Camila de Toledo Castanho

Facilitação entre plantas e suas implicações
para a dinâmica e restauração de restingas

Plant facilitation and its implications for the
dynamics and restoration of coastal dunes

*Versão corrigida **

São Paulo

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Camila de Toledo Castanho

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dynamics and restoration of coastal dunes

Tese apresentada ao Instituto de
Biociências da Universidade de São
Paulo, para a obtenção de Título de
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Ecologia.

Orientador: Paulo Inácio de Knegt
López de Prado

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Dedicatória

Ao Alê, pela parceria na ciência
e em tudo o que importa
nesta vida

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Resumo

Nas últimas duas décadas, estudos empíricos têm demonstrado a importância da facilitação entre plantas, especialmente sob condições ambientais severas. Tal constatação inspirou a proposição da hipótese do gradiente de estresse (HGE), um modelo conceitual que prediz que a frequência relativa entre facilitação e competição deve variar inversamente ao longo de um gradiente de estresse, sendo a facilitação mais comum sob condições extremamente severas. As restingas (ou planícies costeiras arenosas) são ambientes caracterizados por condições ambientais limitantes para o desenvolvimento das plantas, característica que as tornam um ambiente propício para o predomínio de facilitação. Além disso, o gradiente de intensidade de estresse e perturbação relacionado à distância do mar faz ainda deste ambiente um modelo ideal para testar a HGE.

O objetivo geral desta tese foi estudar facilitação entre plantas de restinga através dos seguintes objetivos específicos: i) Apresentar uma revisão sistemática dos trabalhos já publicados sobre facilitação entre plantas de restinga em escala mundial, assim como investigar, através de meta-análise, que fatores influenciam a presença e intensidade da facilitação entre plantas; ii) Testar se os padrões de associação espacial entre árvores adultas isoladas e plantas de distintas formas de vida se alteram ao longo de um gradiente ambiental praia-interior, conforme esperado pela HGE; iii) Testar a HGE através de experimentos de campo envolvendo transplante da espécie potencialmente beneficiada (espécie alvo), assim como manipulação de recurso limitante ao longo do gradiente praia-interior; iv) Testar se o sombreamento é um mecanismo de facilitação na restinga. Para os testes empíricos (objetivos ii-iv), as observações e experimentos foram realizados em um gradiente de restinga arbustiva do Parque Estadual da Ilha do Cardoso (PEIC) localizado em Cananéia, São Paulo, Brasil.

Os resultados indicaram que: i) Diversas condições e aspectos da facilitação entre plantas de planícies costeiras têm sido pouco exploradas, como por exemplo, há poucos estudos nas regiões tropicais e poucos estudos que consideraram estágios de vida de semente ou de adultos da espécie alvo da interação. Dentre os estudos publicados, fatores como precipitação, região geográfica e estágio de vida da planta alvo definitivamente influenciam a existência e magnitude da facilitação entre plantas de restinga; ii) Para a maioria das formas de vida, o padrão de associação espacial com árvores adultas não se altera ao longo do gradiente ambiental conforme predito pela HGE. Apenas árvores jovens apresentam associação espacial positiva com árvores adultas, o que sugere efeito de planta-berçário entre árvores da restinga arbustiva; iii) Tanto a intensidade quanto a importância da interação entre árvores foram negativamente relacionadas ao estresse, rejeitando então a proposição clássica da HGE. Além disso, o sinal da interação foi dependente do estágio de vida da espécie alvo, uma vez que a presença do adulto

vizinho foi predominantemente negativa sobre o estágio de semente, mas positiva sobre a sobrevivência das plântulas; iv) O efeito de planta-berçário entre árvores da restinga é, pelo menos parcialmente, explicado pelo sombreamento gerado pela copa da espécie facilitadora.

Dessa forma, conclui-se que a facilitação via sombreamento é uma interação relevante entre árvores adultas e jovens na restinga. Entretanto, ao contrário do previsto pela HGE, o efeito de planta-berçário tende a ser mais intenso em condições ambientais mais amenas. Estes resultados sugerem a existência de um ciclo de retroalimentação positiva gerado a partir do estabelecimento das primeiras árvores isoladas. Este ciclo positivo tem implicações importantes para a compreensão da organização estrutural da vegetação da restinga arbustiva, em que muitas de espécies lenhosas estão distribuídas em uma matriz predominantemente herbácea. Adicionalmente, a facilitação entre árvores e sua dependência em relação às condições ambientais locais devem ser mecanismos essenciais para explicar o gradiente de fisionomias vegetacionais sobre os cordões arenosos, a qual inicia-se em uma vegetação aberta e termina em uma floresta, assim como para entender a dinâmica temporal desta vegetação ao longo do tempo. Por fim, os resultados também trazem implicações práticas, relacionadas ao uso potencial de plantas-berçário e sombra artificial como técnicas de manejo para aumentar o estabelecimento de mudas transplantadas em projetos de restauração de restingas arbustivo-arbóreas.

Summary

In the last two decades, empirical studies have shown the importance of plant interaction, especially under harsh environmental conditions. These observations led to the proposition of the stress gradient hypothesis (SGH), a conceptual model predicting that the relative frequency of facilitation and competition will vary inversely across gradients of stress, with facilitation being the dominant interaction under highly stressful conditions. Coastal dunes (known as restinga in Brazil) are environments with limiting conditions for plant performance, which makes them suitable for facilitation predominance among plant interactions. Furthermore, there is a gradient of stress and disturbance related to the presence of the sea, making this environment an ideal model to test the SGH.

The general goal of this thesis was to study plant facilitation in coastal dunes with the following specific objectives: i) to perform a systematic review of published studies on plant facilitation in coastal dunes around the world as well as to investigate, using a meta-analysis approach, factors that affect the existence and magnitude of plant facilitation; ii) to test if spatial association between isolated adult trees and understory plants of distinct life forms changes along a beach-to-inland gradient, as expected by the SGH; iii) to test the SGH through field experiments involving target species transplantation coupled with manipulation of limiting resource along a beach-to-inland gradient; iv) to test if shading is a facilitation mechanism in coastal dunes. The empirical tests (objectives ii-iv) were conducted in an open scrub coastal dune located at Ilha do Cardoso State Park, Cananéia, São Paulo, Brazil.

Our results indicate that: i) several aspects and conditions of plant facilitation in coastal dunes have been little studied. For instance, few studies were conducted in tropical regions and few of them studied the effect of neighbor presence on seed and adult life stage of the target species. Precipitation, geographic region and target life stage affect the existence and magnitude of plant facilitation; ii) For most of the understory life forms, the spatial association between adult trees and understory plants do not change along the environmental gradient as predicted by the SGH. Among all life forms, only young trees were positively associated with adult trees, suggesting a nurse plant effect among trees in coastal dunes; iii) Both intensity and importance of the interaction among trees were negatively related to stress, rejecting the classic proposition of the SGH. Furthermore, the signal of the net interaction depends on the life stage of the target species since the adult neighbor had mostly negative effects on target species seeds but positive effects on seedlings survival; iv) The nurse plant effect among trees was, at least partly, due to the shading provided by the facilitator crown.

Overall, we concluded that facilitation driven by shade is a relevant interaction between adult and young trees in the studied coastal dune. However, contrary to what was expected by

the early propositions of the SGH, the observed nurse plant effect tends to be more intense under mild conditions. Our results suggest a positive feedback relationship started with the establishment of the first isolated trees. This positive feedback has important implications to understand the vegetation organization on open scrub vegetation, where patches of woody species are scattered in a matrix of herbaceous plants. Furthermore, the facilitation between trees and their dependency on local environmental conditions could be fundamental to explain the gradient of vegetation physiognomies from open vegetation to forest observed along the beach-to-inland gradient, as well as to understand the dynamics of this vegetation over time. Finally, our results also have practical implications, highlighting the potential use of nurse plants and artificial shade as techniques to restore shrubland or forest physiognomies in coastal dunes.

Capítulo 1

Introdução geral

1.1. Interações entre plantas

Assim como todos os outros organismos vivos, plantas também interagem entre si. Estas interações são classificadas em negativas (competição) ou positivas (facilitação) de acordo com o efeito que uma planta tem sobre a sobrevivência, crescimento e reprodução de outra planta (Callaway 2007). Historicamente, o reconhecimento de que ambas as interações têm importante papel na organização de comunidades vegetais data do início da ecologia como disciplina (Clements et al. 1929). No entanto, durante a maior parte do século XX, a competição foi o foco de pesquisa na área de interações ecológicas e, conseqüentemente, norteou a elaboração de teorias desenvolvidas durante tal período (Bertness & Callaway 1994; Bruno et al. 2003). Embora competição seja ainda a interação predominantemente estudada, o início da década de 90 foi marcado por uma crescente renovação no interesse pela facilitação entre plantas (Figura 1). Estas pesquisas recentes fundamentaram o atual reconhecimento do papel da facilitação na estruturação e organização de comunidades vegetais de ecossistemas diversos (Callaway 2007; Brooker et al. 2008) e vem continuamente estimulando o desenvolvimento de modelos teóricos integrados com outros aspectos da ecologia (Bruno et al. 2003; Michalet et al. 2006; Scheffer 2009).

1.2. Como uma planta beneficia outra? Mecanismos de facilitação

Para entendermos mais profundamente a facilitação entre plantas e compreendermos questões como, quais as condições que a promovem, ou entre que tipo de espécies ela é mais comum, é fundamental compreendermos como uma planta pode beneficiar outra, ou seja, os mecanismos de facilitação (Brooker et al. 2008). Tais mecanismos podem ser divididos em duas categorias: diretos e indiretos. Entre os mecanismos diretos estão incluídas as modificações favoráveis que uma planta exerce diretamente sobre as condições e/ou recursos de outra planta. Nos mecanismos indiretos, os benefícios são alcançados através do envolvimento de um terceiro organismo.

Figura 1. Porcentagem de artigos que investigaram facilitação (barras pretas) e competição (barras cinzas) entre plantas, do total de artigos publicados em cinco importantes revistas da área de Ecologia (American Naturalist, Ecology, Journal of Ecology, Oikos e Oecologia) entre 1990 e 2011. Os dados foram obtidos do ISI Web of Knowledge em 29 de fevereiro de 2012, usando como palavras chaves [(positive interaction* OR facilitation) AND plant*] para facilitação e [(negative interaction* OR competition) AND plant*] para competição. Modificado de Dormann & Brooker (2002).

Entre os mecanismos diretos está o sombreamento proporcionado pela copa de plantas maiores, que diminui temperaturas extremas, diminui o excesso de luz e aumenta a disponibilidade de água no solo através de redução na evapotranspiração (Shumway 2000; Yang et al. 2010). Mecanismos adicionais incluem o transporte de água realizada por algumas espécies lenhosas cujas raízes transportam água de camadas profundas e úmidas para camadas mais secas da superfície do solo (Zou et al. 2005), a proteção mecânica contra vento (Baumeister & Callaway 2006) e o aumento na oxigenação do solo de ambientes alagados (Hacker & Bertness 1995).

Entre os mecanismos indiretos, um dos mais conhecidos e estudados é a proteção contra herbívoros proporcionada por espécies pouco palatáveis (Callaway et al. 2005;

Smit et al. 2006). Interações indiretas também podem ocorrer através do reforço de uma interação positiva entre uma planta e um terceiro organismo. Este é o caso de plantas que compartilham o mesmo polinizador, e cujo sucesso de polinização é positivamente afetado pela proximidade às flores de outra espécie (Juillet et al. 2007; Peter & Johnson 2008). Mecanismos indiretos de facilitação também incluem o aumento na disponibilidade de nutrientes do solo proporcionados por espécies vizinhas associadas com micorrizas e bactérias fixadoras de nitrogênio (Shumway 2000; van der Heijden & Horton 2009).

1.3. Competição e facilitação: saldo das interações

Embora a facilitação e a competição tenham efeitos opostos, ambas interações podem ocorrer simultaneamente. Dessa forma, o saldo da interação entre duas espécies é o resultado do balanço entre os efeitos positivos e negativos. Por exemplo, Maestre et al. (2003) estudaram o efeito da gramínia *Stipa tenacissima* sobre as plântulas do arbusto *Pistacia lentiscus* em campos semi-áridos mediterrâneos. Os autores encontraram evidências de que a gramínia altera positivamente as condições microclimáticas e que tal efeito contrabalança os efeitos negativos de competição abaixo do solo, resultando em um saldo positivo da gramínia sobre o desempenho das plântulas de *P. lentiscus*. Em um outro estudo desenvolvido em um deserto da Califórnia, Holzapfel & Mahall (1999) identificaram que o forte efeito negativo de espécies anuais sobre o arbusto *Ambrosia dumosa* é apenas parcialmente balanceado pelos efeitos positivos, resultando em um saldo negativo das espécies anuais sobre o arbusto.

1.4. Como avaliar o saldo das interações e potenciais mecanismos?

O saldo das interações entre duas espécies pode ser avaliado basicamente através de duas abordagens: observacional-correlativa e experimental (Callaway 1995). Na abordagem observacional-correlativa, a associação espacial positiva (agregação) entre duas espécies é interpretada como evidência de facilitação. De maneira inversa, a

associação espacial negativa (segregação) é interpretada como evidência de competição. O principal problema desta abordagem é que diferentes mecanismos podem gerar o mesmo padrão de associação espacial. A agregação espacial pode ser resultado de facilitação, mas também de processos alternativos como preferência compartilhada por um tipo de hábitat (Harms et al. 2001) ou dispersão preferencial, geralmente observada sob espécies lenhosas que funcionam como poleiros para aves dispersoras de sementes (Slocum & Horvitz 2000; Holl 2002).

Para esclarecer de maneira conclusiva se a facilitação é o processo gerador de padrões espaciais positivos são necessários experimentos em campo. De maneira semelhante à abordagem observacional-correlativa, os experimentos em campo conduzidos para avaliar facilitação não são diferentes daqueles usados para avaliar competição. Basicamente compara-se o desempenho da espécie alvo (a espécie potencialmente facilitada) em duas condições: na presença do vizinho (potencial facilitador) e em sua ausência. Se o desempenho da espécie alvo na presença do vizinho é melhor do que em sua ausência, interpreta-se que facilitação é a interação predominante (saldo final positivo); se o resultado é inverso interpreta-se como evidência de predominante competição (saldo final negativo).

Enquanto o poder de evidência da abordagem experimental é muito mais forte do que aquele alcançado através da observação de padrões espaciais, a primeira abordagem é porém muito mais custosa em termos de tempo, logística e dinheiro. Como consequência, os experimentos em campo são, em geral, restritos a pares de espécies e quase sempre impeditivos para a escala da comunidade. Além disso, enquanto os experimentos em campo refletem os processos operantes no momento ou em período um pouco anterior àquele em que o experimento foi conduzido, o padrão de associação espacial entre espécies reflete um histórico de interações muito mais extenso. Considerando então as vantagens e desvantagens de cada abordagem e a potencial complementariedade entre elas, a combinação de levantamentos observacionais-correlativos com experimentos em

campo oferece boas perspectivas para desenhar um quadro mais completo das interações que podem ocorrer em comunidades vegetais ao longo do tempo e espaço (ver Callaway 1992; Choler et al. 2001; Rudgers & Maron 2003).

Abordagens observacionais-correlativas e experimentais também são adotadas para investigar mecanismos de facilitação. Neste caso, a abordagem observacional-correlativa é útil para indicar potenciais mecanismos. Vários estudos que encontraram, por exemplo, saldo positivo no efeito de espécies lenhosa adultas sobre jovens de outras espécies (tipo de facilitação conhecido como efeito de planta-berçário) detectaram melhor condição microclimática ou maior disponibilidade de nutrientes sob os adultos do que em áreas abertas (Joy & Young 2002; Martínez 2003; Armas & Pugnaire 2009; Cushman et al. 2010). Embora tais observações sejam boas pistas, não são provas inequívocas de que a melhoria das condições microclimáticas ou nutricionais promove o melhor desempenho da espécie alvo. Para tanto, é necessário realizar experimentos manipulativos em que o potencial efeito de facilitação é removido ou simulado por uma estrutura artificial.

Em um estudo realizado em uma planície costeira temperada, Shumway (2000) encontrou evidências de que o arbusto fixador de nitrogênio *Myrica pensylvanica* facilita o crescimento e reprodução de duas espécies herbáceas. Medidas de parâmetros abióticos indicaram menores temperaturas e maiores níveis de nitrogênio do solo sob o arbusto do que em áreas abertas. Para confirmar se o efeito facilitador do arbusto era decorrente do sombreamento e/ou enriquecimento do solo, o autor conduziu um experimento em campo com o uso de estruturas artificiais para simular o sombreamento do arbusto, assim como um tratamento de fertilização para simular a maior concentração de nitrogênio sob o arbusto. Adicionalmente, o autor conduziu um experimento complementar em casa de vegetação em que examinou o crescimento da espécie alvo em solo coletado sob *M. pensylvanica* e em solo coletado em áreas abertas para confirmar se o efeito facilitador do arbusto estava relacionado a alterações no solo. Com essa seqüência de experimentos, Shumway (2000) encontrou fortes evidências de que *M. pensylvanica* facilita as duas

espécies herbáceas tanto pela melhoria das condições microclimáticas via sombreamento quanto pelo enriquecimento de nitrogênio no solo.

Em um outro exemplo de estudo que adotou abordagem experimental para entender mecanismos de facilitação, Callaway et al. (2005) testaram se *Cirsium obalatum* e *Veratum lobelianum*, duas espécies herbáceas impalatáveis, facilitam suas vizinhas palatáveis através de proteção contra herbívoros. Para tanto, os autores conduziram experimentos em campo com remoção dos vizinhos impalatáveis acoplada a exclusão dos herbívoros. Os autores observaram que o efeito positivo de *C. obalatum* e *V. lobelianum* sobre a riqueza da comunidade estava condicionada à pressão por herbívoros e que, portanto, o mecanismo responsável pelos efeitos positivos das herbáceas estava ligado à proteção contra herbívoros.

Como ilustrado nos dois exemplos anteriores, a investigação dos mecanismos de interação permite o entendimento mais profundo de como se dão as interações entre plantas. Além do avanço teórico, o entendimento mecanístico das interações entre plantas pode trazer implicações práticas, como por exemplo, para o crescente interesse pela facilitação como técnica de manejo na recuperação de áreas degradadas (Padilla & Pugnaire 2006; Gómez-Aparicio 2009). O conhecimento dos mecanismos de facilitação é essencial para fundamentar a seleção de espécies facilitadoras apropriadas, assim como para manejar as condições ambientais de forma a simular os efeitos benéficos de tais espécies (ver Rey Benayas et al. 2005; Badano et al. 2011).

Todos os exemplos descritos até o momento ilustram o uso de abordagem observacional e/ou experimental para elucidar interações entre plantas. Como ponto comum entre todos esses trabalhos está a coleta de dados primários. No entanto, o avanço da ciência também se dá através da síntese e análise de dados primários coletados de forma independente (Borestein et al. 2009). Se temos interesse, por exemplo, em saber se a frequência de facilitação entre plantas varia entre ambientes temperados e tropicais, podemos desenhar experimentos para identificar a frequência de facilitação nas duas

regiões geográficas. No entanto, as complicações e custos de um projeto como este poderiam impedir sua execução. Uma maneira muito mais simples e barata de responder a mesma questão é compilar os resultados dos trabalhos que investigaram a frequência de facilitação e testar se há diferenças em relação à região geográfica onde o estudo foi desenvolvido. Embora mais simples do que a coleta direta dos dados, tal abordagem exige que um número razoável de estudos independentes tenha sido acumulado para que a revisão atinja um nível desejável de generalização.

Apesar do aumento nas pesquisas com facilitação entre plantas seja relativamente recente (Figura 1), o acúmulo de estudos indica que o uso de ferramentas de revisão e síntese tem grande potencial para desenharmos conclusões com alto poder de generalização, assim como apontar lacunas do conhecimento em diversos aspectos do estudo de interações entre plantas. De fato, nos últimos anos, alguns estudos têm usado ferramentas de revisão, sejam elas qualitativas (como revisões narrativas) ou quantitativas (como revisões sistemáticas acompanhadas de sínteses estatísticas - meta-análise) para entender diversos aspectos da facilitação entre plantas (Callaway 1995; Flores & Jurado 2003; Martínez & García-Franco 2004; Maestre et al. 2005; Brooker et al. 2008; Gómez-Aparicio 2009; Bonanomi et al. 2011). O acúmulo de estudos fornecerá cada vez mais material para revisões e sínteses de distintos aspectos das interações entre plantas, o que em contrapartida poderá orientar o foco das pesquisas primárias e o poder de generalização de suas conclusões.

1.5. Hipótese do gradiente de estresse

Descrever o saldo das interações positivas e negativas, assim como os mecanismos específicos, representa um avanço importante para uma compreensão mais ampla das interações entre plantas. Outra questão fundamental é entender como o saldo das interações varia no tempo e espaço (Callaway & Walker 1997). O balanço entre facilitação e competição pode variar, por exemplo, de acordo com o estágio de vida das espécies

(Miriti 2006; Armas & Pugnaire 2009), aspectos de sua história de vida (Liancourt et al. 2005) e também conforme as condições abióticas (Bertness & Callaway 1994; Brooker & Callaghan 1998; Maestre et al. 2009; Holmgren & Scheffer 2010).

Uma das proposições teóricas mais frutíferas em termos de volume de testes empíricos e consequente avanço no entendimento das interações entre plantas é a hipótese do gradiente de estresse (HGE; Bertness & Callaway 1994; Brooker & Callaghan 1998). Desenvolvida a partir da freqüente observação de facilitação em ambientes com condições ambientais severas, a HGE propõe que o saldo das interações entre plantas é linearmente influenciado pelas condições ambientais, de forma que em ambientes severos a facilitação é a interação predominante, enquanto em ambientes com condições ambientais mais amenas a competição predomina no saldo final das interações (Bertness & Callaway 1994; Brooker & Callaghan 1998). Logo após sua proposição, seguiram-se diversos testes empíricos, incluindo estudos que validaram suas predições (Callaway et al. 2002; Gómez-Aparicio et al. 2004; Holzapfel et al. 2006) e outros que as rejeitaram (Pennings et al. 2003; Maestre & Cortina 2004; Bowker et al. 2010).

A divergência entre os diferentes testes empíricos são fundamentais para o refinamento da teoria. Por exemplo, estudos empíricos encontraram evidências de que o saldo de interações é neutro ou negativo em ambientes extremamente severos (Maestre et al. 2004; de Bello et al. 2011), sugerindo que a predominância da facilitação não deve ser crescente ao longo de todo gradiente ambiental, como predito pelas primeiras proposições da HGE. Tais constatações levaram a uma proposição mais refinada da HGE, em que o estresse e o saldo das interações tem relação unimodal e, conseqüentemente, o papel da facilitação é mais importante em ambientes moderadamente severos do que sob estresse extremo (Michalet et al. 2006; Maestre et al. 2009; Holmgren & Scheffer 2010; Kikvidze et al. 2011). A natureza basicamente teórica destas recentes alterações da HGE ressalta a importância de testes empíricos explicitamente desenhados para testá-las. Esse fluxo constante e de duas vias entre a teoria e empirismo é fundamental para o avanço do

entendimento da influência das condições ambientais sobre as interações entre plantas e para definirmos com maior clareza o domínio de aplicação da HGE.

