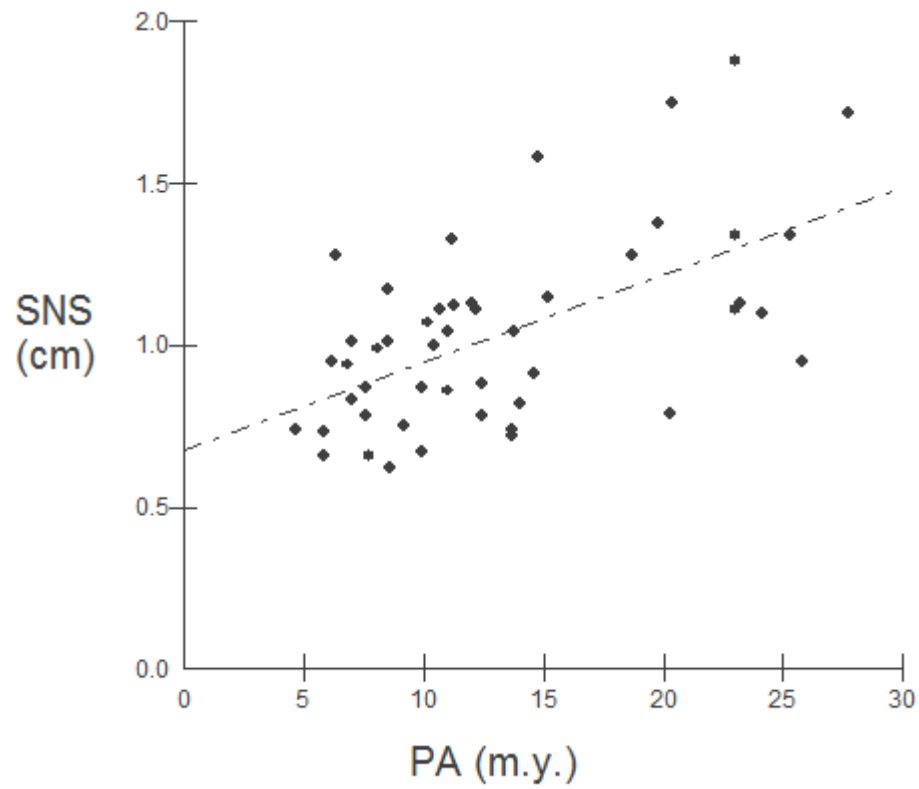
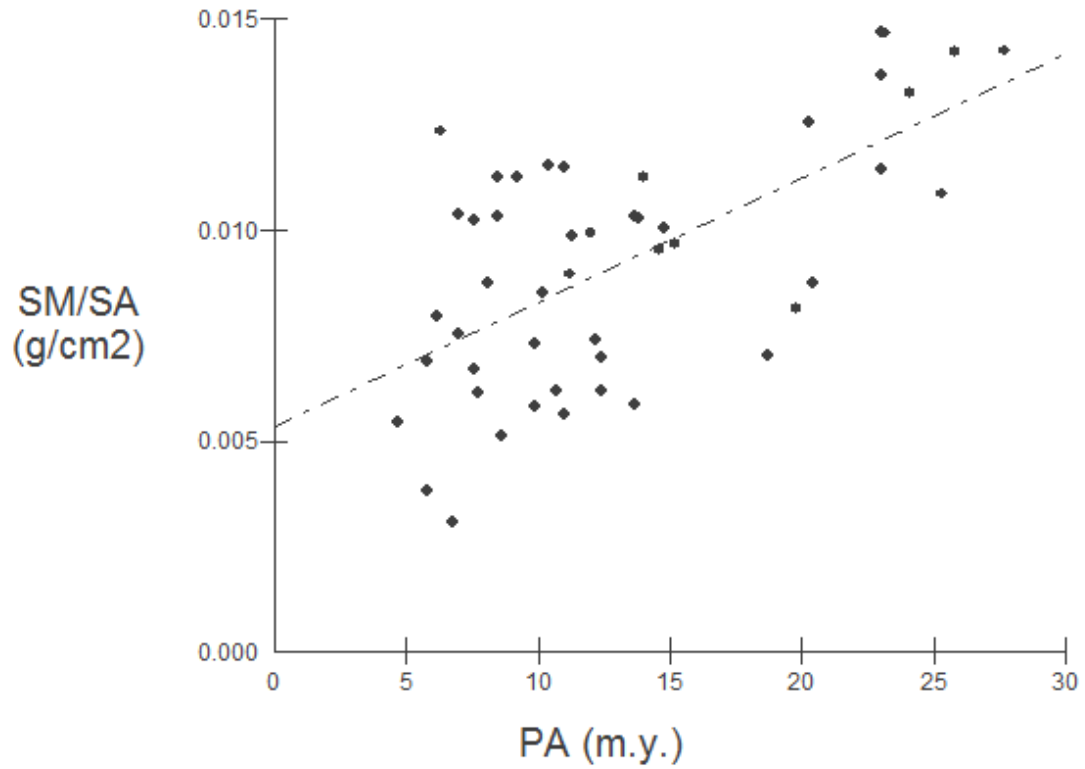