1.6. Vegetação de restinga como modelo de estudo

Entre os ambientes mais estudados em relação à facilitação entre plantas estão ambientes áridos e semi-áridos, assim como regiões alpinas (Choler et al. 2001; Callaway et al. 2002; Flores & Jurado 2003; Maestre et al. 2005). Além de condições ambientais severas, tais ambientes muitas vezes possuem gradientes ambientais, como por exemplo, os gradientes altitudinais de regiões alpinas (ver Choler et al. 2001; Callaway et al. 2002), o que os tornam ambientes adequados para testar a HGE. Um ambiente muito menos estudado, mas extremamente adequado para estudar facilitação e testar a HGE, é a vegetação sobre planície costeira arenosa (conhecida como vegetação de restinga no Brasil). Planícies costeiras são usualmente ambientes caracterizados por condições ambientais limitantes para o desenvolvimento das plantas devido à baixa disponibilidade de água e nitrogênio no solo, à presença de sal no solo e nos borrifos soprados do mar, à intensa exposição ao vento que promove abrasão por movimentação de areia (Wilson & Sykes 1999; Lane et al. 2008). Considerando que a presença de plantas pode melhorar as condições severas de seus arredores, facilitação entre plantas é uma interação bastante plausível em tal ambiente. De fato, tem sido demonstrado o efeito positivo de espécies lenhosas adultas sobre o estabelecimento de espécies tardias em vegetação de planície costeira de distintas regiões geográficas (Kellman & Kading 1992; Shumway 2000; Joy & Young 2002; Martínez 2003).

Apesar das planícies costeiras serem consideradas ambientes limitantes, as condições ambientais severas e as freqüentes perturbações não são espacialmente homogêneas, mas sim distribuídas ao longo de um gradiente ambiental relacionado à presença do mar (Wilson & Sykes 1999; Lortie & Cushman 2007; Lane et al. 2008; Carboni et al. 2011). Então, além de ser um ambiente adequado para estudar facilitação entre

plantas de forma geral, o gradiente natural de estresse e perturbação da praia para o interior faz com que a vegetação sobre planície costeira arenosa seja também um ambiente ideal para testar a HGE. Embora alguns estudos tenham investigado interações entre plantas ao longo deste gradiente costeiro (ver Forey et al. 2009; Maltez-Mouro et al. 2010; Santoro et al. 2011), poucos foram conduzidos em regiões tropicais ou subtropicais (ver Franks 2003). Além disso, resultados discordantes entre os diferentes estudos demonstram que ainda não está claro como as condições ambientais e as características das espécies envolvidas afetam o saldo das interações entre plantas ao longo de gradientes costeiros.

1.7. A tese

O objetivo geral desta tese foi estudar, através de diferentes abordagens, facilitação entre plantas de planície costeira arenosa (ou restinga). Para atingir esta meta geral, esta tese é composta de seis capítulos. O primeiro e presente capítulo faz uma apresentação sucinta dos conceitos, métodos e principais teorias que permeiam os quatro capítulos subseqüentes. Com esta introdução, espero ajudar o leitor a compreender o plano de pesquisa representado por esta tese, assim como a unidade que existe entre os quatro capítulos seguintes, mesmo que apresentados de forma independente. Os quatro capítulos seguintes (capítulos 2 a 5) formam o corpo principal de tese. Tratam-se de capítulos independentes que investigam diferentes aspectos da facilitação entre plantas de planície costeira. Cada um destes capítulos está redigido em forma de artigo científico, nos formatos exigidos pelas revistas às quais serão submetidos (ou da revista a qual já foi publicado, caso do capítulo 3). Para concluir a tese, o último capítulo (capítulo 6) apresenta as considerações finais, cujo objetivo é discutir implicações dos resultados obtidos nesta tese para o entendimento da organização e dinâmica da comunidade vegetal na restinga. A seguir, é apresentado de forma sucinta os objetivos gerais dos capítulos 2 a 5.

Capítulo 2. Facilitation between plants in coastal dunes: what we know and what we need to know

Neste capítulo, apresentamos uma revisão sistemática dos trabalhos já publicados sobre facilitação entre plantas de planície costeira arenosa em escala mundial. O objetivo da revisão é organizar de maneira objetiva o conhecimento adquirido, assim como identificar lacunas e indicar direções para estudos futuros. Adicionalmente, utilizamos técnicas de meta-análise para investigar se fatores considerados importantes para o saldo final das interações entre plantas explicam a variação na existência e na intensidade de facilitação entre os diversos estudos considerados.

Capítulo 3. The importance of plant life form on spatial associations along a subtropical coastal dune gradient

Neste capítulo, adotamos uma abordagem observacional-correlativa para fazer as primeiras inferências sobre as interações entre plantas em um gradiente de restinga subtropical. Investigamos padrões de associação espacial entre árvores adultas isoladas e plantas de diferentes formas de vida com até 0,5 m de altura ao longo de um gradiente ambiental praia-interior. Pressupondo que a distância do mar representa o gradiente de estresse, de acordo com a HGE, seria esperado predomínio de associações espaciais positivas decorrentes de predominância de facilitação, quanto menor a distância do mar (maior estresse). Por outro lado, seriam esperadas associações espaciais negativas, decorrentes do predomínio de competição entre as espécies, conforme aumenta a distância do mar (menor estresse). Além disso, investigamos se os padrões de associação espacial variam de acordo com a forma de vida da espécie alvo, sendo estas classificadas em herbáceas, lianas, arbustos e árvores. Este capítulo teve importância fundamental como o primeiro indicador de facilitação entre plantas de restinga em uma escala muito mais ampla (em termos de número de espécies envolvidas) do que a usualmente viável

para experimentos em campo. A partir desses resultados, foi possível planejar os experimentos que investigaram de maneira conclusiva o saldo de interações entre um par de espécies (capítulo 4), assim como o potencial mecanismo de facilitação em restinga (capítulo 5).

Capítulo 4. Does extreme stress beget plant facilitation? Experimental evidences from a subtropical coastal dune

No capítulo 3, encontramos associação espacial positiva entre árvores adultas e árvores jovens ao longo de todo gradiente ambiental, sugerindo efeito de planta-berçário entre árvores da restinga. Embora tal interpretação não seja inequívoca (conforme argumentos apresentados anteriormente), os resultados do capítulo 3 representam boas pistas de que a facilitação predomine no saldo final das interações entre árvores de restingas. Sendo assim, no capítulo 4 testamos, através de experimentos em campo envolvendo transplante da espécie alvo e manipulação de recurso limitante, se o saldo das interações de um par de espécies arbóreas é afetado pela variação nas condições abióticas, conforme predito pela HGE. Também avaliamos se o estágio de vida e a variável adotada para estimar desempenho da espécie alvo afeta a relação entre condições abióticas e o saldo das interações.

Capítulo 5. Nurse effect is driven by shade in a subtropical coastal dune: implications for restoration

No capítulo 4, confirmamos de maneira conclusiva que há efeito de planta-berçário entre o par de espécies arbóreas estudado. Desta maneira, o objetivo geral do capítulo 5 foi investigar, através de experimentos manipulativos em campo, se o sombreamento promovido pela copa da planta-berçário é o mecanismo responsável pelo aumento na sobrevivência das plântulas da espécie alvo. Neste capítulo discutimos como a

compreensão do mecanismo de facilitação entre plantas pode ter implicações práticas para a recuperação de áreas degradadas de restinga.

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Capítulo 2

Facilitation between plants in coastal dunes: what we know and what we need to know

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2.1 Abstract

Empirical studies in salt marshes, arid and alpine systems have given support to ecological models predicting that facilitation between plants is an important ecological process in severe environments. In coastal dunes, a stressful and frequently disturbed system, some studies have also been showing that facilitation is important, however the presence and magnitude of the interaction are context-dependent. We performed a systematic review and meta-analysis in order to examine potentially causative differences in the facilitation magnitude and highlight gaps in the plant interaction research in coastal dunes. Our meta-analyses indicate that factors influencing the facilitation existence or magnitude in coastal dunes depended on the performance estimator. For density, mean annual precipitation (MAP) and regional normalized difference vegetation index (NDVI) negatively affected facilitation. On the other hand, for growth, the effect of MAP on the facilitation magnitude was positive. Furthermore, for growth and also survival, the presence of a neighbor was positive in the tropics, whereas in the temperate region the effect was neutral for both performance estimators. Finally, for survival, the neighbor presence was positive in the early phase and negative during the adult life. In order to better understand these results we need to comprehend how the neighbor changes the conditions and resources in its neighborhood and how it affect the distinct performance estimators. Furthermore, the systematic review highlighted the necessity to improve the number of researches for some less studied conditions, such as tropical systems, latter target life stage and specifics performance estimators like seed emergence.

Keywords: coastal sand dunes, plant-plant interactions, life forms, synthesis

2.2 Introduction

The role of positive interactions between plants as key drivers of plant community dynamics and structure is widely recognized nowadays (Brooker et al. 2008; Butterfield 2009). Most of the recent knowledge in this topic results from empirical studies and theoretical models which have been suggesting that facilitative effects are more important in severe environments, where neighbors frequently buffer other individuals from potential limiting stresses (Bertness and Callaway 1994; Callaway and Walker 1997). The classical systems, which gave support for these ideas, are deserts (Flores and Jurado 2003; Franco and Nobel 1989), salt marshes (Bertness and Hacker 1994; Bertness and Leonard 1997) and alpine systems (Badano et al. 2006; Callaway et al. 2002).

In the last few years, studies performed in coastal dunes, a stressful and frequently disturbed system, have also been accumulating evidences of facilitation as an important interaction on this plant community. Several factors are liable to limit plant performance on coastal dune, such as soil moisture, soil nutrient, wind exposure, sand burial, salt spray and soil salinity (Wilson and Sykes 1999). Since plants might be able to ameliorate these harsh conditions, plant facilitation is likely to occur in this system. Indeed, in a tropical dune in Mexico, Martínez (2003) showed that the shrub *Chamaecrista chamecristoides* reduces the surface temperature, wind speed and sand accretion beneath its canopy and increases the establishment success for two late colonizer grasses. In a similar way, in a temperate dune in the United States a wood nitrogen-fixing shrub facilitated recruitment, growth and reproduction of two herbaceous species through canopy shading and soil nutrient enrichment (Shumway 2000). However, as showed in other systems (Dullinger et al. 2007; Gómez-Aparicio 2009), the existence and the magnitude of the positive interaction are variable in context-dependent. Franks (2003), for example, found that the existence of facilitation depends on the plant performance estimator considered while Armas and Pugnaire (2009) suggested that the life stage of the target individual highly influences the interaction balance. Understanding in what conditions facilitation between

plants are stronger will have a great importance for a better understanding of the organization and dynamics of the coastal dunes. Moreover, it might be of great value for practices of restoration of degraded areas in which remaining vegetation could be used to accelerate the recovery process.

The advance of science takes place normally in two different ways: through primary research studies, which is the most common method; and through research synthesis, where the results from a set of primary research are evaluated in terms of the same hypothesis (Rosenberg et al. 2000). Although less studied than other systems, we already have enough set of published studies on plant facilitation in coastal dunes, which makes this moment a good one for a synthesis. For that purpose, systematic reviews combined with meta-analysis represent a power and objective approach used to combine results from different studies in order to highlight gaps and reach general conclusions (Gurevitch and Hedges 2001). Although narrative reviews, as done by Martínez and García-Franco (2004), are useful as summaries of the knowledge within a discipline, a quantitative and direct comparison of effect sizes between studies via meta-analysis provides the same quantitative rigor as primary studies (Osenberg et al. 1999).

In this study we used formal systematic review and meta-analyses to highlight gaps in the plant facilitation research in coastal dunes, and also to estimate the average magnitude of facilitation between plants in coastal dunes and examine potentially causative differences in the interaction magnitude.

2.3 Methods

2.3.1 Data collection

We conducted a survey of the published studies that explicitly tested the presence of facilitation between plants in coastal dunes. Studies were located in ISI Web of Science in October 2010 by using a combination of three groups of terms: i) “dune*” or “restinga” or “coastal sand vegetation”, and ii) “facilitation” or “positive interaction*” and iii) “plant*” or

“tree*” or “shrub*” or “herb*”. This search led to a large number of papers that were subsequently examined firstly for their suitability in the review and secondly in the meta-analysis. For the first selection were included only the studies that explicitly addressed facilitation interaction between plants in coastal dune systems. Using these criteria, reviews, studies on non-coastal dunes and those in which at least one of the interacting organisms was not a plant were appropriately excluded. Furthermore, for the meta-analysis the studies had the additional following criterions: i) to report the data in a usable form; ii) to be conducted under natural conditions in the field; and iii) to evaluate the effect of neighbours on target species comparing the performance of plants growing in the vicinity of a neighbour with plants growing in open areas. When the required data were only reported in graphical form, the graphics were scanned and extracted in table format using TechDig software (Jones 1998). In the cases in which the same publication evaluated the effect of different combinations of neighbour-target species, or different life stages, or the experiment was conducted in different sites, each result was considered as an independent case. However, if repeated measures were taken from the same experiment, only the results obtained in the end of the experiment were used. In the same way, when the same experiment was done in different years just the last one was taken in consideration. When the data required for meta-analysis were not provided in the papers nor obtained by contacting the authors the studies were excluded from the analyses.

In order to understand the variation found between the different cases, each case was classified according to some independent variables that had potential to explain such variations. First of all, each case was classified according to the neighbour and target life forms (herb, shrub or tree). Herbaceous life form was further subdivided into grass and forb when the information was available. Information about the target life stage (seed, young or adult) and the kind of approach adopted (observational or experimental) were also taken into consideration. We classified each case according to the geographic region, *i.e.*, as tropical (from latitude 0° to 28°), temperate (29° to 50°) and artic-antartic (more

than 51°) using the reported latitudes. Based on the site localization provided by each study, we used remote sensing techniques to record information about the mean annual precipitation (MAP) and the normalized difference vegetation index (NDVI), a surrogate for plant biomass. To estimate the MAP for each study site we used the Global Land Data Assimilation System (GLDAS), which is a global, high-resolution, terrestrial modelling system that incorporates satellite- and ground-based observations in order to produce optimal fields of land surface states and fluxes in near-real time (Rodell et al. 2004). For NDVI calculation, we used two kinds of images with different resolutions: aster images with 15 m resolution, which provided a local estimate of biomass vegetation; and modis images with 250-500 m resolution, which, on the other hand, provided a more regional estimation. For the NDVI based on aster images, hereafter called local NDVI, we used the coordinates and description of the site (Reserve, National Park, etc) and local vegetation provided by each study in order to localize the study site in the image as precisely as possible. After that, we selected, among the aster images available for each site, one with less clouds and which was taken around the period in which the study was done. On the other hand, for NDVI based on modis images (hereafter called regional NDVI), the NDVI was calculated from mensal images took from 2001 to 2009. In order to synthesize this information for each site, the mensal NDVI was summed for each year to finally calculate the mean annual NDVI. All NDVI calculation was done using the software ERDAS IMAGINE.

2.3.2 Meta Analysis

Suitable studies were grouped in eight different datasets according to the performance estimator: density, survival, growth (which includes biomass and growth in height), richness (number of species), reproductive output (which includes any quantitative measure of flower, fruit or seeds production), occurrence and emergence. Since we had two types of response variables, we used different measures of effect size: the natural log of the response ratio ($\ln(RR)$) for continuous response variables (density, growth, richness

and reproductive output) and the natural log odds ratio ($\ln(\text{OR})$) for categorical responses (survival, occurrence and seed emergence).

The natural log of the response ratio ($\ln(\text{RR})$) estimation and its associated variance, calculated for each case, is based on means, standard deviation (SD) and sample size (n) for control (without neighbor) and treatment (with neighbor). In the cases in which only the standard error (SE) was provided, it was transformed according to the equation: $\text{SD} = \text{SE} \cdot (n^{1/2})$. Values of $\ln(\text{RR})$ higher than 0 indicate a positive effect of the neighbor on the target performance (facilitation) while values lower than 0 indicate a negative effect of the neighbor (competition). For categorical responses, the estimation of the natural log of the odds ratio ($\ln(\text{OR})$) and its associated variance for each case is based on the number of success and failure for each treatment. In the case of survival for example, it means: the number of survival and dead plants with and without neighbors. As for $\ln(\text{RR})$, positive values of $\ln(\text{OR})$ indicate facilitation and negative values indicate competition.

The effect of the neighbor was assessed for each one of the performance estimator dataset, once it had at least five studies (publications) included. This arbitrary criterion was considered in order to avoid trends resulting from few studies. Bias-corrected bootstrap 95% confidence intervals (CIs) were calculated for each overall effect size. If the CI did not overlap zero, the effect was considered significant. Furthermore, the Q-statistics were used for each dataset in order to examine the heterogeneity among the effect sizes. When the variance among effect sizes (Q_T) was greater than expected by chance ($P < 0.05$), we evaluate if the independent variables help to explain the total heterogeneity (Q_T). The percentage of variation in the effect sizes explained by each independent variable was estimated as Q_M/Q_T (Rosemberg et al. 2000) and the significance of the model structure (Q_M) was tested by randomization tests with 999 iterations ($\alpha = 0.05$). The independent variables selected were: i) geographic region (tropical, temperate and subarctic-subantartic regions), ii) neighbor life-form (i.e. tree, shrub, grass or forb); iii)

target life-form (i.e. tree, shrub, grass or forb); iv) target life stage; v) mean annual precipitation (MAP); vi) local NDVI and vii) regional NDVI.

Data were analyzed using random-effect models which assumed that, in addition to sampling error, there is a true random component of variation in the effect sizes between the studies (Gurevitch and Hedges 2001). In the present context, this assumption makes the random-effect models more reasonable than fixed-effect models since the complex interactions in ecology generally result in ecologically important heterogeneity between studies (Pullin and Stewart 2006). Additionally, the use of random-effect models instead of fixed-effect models fits the goal of generalization usually present in reviews (Borenstein et al. 2009). Publication bias was tested by calculating the Rosenthal's fail number, which is the number of non-significant missing studies that would have to be added to the meta-analysis in order to change the results from significant to nonsignificant (Rosemberg et al. 2000). If the fail-safe number is larger relatively to the number of observed cases, the observed results can be treated as reliable estimate of the true effect (Rosemberg et al. 2000). However, Rosenthal (1979) suggests that a fail-safe number larger than $5n + 10$ (where n is the number of studies) is a more conservative critical value against which to test a fail-safe calculation. Moreover, we used funnel plots as a graphical method to assess publication bias and conducted Spearman rank correlation tests to analyze the correlation between the standardized effect size and the variance (Rosemberg et al. 2000). All the meta-analysis were conducted using MetaWin 2.1 (Rosenberg et al. 2000).

2.4 Results

2.4.1 Systematic Review

A total of 68 articles were recorded using the proposed keywords in the Web of Science. However, within this set of publications, only 24 articles met the selection criteria for

systematic review (Appendix 1). The 24 articles, published in 14 different journals between 1997 and 2010, yielded 316 suitable cases.

The 24 studies were done in 11 countries around the world, but most of them (10 studies - 42%) in the United States of America and only one or two in the each remaining countries. In relation to geographic position, 63% of the studies were done in temperate zone, 29% in the tropics and only 8% in the subarctic zone. Regarding the approach adopted, from 24 studies 11 (46%) used only the observational approach, 5 (21%) only the experimental and 8 studies (33%) used both of them. If we consider the cases instead of the publications, the observational approach is still dominant with 195 of 316 (62%) against 121 (38%) of experimental cases.

From 316 cases seven plant performance estimators were recorded. Density was the most frequent, representing 32% of the total, followed by survival (21%), growth (19%), reproductive output (10%), richness (9%), occurrence (6%) and emergence (2%). The life stage recorded most commonly was the young stage (seedlings, saplings and juveniles) representing 46% of the total number of measurements versus 18% of studies recording adults and only 2% recording seed stage. The remaining studies (33%) recorded a mix of stages, from young to adult.

Among the neighbor life form, shrub is the most common representing 50% of the cases, followed by herb (38%), tree (7%) and a mix of life-forms used in the 5% of the cases. On the other hand, among the target life forms, the most common is herb (50%), followed by mix of life-forms (26%), shrub (22%), tree (2%) and moss (1%).

2.4.2 Meta-analysis

The number of cases suitable for the meta-analyses varied according to the performance estimator (Table 1). As an arbitrary limit we considered as enough sample size the performance estimator with at least 10 cases from at least 5 different publications. In this way, only density (Appendix 2), growth (Appendix 3) and survival (Appendix 4)

datasets had enough cases and original publications to be considered in the meta-analysis (Table 1).

Regarding the publication bias, Spearman rank correlation tests between effect size and variance were not significant for the three performance estimators analyzed, which indicates no publication bias ($R_s = 0.20$, $P = 0.22$ for density; $R_s = 0.06$, $P = 0.73$ for growth; $R_s = -0.24$, $P = 0.21$ for survival). Fail-safe number was higher than the number of cases for the three performance estimators (for density= 125, for growth= 313, for survival= 73). However, for density and survival these values were smaller than the threshold recommended by Rosenthal (1979). The effect size and sample size scatter plots of each of the three datasets showed the funnel shape with large opening at the smallest sample sizes (data not showed), which indicates no biases in publication. Taken as a whole, these results indicate that there is little publication bias among the cases considered and that the meta-analyses are reliable.

For plant density, the overall effect of the neighbor presence was neutral (i.e. 95% CI crossed zero) and the overall heterogeneity test was significant, indicating that the different cases do not share a common effect ($Q_T = 105.7$; $df = 37$, $P = 0.00000$). Indeed, among the predictors variables tested, the mean annual precipitation (MAP) and the regional NDVI helped to explain such internal variation (Table 2). Mean annual precipitation (MAP) and regional NDVI was negatively related to the effect size for plant density (Table 2, Fig. 1 and Fig. 2).

Regarding the plant growth, across all studies, the overall effect size was neutral (Fig. 3) and the overall heterogeneity test was significant ($Q_T = 65.7$; $df = 35$, $P = 0.001$). In this case, geographic region and MAP were significant predictors variables (Table 3). While in the tropics the neighbor effect was positive, in the temperate region the effect was neutral (Fig. 3). Furthermore, opposite from the density result, there was a positive relationship between MAP and effect size for plant growth (Fig. 4).

For plant survival, the overall effect size indicated a positive effect of the neighbor presence (Fig. 5). The test of internal heterogeneity was not significant ($Q_T=19.2$; $df= 29$, $P=0.91$), but significant effects were identified for geographic region and target life-stage (Table 4). As observed for growth, the neighbor presence in the tropical region was positive for plant survival whereas neutral in the temperate region (Fig. 5). Regarding target life stage, the neighbor presence was positive for young phase while negative for adult individuals (Fig. 5).

2.5 Discussion

2.5.1 Systematic review: highlighting gaps

The systematic review showed a clear concentration of dune facilitation studies in temperate dunes. In order to improve the degree of generalization and even to better understand in which way climatic conditions affect the magnitude of facilitation between plants more studies need to be done in tropical dunes. As highlighted by Hesp (2004), even though few comparative studies have been carried out, differences in factors such as species, adaptative strategies and rates of plants growth indicate that ecological processes may be distinct between tropical and temperate dunes. Another point highlighted by systematic review is the predominance of observational studies over experimental studies. Observational studies are generally spatial associations analysis among species. Although positive associations provide evidence of facilitation, this associational pattern does not exclude alternative explanations, as shared physical microhabitats requirements and the tendency of some plants to act as foci for seed deposition (Callaway 1995). On the other hand, experimental approach provides a strongest evidence for plant facilitation since the alternative explanations cited before might be eliminated in this kind of approach. Moreover, with an experimental approach is possible to test not only the existence and magnitude of the interaction, but the mechanism behind the phenomenon (Callaway 2007). In this way, it would be of great value to increase the number of studies that adopt

experimental, or a combination of observational and experimental approaches, in order to improve the degree of evidence of facilitation in coastal dunes and to explore with details the still poorly understood mechanisms behind this interaction.

The systematic review also pointed that several performance estimators have been used to estimate facilitation between plants in coastal dunes. However, some of them are more commonly used than others. Reproductive output, richness and seed emergence are important estimators but hardly used. As showed in another meta-analysis including several ecosystems, the effect of neighbors on emergence is significantly positive in semiarid and tropical habitats (Gómez-Aparicio 2009). Emergence is less studied probably due to the demanding time to monitor the emergence pattern. For reproductive output the challenge is probably related to the logistic of the experiment, since transplanting reproductive adult individual could be harder than transplanting seedlings or samplings. This explanation might also be partially relevant to the frequency of life stages usually used in dune facilitation studies, since most of them are young individuals while adults are much less represented. Although the benefits provided by a neighbor is more prone to happen in the young phase, usually the most vulnerable to stress conditions, we still need to increase the number of studies for seeds and adults to better understand how the facilitation magnitude changes along the ontogenetic life in coastal dunes.

2.5.2 Meta-analysis: reaching general conclusions

All the meta-analyses indicated that the factors influencing facilitation existence or magnitude in coastal dunes depended on the performance estimator. For example, survival data suggested that life stage affected the outcome of the interaction, with the presence of a neighbor being positive for young individuals and negative for adults, whereas density and growth data suggested that the net effect of neighbors did not differ among life stages. This general conclusion is in agreement with a previous meta-analysis performed with studies done in arid and semi-arid environments, which detected that the

effect of abiotic stress on the outcome of interactions depended on the performance estimator (Maestre et al. 2005). Since the resource requirements and abiotic conditions which affect different performance estimators are likely to differ, the change in resources or conditions generated by the neighbor presence might affect positively one performance estimator but not another. For example, in a study done in two barrier islands in the USA, Franks (2003) showed that neighbors increased target plant survival but reduced biomass. Moreover, we found here that although some conditions arising from neighbor presence might influence the plant performance, this effect may vary according to some factors. However, what defines which factors will affect each performance estimator? To know the answer, we probably need to better understand the mechanisms behind the interaction and how the neighbor changes the conditions and resources in its neighborhood.

For density, MAP and regional NDVI negatively affected facilitation, which means that as the precipitation and vegetation biomass become higher, the magnitude of facilitation is smaller. If we consider MAP and NDVI as surrogates of stress, these results are in accordance with the Stress Gradient Hypothesis (SGH), which states that the relative frequency of facilitation becomes smaller as stressful conditions decreases (Bertness and Callaway 1994; Callaway and Walker 1997). However, although these results are in accordance with a common hypothesis in the facilitation literature, it is hard to understand the mechanism behind this pattern since density is a result from different processes, such as seed emergence and survival. Moreover, measurement of density in naturally occurring plants, as measured in all of the cases included in the meta-analysis, could be the result of processes beyond the plant-plant interaction, such as shared microhabitat requirements and distinct seed deposition (Callaway 1995, Holl 2002).

MAP is also important for growth dataset, although in this case the relationship was positive, suggesting that the magnitude of facilitation increases with the precipitation. In this case the result do not support SGH. Since competition and facilitation seem to occur

simultaneously (Maestre et al. 2003), a neighbor can facilitate a target individual ameliorating the nitrogen availability but, at the same time, they can compete for water. The net effect will be the sum of both interactions. One possible explanation for the result found here is that the increase in water availability provided by the rain reduces the competition for water, increasing the net interaction for growth.

Growth data suggested that the geographic region also affected the existence of facilitation. Moreover, similar results were found for survival data. Altogether, these results suggested that the presence of a neighbor was positive for plant survival and growth in the tropical region, whereas in the temperate region the effect was neutral for both performance estimators. The environment severity is relative to the stress tolerance and resource use adaptations of the species (Lortie 2010). The species composition and predominant life forms differ between tropical and temperate dunes (Hesp 2004). Therefore, the observed outcome might be the result of different traits and, consequently, distinct sensibility to the changes in conditions and resources generated by the neighbor presence in the tropical and temperate dunes. However, the limited number of tropical studies indicates that we need to be cautious in relation to the generalization of the results. More studies in tropical dunes are clearly needed in order to confirm the effect of geographic region on the outcome of the interaction. At the same time, studies comparing tropical and temperate systems will be very interesting in order to test the hypothesis arose here.

Beyond the geographic effect, survival data suggests that the outcome of interaction also varies depending on the life stage, with the neighbor presence being positive in the early phase and negative during the adult life. The ontogenetic divergence in the response to neighbor presence might be because the habitat requirements of early stages are not the same as those of adults, and sometimes they could be even conflicting (Schupp 1995). The effect of life stage on the interaction outcome was also reported in arid systems (Miriti 2006; Valiente-Banuet et al. 1991). Because the survival of seedlings is

usually extremely low in sand dunes (Maun 2004) and the recruitment limitation is a key determinant of long-term community dynamics (Grubb 1977), the increase in the survival provided by the presence of neighbor in the early stages of life is probably essential for the maintenance of dune vegetation, even considering the latter change in the outcome of the interaction.

Some characteristics of the datasets used in the meta-analyses impose certain limitations to the generalization of the synthesis. Although we have a substantial number of cases for each performance estimator evaluated, for some conditions the number of cases is very low, such as for tropical systems and adult life stage. In the same way, the systematic review indicated other gaps in the number of dune interaction studies for certain conditions. Beyond expand the geographic region and life stage studied; it will be of great value increase the researches considering less studied performance estimators such as emergence and reproductive output. Furthermore, it is recommended the use of experimental approach in order to strengthen the degree of evidence of facilitation existence and to explore the underling mechanisms behind the interaction.

We conclude that the factors, which affect the facilitation in coastal dunes, were tightly dependent on performance estimator. In order to explain this complex pattern we need to understand how the neighbor presence changes the conditions and resources in its neighborhood in coastal dunes and how it affects the plants distinct performance estimators.

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TABLES AND FIGURES

Table 1 Total of suitable cases for meta-analysis and respective total publications for each performance estimator.

PERFOMANCE	N CASES	N PUBLICATIONS
Density	38	9
Growth	36	9
Survival	30	6
Richness	17	4
Reproductive output	7	3
Emergence	4	2
Occurrence	4	1

Table 2 Summary of random models analyzing the effect of independent variables on neighbor effect for plant density. d.f= degrees of freedom; Q_M = heterogeneity explained by the model; Q_E = residual error variance; Q_M/Q_T = fraction of the total heterogeneity explained by the model; Slope= only applicable for continuous predictors.

EFFECT	DF	Q_M	Q_E	Q_M/Q_T	SLOPE	P
Geographic region	1,35	0.71	101.01	0.007	-----	0.63
Neighbor life form	2,35	0.29	99.58	0.003	-----	0.95
Target life form	2,33	1.86	98.1	0.02	-----	0.69
Target life stage	2,35	0.48	96.71	0.005	-----	0.91
MAP	1,36	1.23	99.63	0.01	-0.0005	0.02
NDVI - local	1,27	0.16	70.31	0.002	0.40	0.24
NDVI - regional	1,34	6.78	102.44	0.06	-0.27	0.002

Table 3 Summary of random models analyzing the effect of independent variables on neighbor effect for plant growth. d.f= degrees of freedom; Q_M = heterogeneity explained by the model; Q_E = residual error variance; Q_M/Q_T = fraction of the total heterogeneity explained by the model; Slope= only applicable for continuous predictors.

EFFECT	DF	Q_M	Q_E	Q_M/Q_T	SLOPE	P
Geographic region	1,33	13.43	51.78	0.21	-----	0.02
Neighbor life form	2,33	0.18	57.32	0.003	-----	0.96
Target life form	2,32	5.89	47.84	0.11	-----	0.19
Target life stage	2,33	9.28	53.30	0.15	-----	0.10
MAP	1,34	6.52	57.26	0.10	0.0011	0.02
NDVI - local	1,15	0.17	35.96	0.005	-0.1945	0.43
NDVI - regional	1,33	0.002	59.31	0.00003	0.0026	0.43

Table 4 Summary of random models analyzing the effect of independent variables on neighbor effect for plant survival. d.f= degrees of freedom; Q_M = heterogeneity explained by the model; Q_E = residual error variance; Q_M/Q_T = fraction of the total heterogeneity explained by the model; Slope= only applicable for continuous predictors.

EFFECT	DF	Q_M	Q_E	Q_M/Q_T	SLOPE	P
Geographic region	1,28	3.96	18.24	0.18	-----	0.02
Neighbor life form	3,26	3.12	14.65	0.18	-----	0.32
Target life form	3,26	1.74	17.58	0.09	-----	0.57
Target life stage	2,28	3.35	24.78	0.12	-----	0.05
MAP	1,28	0.78	17.75	0.04	-0.001	0.26
NDVI - local	1,28	0.63	16.96	0.04	-1.570	0.09
NDVI - regional	1,28	0.88	18.13	0.05	-0.110	0.29

Fig. 1 Relationship between mean effect size (lnRR) and mean annual precipitation (MAP) for plant density.

Fig. 2 Relationship between mean effect size (lnRR) and regional NDVI for plant density.

Fig. 3 Mean effect sizes by geographical region and the overall effect for plant growth. Error bars are bias-corrected bootstrap 95% confidence intervals. The number of cases is shown in parenthesis. Significant geographic region effect is indicated by confidence intervals that do not overlap zero.

Fig. 4 Relationship between mean effect size (lnRR) and mean annual precipitation (MAP) for plant growth.

Fig. 5 Mean effect sizes by target life stage, geographical region and the overall effect for plant survival. Error bars are bias-corrected bootstrap 95% confidence intervals. The number of cases is shown in parenthesis. Significant effect is indicated by confidence intervals that do not overlap zero.

2.8 Supplementary material

Appendix 1 List of 24 studies included in systematic review.

study	Author and year	Journal	Country	Region	Approach	Number of cases for Systematic Review
1	Cushman et al. 2010	JOURNAL OF VEGETATION SCIENCE	USA	temperate	observational	22
2	Maltez-Mouro et al. 2010	ACTA OECOLOGICA-INTERNATIONAL	Portugal	temperate	observational	8
3	Forey et al. 2010	PLANT ECOLOGY	France	temperate	experimental	32
4	Forey et al. 2009	JOURNAL OF VEGETATION SCIENCE	France	temperate	observational	33
5	Armas and Pugnaire 2009	JOURNAL OF VEGETATION SCIENCE	Spain	temperate	both	27
6	Brancalion et al. 2009	BIOTROPICA	Brazil	tropical	observational	1
7	Bonanomi et al. 2008	PLANT ECOLOGY	Italy	temperate	observational	9
8	Feagin and Wu 2007	RANGELAND ECOLOGY & MANAGEMENT	USA	temperate	observational	5
9	Cheplick 2005	PLANT ECOLOGY	USA	temperate	observational	10
10	Dias et al. 2005	JOURNAL OF TROPICAL ECOLOGY	Brazil	tropical	both	15
11	Feagin et al. 2005	ECOLOGICAL MODELLING	USA	temperate	observational	2
12	Martinez et al. 2004	ECOSCIENCE	Mexico	tropical	both	11
13	Sternberg et al. 2004	ISRAEL JOURNAL OF PLANT SCIENCES	Israel	temperate	observational	4
14	Franks 2003	PLANT ECOLOGY	USA	tropical	experimental	1
15	Franks and Peterson 2003	PLANT ECOLOGY	USA	tropical	experimental	4
16	Martinez 2003	PLANT ECOLOGY	Mexico	tropical	both	5
17	Rudgers and Maron 2003	OIKOS	USA	temperate	both	12
18	Franks SJ 2003	CANADIAN JOURNAL OF BOTANY	USA	tropical	experimental	43
19	El-Bana et al. 2002	PLANT AND SOIL	Egito	temperate	observational	15
20	Joy and Young 2002	PLANT ECOLOGY	USA	temperate	both	8
21	De Villiers et al. 2001	JOURNAL OF ARID ENVIRONMENTS	South Africa	temperate	both	25
22	Gagne and Houle 2001	CANADIAN JOURNAL OF BOTANY	Canada	subartic	observational	5
23	Shumway 2000	OECOLOGIA	USA	temperate	both	11
24	Houle 1997	CANADIAN JOURNAL OF BOTANY	Canada	subartic	experimental	8

Appendix 2 List of 38 cases included in the meta-analysis of density data.

Case	Author and year	Region	MAP (mm)	Local NDVI	Regional NDVI	part of the gradient	Neighbor life form	Neighbor species	Target life form	Target species	Target life stage	Effect Size (lnRR)	Variance (lnRR)
1	Cushman et al. 2010	temperate	482	0.652	4.2	hind-dune	shrub	<i>Lupinus chamissonis</i>	forb	<i>Claytonia perfoliata</i>	several	4.297	0.165
2	Cushman et al. 2010	temperate	482	0.65	4.2	hind-dune	shrub	<i>Ericameria ericoides</i>	forb	<i>Claytonia perfoliata</i>	several	4.099	0.161
3	Cushman et al. 2010	temperate	482	0.65	4.2	hind-dune	shrub	<i>Lupinus chamissonis</i>	grass	<i>Bromus diadruns</i>	several	0.627	0.296
4	Cushman et al. 2010	temperate	482	0.65	4.2	hind-dune	shrub	<i>Ericameria ericoides</i>	grass	<i>Bromus diadruns</i>	several	0.319	0.330
5	Cushman et al. 2010	temperate	482	0.65	4.2	hind-dune	shrub	<i>Lupinus chamissonis</i>	grass	<i>Vulpia bromoides</i>	several	-2.860	2.271
6	Cushman et al. 2010	temperate	482	0.65	4.2	hind-dune	shrub	<i>Ericameria ericoides</i>	grass	<i>Vulpia bromoides</i>	several	-0.915	0.119
7	Cushman et al. 2010	temperate	482	0.65	4.2	hind-dune	shrub	<i>Lupinus chamissonis</i>	moss	several	several	-2.005	0.168
8	Cushman et al. 2010	temperate	482	0.65	4.2	hind-dune	shrub	<i>Ericameria ericoides</i>	moss	several	several	0.836	0.046
9	Forey et al. 2009	temperate	749	0.30	7.6	foredune	grass	<i>Elymus farctus</i>	several	several	several	1.748	0.260
10	Forey et al. 2009	temperate	772	0.216	7.7	foredune	grass	<i>Elymus farctus</i>	several	several	several	0.742	0.219
11	Forey et al. 2009	temperate	699	NA	6.5	foredune	grass	<i>Elymus farctus</i>	several	several	several	-0.045	0.105
12	Forey et al. 2009	temperate	749	0.304	7.6	whitedune	grass	<i>Ammophila arenaria</i>	several	several	several	0.064	0.110
13	Forey et al. 2009	temperate	772	0.216	7.7	whitedune	grass	<i>Ammophila arenaria</i>	several	several	several	0.541	0.074
14	Forey et al. 2009	temperate	699	NA	6.5	whitedune	grass	<i>Ammophila arenaria</i>	several	several	several	0.126	0.024
15	Forey et al. 2009	temperate	749	0.304	7.6	greydune	forb	<i>Helichrysum stoechas</i>	several	several	several	0.136	0.020
16	Forey et al. 2009	temperate	772	0.216	7.7	greydune	forb	<i>Helichrysum stoechas</i>	several	several	several	0.340	0.016
17	Forey et al. 2009	temperate	699	NA	6.5	greydune	forb	<i>Helichrysum stoechas</i>	several	several	several	-0.319	0.017
18	Forey et al. 2009	temperate	749	0.304	7.6	greydune	shrub	<i>Ephedra distachya</i>	several	several	several	0.457	0.011
19	Forey et al. 2009	temperate	699	NA	6.5	greydune	forb	<i>Pancratium maritimum</i>	several	several	several	-0.243	0.017
20	Bonanomi et al. 2008	temperate	737	0.264	6.0	open shrub	shrub	<i>Medicago marina</i>	grass	<i>Lophochloa pubescens</i>	several	1.386	0.184
21	Cheplick 2005	temperate	1874	NA	8.4	pioneer zone	grass	<i>Ammophila breviligulata</i>	grass	<i>Triplasis purpurea</i>	several	-0.065	0.011
22	Cheplick 2005	temperate	1874	NA	8.4	bpioneer zone	grass	<i>Ammophila breviligulata</i>	grass	<i>Cenchrus tribuloides</i>	several	-0.571	0.010
23	Cheplick 2005	temperate	1874	NA	8.4	pioneer zone	grass	<i>Ammophila breviligulata</i>	forb	<i>Heterotheca subaxillaris</i>	several	-0.819	0.097
24	Martinez et al. 2004	tropical	657	0.151	6.7	parabolic mobile dunes	shrub	<i>Chamaecrista chamaecristoides</i> var. <i>chamaecristoides</i>	grass	<i>Trachypogon plumosus</i>	adult	2.754	0.372
25	Martinez et al. 2004	tropical	657	0.151	6.7	parabolic mobile dunes	shrub	<i>Chamaecrista chamaecristoides</i> var. <i>chamaecristoides</i>	grass	<i>Schizachyrium scoparium</i> var. <i>littoralis</i>	adult	0.000	0.404
26	Martinez et al. 2004	tropical	657	0.151	6.7	parabolic mobile dunes	shrub	<i>Chamaecrista chamaecristoides</i> var. <i>chamaecristoides</i>	grass	<i>Trachypogon plumosus</i> and <i>Schizachyrium scoparium</i> var. <i>littoralis</i>	young	-1.315	0.168
27	Martinez et al. 2004	tropical	657	0.151	6.7	parabolic mobile dunes	shrub	<i>Chamaecrista chamaecristoides</i> var. <i>chamaecristoides</i>	grass	<i>Trachypogon plumosus</i>	adult	1.689	0.254
28	Martinez et al. 2004	tropical	657	0.151	6.7	parabolic	shrub	<i>Chamaecrista</i>	grass	<i>Schizachyrium</i>	adult	-2.019	0.116

Case	Author and year	Region	MAP (mm)	Local NDVI	Regional NDVI	part of the gradient	Neighbor life form	Neighbor species	Target life form	Target species	Target life stage	Effect Size (lnRR)	Variance (lnRR)
29	Martinez et al. 2004	tropical	657	0.151	6.7	mobile dunes parabolic mobile dunes	shrub	<i>chamaecristoides</i> var. <i>chamaecristoides</i> <i>Chamaecrista</i> <i>chamaecristoides</i> var. <i>chamaecristoides</i>	grass	<i>scoparium</i> var. <i>littoralis</i> <i>Trachypogon plumosus</i> and <i>Schizachyrium</i> <i>scoparium</i> var. <i>littoralis</i>	young	-0.644	0.266
30	Sternberg et al. 2004	temperate	542	NA	NA	open shrub	shrub	<i>Retama raetam</i>	herb	several	young	-0.934	0.027
31	Sternberg et al. 2004	temperate	542	NA	NA	open shrub	shrub	<i>Retama raetam</i>	herb	several	several	-2.020	0.058
32	Joy and Young 2002	temperate	958	0.256	6.9	open shrub	tree	<i>Juniperus virginiana</i>	several	several	several	-0.408	0.208
33	Joy and Young 2002	temperate	958	0.256	6.9	open shrub	tree	<i>Juniperus virginiana</i>	several	several	several	0.640	0.091
34	Gagne and Houle 2001	subartic	680	0.116	3.3	embryo dunes	forb	<i>Honckenya peploides</i>	grass	<i>Leymus mollis</i>	young	3.058	0.400
35	Shumway 2000	temperate	1049	0.114	7.1	open shrub	shrub	<i>Myrica pensylvanica</i>	grass	<i>Ammophila</i> <i>breviligulata</i>	adult	0.207	0.010
36	Shumway 2000	temperate	1049	0.114	7.1	open shrub	shrub	<i>Myrica pensylvanica</i>	forb	<i>Solidago sempervirens</i>	adult	-0.161	0.048
37	Shumway 2000	temperate	1049	0.114	7.1	open shrub	shrub	<i>Myrica pensylvanica</i>	grass	<i>Ammophila</i> <i>breviligulata</i>	young	-0.317	0.579
38	Shumway 2000	temperate	1049	0.114	7.1	open shrub	shrub	<i>Myrica pensylvanica</i>	forb	<i>Solidago sempervirens</i>	young	4.928	0.399

(Appendix 2 – continued)

Appendix 3 List of 36 cases included in the meta-analysis of growth data.