Figure 5. Linear regression between phylogenetic age (PA - m.y.) and the ratio seed mass/seed area (SM/SA - g/cm²) for 48 Bignoniaceae species ($R^2 = 0.40$; $p < 0.0001$; $y = 0.0003x + 0.0054$; $n = 48$).



CAPÍTULO 4

Are there morphological and functional differences between herbarium versus field collected Bignoniaceae seeds ?

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Abstract

Herbaria represent vast databases on several aspects of many plant species, as well as a source of biological material for numerous studies in botany, ecology and evolution. In order to validate the results of studies realized with seeds from herbarium we measured several morphological traits in field collected seeds and compared them with the same measures made after the material have been herborized. We also tested the seed flight capacities in a wind tunnel. We found no significant differences in the seed traits before and after the seeds had been herborized. The results showed that anemochory studies realized with Bignoniaceae herbarium seeds produces useful and applicable results that could be considered compatible with those realized with fresh material from field collections.

Keywords: dispersal, Bignoniaceae, winged seeds, seed traits, herborization

Introduction

Herbaria are valuable databases that store extensive information about plants that are representative of natural and cultured individual species and populations. They represent vast collections of directly available data on several aspects of plants, like morphological and distributional patterns. Often herbarium data and/or material are used to make scientific investigations, providing essential material for studies in taxonomy, systematics, ecology, anatomy, morphology, conservation biology, biodiversity, ethnobotany, and paleobiology, as well as teaching and public purposes (Funk, 2003a).

According to the Index Herbariorum (Thiers, 2012), there are at least 3614 herbaria in the world, and at least 212 (5.86%) in Brazil (Vieira, 2012), all of them representing a reasonable fraction of our flora. Funk (2003b) have listed at least 72 uses for herbaria, such as discover or confirm identities of plants and determine if it is new to science (taxonomy); provide data and material for floristic studies and locality data for planning field trips (systematics, teaching); serve as a secure repository for "type" specimens and new collections (taxonomy and systematics); allow for the documentation of flowering and fruiting times and juvenile forms of plants (ecology and phenology); and many others.

But once the materials are pressed and dried, they may have changes in their morphological structures and/or functional features (like mass reduction, for example), as it is widely recognized with the color of some flowers and fruits. For this reason and in order to validate studies and experiments realized with herborized anemochoric seeds, we investigated if there are significant changes in morphological and functional traits in anemochoric seeds after they have gone through the herborization process.

Methods

We monitored populations of three Bignoniaceae species waiting for their fruits to open and release their seeds. The populations were located in forest fragments near the campus of University of Campinas (Campinas, São Paulo state, Brazil), in the Ribeirão Cachoeira Forest and in the Itirapina Ecological Station (Itirapina, São Paulo, Brazil). The species were: *Fridericia platyphylla* (Cham.) L.G. Lohmann, *Pyrostegia venusta* (Ker Gawl.) Miers and *Amphilophium crucigerum* (L.) L.G. Lohmann. They exhibited substantial variation in seed mass (ranging from 0.0065 g of *Pyrostegia venusta* to 0.0905 g of *Fridericia platyphylla*) and seed total size (ranging from 1.8 cm of *Pyrostegia venusta* to 7.1 cm of *Amphilophium crucigerum*).

The seeds were collected just after they had fallen naturally and were stored in a hermetic plastic box to prevent moisture evaporation. In laboratory we selected 30 seeds from each individual from two different individuals from each species collected in different places. We choose the more intact fertile seeds to use in the study; i.e. seeds without defects like broken wings and which had the seminal nucleus fully developed. Then, with a digital caliper (Digimatic Caliper, Mitutoyo, Japan) we measured the following seed morphological traits: (1) seed total size (STS), (2) seminal nucleus size (SNS), and (3) seed wings size (SWS). The dimensions were taken with the seed longitudinally oriented. With a high precision analytical balance (METTLER AE240(s), Instrument Corporation) we measured the (4) seed mass (SM), and with a Area Meter (LI-2100C Area Meter, LI-COR Biosciences, Lincoln, Nebraska, USA) we measured the (5) seed area (SA).