Case	Author and year	Region	MAP (mm)	local NDVI	regional NDVI	part of the gradient	Neighbor life form	Neighbor species	Target life form	Target species	Target life stage	Effect Size (lnRR)	Variance (lnRR)
1	Cushman et al. 2010	temperate	482	0.652	4.2	hind-dune	shrub	<i>Lupinus chamissonis</i>	grass	several	several	0.538	0.091
2	Cushman et al. 2010	temperate	482	0.652	4.2	hind-dune	shrub	<i>Ericameria ericoides</i>	grass	several	several	0.385	0.086
3	Cushman et al. 2010	temperate	482	0.652	4.2	hind-dune	shrub	<i>Lupinus chamissonis</i>	forb	several	several	-0.480	0.127
4	Cushman et al. 2010	temperate	482	0.652	4.2	hind-dune	shrub	<i>Ericameria ericoides</i>	forb	several	several	-0.728	0.229
5	Forey et al. 2010	temperate	772	NA	7.7	foredune	grass	<i>Elymus farctus</i>	grass	<i>Elymus farctus</i>	young	0.728	0.182
6	Forey et al. 2010	temperate	772	NA	7.7	foredune	grass	<i>Elymus farctus</i>	grass	<i>Ammophila arenaria</i>	young	2.838	16.823
7	Forey et al. 2010	temperate	772	NA	7.7	whitedune	grass	<i>Ammophila arenaria</i>	grass	<i>Elymus farctus</i>	young	2.539	8.509
8	Forey et al. 2010	temperate	772	NA	7.7	whitedune	grass	<i>Ammophila arenaria</i>	grass	<i>Ammophila arenaria</i>	young	2.781	6.255
9	Forey et al. 2010	temperate	772	NA	7.7	whitedune	grass	<i>Ammophila arenaria</i>	forb	<i>Helichrysum stoechas</i>	young	0.030	0.234
10	Forey et al. 2010	temperate	772	NA	7.7	whitedune	grass	<i>Ammophila arenaria</i>	grass	<i>Corynephorus canescens</i>	young	-0.396	0.668
11	Forey et al. 2010	temperate	772	NA	7.7	transition dune	forb	<i>Helichrysum stoechas</i>	grass	<i>Elymus farctus</i>	young	0.162	0.647
12	Forey et al. 2010	temperate	772	NA	7.7	transition dune	forb	<i>Helichrysum stoechas</i>	grass	<i>Ammophila arenaria</i>	young	2.890	7.225
13	Forey et al. 2010	temperate	772	NA	7.7	transition dune	forb	<i>Helichrysum stoechas</i>	forb	<i>Helichrysum stoechas</i>	young	0.599	0.965
14	Forey et al. 2010	temperate	772	NA	7.7	transition dune	forb	<i>Helichrysum stoechas</i>	grass	<i>Corynephorus canescens</i>	young	0.301	0.252
15	Forey et al. 2010	temperate	772	NA	7.7	grey dune	grass	<i>Corynephorus canescens</i>	grass	<i>Elymus farctus</i>	young	0.662	0.705
16	Forey et al. 2010	temperate	772	NA	7.7	grey dune	grass	<i>Corynephorus canescens</i>	grass	<i>Ammophila arenaria</i>	young	2.825	3.206
17	Forey et al. 2010	temperate	772	NA	7.7	grey dune	grass	<i>Corynephorus canescens</i>	forb	<i>Helichrysum stoechas</i>	young	-0.350	0.272
18	Forey et al. 2010	temperate	772	NA	7.7	grey dune	grass	<i>Corynephorus canescens</i>	grass	<i>Corynephorus canescens</i>	young	0.007	0.310
19	Armas and Pugnaire 2009	temperate	313	0.208	2.5	open shrub	shrub	Several	shrub	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	adult	0.223	0.008
20	Armas and Pugnaire 2009	temperate	313	0.208	2.5	open shrub	shrub	Several	shrub	<i>Pistacia lentiscus</i>	adult	0.088	0.005
21	Bonanomi et al. 2008	temperate	737	0.264	6.0	open shrub	shrub	<i>Medicago marina</i>	grass	<i>Lophochloa pubescens</i>	adult	1.705	0.151
22	Sternberg et al. 2004	temperate	542	NA	NA	open shrub	shrub	<i>Retama raetam</i>	herb	several	several	-1.365	0.103
23	Rudgers and Maron 2003	temperate	482	0.652	5.0	open shrub	shrub	<i>Baccharis pilularis pilularis</i>	shrub	<i>Lupinus arboreus</i>	young	0.246	0.013
24	Rudgers and Maron 2003	temperate	482	0.652	5.0	open shrub	grass	<i>Ammophila arenaria</i>	shrub	<i>Lupinus arboreus</i>	young	0.379	0.013
25	Franks 2003	tropical	1116	NA	5.9	foredune, mid-dune and rear dune	grass	<i>Uniola paniculata</i>	grass	<i>Uniola paniculata</i>	young	1.806	0.247
26	Franks 2003	tropical	1116	NA	5.9	foredune, mid-dune and rear dune	shrub	<i>Iva imbricata</i>	grass	<i>Uniola paniculata</i>	young	2.517	0.406
27	Franks 2003	temperate	881	0.193	8.0	foredune, mid-dune and rear dune	grass	<i>Uniola paniculata</i>	grass	<i>Uniola paniculata</i>	young	-1.053	0.126

Case	Author and year	Region	MAP (mm)	local NDVI	regional NDVI	part of the gradient	Neighbor life form	Neighbor species	Target life form	Target species	Target life stage	Effect Size (lnRR)	Variance (lnRR)
28	Franks 2003	temperate	881	0.193	8.0	foredune, mid-dune and rear dune	shrub	<i>Iva imbricata</i>	grass	<i>Uniola paniculata</i>	young	-1.925	0.862
29	Franks 2003	tropical	1116	NA	5.9	foredune, mid-dune and rear dune	grass	<i>Uniola paniculata</i>	shrub	<i>Iva imbricata</i>	young	-0.024	3.548
30	Franks 2003	tropical	1116	NA	5.9	foredune, mid-dune and rear dune	shrub	<i>Iva imbricata</i>	shrub	<i>Iva imbricata</i>	young	0.915	1.093
31	Franks 2003	temperate	881	0.193	8.0	foredune, mid-dune and rear dune	grass	<i>Uniola paniculata</i>	shrub	<i>Iva imbricata</i>	young	-0.659	0.085
32	Franks 2003	temperate	881	0.193	8.0	foredune, mid-dune and rear dune	shrub	<i>Iva imbricata</i>	shrub	<i>Iva imbricata</i>	young	-0.733	0.078
33	Gagne and Houle 2001	subartic	680	0.116	3.3	embryo dunes	forb	<i>Honckenya peploides</i>	grass	<i>Leymus mollis</i>	young	-0.034	0.005
34	Shumway 2000	temperate	1049	0.114	7.1	primary dunes (open shrub)	shrub	<i>Myrica pensylvanica</i>	grass	<i>Ammophila breviligulata</i>	adult	0.775	0.035
35	Shumway 2000	temperate	1049	0.114	7.1	primary dunes (open shrub)	shrub	<i>Myrica pensylvanica</i>	forb	<i>Solidago sempervirens</i>	adult	1.363	0.046
36	Shumway 2000	temperate	1049	0.114	7.1	primary dunes (open shrub)	shrub	<i>Myrica pensylvanica</i>	forb	<i>Solidago sempervirens</i>	adult	0.365	0.014

(Appendix 3 – continued)

Appendix 4 List of 30 cases included in the meta-analysis of survival data.

Case	Author and year	Region	MAP (mm)	local NDVI	regional NDVI	part of the gradient	Neighbor life form	Neighbor species	Target life form	Target species	Target life phase	Effect Size (lnOR)	Variance (lnOR)
1	Forey et al. 2010	temperate	772	0.22	7.70	foredune	grass	<i>Elymus farctus</i>	grass	<i>Elymus farctus</i>	young	-0.345	0.690
2	Forey et al. 2010	temperate	772	0.22	7.70	foredune	grass	<i>Elymus farctus</i>	grass	<i>Ammophila arenaria</i>	young	-0.345	0.690
3	Forey et al. 2010	temperate	772	0.22	7.70	foredune	grass	<i>Elymus farctus</i>	forb	<i>Helichrysum stoechas</i>	young	0.000	4.000
4	Forey et al. 2010	temperate	772	0.22	7.70	foredune	grass	<i>Elymus farctus</i>	grass	<i>Corynephorus canescens</i>	young	0.000	4.000
5	Forey et al. 2010	temperate	772	0.22	7.70	whitedune	grass	<i>Ammophila arenaria</i>	grass	<i>Elymus farctus</i>	young	1.818	0.455
6	Forey et al. 2010	temperate	772	0.22	7.70	whitedune	grass	<i>Ammophila arenaria</i>	grass	<i>Ammophila arenaria</i>	young	0.667	0.444
7	Forey et al. 2010	temperate	772	0.22	7.70	whitedune	grass	<i>Ammophila arenaria</i>	forb	<i>Helichrysum stoechas</i>	young	0.486	0.486
8	Forey et al. 2010	temperate	772	0.22	7.70	whitedune	grass	<i>Ammophila arenaria</i>	grass	<i>Corynephorus canescens</i>	young	0.625	0.625
9	Forey et al. 2010	temperate	772	0.22	7.70	transition dune	forb	<i>Helichrysum stoechas</i>	grass	<i>Elymus farctus</i>	young	0.909	0.455
10	Forey et al. 2010	temperate	772	0.22	7.70	transition dune	forb	<i>Helichrysum stoechas</i>	grass	<i>Ammophila arenaria</i>	young	0.000	0.438
11	Forey et al. 2010	temperate	772	0.22	7.70	transition dune	forb	<i>Helichrysum stoechas</i>	forb	<i>Helichrysum stoechas</i>	young	-1.273	0.509
12	Forey et al. 2010	temperate	772	0.22	7.70	transition dune	forb	<i>Helichrysum stoechas</i>	grass	<i>Corynephorus canescens</i>	young	-0.539	0.539
13	Forey et al. 2010	temperate	772	0.22	7.70	grey dune	grass	<i>Corynephorus canescens</i>	grass	<i>Elymus farctus</i>	young	1.111	0.444
14	Forey et al. 2010	temperate	772	0.22	7.70	grey dune	grass	<i>Corynephorus canescens</i>	grass	<i>Ammophila arenaria</i>	young	-0.455	0.455
15	Forey et al. 2010	temperate	772	0.22	7.70	grey dune	grass	<i>Corynephorus canescens</i>	forb	<i>Helichrysum stoechas</i>	young	-0.217	0.433
16	Forey et al. 2010	temperate	772	0.22	7.70	grey dune	grass	<i>Corynephorus canescens</i>	grass	<i>Corynephorus canescens</i>	young	-0.345	0.690
17	Armas and Pugnaire 2009	temperate	313	0.21	2.50	open shrub	shrub	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	shrub	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	young	1.833	0.282
18	Armas and Pugnaire 2009	temperate	313	0.21	2.50	open shrub	shrub	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	shrub	<i>Pistacia lentiscus</i>	young	2.438	0.406
19	Armas and Pugnaire 2009	temperate	313	0.21	2.50	open shrub	shrub	<i>Pistacia lentiscus</i>	shrub	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	young	1.671	0.304
20	Armas and Pugnaire 2009	temperate	313	0.21	2.50	open shrub	shrub	<i>Pistacia lentiscus</i>	shrub	<i>Pistacia lentiscus</i>	young	1.219	0.609
21	Armas and Pugnaire 2009	temperate	313	0.21	2.50	open shrub	shrub	several	shrub	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	adult	-1.229	0.028
22	Armas and Pugnaire 2009	temperate	313	0.21	2.50	open shrub	shrub	several	shrub	<i>Pistacia lentiscus</i>	adult	-0.051	0.563
23	Martinez 2003	tropical	657	0.15	6.70	parabolic mobile dunes	shrub	<i>Chamaecrista chamaecristoides</i> var. <i>chamaecristoides</i>	grass	<i>Trachypogon plumosus</i>	young	2.073	0.276
24	Martinez 2003	tropical	657	0.15	6.70	parabolic mobile dunes	shrub	<i>Chamaecrista chamaecristoides</i> var. <i>chamaecristoides</i>	grass	<i>Schizachyrium scoparium</i> var. <i>littoralis</i>	young	2.046	0.409
25	Rudgers and Maron 2003	temperate	482	0.65	5.00	open shrub	shrub	<i>Baccharis pilularis pilularis</i>	shrub	<i>Lupinus arboreus</i>	young	0.683	0.085
26	Rudgers and Maron 2003	temperate	482	0.65	5.00	open shrub	grass	<i>Ammophila arenaria</i>	shrub	<i>Lupinus arboreus</i>	young	-1.119	0.124
27	Joy and Young 2002	temperate	958	0.26	6.90	open shrub	tree	<i>Juniperus virginiana</i>	tree	<i>Sassafras albidum</i>	young	0.000	4.000

Case	Author and year	Region	MAP (mm)	local NDVI	regional NDVI	part of the gradient	Neighbor life form	Neighbor species	Target life form	Target species	Target life phase	Effect Size (lnOR)	Variance (lnOR)
28	Joy and Young 2002	temperate	958	0.26	6.90	open shrub	tree	<i>Juniperus virginiana</i>	tree	<i>Prunus serotina</i>	young	1.555	0.222
29	Shumway 2000	temperate	1049	0.11	7.10	open shrub	shrub	<i>Myrica pensylvanica</i>	grass	<i>Ammophila breviligulata</i>	young	-0.442	0.221
30	Shumway 2000	temperate	1049	0.11	7.10	open shrub	shrub	<i>Myrica pensylvanica</i>	forb	<i>Solidago sempervirens</i>	young	0.059	0.118

(Appendix 4 - continued)

Appendix 5 References included in Appendices 1-4 and not cited in the main text.

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Capítulo 3

The importance of plant life form on spatial associations along a subtropical coastal dune gradient

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3.1 ABSTRACT

Questions: Does the spatial association between isolated adult trees and understory plants change along a gradient of sand dunes? Does this association depend on the life form of the understory plant?

Location: Coastal sand dunes, southeast Brazil

Methods: We recorded the occurrence of understory plant species in 100 paired 0.25 m² plots under adult trees and in adjacent treeless sites along an environmental gradient from beach to inland. Occurrence probabilities were modeled as a function of the fixed variables of the presence of a neighbor, distance from the seashore and life form, and a random variable, the block (i.e., the pair of plots). Generalized linear mixed models (GLMM) were fitted in a backward stepwise procedure using Akaike's Information Criterion (AIC) for model selection.

Results: The occurrence of understory plants was affected by the presence of an adult tree neighbor but the effect varied with the life form of the understory species. Positive spatial association was found between isolated adult neighbor and young trees, whereas a negative association was found for shrubs. Moreover, neutral association was found for lianas, whereas for herbs the effect of the presence of an adult neighbor ranged from neutral to negative, depended on the subgroup considered. The strength of the negative association with forbs increased with distance from the seashore. However, for the other life forms, the associational pattern with adult trees did not change along the gradient.

Conclusions: For most of the understory life forms there is no evidence that the spatial association between isolated adult trees and understory plants changes with the distance from the seashore as predicted by the stress gradient hypothesis, a common hypothesis in the literature about facilitation in plant communities. Furthermore, the positive spatial association between isolated adult trees and young trees identified along the entire gradient studied indicates a positive feedback that explains the transition from open vegetation to forest in subtropical coastal dune environments.

Keywords: Brazil; Competition; Environmental gradient; Facilitation; Plant interactions; Restinga; Sand dune vegetation; Stress gradient hypothesis; Succession

Abbreviations: Stress Gradient Hypothesis (SGH)

Nomenclature: Forzza et al. 2010

Running head: Plant spatial association in a coastal dune

3.2 INTRODUCTION

It is broadly accepted that facilitation and competition can occur simultaneously between interacting plants (Holzapfel & Mahall 1999; Maestre et al. 2003), but the conditions under which one type of interaction prevails are not well understood. The stress gradient hypothesis (SGH) is a general conceptual model predicting that the relative frequency of facilitation and competition will vary inversely across gradients of stress, with facilitation being the dominant interaction under highly stressful conditions (Bertness & Callaway 1994; Brooker & Callaghan 1998). Several empirical studies conducted in different ecosystems have confirmed the predictions of the SGH (Callaway et al. 2002; Gómez-Aparicio et al. 2004; Holzapfel et al. 2006), although some empirical works do not support SGH (Pennings et al. 2003; Maestre & Cortina 2004; Bowker et al. 2010). It is possible that these contradictions are due, at least in part, to uncontrolled factors that also influence the outcome of plant interactions, such as ontogenetic effects (Armas & Pugnaire 2009), the performance measure used (Goldberg et al. 1999), the nature of the stress factor (Dullinger et al. 2007; Kawai & Tokeshi 2007), the methodology used to quantify biotic interactions (Michalet 2006) and, to a large degree, the traits of both the beneficiary and the benefactor species being investigated (Gómez-Aparicio et al. 2004; Liancourt et al. 2005). Recently, Maestre et al. (2009) argued that SGH should be refined by incorporating species traits to explain why co-occurring species may not show the same response to a common neighbor under the same environmental conditions. They suggest that species might be classified according to their life histories as “competitive” or “stress-tolerant” - following the CSR classification of Grime (1977, 2001).

Although the proposal of Maestre et al. (2009) refines the SGH, the application of their ideas is still challenging in tropical and subtropical systems. The information needed to classify species according to their life histories includes not only morphology but also physiology and morphogenetic responses to stress (Grime 2001), information rarely available for the numerous species common in these regions. Thus, an alternative is the

simpler distinction of life forms of interacting species. In fact, some studies have shown that the life form of the interacting plant species largely influences the outcome of interaction (Dullinger et al. 2007; Gómez-Aparicio 2009). Although each life form exhibits a wide range of strategies linked to the tolerance-competitive tradeoff (Grime 2001), in a general way, different life forms may reveal general tendencies in their abiotic tolerances and requirements. In this way, despite its simplicity, life form classification could represent a first step toward refining the SGH in environments where species life history information is scarce.

A common approach used to infer interactions between plants is spatial association (Callaway 1995), in which interspecific aggregation is interpreted as facilitation and segregation is interpreted as competition. However, aggregation may result from other processes, such as shared microhabitat requirements and dispersal processes (Callaway 1995). Manipulative experiments, provides stronger evidence but has intrinsic logistic limitations, which may explain why most experimental studies have been conducted using only pair-wise interactions. Accordingly, despite its limitations, the spatial association approach is a key tool as the first step toward identifying patterns in the entire community, generating hypotheses and guiding further experiments.

In coastal dune vegetation, the natural gradient from the beach to inland areas makes these communities ideal for testing the SGH. Because of the proximity of the ocean and the age of the substrate, there is a gradient of stress and disturbance from wind exposure, salt spray, sand burial, soil salinity and moisture, that decrease towards inland (Wilson & Sykes 1999; Lortie & Cushman 2007; Lane et al. 2008; Carboni et al. 2011). While several studies have investigated plant interactions along such environmental gradients (see Forey et al. 2009; Maltez-Mouro 2010; Santoro et al. 2011), few of them were conducted in subtropical or tropical coastal dunes (see Franks 2003).

In this study, we addressed two questions: (1) Does the spatial association between isolated adult trees and understory plants change along a gradient of subtropical

sand dunes? (2) Does this association depend on the life form of the understory plant? Assuming that the distance from the seashore is a surrogate for the stress gradient, we predicted that the probability of understory plants occurring under trees would be comparatively higher near the sea than in the adjacent treeless areas (positive association) as a consequence of facilitation. However, as the distance from the seashore increases, we expected a higher probability of understory plants occurring in the treeless areas (negative association) as a result of intensified competition. We also predicted that the spatial pattern of association would change in magnitude or type depending on the life form of the understory species, classified here as tree, shrub, herb or liana.

3.3 METHODS

3.3.1 Study area and vegetation

The study was conducted along a sand dune gradient near Marujá, a small fishing village located on the southern shore of Ilha do Cardoso State Park, a coastal island in southeastern Brazil (25°12'S, 44°17'W; Figure 1). The mean annual precipitation in Ilha do Cardoso ranges from 1400 mm to 2380 mm, with 70% of the rain falling between November and April. The mean annual temperature ranges from 21 to 23°C, but summers are warmer (mean monthly maximum of 26.0°C in February) and winters are cooler (mean monthly minimum of 18.3°C in July).

The sand dune gradient of southeastern Brazil is formed by a mosaic of plant communities that occupy sandy plains formed by marine deposits in the late Quaternary and which lie between the sea and the Atlantic forest, that grows in more ancient and fertile soils inland (see details in Lacerda et al. 1993). At the local scale, the dune system at the study area is formed by parallel beach ridges occupying an approximately 400 m strip of land between the ocean and an inland estuary. The first vegetation along the beach-to-inland gradient is a narrow strip of beach community, in which creeping psammophytes grow on the shifting sands of the upper part of the beach. Behind these embryo dunes is

the foredune, a slightly higher and older beach ridge dominated by grasses. Just shorewards of the foredune are the rear dunes, which are several parallel older and slightly higher beach ridges that are not directly affected by the beach-exchange process. Between the ridges of the rear dunes there are depressions flooded by the water table during the summer, the dune slacks. On the ridges of the rear dunes, there is open scrub vegetation with sparse, isolated 1-3 m trees and shrubs, wood thickets of various sizes and a perennial herbaceous cover on the sandy substrate (Photo S1). Vegetation cover and biomass increase with increasing distance from the seashore, and on the inland end of the gradient there is a strip of forest with a 4-6 m high canopy. Communities with similar structures but different species compositions along a beach-to-inland gradient have been described in other regions of the tropical and subtropical coast (Araujo 1992; Araujo & Pereira 2004; Lubke 2004).

Sampling was conducted in the open scrub vegetation of the rear dunes where isolated adult trees occur, allowing us to test their effect on other plants. All sampling was carried out on the portions of the ridges facing the sea and not flooded by the water table.

3.3.2 Sampling design

In September 2008, 100 isolated adult trees of similar height and canopy size were randomly selected along the open scrub vegetation (70 to 270 m from the seashore) in an area of 30 ha (Appendix 1). We used 50 cm x 50 cm randomly placed plots to sample the understory vegetation beneath the canopy of the trees and placed a paired plot (1 m away) in the adjacent, open microsite. The small size of the plot was selected to guarantee that all understory plants recorded beneath an adult tree were under its canopy influence. In the present study, we define understory plants as the layer of vegetation shorter than the canopy of trees (specifically less than 0.5 m high), but not necessarily under trees, since this short layer may occur in treeless patches. In our site, this understory assemblage includes herbs, lianas and young shrubs and trees. To place the plot beneath

the tree, we randomly chose a direction from 0 to 359° and placed the plot between the tree trunk and the canopy projection limit. Then, we used the same direction to place the paired plot 1 m away from the canopy projection, selecting an open microsite without direct canopy influence from any adult woody plant. If this was not possible, we randomly sampled another microsite that met these criteria to place the paired plot. For each block formed by a plot under a tree and its pair in an open microsite, we recorded its distance from the seashore as well as the height, canopy size and neighbor-tree identification. In each plot, we identified all of the understory species and classified them according to one of four life forms: trees, shrubs, lianas or herbs. To avoid positive pattern associations between trees resulting from the high occurrence of young individuals originating from each isolated parent tree, we excluded all conspecifics from analysis. Additionally, to refine the results for herbs (the life form that includes most of the understory species found), we subdivided these into grasses, forbs, bromeliads and orchids.

3.3.3. Statistical analyses

If there is spatial association between trees and understory, the proportion of plots occupied by understory plants under trees and in open microsites will differ. If the distance from seashore affects the association as predicted by SGH, this difference will vary along the shore-inland gradient. To test these statistical effects for each life form, we used a general linear mixed model (GLMM). A GLMM combines the properties of two statistical frameworks, generalized linear models (which handle non-normal data by using link functions to keep the response linear) and linear mixed models (which incorporate random effects; Bolker et al. 2009). GLMM was used to describe the probability of the occurrence of understory plants (assuming a binomial error distribution with the logit link function) as function of the fixed prediction variables of the presence of a neighbor, distance from the seashore, type of life form and a random variable, the block (each pair of plots).

To evaluate the importance of each fixed effect inside each block, we compared models with and without each effect. The full model included all fixed effects, second and third order interactions, and the random effect. The comparison was done hierarchically, thus, progressively simpler models were fitted by dropping first the third order interaction, then second order interactions and finally each single effect. In all models, including the model without any fixed term (here called minimal model), the random effect was kept.

In this study, we assumed that distance from the seashore was a good surrogate for abiotic stress. To reinforce this assumption, in Appendix 2 we presented additional analyses indicating that potentially confounding variables that vary with distance from the seashore, such as canopy size and the species of the tree-neighbor individual, were insufficient to explain the effect of distance from the seashore on the occurrence of understory plants.

For statistical inferences, we employed model selection using Akaike's information criterion (AIC), a likelihood-based measure of model plausibility that penalizes more complex models, i.e., those with a greater number of parameters (Burnham & Anderson 2002). Model selection is highly recommended in GLMM inference because it allows a true concomitant comparison of multiple models in a single step and avoids the drawbacks of stepwise multiple regressions based on multiple p-values (Whittingham et al. 2006). Models were ranked using AIC, in which the best model, the one that sacrifices the least information when it is used to approximate the truth, had the lowest AIC value (Hobbs & Hilborn 2006). The differences between the AIC value of the best model and the values of each model ranked below it (ΔAIC) provide information for evaluating which models in a set are as plausible as the best model. Values of ΔAIC between 0 and 2 indicate similar support (Burnham & Anderson 2002). We used the R environment (version 2.11.1, R Development Core Team 2010, Vienna, Austria) with the lme4 package for all statistical analyses.

3.4 RESULTS

The 100 isolated adult trees sampled as neighbors had heights of 1.4 ± 0.4 m (mean $\pm$ SD) and canopy areas (assuming the canopy shape was elliptical) of 3.1 ± 2.0 m². The trees belonged to 11 species (Table 1). The understory plants sampled under or near the trees included 56 species: 34 herbs, 12 young trees, seven shrubs and three lianas.

The selected model for probability of occurrence of understory plants included all main effects as well as the interaction between the presence of a neighbor and understory plant life form and the interaction between the distance from the seashore and the understory plant life form (Table 2). The model that included these same terms as well as the second-order interaction between neighbor and distance was equally plausible (Table 2), indicating that there is no certainty about the importance of this last term.

The presence of an isolated adult tree had a strong influence on the occurrence of an understory plant. However, the associational pattern depended on the life form considered, which causes the interaction between neighbor and life form (Figure 2). For lianas and herbs, the probabilities of occurrence under an isolated adult tree were very similar to those found in treeless microsites along the entire gradient (neutral association); for shrubs, the probability of occurrence was higher in treeless areas than under trees (negative association; Figure 2). On the other hand, the occurrence of young trees was positively associated with the presence of adult tree neighbors along the entire gradient (Figure 2). In accordance with the SGH, we expected that the effect of the presence of a neighbor would change along the gradient. However, the model that included the interaction between the presence of a neighbor and distance from the seashore and the model without this term had similar support. In general, the type of spatial association between isolated adult trees and the four life forms of understory plants did not change along the gradient for any life form; for young trees, it was always positive whereas it was always negative for shrubs and neutral for lianas and herbs.

Of the 34 herb species, 19 were forbs, eight were grasses, five were bromeliads, and two were orchids. The best-competing model for occurrence of herbs was the full model, which included all of the main effects and interactions (Table 3). However, the model that excluded the third order interaction and the one that excluded the third order interaction and the interaction between the presence of a neighbor and the distance from the seashore were equally plausible to the best one (Table 3).

The subdivision of herbs into four groups revealed different responses among herbs. The spatial association between isolated adult trees and herbs depended greatly on the subgroup of herbs. Although for bromeliads and orchids the occurrence probabilities were very similar with and without a neighbor along the entire gradient (neutral association), for grasses there was evidence of a negative association (Figure 3). For forbs, the probability of occurrence was higher in treeless areas than beneath crown trees, and the strength of this negative association increased with distance from the seashore (Figure 3).

3.5 DISCUSSION

This study shows that the spatial association between isolated adult trees and understory plants clearly depends on the life form of the understory plant, which is consistent with other recent studies of plant interactions (Dullinger et al. 2007; Gómez-Aparicio 2009). The positive association expected in a harsh environment such as the dune system was found only when the understory plant was a young tree. On the other hand, grasses and forbs were negatively associated with isolated adult trees. The variation in the spatial association with the life form of the understory species may be a result of differences in stress tolerance and the competitive responses of different life forms, since the tradeoff between these traits is of great importance to the net outcome of plant interactions (Liacourt et al. 2005). Although each life form comprises a wide range of strategies linked with the tolerance-competitive tradeoff, in a general way, trees have a

higher competitive ability and are less stress-tolerant than herbs, which present a wider range of strategies (Grime 2001). High competitive ability and low tolerance to stress enable a species to minimize the costs of negative interactions and to maximize the benefits of habitat amelioration provided by neighbors (Liancourt et al. 2005). Because the most vulnerable phase in the tree life cycle is the early phase (Kitajima & Fenner 2000), the observed positive association between isolated adult trees and young trees may be explained by the well-documented nurse-plant effect (Franco & Nobel 1989). Indeed, some studies performed in dune systems have found high performance of the early stages of tree species under woody neighbors (Kellman & Kading 1992; Joy & Yong 2002).

Although the positive association between adult and young trees could be a result of plant facilitation, the same aggregation pattern could be generated by preferential dispersal. Since seed-dispersing animals generally perch in woody vegetation, the number of animal-dispersed seeds below trees is higher than in the open areas (Holl 2002; Slocum & Horvitz 2000). In the present study, the tree understory group (young trees) was composed of 12 species, all of them dispersed by animals, mainly birds (Campassi 2002). Because ten of the 11 isolated adult tree species are also dispersed mainly by birds and therefore probably provide perches for these frugivorous dispersers, the positive association between adult and young trees could result from preferential dispersal. Further experimentation is needed to understand whether the positive associational pattern observed here between isolated adults and young trees is a result of seed shadow effects, true facilitation, or both.

For most life forms considered, the distance from the seashore, a surrogate for abiotic stress did not change the associational pattern between adult trees and understory plants as predicted by the SGH. One exception was observed for forbs; their occurrence was higher farther from adult trees than under them as the distance from the seashore increases. This result is in accordance with the SGH because although there is no evidence of a shift in the outcome of interactions, there is evidence that negative interactions

between tree neighbors and forbs become more intense as the environmental stress decreases.

Why did the distance from the seashore not affect the spatial association between isolated adult trees and the other life forms? Studies on coastal sand dunes have demonstrated a gradient of stress and disturbance strongly related to distance from the sea (Wilson & Sykes 1999; Lortie & Cushman 2007; Lane et al. 2008; Carboni et al. 2011), which makes the distance from the sea a good proxy for abiotic stress. However, it is possible that the stress gradient range considered in this study was too short and insufficiently heterogeneous for abiotic conditions, preventing observations of their effect on associational pattern of most life forms. Indeed, some studies conducted on coastal dunes have found that the shift in plant associational patterns along environmental gradients varied with the spatial scale. Forey et al. (2009) did not find support for the SGH when they studied plant interactions in coastal dunes of France at a local scale, but found support to SGH when the authors extended the observation to a regional scale, where the environment differences were stronger. Similar results were found by Maltez-Mouro et al. (2010) studying plant co-occurrence patterns on yellow coastal dunes in Portugal. In the literature about plant interactions on coastal dunes, the SGH have been highlighted mainly in temperate ecosystems and there is scarce information about plant interaction in tropical and subtropical ecosystems. In tropical and subtropical coastal dunes with high precipitation indices, the sea-inland gradient might be buffered by the more favorable general conditions, making the stress gradient less marked than in temperate region. Indeed, the only previous study we know that investigate how plant interactions shift along a sea-inland gradient in a subtropical region did not support SGH either (Franks 2003). More studies in tropical and subtropical region are clearly needed in order to understand how the relation between stress and plant interaction varies among coastal dunes under different geographic climatic regimes.

The positive association observed only between isolated adult trees and young trees along the environmental gradient suggests a positive feedback relationship with potential importance for accelerating the rate of succession in this subtropical dune system. If we assume a chronosequence in dunes along the beach-to-inland gradient, we can see a change in the vegetation physiognomy through succession, with an initial predominance of herbs changing to a later predominance of woody species (forest), as observed in other dune systems (Litcher 1998; Lubke 2004). The positive feedback created by the presence of initial trees results in patches of woody species that grow in size until they coalesce to create a continuous forest canopy. This rationale also explains the pattern found in intermediate areas of the dune gradient formed by patches of woody species scattered in a matrix of white-sand herbaceous plants (Araujo 1992). This process is very similar to the nucleation process proposed by Yarranton & Morrison (1974) to explain primary succession in temperate dunes. The authors found that nucleation is initiated by a tree species, *Juniperus virginiana* L., which benefits persistent subsequent species. A similar process has been suggested for the tropical dunes of Rio de Janeiro (southeast Brazil), where the formation of vegetation islands and succession are triggered by the colonization of pioneer plants, such as the geophyte palm species *Allagoptera arenaria* (Gomes) Kuntze. and the tree species *Clusia hilariana* Schlecht (Zaluar & Scarano 2000; Scarano 2002). The role of pioneer woody species in nucleating the settlement of more woody species in open vegetation have been reported in other studies, but most of them have been conducted in secondary successional habitats, such as abandoned pastures (Vieira et al. 1994; Slocum & Horvitz 2000; Holl 2002). The positive pattern association between trees observed in this study seems to be a key to understanding the transition between herbaceous-woody physiognomies along the successional development of this subtropical dune vegetation.

In conclusion, the associational pattern between isolated adult trees and understory plants along the coastal dune gradient depends on the life form of the

understory plant. The positive association expected in a harsh environment, such as dune systems, was found only for young trees. However, an experimental approach is needed to determine whether the observed pattern results from higher seed shading under trees or if adult trees truly facilitate the youngest trees under their canopy, or if both processes are present. Regardless of the process behind the positive association between trees, the potential feedback identified in this study may be a crucial element to understanding the transition between open vegetation, dominated by light-demanding herbs, and communities where trees are the dominant life form. In this way, our study contributes to understanding the dynamics of plant communities in subtropical coastal dunes through the pattern-process approach, which has proven to be an essential method for understanding community organization (Watt 1947; Brown 1995). Moreover, the shift in the associational pattern expected by the SGH prediction also depends on the life form of the understory plant, adding one more condition for refining the effects of stress on net plant interactions.

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ELECTRONIC APPENDICES

Appendix S1. Distribution of the experimental blocks in the study area.

Appendix S2. Testing potentially confounding factors along the stress gradient.

Photo S1. Open scrub vegetation at the study site.

TABLES AND FIGURES

Table 1. Species and number of isolated adult trees in a random sample of 100 trees taken along a coastal sand dune gradient at Ilha do Cardoso State Park, Cananéia, SP, southeastern Brazil.

SPECIES	FAMILY	NUMBER OF INDIVIDUALS
<i>Myrsine parvifolia</i> A.DC.	Myrsinaceae	28
<i>Ternstroemia brasiliensis</i> Cambess.	Pentaphylacaceae	26
<i>Clusia criuva</i> Cambess.	Clusiaceae	16
<i>Guapira opposita</i> (Vell.) Reitz	Nyctaginaceae	14
<i>Erythroxylum amplifolium</i> (Mart.) O.E. Schulz	Erythroxylaceae	5
<i>Ilex theezans</i> Mart. ex Reissek	Aquifoliaceae	3
<i>Sophora tomentosa</i> L.	Fabaceae	2
<i>Ocotea pulchella</i> (Nees & Mart.) Mez	Lauraceae	2
<i>Psidium cattleianum</i> Afzel. ex Sabine	Myrtaceae	2
<i>Maytenus robusta</i> Reissek	Celastraceae	1
<i>Myrcia multiflora</i> (Lam.) DC.	Myrtaceae	1

Table 2. Model selection results for the probability of occurrence of understory plants. The models were GLMM with binomial errors and presence of understory plant as response variables; presence of a tree neighbor, distance from the seashore, understory life form and their interactions as fixed predictor variables and block as a random variable. The selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta AIC = AIC$ of each model – AIC best model.

MODELS	TERMS REMOVED	AIC	ΔAIC
Full	_____	702.8	6.0
Reduced	Neighbor : Distance : Life form	697.6	0.8
	Neighbor : Distance : Life form + Neighbor : Distance	696.8	0.0
	Neighbor : Distance : Life form + Neighbor : Life form	734.8	38.0
	Neighbor : Distance : Life form + Distance: Life form	735.6	38.8
Minimal	All fixed predictors and interactions	1071	374.2

Table 3. Model selection results for the probability of occurrence of herbs. The models were GLMM with binomial errors and presence of herb as response variables; presence of a tree neighbor, distance from the seashore, herb subgroup and their interactions as fixed predictor variables and block as random variable. The selected models ($\Delta\text{AIC} < 2$) are shaded. AIC = Akaike's Information Criterion and $\Delta\text{AIC} = \text{AIC of each model} - \text{AIC best model}$.

MODELS	VARIABLE REMOVED	AIC	ΔAIC
Full	————	882.1	0.0
Reduced	Neighbor : Distance : Subgroup	883.1	1.0
	Neighbor : Distance : Subgroup + Neighbor : Distance	882.3	0.2
	Neighbor : Distance : Subgroup + Neighbor : Subgroup	900.4	18.3
	Neighbor : Distance : Subgroup + Distance: Subgroup	983.0	100.9
Minimal	All fixed predictors and interactions	1108.0	225.9

Fig. 1. Location of the study area at Ilha do Cardoso State Park, Cananéia, São Paulo, Brazil.

Fig. 2. Observed proportions and predicted probabilities of occurrence of four life form plants under the canopy tree and adjacent open microsites with distance from the seashore. The lines represent the occurrence probabilities predicted by the selected model ($\text{logit}(y) \sim \text{neighbor} + \text{distance} + \text{life-form} + \text{neighbor}:\text{life-form} + \text{distance}:\text{life-form} + \text{block}$). Circles and triangles represent the observed proportion in five classes of distance and their respective standard errors.

Fig. 3. Observed proportions and predicted probabilities of occurrence of four herb subgroups under the canopy tree and adjacent open microsites with distance from the seashore. The lines represent the occurrence probabilities predicted by the selected model ($\text{logit}(y) \sim \text{neighbor} + \text{distance} + \text{subgroup} + \text{neighbor}:\text{subgroup} + \text{neighbor}:\text{distance} + \text{distance}:\text{subgroup} + \text{neighbor}:\text{distance}:\text{subgroup} + \text{block}$). Circles and triangles represent the observed proportion in five classes of distance and their respective standard errors.

3.8 ELECTRONIC APPENDICES

Appendix S1. Aerial photograph of the study area with the distribution of the experimental blocks represented as yellow circles.

Appendix S2. Testing potentially confounding factors along the stress gradient

In this study, we assumed that distance from the seashore was a good surrogate for abiotic stress. However, other factors beyond the abiotic stress could change with distance and affect the interaction outcome. This is the case for the canopy size and the species of the adult tree neighbors. To guarantee that these variables were insufficient to explain the effect of distance from the seashore on the occurrence of understory plants (and consequently, reinforce our assumption) we ran one model selection for each of these potentially confounding factors to test if distance is still an important factor when these variables are already included in the model. We expected that even with these factors included in the model, the addition of the distance term would improve the model, supporting our assumption that distance is a good surrogate for abiotic stress.

A) Canopy size of the neighbor

Although we selected isolated adult trees with similar canopies, because the size of vegetation increases with increasing distance from the seashore, this uniformity could be hard to maintain. To guarantee that a variation in canopy size was not enough to explain the effect of distance over occurrence of understory plants, we ran a model selection comparing the following models:

Model 1. Based on the model selected in the main analysis (model with $\Delta AIC = 0$ at Table 2 in the main text), we replaced the terms that included distance by canopy size:

Logit (p) occurrence $\sim$ neighbor + life-form + canopy + neighbor:life-form + canopy:life-form

Model 2. We added distance and the related interaction:

Logit (p) occurrence $\sim$ neighbor + life-form + canopy + neighbor:life-form + canopy:life-form + distance + distance: life-form

The model without distance from the seashore was much less plausible ($\Delta AIC=45.5$) indicating that the variation in the size of neighbor does not explain the differences in occurrence of understory plants along the distance from the seashore.

B) Neighbor species

One of the goals of this study was to test whether the occurrence of understory plants is higher under isolated adult trees than in treeless adjacent areas. In this sense, our focus was at the potential facilitative effect of the tree life form and not in the species-specific interaction between trees of different species and understory plants. However, considering that the abundance of each neighbor tree species peaks at different points along the gradient and the effect of adult tree on understory plant might vary according the neighbor species, the effect of distance could be result from shifts in the species of the neighbor trees along the gradient. To assure that a variation in the neighbor species along the gradient was not enough to explain the effect of distance over occurrence of understory plants, we ran a model selection comparing the following models:

Model 1. Based on the model selected in the main analysis (model with $\Delta AIC = 0$ at Table 2 in the main text), we replaced the terms that included distance by neighbor species:

Logit (p) occurrence $\sim$ neighbor + life-form + neighbor spp. + neighbor:life-form + neighbor spp.:life-form

Model 2. We added distance and the related interaction:

Logit (p) occurrence $\sim$ neighbor + life-form + neighbor spp. + neighbor:life-form + neighbor spp.:life-form + distance + distance:life-form

The 100 adult tree neighbors sampled in this study included 11 species. However, to have enough samples for each species, we combined species with less than 10 individuals (see Table 1 in the main text) in a single class. Therefore, the fixed factor neighbor species had 5 levels (four species plus the combined class), instead of 11.

As we found for canopy size, the model that did not include distance from the seashore was much less plausible ($\Delta AIC = 6.5$) indicating that the variation in the species of neighbor does not explain the differences in occurrence of understory plants along the distance from the seashore.

As a whole, these results indicate that variation in canopy size and species of the tree neighbor along the beach-inland gradient are not enough to explain the effect of distance from the seashore on the occurrence of understory plants found in this study. Therefore, these results support our assumption that distance from the seashore is a good surrogate for abiotic stress.

Photo S1. Open scrub vegetation at the study site.

Capítulo 4

Does extreme stress beget plant facilitation? Experimental evidences from a subtropical coastal dune

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4.1 Summary

1. The stress gradient hypothesis (SGH) postulates how the balance between plant competition and facilitation shifts along environmental gradients. The early SGH proposals predict that importance of facilitation should linearly increase with stress. However, divergent empirical tests stimulated a recent refinement of the SGH, which postulates higher facilitation under moderate stress and the decreasing role of facilitation at the most severe environment.

2. We conducted field experiments along the most severe part of a coastal dune gradient in southeast Brazil to test the effect of stress on the intensity and importance of the net interactions between two tree species. This was done by comparing the performance of distinct life stages of *Ternstroemia brasiliensis* in the presence and absence of *Guapira opposita* adults, coupled with water manipulation, along a beach-to-inland gradient.

3. At the most severe part of the coastal gradient, both interaction intensity and importance of *G. opposita* on *T. brasiliensis* were negatively related to stress.

4. However, the signal of the net interaction depends on the life stage of the target species. *G. opposita* had a decreasingly negative effect on the removal of *T. brasiliensis* seeds, while its effect on seed emergence shifted from negative to positive as stress was reduced. On the other hand, *G. opposita* facilitated survival of *T. brasiliensis* seedlings in all conditions, but the interaction intensity and importance increased as stress reduced.

5. *Synthesis.* Our results provide empirical evidences that the role of facilitation tends to wane, leading to neutral or even negative net interactions as stress reaches its maximum. These results support the predictions of the recent refinements of the SGH, at least regarding the most severe part of the environmental gradient.

Key-words: competition, growth, life stages, multistate models, ontogenetic shift, plant-plant interactions, restinga, stress gradient hypothesis, survival analysis

4.2 Introduction

The stress gradient hypothesis (SGH) is a general conceptual model that postulates how the balance between competition and facilitation among plants shifts along environmental gradients (Bertness & Callaway 1994; Brooker & Callaghan 1998; Michalet *et al.* 2006; Maestre *et al.* 2009; Holmgren & Scheffer 2010; Kikvidze *et al.* 2011). The early proposals of the SGH predict that the frequency and importance of facilitation should linearly increase with increasing environmental severity (Bertness & Callaway 1994; Brooker & Callaghan 1998). The basic idea behind this simple model is that under severe physical conditions which restrict resource acquisition, amelioration of severe stress by a neighbor may be more likely to favor performance than competition with the same neighbor is to reduce it (Callaway 2007). Several empirical tests supported the linear predictions of the early SGH (Choler *et al.* 2001; Callaway *et al.* 2002; Gómez-Aparicio *et al.* 2004; Armas *et al.* 2011). However, other studies indicate that the role of facilitation may not increase along all the gradient, but actually decrease in extreme severe environments (Maestre *et al.* 2004; de Bello *et al.* 2011), generating a hump-shaped relation. Recently the SGH has been refined in order to incorporate some of this divergence. Theoretical models have proposed that the positive impact of the interaction on the recipient species is higher under moderate stress rather than in extreme conditions (Michalet *et al.* 2006; Maestre *et al.* 2009; Holmgren & Scheffer 2010; Kikvidze *et al.* 2011). The reasoning behind this alternative pattern is that the abiotic conditions may deteriorate to the point where the neighbors are unable to ameliorate the limiting factors, leading to a neutral or even negative interaction in the extreme end of the severity gradient (Maestre *et al.* 2009). However, these recent discussions about the refinements of the stress gradient hypothesis remain mostly theoretical, due to the scarce number of field surveys at the severe end of the environmental gradient.