With this variables we calculated three other variables that are related with the seed flight potential: (6) seminal nucleus size/seed wing size ratio (SNS/SWS), (7) seed mass/seed wing size ratio (SM/SWS), and (8) seed mass/seed area ratio (SM/SA).

Then, we used a wind tunnel to assess the seed flight potential. The wind tunnel consisted of a semi-cylindrical structure made of polycarbonate coupled with a fan with speed regulation (dimmer). The tunnel dimensions were 70 x 70 x 240 cm, in height, width and length, respectively. The wind tunnel was constructed within the dependences of herbarium UEC (Campinas State University, Campinas, São Paulo, Brazil), because this way we could also have control on air humidity and temperature, which were set to $65 \pm 5\%$ and $18 \pm 1^\circ\text{C}$, respectively. This way, we could measure the 'seed flight distance' (SFD) in controlled conditions for the different seeds of different species. The SFD was our measure of dispersal potential, because for a seed that is carried by the wind, the greater its SFD, the better its dispersal. The SFD was measured setting the fan speed at a fixed value (1 m/s) and measuring the distance traveled by the seed inside the tunnel after it had been released from an opening at the top of the tunnel (0.7 m of height). All the seeds were released under the same conditions and in the same orientation.

All the measures and flight experiments were realized in two distinct phases. With the fresh seeds (i.e., immediately after they have been collected) and with the herborized seeds (i.e., after they have been pressed and dried for 72 hours in 65°C). The variable values were compared before and after the herborization with a paired *t*-test.

Results

None of the variables showed significant changes in their values after herborization. The variables STS, SNS, SWS, and SA did not showed any changes after herborization exhibiting the exactly same values before and after herborization.

The only variable that showed a slight alteration was the SM, but the observed changes were not significant (Table 1; Figure 1). The small changes in SM affected the values of the ratio SM/SWS and ratio SM/SA, although not in a significant manner (Table 1).

SFD also showed small alterations in their values, with slightly greater values after herborization, probably due to the non-significant alteration in SM, but the changes were not considered significant (Table 1).

Discussion and conclusion

Our results demonstrated that the herborization process necessarily applied to the herbarium plants did not changed the morphology neither the flight potential of the winged seeds from the three Bignoniaceae species we tested. Therefore, we conclude that studies and experiments conducted with herborized seeds from the family Bignoniaceae will gather reliable and valid data, because most part of the species have the same type of seed and the herborization process did not caused any significant change in their morphology and flight ability.

This conclusion has important practical implications, because as the scientific knowledge advances, questions tend to become more complex and the spatial scale adopted by the researchers also increases. Therefore, using herbarium material to realize scientific studies and experiments represents a practical and efficient manner to perform studies involving a great variety of taxa in wider geographical scales, since the researcher would not have the opportunity (i.e., the time or the money) to perform all the needed collections during the available time they have to realize their studies (usually, a few years).

Despite the fact that scientific collections seem to be going through a declining phase (Dalton, 2003; Gropp, 2003), our results highlights the importance of herbarium as a source of directly available scientific material and information for scientific studies.

To our knowledge, there are not any other study investigating possible changes in morphological or functional features of seeds caused by the herborization process. As a recommendation for further studies we emphasize the importance of a careful preliminar preparation of the material before the herborization aiming to preserve the material the more intact as possible.