Besides the controversy related to the most severe end of the stress gradient, additional factors could alter the interactions outcome. First, the neighbor effect may

change along the life stages of the target species (Callaway & Walker 1997). For example, adult neighbors facilitate seedlings and juveniles but compete with larger target individuals (Miriti 2006; Armas & Pugnaire 2009). Second, the effect of neighbor is dependent on the variable used to estimate plant performance. For instance, neighbors usually facilitate the target plant survival, but have neutral or even negative effect on the target growth (Franks 2003a; Gómez-Aparicio 2009). And last but not least, SGH tests often do not clearly distinguish between intensity and importance of the interactions (Brooker *et al.* 2005). Interaction intensity refers to the change in plant performance due to interactions with neighboring plants relative to the plant's performance in the absence of neighbors. On the other hand, interaction importance is the interaction intensity relative to the overall impact of the environment (Welden & Slauson 1986; Kikvidze *et al.* 2011). Some of the last refinements of the SGH explicitly state that not just intensity, but also importance of the facilitation should be higher under moderate stress and may decrease at the most severe conditions (Michalet *et al.* 2006; Kikvidze *et al.* 2011). However, the few field studies that tested SGH predictions regarding both intensity and importance of the interactions demonstrate that they showed different patterns of variation along environmental gradients (e. g. Gaucherand *et al.* 2006; le Roux & McGeoch 2010; but see Armas *et al.* 2011).

Experiments that take into account these recent developments of the SGH are a fundamental step to improve our understanding of the relation between plant net interactions and environment severity (Brooker *et al.* 2008). In coastal dune vegetation, the natural gradient from the beach-to-inland makes these communities ideal for such experimental studies of the SGH. Because of the proximity to the ocean and the age of the soil substrate, there is a gradient of stress and disturbance from wind exposure, salt spray, sand burial, soil salinity, fertility and moisture, which decreases towards inland (Wilson & Sykes 1999; Lane *et al.* 2008), and makes the distance from the sea a good proxy for stress intensity (Lortie & Cushman 2007; Carboni *et al.* 2011). The shortest distance from the sea

in which a species occurs represents the most severe conditions along the beach-inland gradient that this species can tolerate. Therefore, the coastal dune is also an appropriate system to empirically test the controversial effect of environmental conditions on the net interactions at the most severe end of the stress gradient.

We performed a field experiment where neighbor presence and water availability were manipulated along a beach-to-inland gradient to test the effect of environmental severity on the intensity and importance of plant net interaction. We conducted the experiments on the most severe part of the coastal dune gradient where a target species occurs. We aimed to test two competing hypotheses on the relationship between environment severity and net interspecific interaction. The first, based on the early propositions of the SGH (Bertness & Callaway 1994; Brooker & Callaghan 1998), is the linear relation which predicts a monotonically decrease in the facilitation intensity and importance as stress is reduced (see linear relationship in Fig. 01). The alternative hypothesis, based on recent refinements of the SGH (Michalet *et al.* 2006; Holmgren & Scheffer 2010; Kikvidze *et al.* 2011), predicts that the facilitation intensity and importance should increase from the most severe environment and be higher under moderate stressful condition (see hump-shaped relationship in Fig. 01). To test these hypotheses, along the most severe part of the beach-to-inland gradient, we investigated: (1) interaction intensity of the potential nurse tree *Guapira opposita* on seed removal, emergence, survival and growth of the seedlings of the tree species *Ternstroemia brasiliensis*, coupled with experimentally altered resource (water); (2) the interaction importance of *G. opposita* on *T. brasiliensis* seedlings survival, coupled with experimentally altered resource (water). According to the linear proposition of the SGH, we expected that both intensity and importance of the facilitation between *G. opposita* and *T. brasiliensis* decrease with the increase in the distance from the sea and with the addition of water (lower stress). On the other hand, according to the alternative SGH proposal, we expected

that facilitation intensity and importance increase with the increase of the distance from the sea, as well as with the addition of water.

4.3 Material and methods

4.3.1 STUDY SITE AND SPECIES

The study was conducted in a coastal sand dune near Marujá, a small fishing village located on the southern shore of Ilha do Cardoso State Park, a coastal island in southeastern Brazil (25°12'S, 44°17'W). The mean annual precipitation in Ilha do Cardoso ranges from 1392 mm to 2379 mm, with almost 70% of the rain falling between November and April. The mean annual temperature ranges from 21 to 23°C, but summers are warmer (mean monthly maximum of 26.0°C in February) and winters are cooler (mean monthly minimum of 18.3°C in July).

The sand dune gradient in southeastern Brazil is formed by a mosaic of plant communities that occupy sandy plains formed by marine deposits in the late Quaternary and which lie between the sea and the Atlantic forest (see details in Lacerda *et al.* 1993). The dune system in the study area is formed by parallel beach ridges occupying an approximately 400 m strip of land between the ocean and an inland estuary. The first vegetation along the beach-to-inland gradient is a narrow strip of beach community called embryo dunes, in which creeping psammophytes, such as *Blutaparon portulacoides* (A.St.-Hil.) Mears and *Ipomea pes-caprae* Roth, grow on the shifting sands of the upper part of the beach. Behind the embryo dunes is the foredune, a slightly older and higher beach ridge dominated by the grass *Spartina ciliata* Brongn. and the legume shrub *Dalbergia ecastaphyllum* (L.) Taub.. Just shoreward of the foredune are the rear dunes, which consist of several older, slightly higher, parallel, beach ridges that are not directly affected by the beach-exchange process. Between the ridges of the rear dunes are the dune slacks, which are depressions flooded by the water table during the summer. On the ridges of the rear dunes, there is an open scrub vegetation with sparse, isolated 1-3 m treelets and shrubs,

wood thickets of various sizes and a perennial herbaceous cover on the sandy substrate. Along the ridges of the rear dunes, vegetation cover and biomass increase with increasing distance from the seashore. Finally, on the inland-most part of the beach-to-inland gradient, there is a strip of forest with a 4-6 m high canopy. Experiments were conducted in the open scrub vegetation of the rear dunes, on the portions of these ridges facing the sea and not flooded by the water table.

The two tree species chosen to test our questions were: *Guapira opposita* (Vell.) Reitz (Nyctaginaceae) as the potential benefactor and *Ternstroemia brasiliensis* Cambess. (Pentaphyllacaceae) as the potential beneficiary. We selected two tree species because a previous study on the same study area found positive spatial association between adult trees and young trees from distinct species, suggesting a widespread nurse effect among tree species (see chapter 3 in this thesis). *G. opposita* is a tree or a treelet widely distributed around Brazilian ecosystems, including Amazonia, Brazilian Savanna and Atlantic forest (Sá 2010). Fruits, produced from January to March, are primarily dispersed by birds (Campassi 2002). In the study area, *G. opposita* is found along almost all the gradient, extending from rear dunes to forest. *Guapira opposita* was chosen as the potential beneficiary because isolated individuals are relatively common along the rear dunes, the most severe part of the beach-to-inland gradient for tree species. The adults of *G. opposita* from open scrub vegetation are shorter (on average 1-2 m height) than those found in forest physiognomies, probably due to the harsh abiotic conditions. In the open scrub vegetation there is a considerable reduction on extreme temperatures and PAR during midday under *G. opposita* canopy compared to open microsites (Appendix S1), which also indicates *G. opposita* potential role as a nurse plant in this part of the coastal gradient. *Ternstroemia brasiliensis*, the potential beneficiary, is a Brazilian endemic tree relatively common on altitude forests and coastal plains (Souza & Lorenzi 2008; Sobral & Bittrich 2010). The seeds, surrounded by a red aril, are dispersed by birds (Campassi 2002). In the study area, *T. brasiliensis* also occurs from the rear dunes to the forest

physiognomy. The abundance of *T. brasiliensis* increases along the rear the dunes, with lower abundance closer to the sea. The experiments were carried out from the ridge closest to the sea where *T. brasiliensis* occurs because it probably represents the distribution end of *T. brasiliensis* along this extreme of the beach-to-inland gradient.

4.3.2 EXPERIMENTAL DESIGN

To test how environmental severity influences the effect of *G. opposita* adults on *T. brasiliensis* performance, in October 2009 we set up 90 experimental blocks in the field. Each experimental block comprised two treatments (sub-blocks): with an adult of *G. opposita* and the control, i. e. without *G. opposita* (Fig. 2). To define the experimental blocks, 90 isolated adult trees of *G. opposita* with similar height (0.87 ± 0.20 m; mean $\pm$ SD) and canopy areas (0.42 ± 0.22 m²; assuming an elliptical shape) were randomly selected along the open scrub vegetation. To place the paired control treatment, we randomly chose a direction from 0 to 359° centered on the trunk of *G. opposita* and set a control area 2 m away from the canopy edge of *G. opposita* treatment since it was an open microsite without shading influence from any adult woody plant. If the microsite that was drawn was occupied by an adult tree or presented marked differences in the soil or terrain, we randomly selected another microsite until we met the described criteria. Except for *G. opposita* adult in the neighbor treatment, all other plants in a 0.5m radius were regularly clipped in the ground level for both treatments (Fig. 2).

Assuming that the distance from the sea is a surrogate for the stress gradient, the 90 experimental blocks were placed in three different distance classes from the sea (30 blocks for each class) in order to test how stress affects the interaction between *G. opposita* and *T. brasiliensis*. To reinforce the stress-interaction question we also manipulated the availability of water, a limited resource, to test if the reduction in water stress affects the net interaction. At each sub-block we put a 2L plastic bottle tied to a wood stake and buried around 5 cm in the soil (Fig. 2). In the watering treatment, the

bottle had a 1mm hole in the bottom and it was filled with water every two weeks. As the bottle was capped, the water just went out of the bottle if the soil was dry enough for the soil water pressure to overcome the pressure inside the plastic bottle, which then gradually crumpled. This is a cheap and simple method to maintain soil humidity relatively constant (Dias 2003). In half of the experimental blocks (45 blocks being 15 in each distance from the sea), the bottles were water filled every two weeks (watering treatment) and in the other half, the bottles remained empty along the experiment (control treatment). For each treatment combination we had 15 replicates, with a total of 90 experimental blocks (15 replicates x 3 distances x 2 watering levels).

4.3.3. SEED REMOVAL AND EMERGENCE

Ripe fruits were collected from *T. brasiliensis* trees around the study site in April 2010. Viability of seeds was $80 \pm 12\%$ (mean $\pm$ SD), determined by sowing 20 seeds in each of the ten transparent germination boxes with vermiculite in a germination camera, and counting seedlings that emerged over three months. On each field experimental block, twenty *T. brasiliensis* seeds were sown (ten under *G. opposita* canopy and ten in the respective open microsite). The experimental design included 90 experimental blocks (15 replicates x 3 distances from the sea x 2 water levels) with two unreplicated subplots per block (2 neighbor levels) and 10 seeds per treatment combination, with a total of 1800 *T. brasiliensis* seeds sown into the field experiment. In order to follow the fate of each seed and not lose them due to the rain, we used transparent plastic rings with 3 cm of diameter and 5 cm height. The rings were half buried in the soil and one seed was sown per ring. We inspected the blocks every two weeks and counted the removed seeds (missing or damaged) and emerged seedlings. Inspections took place until no emergence was observed (109 days after sowing; from 08 April to 26 July, 2010). At this time, remaining seeds had probably lost their viability since *T. brasiliensis* seeds have low longevity, with germination concentrated until 60 days after sown (Pires *et al.* 2009).

In order to test how the presence of *G. opposita* and environmental severity affect the removal and emergence of *T. brasiliensis* seeds, we used a multistate model, a special case of multistate capture-recapture models that have been widely used in animal ecology and evolution (Nichols & Kendall 1995; Lebreton *et al.* 2009), but are still scarcely explored in plant ecology (but see Shefferson & Tali 2007; Breininger *et al.* 2010). Multistate models describe the temporal evolution of discrete phenomena over time (Hougaard 1999). A simple special case is survival analysis, where we can, for example, describe the temporal evolution of an organism survivorship. In this case, there is a single state (alive) and we estimate how likely it is to stay alive. Multi-state models are extensions of these models in which more than a single state is possible (Hougaard 1999). As a consequence of the multi states feature, besides the survival probability of each state (denoted as S), the transition probability between states (denoted as Ψ ; Cooch & White 2011) is also estimated. It is a useful framework for modeling processes in cases in which plant features or conditions can be characterized by discrete stages or states, as similarly used in models for population dynamics (e.g. Caswell 2001). By adopting this approach we modeled the entire set of the seed history data, in which the data reflect the state of each seed firstly sowed at each time period of observation.

To analyze the dataset as a multistate model we defined three states: seed (s), seedling (l) and seedling death (d) (Fig. 3). Hence, for each of the 1800 seeds sowed we had their state history, which is their state at each inspection (26, 40, 61, 75 and 90 days after sowing). For example, the state history for seed j can be written as $h_j = sssld$, indicating a seed that was recorded intact until 61 days, then emerged between 61 and 75 days and finally died between 75 and 90 days after sowing. The seed removal was indicated by a 0 in the state history. So, a seed removed in the third interval had the following history: $sss00$. The model has parameters for: the probability of seed permanency (S^s - which means the seed was not removed and is available to germinate), the transition from seed to seedling (ψ^{sl} - which means seed emergence), the transition

from seedling to death (ψ^{ld} – seedling death) and transitions for states that remained the same (ψ^{ss} , ψ^{ll} , ψ^{dd} ; Fig. 3). Because seedling death was considered as a state, the seedling survival parameter for the seedling state was constrained to 1 ($S^l = 1$). The same was done for the survival parameter of the state death ($S^d = 1$), an absorbing state since any transition is possible from it (Fig. 3). Multistate models usually have extra parameters related to detection probability, used to account for the failure to detect the organism when it is present (Cooch & White 2011). Due to the use of the rings to delimit the seeds position and the sessile nature of seedlings, we assumed perfect detection for the three states (detection probability=1).

This multistate modeling approach allows inference about ecological covariates that might influence survival (S) and state transition probabilities (ψ). Hence, we used logistic models with time constant to test how neighbor presence and environmental severity influence the permanency (S^s) and emergence (ψ^{sl}) of *T. brasiliensis* seeds. The full model, defined as the fully parameterized, biologically relevant model analyzed, included neighbor presence (NEI), distance from the sea (DIS) and their interaction for seed permanency (S^s), and the previous terms plus watering treatment (WA) and interaction between neighbor and watering for emergence (ψ^{sl}). So, the full model was:

$$S^s \sim \text{NEI} + \text{DIS} + \text{NEI:DIS}$$

$$\psi^{sl} \sim \text{NEI} + \text{DIS} + \text{NEI:DIS} + \text{WA} + \text{NEI:WA}$$

To make the statistical inferences about the importance of predictors affecting seed permanency (S^s) and emergence (ψ^{sl}) we employed model selection using Akaike's information criterion (AIC), a likelihood-based measure of model plausibility that penalizes more complex models, i.e., those with a greater number of parameters (Burnham & Anderson 2002). Models were ranked using AIC, in which the best model, the one that sacrifices the least information when it is used to approximate the truth, had the lowest AIC value (Hobbs & Hilborn 2006). The differences between the AIC value of the best model and the values of each model ranked below it ($\Delta\text{AIC} = \text{AIC of each model} - \text{AIC}$

of the best model) provide information for evaluating which models in a set are close competitors to the best model. Values of ΔAIC between 0 and 2 indicate similar support (Burnham & Anderson 2002). As the null model, we used a time constant model having the same states, survival and transitions parameters, but no ecological predictors. The multistate modeling was done in program MARK (White & Burnham 1999).

4.3.4 SEEDLING SURVIVAL AND GROWTH

In April 2009 *T. brasiliensis* seeds collected in the study site were sown into a mixture of 1:1 dune soil:organic compost Biomix® within plastic pots of 43 cm³ (28 mm diameter and 115 mm height) in a greenhouse located in the northeast of Ilha do Cardoso State Park. Seedlings were grown for six months in the greenhouse before being transported to the study site. During this period seedlings were watered daily, and in the last month before transportation to the study site they were kept under direct sunlight outside the greenhouse in order to acclimate.

On 10 and 11 November 2009, twenty randomly selected seedlings of *T. brasiliensis* were planted in each experimental block (ten seedlings under *G. opposita* and ten in the adjacent open area). In the following days the seedlings were watered to alleviate transplant shock. Still, 222 seedlings died in the following week and were substituted and watered as just described. Only after that the experiment started (18 November 2009). In summary, our experimental design included 90 experimental blocks (15 replicates x 3 distances from the sea x 2 water levels) with 2 unreplicated subplots per experimental block (2 neighbor levels) and 10 seedlings per sub-block, with a total of 1800 *T. brasiliensis* seedlings transplanted into the field experiment.

All seedlings were measured for initial height, diameter at ground level and leaf number. To calculate the increment in biomass during the course of the experiment, the initial dry biomass of the experimental seedlings was estimated using an allometric equation based on a subsample of 36 seedlings in which height, diameter at the ground

level, leaf, node number and dry biomass were measured. We decided to use only the aboveground biomass to make inferences about the growth of *T. brasiliensis* because, despite being careful in the removal of each seedling from the field at the end of the experiment, some fine root material was likely lost. Adopting a stepwise AIC procedure, we selected the allometric model with lower AIC. The selected equation included height (h), diameter at the ground level (d) and leaf number (l) and had a $R^2=0.59$:

Initial dry aboveground biomass of *T. brasiliensis* $\sim -0.062 + 0.037*d + 0.011*h + 0.004*l$

Seedlings survival was monitored once each two weeks until the end of the experiment on May 2011, totaling 546 days. At the end of the experiment all surviving seedlings were measured for height and then harvested for final aboveground biomass calculation. Harvested seedlings were gently washed, dried at 62°C to constant mass and weighted for aboveground biomass.

We analyzed seedling survival data with accelerated failure time (AFT) models (Hosmer *et al.* 2008). These models can accommodate censored data – that is, cases for which the exact timing of the event is unknown. This is necessary because in our experiment we had interval-censored data in which the exact time of the seedling death was between the census at which it was recorded and the prior census. Furthermore, plants still living at the end of the experiment were considered right censored; that is, the true death time is sometime after that date. Accelerated failure time models characteristically do not have symmetric errors and can use a variety of error distributions (Hosmer *et al.* 2008). We fit models using exponential, weibull, lognormal and loglogistic distribution and we used AIC to choose the best distribution.

To make statistical inferences about how environmental severity influences the effect of *G. opposita* on the survival of *T. brasiliensis* seedlings, we used stepwise AIC procedure to select the best model, as described previously. The full model included neighbor presence (*G. opposita*), distance from the sea, watering treatment, and the interactions between neighbor and distance and neighbor and watering. Besides these

fixed terms, we also included a frailty term, analogous to a random variable in mixed models, to account for the block effect. The null model included only the frailty term. We used the R environment (version 2.13.1, R development Core Team 2011) with the survival package (Therneau 2011) to do the survival analyses.

We analyzed the growth of *T. brasiliensis* seedlings with linear mixed models (LMM). Aboveground biomass increment, as well height increment, was analyzed as a function of fixed variables presence of *G. opposita*, distance from the seashore, and their interaction and a random variable, the individual seedling within neighbor treatment within the block. It was not possible to assess the effect of watering on seedlings growth because of the low number of surviving individuals under the control treatment (without extra water). For the same reason, the level 1 from the fixed variable “distance from the seashore” was also not included in this analysis. For statistical inferences, we employed model selection using Akaike’s information criterion (AIC). The analysis was done in R environment (version 2.13.1, R development Core Team 2011) with lme4 package (Bates *et al.* 2011).

4.3.5 IMPORTANCE INDEX (I_{imp})

The previous analyses were done to test how environmental severity affects the interaction intensity of *G. opposita* at distinct life stages of *T. brasiliensis*. Additionally, we estimated the importance of *G. opposita* on survival of *T. brasiliensis* seedlings using I_{imp} as an importance index (Seifan *et al.* 2010). This index scales the intensity of biotic interaction relative to the total of environmental and biotic factors that impact the plant performance. It is defined as:

$$I_{imp} = N_{imp} / |N_{imp}| + |E_{imp}|$$

$$N_{imp} = P_{+N} - P_{-N}$$

$$E_{imp} = P_{-N} - MP_{+N}$$

where N_{imp} is the contribution of the neighbor *G. opposita* to the survival of *T. brasiliensis* seedlings (i. e. interaction intensity) and E_{imp} is the environmental contribution to the survival of *T. brasiliensis*. P_{+N} is the survival of *T. brasiliensis* seedlings beneath *G. opposita* crown and P_{-N} is the survival of *T. brasiliensis* seedlings in the paired adjacent open area. MP_{+N} is the maximum value of *T. brasiliensis* survival regardless of the neighbor presence (an estimate of the optimum performance). I_{imp} has limited range $[-1,+1]$ where negative values indicate competition, positive ones indicate facilitation and 0 indicates neutral interaction (Seifan *et al.* 2010).

To test if environmental severity influences the importance of *G. opposita* on survival of *T. brasiliensis* seedlings we used beta regression models, which assumed a beta distribution for the response variable. Beta distribution is suitable for modeling our response variable I_{imp} since it is a bounded continuous variable (Ferrari & Cribari-Neto 2004). In order to be within the limits of beta distribution, I_{imp} was scaled to range between 0 and 1 to perform the analysis. The response variable, I_{imp} , was modeled as a function of the predictor variables distance from the sea and watering treatment. To make statistical inferences about how environmental severity influences the importance of *G. opposita* on *T. brasiliensis* survival we used stepwise AIC procedure to select the best model, as described previously.

4.4 Results

4.4.1 SEED REMOVAL AND EMERGENCE

From 1800 seeds of *T. brasiliensis*, 1080 (60%) were not removed and just 213 (12%) emerged. The best models selected by multistate modeling indicated that both permanency (S^s) and emergence (ψ^{sl}) of seeds were affected by neighbor presence, distance from the seashore, and their respective interaction (model 7 in Table 1). Additionally, emergence (ψ^{sl}) was also affected by watering (Table 1). The interaction between neighbor and distance suggest that, as expected by our predictions, the effect of

G. opposita on permanency and emergence of *T. brasiliensis* seeds is influenced by environmental conditions. The model that includes the same terms of the model 7 plus the interaction between neighbor presence and watering (model 3 in Table 1) was equally plausible, meaning there is uncertainty about the effect of watering on net interaction.

The proportion of *T. brasiliensis* seeds that remained beneath *G. opposita* crown was lower than in open areas, indicating that *G. opposita* increases the removal of seeds (Table 2). However, that effect was not homogeneous along the gradient, since as the distance from the seashore increased, the permanency probabilities of the seeds beneath *G. opposita* and in open areas became similar (Table 2). These results indicate that the impact of *G. opposita* on permanency of the *T. brasiliensis* seeds shifts from negative to neutral as the distance from the sea increases.

Similarly, distance from the seashore influenced the effect of *G. opposita* on *T. brasiliensis* emergence. Near the sea and at an intermediate distance (distances 1 and 2), the proportion of emerged *T. brasiliensis* seeds was higher in open areas than beneath *G. opposita* crown (Fig. 4). At distance 3, however, the opposite was observed (Fig. 4). Therefore, these results indicate that the effect of *G. opposita* on *T. brasiliensis* emergence shifts from negative to positive as the distance from the seashore increases.

In summary, the interaction intensity of *G. opposita* on *T. brasiliensis* seeds was predominantly negative, but tends to be neutral or even positive as environmental severity decreased.

4.4.2 SEEDLING SURVIVAL AND GROWTH

From 1800 transplanted, only 74 seedlings (4%) survived after 546 days of experiment (Fig. 5). The survival data of *T. brasiliensis* seedlings were best fit by accelerated failure time models with log-logistic distribution (see Table S1). The model selected for *T. brasiliensis* seedlings survival includes the effect of neighbor, distance from the seashore, watering, and the interactions between neighbor and distance and neighbor and watering

(model 1 in Table 3). The interaction terms mean that environmental severity altered the effect of *G. opposita* on survival *T. brasiliensis* seedlings. However, the model that included the same terms, with the exception of the interaction between neighbor and watering (model 2 in Table 3), was equally plausible, meaning there is an uncertainty about the effect of the watering on the net interaction.

The odds of survival of *T. brasiliensis* seedlings beneath *G. opposita* were two to seven times higher than that for seedlings in open adjacent areas (Table 4), indicating facilitation along the entire gradient studied and in both watering treatments. However, the intensity of the positive interaction increases with the distance from the seashore and with the addition of water (Table 4).

The model selection for increment in aboveground biomass showed an uncertainty about the effect of the neighbor and distance since the models that include these terms (models 2 and 3 in Table 5) were equally as plausible as the null model (model 4 in Table 5). The only term that did not improve the model and, as a consequence, was considered not important was the interaction between neighbor and distance (Table 5), meaning that distance from the seashore definitively did not affect the effect of *G. opposita* on biomass increment of the *T. brasiliensis* seedlings.

Regarding height increment, we also found uncertainty about the effect of predictor variables. The model that includes neighbor, distance and their respective interaction was equally as plausible as models that include only distance and neighbor or only distance (models 1, 2 and 4 in Table 6). It means that there is neither any certainty about the effect of *G. opposita* on height increment of seedlings nor about the effect of distance on the interaction.

As a whole, these results indicate that the effect of *G. opposita* on *T. brasiliensis* seedlings depends on the performance parameters considered. There are evidences that *G. opposita* facilitates seedlings survival along the environmental gradient, as well as that the

intensity of the facilitation is negatively related to environmental severity. On the other hand, there is no evidence that *G. opposita* affected the growth of *T. brasiliensis* seedlings.

4.4.3 IMPORTANCE INDEX (I_{imp})

The importance of *G. opposita* facilitation on survival of *T. brasiliensis* seedlings increases with distance from the sea and water addition (Table 7; Fig. 6). At the nearest distance from the sea and without extra water (higher stress condition in the experiment), the importance of the interaction of *G. opposita* on survival of *T. brasiliensis* seedlings was zero (Fig. 6). On the other hand, at the greatest distance from the sea and with water (the less stressful condition) facilitation reached the highest importance observed in the experiment (Fig. 6). These results indicate a negative relation between interaction importance and environmental severity in this extreme part of the coastal dune gradient.

4.5 Discussion

4.5.1 STRESS GRADIENT HYPOTHESIS

Our results showed that the removal of *T. brasiliensis* seeds was higher beneath *G. opposita* canopy, but this negative effect decreased as stress was reduced. Regarding *T. brasiliensis* emergence, the effect of *G. opposita* shifts from negative to positive as stress was reduced. On the other hand, the net effect of *G. opposita* on survival of *T. brasiliensis* seedlings was always positive, but increases in intensity and importance as stress decreased. In summary, these results indicate that besides the variation on the interaction signal depending on the life stage of the target species, at the most severe part of the coastal dune gradient, both intensity and importance of *G. opposita* on *T. brasiliensis* were negatively related to environmental severity (Fig. 7). These results do not support the monotonic increase in the severity-interaction relationship predicted by the early propositions of the SGH (Bertness & Callaway 1994; Brooker & Callaghan 1998). In contrast, our results are consistent with recent SGH refinements, which predict that under

high abiotic severity the intensity and/or importance of positive effects may wane, reaching a neutral or even negative net interaction (Michalet *et al.* 2006; Maestre *et al.* 2009; Homlgren & Scheffer 2010; Kikvidze *et al.* 2011). Our experiments were conducted at the most severe part of the beach-to-inland gradient and did not consider the entire range of the coastal gradient. Therefore, we cannot guarantee that the whole extension of the gradient range would still support the refined SGH hypothesis (hump-shaped relation). However, regarding only the most severe part of the stress gradient, where early and refined SGH propositions diverge, our results reject the early SGH proposition and support the refined one. Accordingly, we found that, as stress reaches its highest levels, the net interaction tends to decrease, being more negative or less positive depending on the life-stage of the target species.

Empirical studies conducted in very severe environments found evidences that facilitation does not increase constantly with stress. Some studies found that at the extreme end of the gradient the intensity of positive net interaction reaches an asymptote (Kawai & Tokeshi 2007; le Roux & McGeoch 2010), or may wane, reaching a neutral (Kitzberger *et al.* 2000; Forey *et al.* 2010) or even negative net interaction (Maestre & Cortina 2004). Some authors have proposed that the decrease in the net interaction occurs probably because facilitators are less successful in ameliorating stress levels under very severe conditions, while competition for resources may equally decrease, be constant or even increase with stress (Michalet *et al.* 2006; Maestre *et al.* 2004; Maestre *et al.* 2009). Although we have observed that net interaction was negatively related to environmental severity, the difference in the signal of the interaction depending on the life stage of the target species probably indicates that distinct interaction mechanisms are operating during the *T. brasiliensis* establishment.

4.5.2 LIFE STAGE AND INTERACTION SIGNAL

Plants experience distinct resource requirements and tolerance to abiotic conditions along their ontogenetic development (Schupp 1995), possibly resulting in different responses for neighbor presence depending on life stage. Indeed, studies have shown ontogenetic shift in net interaction, especially from facilitative effects on early stages to competitive effects on the adults (Miriti 2006; Armas & Pugnaire 2009). Little is known, however, about ontogenetic shift in net interaction during the early phase of plant life. Here we found a negative effect of *G. opposita* on *T. brasiliensis* post-dispersal seed stage and also a partially negative effect on its emergence, contrasting with positive effects on seedling survival. It may happen because the interaction mechanism behind the net interaction during one stage is not effective in the next stage of the target species life. Consequently, in order to understand the distinct effect of the neighbor presence during the different life stages, we need to better understand the mechanisms driving the interaction.

Seed removal of *T. brasiliensis* was higher under *G. opposita* than in open adjacent areas, but this effect waned as stress decreased. While the fate of seeds that disappeared was uncertain, we assumed that most missing seeds were predated because we found damaged seeds around many rings with missing seeds. An alternative fate for the missing seeds could be the removal by secondary dispersers, such as ant species found in the dune forest near the study site (Passos & Oliveira 2003). However, considering that the ants are interested in the seed aril that was washed by the rain in the first week of the experiment, we do not believe this potential mutualistic interaction was important to explain the fate of the missing seeds. The higher seed removal under *G. opposita* canopy may be explained by the foraging behavior of granivorous animals. In contrast to secondary disperser ants, rodents forage mostly beneath trees and shrubs and avoid open areas where they are more susceptible to predators (Hulme 1997). Granivorous insects may also prefer to forage under canopies because of the milder microclimatic conditions, such as lower soil temperature. Indeed, Smit *et al.* (2006) found, in a wood pasture, higher seed removal

under shrubs than in open areas, mostly due to insects. But why did the effect of *G. opposita* on *T. brasiliensis* seed removal wane as stress decreased? As the distance from the sea increases, there is an increase in the biomass and cover of the vegetation. It is possible that the importance of *G. opposita* as a potential safe foraging site for granivorous become smaller as new favorable microhabitats appear with the increase in the vegetation cover.

Regarding *T. brasiliensis* emergence, our results demonstrated contrasting effects of environmental stress on the effect of *G. opposita* on the target species. Watering enhanced the seeds emergence, indicating that it is a limiting resource for seed germination. However, there is uncertainty if the change in environmental severity brought by watering change the effect of *G. opposita* on *T. brasiliensis* emergence. On the other hand, the net interaction changed from negative to positive as stress decreased along the coastal gradient. One of the most known positive effects of neighboring plants in stressful environments is the amelioration of microclimatic conditions, including soil moisture improvement (Callaway 2007). Therefore, it would be expected that higher soil moisture under *G. opposita* should increase the emergence of *T. brasiliensis* seeds. Indeed, studies conducted in coastal dunes have found higher seed emergence under vegetation than in open areas (Franks 2003b; Rudgers & Maron 2003). In contrast, we found negative effect of *G. opposita* on *T. brasiliensis* emergence in the two most severe points in the gradient. This unexpected negative effect can not be explained by the reduced light availability under *G. opposita* canopy because *T. brasiliensis* presents neutral photoblastic behavior (Pires *et al.* 2009). Allelopathic effects have been reported to decrease seed viability and germination under neighbor canopy (Herranz *et al.* 2006; Cavieres *et al.* 2007). However, even if an allelopathic effect of *G. opposita* was the mechanism behind the negative effect observed in the most severe part of this coastal gradient, there is no clear reason to expect a shift in net interaction as stress decreased. In order to explain the higher removal rates of *T. brasiliensis* seeds beneath *G. opposita* we hypothesized that the

milder conditions beneath *G. opposita* may favor granivorous insects. A similar process could mediate the reduced *T. brasiliensis* emergence beneath *G. opposita*. It is possible that the milder microclimatic conditions beneath *G. opposita* favored microorganisms, which in turn attacked the seeds, although keeping them visually intact. As the distance from the sea increases, the increase in vegetation cover may reduce the importance of *G. opposita* as safe sites for microorganisms, leading to a decrease in its negative effect.

Contrasting to the predominantly negative effect of *G. opposita* on *T. brasiliensis* seeds, the net effect of *G. opposita* on survival of seedlings was always facilitative. Furthermore, the intensity of this positive effect increased with watering and also with distance from the sea, suggesting that facilitation intensity increases with the reduction of environmental severity, at least in this part of the gradient. In coastal dunes, wood plants can facilitate their neighbors through several mechanisms, such as microclimate amelioration provided by shade (Kellman & Kading 1992; Shumway 2000; Joy & Young 2002), enrichment of soil nutrients (Shumway 2000; Cushman *et al.* 2010) and reduction in wind and sand movement (Martínez 2003). Indeed, several studies conducted on coastal dunes have found higher seedlings survival under wood neighbors (Kellman & Kading 1992; Shumway 2000; Joy & Young 2002; Martínez 2003; Rudgers & Maron 2003; Cushman *et al.* 2010). The lower soil temperature under *G. opposita* canopy (Appendix S1) indicated that microclimate amelioration is a potential mechanism behind the positive effect on seedlings survival. Regardless of the mechanism behind the positive effects observed, why did facilitation tend to decrease as stress became extreme? The collapse of positive interactions at the severe end of the gradient may occur because under these extreme conditions the neighbor amelioration does not reach the minimum conditions that allow the maintenance of fundamental physiological processes of the target species (Malkinson & Tielborger 2010). In a study also conducted in a coastal gradient, vegetation had no effect on survival and growth of their neighbors at the severe end of the environmental gradient, indicating a collapse of biotic interactions when stress reached its

maximum (Forey *et al.* 2010). Although we still detected facilitation at the most severe part of gradient, the observed decrease in facilitation intensity with stress agrees with theoretical propositions and empirical tests that positive interactions tend to collapse under extreme severe conditions.

4.5.3 PERFORMANCE ESTIMATOR AND NET INTERACTION

Besides the variation in net interaction depending on the life stage, we also found that net interaction varies according to the variable used to estimate performance of the target species. The effect of *G. opposita* was positive on the survival of *T. brasiliensis* seedlings, but neutral for seedlings growth. This pattern could be, at least in part, due to the differences in growth and survival requirements (Hastwell & Facelli 2003; Maestre *et al.* 2005). Neighbor presence can alter one condition or resource that is fundamental for survival but not growth. Similar patterns of positive interactions on survival and neutral to negative interactions on growth have been reported in other studies (Foster 2002; Franks 2003a; Gómez-Aparicio 2009). Franks (2003a) attributes the distinct patterns of net interaction for survival and growth to a distinct interaction mechanism: neighbors protect the target species ameliorating the harsh microclimatic conditions that were a source of mortality, but compete for soil resource, reducing biomass.

4.5.4 INTERACTION INTENSITY AND IMPORTANCE

Experimental tests of the SGH have predominantly focused on interaction intensity, while interaction importance has seldom been considered (Kikvidze *et al.* 2011). Our results indicated that, as it was observed for interaction intensity, at the extreme part of coastal dune gradient, importance of facilitation of seedlings survival decreased as conditions became more severe. It happens because at the same time that the negative effect of the environmental increases, the intensity of *G. opposita* effect on survival of *T. brasiliensis* seedlings decreases, resulting in a reduction of facilitation importance. Hence, at the

severe part of the gradient the environmental conditions are so limiting for the plant performance that the positive effect of neighbor is not relevant. This result supports the theoretical prediction that importance of facilitative interaction will peak at moderate stress and wane under extremely stressful conditions (Michalet *et al.* 2006; Kikvidze *et al.* 2011). However, experimental studies have found contrasting results. Instead of facilitation, some studies found that the importance of competition decreased as stress became higher (Brooker *et al.* 2005; Gaucherand *et al.* 2006). The part of the stress gradient where the studies were conducted could explain the contrasting results. While our study considered the extreme severe part of the coastal gradient where *T. brasiliensis* occurs, the other studies possibly not considered the extreme end in the severity gradient of the target species distribution. In a study conducted along an entire altitudinal gradient of a mountain for vascular plants occurrence, le Roux & McGeoch (2010) found evidences, through spatial association pattern, that the importance of interaction between the cushion plant *Azorella selago* and the grass *Agrostis magellanica* was weakly related to altitude. Only for one performance measurement (canopy cover), was the importance of *Azorella* on *Agrostis* more positive on mild altitudes (le Roux & McGeoch 2010), which also agrees with the recent theoretical propositions (Michalet *et al.* 2006; Kikvidze *et al.* 2011). Therefore, the distinct relations between interaction importance and environmental severity found in the empirical studies (including the present study) might be due to the part and the range of the stress gradient considered, as well as the performance estimator of the target plant.

4.5.5 CONCLUDING REMARKS

We have shown complex net effects of *G. opposita* on the establishment of *T. brasiliensis* at the most severe part of a subtropical coastal gradient. While the plant-plant interaction literature has plenty of examples of facilitation of the adult woody species on seedlings (nurse effect), we showed that even during early phases of the establishment of the target

species the effect of neighbor shift from negative to positive depending on the life stage of the target plant. In spite of this, at the most severe part of the coastal dune gradient, both intensity and importance of *G. opposita* on *T. brasiliensis* were negatively related to environmental severity (Fig. 7). This striking result brings empirical evidences to the recent theoretical propositions of the SGH at the extreme end of the severity gradient. Future studies should attempt to clarify the mechanisms behind the net interactions to provide a deeper understanding of the processes governing the relation between net interactions and environment severity.

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Supporting Information

Appendix S1. The effect of *Guapira opposita* adults on abiotic parameters.

Table S1. Model selection comparing different error distributions of accelerated failure time models.

TABLES AND FIGURES

Table 1. Model selection results for the probability of seed permanency (S^s) and seed emergence (ψ^s) of *T. brasiliensis*. The models were multistate models with presence of *G. opposita* neighbor (NE), distance from the seashore (D2 e D3), watering treatment (WA), and their interactions as fixed predictors. The selected models ($\Delta AIC < 2$) are bolded. K= number of parameters; AIC = Akaike's Information Criterion and ΔAIC = AIC of each model – AIC best model.

Model	Seed permanency	Emergence	k	AICc	$\Delta AICc$
1	NE+D2+D3+NE:D2+NE:D3	NE+D2+D3+WA+NE:D2+NE:D3+NE:WA	15	6373.3	3.8
2	NE+D2+D3+NE:D2	NE+D2+D3+WA+NE:D2+NE:D3+NE:WA	14	6380.0	10.5
3	NE+D2+D3+NE:D3	NE+D2+D3+WA+NE:D2+NE:D3+NE:WA	14	6371.5	2.0
4	NE+D2+D3+NE:D2+NE:D3	NE+D2+D3+WA+NE:D2+NE:D3	14	6371.3	1.8
5	NE+D2+D3+NE:D2+NE:D3	NE+D2+D3+WA+NE:D2+NE:WA	14	6380.6	11.1
6	NE+D2+D3+NE:D2+NE:D3	NE+D2+D3+WA+NE:D3+NE:WA	14	6375.5	6.0
7	NE+D2+D3+NE:D3	NE+D2+D3+WA+NE:D2+NE:D3	13	6369.5	0.0
8	NE+D3+NE:D3	NE+D2+D3+WA+NE:D2+NE:D3	12	6378.9	9.4
9	NE+D2+D3+NE:D3	NE+D2+D+NE:D2+NE:D3	12	6383.4	13.9

Table 2. Estimates (mean and SE) of the monthly permanency (S^s) of *T. brasiliensis* seeds (i.e. the proportion of seeds not removed) under *G. opposita* and in the adjacent open microsites at three distances from the seashore, monitored from May to July 2010. The estimates are calculated from the selected model that includes effects of distance from seashore, presence of neighbor, and their interaction (model 7 in Table 2).

Distance from the seashore	Open	Under <i>G. opposita</i>
1	0.85 $\pm$ 0.01	0.73 $\pm$ 0.02
2	0.89 $\pm$ 0.01	0.80 $\pm$ 0.01
3	0.83 $\pm$ 0.01	0.82 $\pm$ 0.01

Table 3. Model selection results for the seedlings survival time. The models were accelerated failure time (AFT) models with log-logistic as error distribution. The fixed predictor variables were presence of *G. opposita* neighbor (NE), distance from the seashore (DI), watering (WA), and their interactions. All models, including the null model, include the block as a frailty term (random effect) with normal distribution. The selected models ($\Delta AIC < 2$) are bolded. K= number of parameters; AIC = Akaike's Information Criterion and ΔAIC = AIC of each model – AIC best model.

Model	Fixed terms included	k	AIC	ΔAIC
1	NE+DI+WA+NE:DI+NE:WA	85	7217.4	0.0
2	NE+DI+WA+NE:DI	84	7218.6	1.2
3	NE+DI+WA+NE:WA	83	7237.5	20.1
4	NE+DI+NE:DI	84	7220.3	2.9
5	-----	80	7498.9	281.5

Table 4. Odds ratio of the survival of *T. brasiliensis* seedlings beneath *G. opposita* crown relative to adjacent open microsites based on the selected model that includes effects of presence of neighbor, distance from seashore, watering treatment, interaction between neighbor and distance, and interaction between neighbor water (model 1 in Table 3).

	Distance from the seashore		
Watering treatment	1	2	3
Control	2.0	4.0	5.1
Water	2.7	5.5	6.9

Table 5. Model selection results for the increment in aboveground biomass of seedlings. The models were linear mixed models (LMM) with presence of a *G. opposita* neighbor (NE) and distance from the seashore (DI) as fixed predictor variables, and the individual seedling within neighbor treatment within the block as a random variable. The selected models ($\Delta AIC < 2$) are bolded. K= number of parameters; AIC = Akaike's Information Criterion and ΔAIC = AIC of each model – AIC best model.

Model	Terms included	k	AIC	ΔAIC
1	NE+DI+NE:DI	8	13.5	3.0
2	NE+DI	7	12.3	1.8
3	NE	6	11.7	1.2
4	-----	5	10.5	0.0

Table 6. Model selection results for the increment in seedlings height. The models were linear mixed models (LMM) with presence of a *G. opposita* neighbor (NE) and distance from the seashore (DI) as fixed predictor variables, and the individual seedling within neighbor treatment within the block as a random variable. The selected models ($\Delta AIC < 2$) are bolded. K= number of parameters; AIC = Akaike's Information Criterion and $\Delta AIC =$ AIC of each model – AIC best model.

Model	Terms included	k	AIC	ΔAIC
1	NE+DI+NE:DI	8	199.2	1.9
2	NE+DI	7	197.9	0.6
3	NE	6	200.9	3.6
4	DI	6	197.3	0.0
5	-----	5	199.8	2.4

Table 7. Model selection results for the importance index (I_{imp}) of the interaction of *G. opposita* on survival of *T. brasiliensis* seedlings after 546 days from transplantation. The models were beta regression models with distance from the seashore (DI) and watering treatment (WA) as fixed predictor variables. The selected models ($\Delta AIC < 2$) are bolded. K= number of parameters; AIC = Akaike's Information Criterion and ΔAIC = AIC of each model – AIC best model.

Model	Terms included	k	AIC	ΔAIC
1	DI+WA	5	-239.5	0.0
2	DI	3	-235.6	3.9
3	WA	4	-236.1	3.4
5	-----	2	-232.6	6.9

Fig. 1. Alternative hypothetical relationships between environmental severity and the net result from interspecific interactions. The linear relation is based on early propositions of the stress gradient hypothesis (SGH; Bertness & Callaway 1994; Brooker & Callaghan 1998) and assumes that even at the most severe part of environmental gradient facilitation should increase linearly with stress. The hump-shaped relation is based on the most recent refinements of the SGH (Michalet *et al.* 2006; Holmgren & Scheffer 2010; Kikvidze *et al.* 2011) and states that facilitation is higher under moderate stress, and that at the most severe part of environmental gradient facilitation should wane, leading to a neutral or negative net interaction. In order to confront the two hypotheses, it is necessary to investigate the extreme severe part of environmental gradients, as done in the present study.

Fig. 2. Field experiment setting at coastal dune vegetation, São Paulo, Brazil. In our field experiment we tested the effect of neighbor presence (with *Guapira opposita* adult and without *G. opposita*), distance from the seashore (distances 1, 2 and 3) and availability of water (with additional water and control) on *Ternstroemia brasiliensis* performance. The photograph shows an experimental block composed by two levels of neighbor treatment: with *G. opposita* tree (bottom left) and without *G. opposita* (bottom right). In both neighbor treatments, all other plants in a 0.5 m radius were regularly clipped. In both neighbor treatments it is also possible to see the plastic bottles used to manipulate water availability. The experimental block depicted was at distance 1, the closest distance to the sea (which can be seen in the upper part of the photograph). Photo: Alexandre A. Oliveira.