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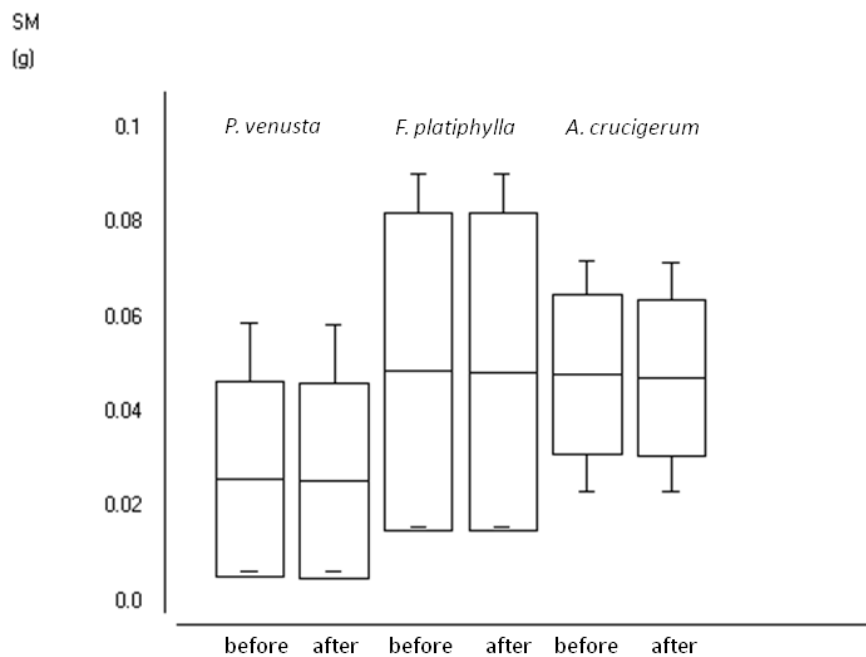
Tables

Table 1. Results of *t*-tests for the seed mass of three Bignoniaceae species before and after herborization.

Species	SM		SM/SWS		SM/SA		SFD	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
<i>Pyrostegia venusta</i>	1.45	0.16	1.11	0.12	1.54	0.08	1.61	0.12
<i>Frideria platiphylla</i>	1.39	0.11	1.23	0.10	1.36	0.15	1.24	0.12
<i>Amphilophium crucigerum</i>	1.64	0.09	1.69	0.17	1.61	0.19	1.27	0.14

Figures

Figure 1. Seed mass (SM) values for *Pyrostegia venusta*, *Frideria platiphylla*, and *Amphilophium crucigerum* seeds before and after herborization.



CONCLUSÃO GERAL

Quase meia década se passou desde que o botânico e biogeógrafo italiano León Croizat publicou sua obra relacionando espaço, tempo e forma (Croizat, 1964). Desde então houve uma grande tendência de especialização dos diferentes campos da ciência que levou a uma excessiva compartimentalização das sub-disciplinas que compõem o conhecimento científico. Neste trabalho, tentamos integrar algumas dessas sub-disciplinas no intuito de gerar um conhecimento mais amplo abrangendo a evolução das formas no espaço e no tempo e as suas implicações práticas relacionadas a distribuição geográfica de espécies vegetais.

Nossos resultados demonstraram que a hipótese idade e área, proposta pelo biogeógrafo inglês John C. Willis (Willis, 1922), não ocorre para as espécies da tribo Bignonieae (Bignoniaceae). Este resultado contradiz outros estudos semelhantes com plantas neotropicais que encontraram relações positivas para espécies do gênero *Piper* (Paul & Tonsor, 2008) e *Psychotria* (Paul *et al.*, 2009). Isto indica a necessidade de se ampliar os estudos sobre tal hipótese abrangendo novos grupos para possibilitar qualquer generalização sobre um tema, ao mesmo tão antigo e ainda tão contraditório.

Na tentativa de se obter dados que ajudassem a entender o porquê da falta de correlação entre a área de distribuição das espécies e sua idade filogenética, realizamos um experimento sobre o potencial de dispersão anemocórica das sementes das diferentes espécies da tribo Bignonieae em um túnel de vento. Através deste experimento, pudemos demonstrar que apesar das sementes aladas seguirem o mesmo padrão morfológico básico, existe grande variação em atributos como, tamanho total, tamanho das asas, tamanho do núcleo seminal, massa e área das sementes, atributos estes que exercem influência sobre a biomecânica do voo destas sementes.

Alguns destes atributos se mostraram fortemente relacionados à distância potencial de voo no túnel de vento, principalmente a relação existente entre a massa e a área da semente, sendo que quanto menor essa relação, ou seja, quanto menos unidade de massa por unidade de área da semente, maior a distância potencial de dispersão por vento.

Posteriormente, relacionando estes atributos, principalmente a razão massa/área, com a área de distribuição atual ocupada pelas espécies e com a sua idade filogenética, demonstramos que as espécies que possuem menores valores para a razão massa/área são espécies que possuem grandes áreas de distribuição geográfica e também são espécies relativamente recentes na filogenia do grupo. Através destes dados, pudemos inferir que alguns atributos morfológicos biomecânicos relacionados à eficiência de voo e consequentemente ao potencial de dispersão anemocórica das sementes podem ter sido selecionados ao longo da evolução do grupo no sentido de promover um aumento no seu potencial de dispersão, amplificando a capacidade de dispersão e colonização de algumas espécies.

Os resultados contraditórios encontrados para a relação idade-área neste e em outros estudos destacam a importância de se aprofundar as pesquisas integrando filogenia e biogeografia e indicam a necessidade de se acrescentar estudos sobre dispersão nas futuras pesquisas sobre a generalidade desta relação com outros grupos de plantas neotropicais. Pois, se em geral, for demonstrado que muitas espécies raras são também recentes, tal informação é crucial para ser incorporada no nosso atual conhecimento sobre as variações na área de distribuição geográfica entre as espécies e, em escala local, variações na abundância que frequentemente possui relação positiva com o tamanho da área de distribuição (Gaston, 1994).

Nossos resultados demonstraram que as relações entre a área de distribuição geográfica e a idade filogenética das espécies podem ser vistas e analisadas de uma maneira mais ampla do que simplesmente através da hipótese proposta por Willis, e que os caminhos evolutivos seguidos por diferentes clados podem ser bem diferentes.

Os dados obtidos em nosso estudo também fornecem informações sobre os fatores relacionados com a distribuição geográfica de um importante e diverso grupo de plantas neotropicais e sobre como alguns atributos vegetais biomecânicos relacionados à reprodução e dispersão podem interagir com o ambiente e responder as pressões seletivas ao longo do espaço e do tempo. Tais dados podem gerar novas hipóteses e teorias sobre o papel de fatores filogenéticos e ecológicos na distribuição atual das espécies no planeta.

O avanço do conhecimento sobre os fatores que moldam a distribuição das espécies possui um importante papel para a conservação, principalmente na região tropical, onde a megadiversidade que agora esta altamente ameaçada é majoritariamente composta por espécies com pequenas áreas de distribuição (Wallace, 1878; Dobzhansky, 1950; Gaston, 1994; Hubbell, 2001) e que estão apenas começando a receber tratamentos ecológicos e genéticos adequados, assim como estimativas de sua amplitude geográfica (Pitman *et al.*, 2001).

Atualmente, atividades humanas estão criando novos processos que isolam, conectam e alteram paisagens em velocidades muito mais altas que as naturais e questões atuais como, a perda da biodiversidade, as invasões biológicas e a disseminação de epidemias, representam grandes problemas ambientais, sociais e políticos. Tais questões têm ganhado crescente interesse se tornando uma preocupação internacional, principalmente diante do aumento da população

mundial e do consequente aumento da demanda por recursos, da fragmentação de habitats e do transporte e introdução de espécies exóticas e invasoras (Gaston, 2003).

Todos estes problemas têm relação com os mecanismos envolvidos na dispersão e na amplitude da distribuição geográfica das espécies, portanto, a necessidade de combater as epidemias e seus vetores, tanto em populações humanas quanto em rebanhos ou plantações, assim como o controle de invasões biológicas, requer o conhecimento dos mecanismos relacionados à dispersão das espécies e dos aspectos que determinam sua abundância (Rogers & Randolph, 1986; Randolph & Rogers, 2000). Também levantam a necessidade de se prever os padrões e taxas de expansão da distribuição geográfica das espécies sobre a superfície terrestre (Hengeveld, 1989; Williamson, 1996; Chown *et al.*, 1998) e os fatores responsáveis pela velocidade dessa expansão.

As respostas a essas questões dependem de um melhor entendimento dos padrões de distribuição dos organismos e dos processos que determinam suas amplitudes geográficas (Davis *et al.*, 1998). Tais conhecimentos constituem uma importante ferramenta para estudos de populações e comunidades e poderão ser usados para a análise dos fatores que inibem ou facilitam a colonização por determinadas espécies (Guasp *et al.*, 1996), sendo importante no planejamento de ações conservacionistas. Portanto, dados sobre o potencial de dispersão das espécies são úteis para a conservação aliada ao planejamento ambiental de paisagens (Verkaar, 1990), tornando os estudos sobre dispersão um requisito básico para a ecologia preditiva (Sutherland *et al.*, 2004).

Além disso, um conhecimento mais aprofundado das causas da variação na distribuição geográfica das espécies no espaço e no tempo, assim como suas relações com a filogenia e

variáveis bióticas e ambientais, propiciará informações novas e relevantes e servirá como base para a elaboração de modelos mais generalizáveis para a Ecologia, Biogeografia e Evolução como um todo, destacando a importância de se aprofundar os estudos integrando biogeografia, ecologia, filogenia e conservação.

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