Fig. 3. Outline of the multistate model adopted to model seed removal and emergence at the experimental blocks in the coastal dune vegetation. The superscripts at seed survival (S) and transition probabilities (ψ) refer to seed, seedling and death states denoted as, respectively, s, l and d. Seed survival (S^s) and emergence (ψ^{sl} ; depicted by heavy solid line) had adequate sample sizes for modeling as a function of neighbor presence and environmental severity. The seedlings death (ψ^{ld} ; depicted by thin solid line) had few occurrences and was not modeled with predictors. Transition probabilities for states that remained the same were estimated by subtraction. For the three states, detection probabilities were constrained to 1, as well as the seedling and dead states survival probability (i.e. $S^l = 1$, $S^d = 1$).

Fig. 4. Estimates proportion (mean and SE) of the monthly emergence (ψ^{sl}) of *T. brasiliensis* beneath *G. opposita* crown and in the adjacent open areas along three distances from the seashore and watering treatment. The experiment was monitored from May to July 2010. The estimates are based on the selected model, which includes neighbor presence, distance from the sea, watering treatment, and the interaction between neighbor and distance (model 7 in Table 1).

Fig. 5. Observed survival of *Ternstroemia brasiliensis* seedlings transplanted under combination of neighboring treatment (beneath *G. opposita* crown and open microsites) and watering treatment (water and control). Transplantation was on 10-11 November 2009.

Fig. 6. Mean and SE of the importance index (I_{imp}) of the interaction of *G. opposita* on survival of *T. brasiliensis* seedlings after 546 days from transplantation. I_{imp} has limited range $[-1,+1]$, where negative values indicate competition, positive ones indicate facilitation and 0 indicates neutral net interaction (Seifan *et al.* 2010).

Fig. 7. Eschematic representation of the interaction intensity of *G. opposita* adults on distinct life stages of *T. brasiliensis*. Regardless of the life stage, the interaction intensity is negatively related to environmental severity. However, the interaction signal is dependent on the life stage of the target species: (a) *G. opposita* increased the removal of *T. brasiliensis* seeds, but this negative effect on seed permanency waned as stress decreased; (b) The effect of *G. opposita* on *T. brasiliensis* emergence shifted from negative to positive as stress decreased, and (c) The positive effect of *G. opposita* on survival of *T. brasiliensis* seedlings became more intense as stress decreased.

4.8 Supporting Information

Appendix S1. The effect of *Guapira opposita* adults on abiotic parameters

To test if *G. opposita* alters abiotic parameters that might be important for plant performance, we measured temperature and photosynthetically active radiation (PAR) under *G. opposita* canopy and in the adjacent open areas in 18 experimental blocks chosen at random from the 90 experimental blocks (see details in the experimental design subsection in material and methods). Surface soil temperature was taken using a UNI-T UT301C infrared thermometer gun and PAR was taken using a Spectrum Technologies 3415FSE solar quantum meter. Under each *G. opposita* canopy and respective open microsite, three subsamples were randomly taken and then averaged prior to analysis (to compensate for heterogeneity found especially under *G. opposita* canopy). The measurements were collected around noon during a sunny summer day in February 2010.

To test the effect of *G. opposita* on abiotic parameters we used linear mixed models (LMM). These models allowed us to describe soil temperature and PAR as a function of the fixed predictor presence of *G. opposita* and a random variable, the block. To evaluate the effect of *G. opposita* on abiotic parameters we compared models with and without this fixed predictor. For statistical inferences, we used likelihood framework and AIC to rank the competing models (see details of model selection in material and methods). We used the R environment (version 2.13.1, R development Core Team 2011) with lme4 package (Bates *et al.* 2011) for the statistical analyses described.

The selected model for both soil temperature and photosynthetic active radiation (PAR) included the presence of a *G. opposita* neighbor (Table 1 and Table 2), which means that both abiotic parameters differed beneath *G. opposita* crown and in the adjacent open areas during noon on a summer day. Soil temperature was, on average, 56°C in open areas and 37°C beneath *G. opposita*. The observed difference of the 19±5°C (mean ± sd) means a

reduction around 34% in soil temperature around noon on a summer day. The PAR beneath *G. opposita* was 158 ± 30 micromoles $\text{m}^{-2}\text{s}^{-1}$ (mean $\pm$ sd), while in the open areas it was at least 2000 micromoles $\text{m}^{-2}\text{s}^{-1}$ (it reached the upper limit measured by the instrument).

Table 1. Model selection results for the effect of *Guapira opposita* adults on soil temperature. The models were gaussian linear mixed models (LMM) with temperature as response variables; presence of a *G. opposita* neighbor as fixed predictor variables and block as a random variable. The selected models ($\Delta AIC < 2$) are bolded. K= number of parameters; AIC = Akaike's Information Criterion and ΔAIC = AIC of each model – AIC best model.

Model	Terms included	k	AIC	ΔAIC
1	Neighbor	4	205.4	0.0
2	-----	3	273.1	67.3

Table 2. Model selection results for the effect of *Guapira opposita* adults on photosynthetic active radiation (PAR). The models were gaussian linear mixed models (LMM) with PAR as response variables; presence of a *G. opposita* neighbor as fixed predictor variables, and block as a random variable. The selected models ($\Delta AIC < 2$) are bolded. K= number of parameters; AIC = Akaike's Information Criterion and ΔAIC = AIC of each model – AIC best model.

Model	Terms included	k	AIC	ΔAIC
1	neighbor	4	317.3	0.0
2	-----	3	587.7	270.4

Table S1. Model selection comparing different error distributions. The models are accelerated failure time (AFT) models with seedlings survival time of *T. brasiliensis* as response variable.

Error distribution	K	AIC	Δ AICc
Exponential	1	9192.5	1228.9
Weibull	2	9194.0	1230.4
Log-normal	2	8234.8	271.2
Log-logistic	2	7963.6	0.0

Capítulo 5

Nurse plant effect is driven by shade in a subtropical coastal dune: implications for restoration practices

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5.1 Abstract

The proximity of adult neighbors often increases the performance of wood seedlings under harsh environmental conditions. However, few studies have elucidated the mechanisms underlying this nurse effect. We tested if shading drove the known nurse effect of adults of the tree *Guapira opposita* on seedling performance of another tree species, *Ternstroemia brasiliensis*. Additionally, we tested if the potential shade-driven facilitation became more intense as stress increased. Assuming that distance from the seashore is a surrogate for stress intensity, at three distinct distances from the seashore, we transplanted *T. brasiliensis* seedlings to three neighbor treatments: under *G. opposita* crown, under artificial shade, and control treatment with no neighbor. Regardless of distance from the seashore, after a year, the odds of *T. brasiliensis* seedlings survival was twice under *G. opposita* and artificial shade than in the control, indicating that the nurse effect of *G. opposita* is, at least partially, driven by shade. However, neighbor treatment did not affect seedlings growth. Overall, this study highlights the potential of nurse plants and artificial shade as techniques to help the establishment of woody seedlings transplanted to restore degraded coastal dunes.

Key-words: alternative states, artificial shade, facilitation, facilitation mechanism, nurse-plants, plant interactions, positive interaction, restinga.

5.2 Introduction

Facilitation and competition occur simultaneously among plants growing close to each other (Holzapfel & Mahall 1999; Maestre et al. 2003). The net balance between these effects determines the signal and the intensity of the plant-plant interaction. Theoretical and empirical studies have shown that the interaction balance is affected by environmental conditions, and the importance and intensity of facilitation increases as the conditions become more severe, a proposition known as stress gradient hypothesis (Bertness & Callaway 1994; Callaway et al. 2002; Gómez-Aparicio et al. 2004; Armas et al. 2011). A common example of facilitative interaction, especially found under severe conditions, is the nurse plant effect, in which adult plants improve the performance of young individuals of the same species or others that grow in their vicinity (Flores & Jurado 2003, Gómez-Aparicio et al. 2004). Some of the potential mechanisms behind the nurse plant effect are amelioration of the microclimatic conditions, increase in nutrient and soil moisture and protection from herbivores (Flores & Jurado 2003; Smit et al. 2006; Gómez-Aparicio et al. 2008).

Since the last decade, there has been an increasing interest on facilitation as a relevant ecological concept applied to restoration of degraded environments (Padilla & Pugnaire 2006; King & Stanton 2008; Gómez-Aparicio 2009; Markham et al. 2011). Although an increasing number of studies have identified nurse plant effects, relatively few of them (Maestre et al. 2003; Weedon & Facelli 2008) have assessed the mechanism behind facilitative interactions. This knowledge is important to select appropriate facilitator species or even to manage the environment to emulate the beneficial effects of nurse plants (Rey Benayas et al. 2005; Badano et al. 2011) when they are not easily available. Hence, to refine the use of facilitation on restoration programs it is necessary to increase the mechanistic understanding of the facilitation process, which is relevant, especially under stressful conditions.

Coastal dunes are recognized as harsh environments where stress and disturbance decrease towards inland, producing a clear environmental gradient (Wilson & Sykes 1999; Lane et al. 2008). In spite of the natural occurrence of stress and disturbance, coastal dunes are considered systems with low resilience because a slight disruption in the disturbance regime (either natural or human-induced) might lead to change and long-term progressive alteration, and their diversity might be affected rather easily (Martínez et al. 2004). Besides their low resilience, coastal dunes have a long history of human exploitation and mismanagement, resulting in an intense net loss of worldwide coastal dune vegetation (Martínez et al. 2004). Their high threat level coupled with their low resilience makes the development of efficient techniques to recover degraded areas of coastal dune vegetation extremely important.

A challenge for restorative plans is that feedbacks between abiotic and biotic factors can make the degraded system resilient to restorative change (Bakker & Barendse 1999). Alternative state models, which emphasize internally reinforced states and recovery thresholds, can provide a constructive framework to guide restoration efforts (Suding et al. 2004). The value of this approach is that it recognizes that the dynamics of a degraded state are different from those in the pristine state and that both, degraded and pristine, represent alternative combinations of environmental conditions that may persist in space and time stabilized by internal feedbacks (Suding et al. 2004). In this context, the restoration goal is to disrupt the internal feedback that constraints restoration of degraded state to induce the transition to the desired state. Several studies conducted on coastal dunes have shown that initial colonizers can act as nurse plants of the wood species (Shumway 2000, Joy & Young 2002, Franks 2003, Martínez 2003), indicating that facilitation has an important role during the primary succession and transition from herbaceous to woody vegetation state. If the restoration goal is to restore a coastal shrubland or forest, then nurse plants have the potential to be used on restoration plans to trigger the transition between degraded and recovery states.

In Brazilian coastal dunes (locally called restinga vegetation), facilitation has been proposed as a key ecological process (Scarano 2002) and recent studies demonstrated nurse plant effects in this vegetation (Correia et al. 2010, Chapter 4). Lower temperature and photosynthetic active radiation beneath nurse plants when compared to sites without vegetation indicate that the shade provided by nurse canopy is potentially responsible for the nurse effect (Chapter 4). If shading is the mechanism behind the nurse effect of adult trees on coastal dunes, in addition to the use of nurse plants itself, artificial shade could be also adopted as an alternative technique to increase the establishment of transplanted seedlings used to restore degraded dunes.

In this study, we performed transplant experiments along a natural coastal gradient to test the following hypotheses: (1) shading is a facilitative mechanism behind the nurse effect of mature individuals of a common tree species and (2) the shade-driven facilitation changes with environmental severity. We transplanted seedlings of a facilitated tree species under a nurse plant, under artificial shade, and to control open microsites to compare seedling survival and growth after one year. We expected higher seedling performance under the nurse plant and artificial shade than in open microsites. Furthermore, as predicted by the stress gradient hypothesis, we expected that such positive effect of shade increased with stress, emphasizing its importance under the severe abiotic conditions usually found in degraded systems.

5.3 Methods

5.3.1 Study Sites

We conducted this study along a beach-inland gradient located on the southern shore of Ilha do Cardoso State Park, a coastal island in southeastern Brazil (25°12'S, 44°17'W). The mean annual precipitation in Ilha do Cardoso ranges from 1400 mm to 2400 mm, with almost 70% of the rain falling between November and April. The mean annual

temperature ranges from 21 to 23 °C, but summers are warmer (mean monthly maximum of 26 °C in February) and winters are cooler (mean monthly minimum of 18 °C in July).

Sand dune vegetation in southeastern Brazil is formed by a mosaic of plant communities that occupy sandy plains formed by marine deposits in the late Quaternary, ranging from creeping types to forests (see details in Lacerda et al. 1993). The dune system in the study area is formed by parallel beach ridges occupying an approximately 400 m strip of land between the ocean and an inland estuary. Along this beach-inland gradient, the vegetation ranges from creeping psammophytes to an open scrub vegetation and a strip of forest on the inland-most part. We conducted the experiments in the open scrub vegetation in the portions of these ridges facing the sea and not flooded by the water table. The open scrub vegetation is composed by sparse, isolated, 1-3 m tall trees, shrubs, wood thickets of various sizes and a perennial herbaceous cover on the sandy substrate. Along the beach-inland gradient, vegetation cover and biomass increase with increasing distance from the seashore. This vegetation pattern, a common feature in coastal communities (Lubke 2004), reflects the reduction in stress and disturbance intensity as the distance from the sea increases (Lortie & Cushman 2007; Carboni et al. 2011).

5.3.2 Study Species

To test our questions we used two treelets species: *Guapira opposita* (Vell.) Reitz (Nyctaginaceae) as the potential benefactor and *Ternstroemia brasiliensis* Cambess. (Pentaphyllacaceae) as the potential beneficiary. We chose this pair of species to test our hypotheses because a previous study conducted in the same study site demonstrated a nurse plant effect of *G. opposita* on the survival of *T. brasiliensis* seedlings (Chapter 4). *Guapira opposita* is a tree or a treelet widely distributed around Brazilian ecosystems, including Amazonia, Brazilian Savanna and Atlantic forest (Sá 2010). Fruits, produced from January to March, are primarily dispersed by birds (Campassi 2002). In the study area, *G. opposita* is found from open scrub to forest. In the open scrub vegetation, where

the experiments were carried out, adults of *G. opposita* are relatively abundant and shorter (on average 1-2 m height) than those found on forest physiognomies, probably due to harsh abiotic conditions. *Ternstroemia brasiliensis* is a Brazilian endemic tree relatively common on altitude forests and coastal plains (Souza & Lorenzi 2008). The seeds, surrounded by a red aril, are dispersed by birds (Campassi 2002). In the study area, *T. brasiliensis* is a common species, occurring from open scrub to the forest physiognomy.

5.3.3 Experimental Design

To test our hypotheses, we established 45 experimental blocks on the scrub vegetation to evaluate the performance of transplanted seedlings of *T. brasiliensis*. Each block comprised three neighbor treatments (sub-blocks): beneath a *G. opposita* adult, beneath artificial shade provided by a mimic of *G. opposita* shade, and control without any shade or neighbor (Figure 1). To define the experimental blocks we randomly selected 45 isolated adult trees of *G. opposita* with similar height and canopy size along the open scrub vegetation. The other two treatments were placed 2 m away from the canopy of *G. opposita* trees, at a random direction from 0 to 359° centered at each tree. If the selected place was occupied by an adult tree or presented marked differences in soil or terrain, we randomly sampled another microsite. The minimum distance between treatments of each block was 2 m. We regularly clipped all other plants in a 0.5 m radius at the ground level for the three treatments (Figure 1).

The artificial shade treatment was a mimic of *G. opposita* shade, which consisted of rectangular bamboo frames covered by black nylon mesh (70% shadow) suspended above the ground by a bamboo stick. Considering that the objective of the artificial shade treatment was to simulate the shade of the paired *G. opposita*, both the frame area and the stick height of each artificial shade structure were equal to the crown area and height of the *G. opposita* nurse tree of the same experimental block. To test how stress affects the potential shade facilitative effect of *G. opposita* on *T. brasiliensis* we assumed that the

distance from the sea is a surrogate for the stress gradient and placed the 45 experimental blocks at three different distance classes from the sea (distance I= 40-50 m from seashore; distance II=120-130 m; distance III= 190-200 m).

In March 2009, we collected *T. brasiliensis* seedlings naturally occurring in the study site and put them into plastic pots of 43 cm³ (28 mm diameter and 115 mm height) with a mixture of 1:1 dune soil:organic compost Biomix®. We kept the seedlings in a greenhouse, located in the northeast of Ilha do Cardoso State Park, until the beginning of the experiments. On 24 and 25 June, 2010, we transplanted 1350 seedlings with 6.6 ± 1.6 cm (mean $\pm$ sd) height to the field experiments. We planted 30 randomly selected seedlings of *T. brasiliensis* in each experimental block (10 per sub-block; Figure 1). In the following days we watered the seedlings to avoid transplant shock. Assuming that seedlings death on the following days after transplantation was the result of transplant shock, we substituted 95 dead seedlings on 12 July, 2010, watered all seedlings again and started the experiment. In summary, our experimental design included 45 experimental blocks (15 replicates x three distances from the sea) with three subplots per experimental block (three neighbor levels) and 10 seedlings per sub-block, with a total of 1350 *T. brasiliensis* seedlings transplanted to the field experiment.

At the start of the experiment, we measured all seedlings for initial height, diameter at the ground level and leaf number. To calculate the increment in biomass over the course of the experiment, we estimated the initial dry biomass of the experimental seedlings using an allometric equation based on a subsample of 60 seedlings for which height, diameter at the ground level, leaf number and dry biomass were measured. We decided to use only the aboveground biomass to make inferences about the growth of *T. brasiliensis* because despite being careful in the removal of each seedling from the field at the end of the experiment, some fine root material was likely lost. Adopting a stepwise Akaike Information Criterion (AIC) procedure, as explained in detail in the next subsection, we selected the best allometric model for initial aboveground biomass of *T.*

brasiliensis seedlings. The selected equation included height (h) and diameter at the ground level (d) and had a $R^2=0.42$: $E[IAB] \text{ of } T. brasiliensis = -0.18 + 0.09*d + 0.03*h$, where $E[IAB]$ is the expected initial aboveground biomass (g).

We monitored seedlings survival monthly until July 2011, totaling 358 days of experiment. At the end of the experiment we harvested all surviving seedlings for calculation of the final aboveground biomass. We gently washed the harvested seedlings, dried them at 62 °C to constant mass and weight.

We also measured temperature and photosynthetically active radiation (PAR) under neighbor treatment in 18 of the 45 experimental blocks. We took surface soil temperature using a UNI-T UT301C infrared thermometer gun, and PAR using a Spectrum Technologies 3415FSE solar quantum meter. We took three subsamples for each location and then averaged prior to analysis to compensate for heterogeneity, especially under *G. opposita* canopy. We collected the measurements around noon during a sunny day in December 2011.

5.3.4 Analysis

To test if the survival of *T. brasiliensis* seedlings was higher under *G. opposita* and artificial shade than in open sites, and if this effect shifted along the environmental gradient, we used general linear mixed models (GLMM). We used GLMM to model proportions of surviving seedlings after one year as linear responses, assuming a binomial error distribution with the logit link function. The expected logit of survival proportion was modeled as a function of two fixed effects (presence of the neighbor and distance from the seashore) and a random effect (the block). To test the effect of neighbor and distance from the seashore on the growth of *T. brasiliensis* seedlings, we used linear mixed models (LMM). Aboveground biomass increment was analyzed as a function of the fixed variables neighbor and distance from the seashore, and a random variable, the block. Finally, to test the effect of the neighbor treatment on abiotic parameters, we also used LMM. In this case,

soil temperature and PAR were modeled as a function of the fixed variable neighbor and the random variable block.

To evaluate the importance of each fixed effect in each model described above, we selected the optimal fixed structure, as well as the random structure of each model following the top-down strategy recommended by Zuur et al. (2009). Although we are interested in the fixed effects, the selection of appropriate random structure is very important since it affects the values and quality of the fixed effects (Zuur et al. 2009). First, we selected the appropriate random component, that is, if the random variable influences the neighbor effect (model slope) or only the intercept. Once the optimal random structure was found, we proceeded with the fixed structure selection. We compared models with and without each fixed term. The full model included the single terms (neighbor and distance for survival and growth, and just neighbor for abiotic parameters) and their interaction (for survival and growth), as well the random component. The comparison was done hierarchically, thus, progressively simpler models were fit by dropping the interaction first, then each single term. In all models, including the model without any fixed term, the random effect was kept.

For statistical inferences, we employed model selection using Akaike's information criterion (AIC), a likelihood-based measure of model plausibility that penalizes more complex models, i.e., those with a greater number of parameters (Burnham & Anderson 2002). We ranked the models using AIC, in which the best model, the one that sacrifices the least information when it is used to approximate the truth, had the lowest AIC value (Hobbs & Hilborn 2006). The differences between the AIC value of the best model and the values of each model ranked below it ($\Delta AIC = AIC \text{ of each model} - AIC \text{ of the best model}$) provide information for evaluating which models in a set are as plausible as the best model. Values of ΔAIC between 0 and 2 indicate similar support (Burnham & Anderson 2002). We used the R environment (version 2.13.1, R Development Core Team 2010) with the lme4 package (Bates et al. 2011) for all statistical analyses.

5.4 Results

5.4.1 Survival

From 1350 *T. brasiliensis* seedlings monitored, 404 (30%) survived after 358 days. The model selection indicates that the random structure of the best model included both the intercept and slope components (Table S1). This means that besides the great variability in seedlings survival among blocks, the neighbor effect also varied among the blocks. A negative correlation of random effects between the control and the other two neighbor levels indicated that blocks with worse survivorship in the open microsites were, on average, more benefited by neighbor presence (*G. opposita* or artificial shade; see Figure S1). On the other hand, a positive correlation of blocks between *G. opposita* and artificial shade levels was found, indicating that blocks with higher seedlings survival under *G. opposita* also had good performance under artificial shade (Figure S1).

In spite of the variation due to random effects, the selected model indicates that neighbor presence, as well as distance from the sea affected the survival of *T. brasiliensis* seedlings (Table 1; Figure 2). The odds of seedling survival beneath *G. opposita* crown or artificial shade were twice those of seedlings in open microsites (odds ratio was calculated as the exponential of the fixed term from Table 2, $e^{0.73} = 2.08$). No consistent difference was identified between *G. opposita* and mimic effects (Table 2). As predicted by the stress gradient hypothesis, the proximity to the shore negatively affected seedlings survival. The odds of seedlings survival were, on average, 11 times higher at distance class II ($e^{2.43}$) and 13 times higher at distance class III ($e^{2.59}$) in comparison with the shortest distance from the seashore (class I; Figure 2). The absence of the interaction term between neighbor and distance in the selected model indicates that the effect of the neighbor presence did not change along the environmental gradient.

5.4.2 Growth

There is no evidence that neighbor affects the increment in aboveground biomass of *T. brasiliensis* seedlings. The model that included only distance, and the model that included distance and neighbor presence were as plausible as the null models in which no fixed effect was included (Table S2; Table 3). This result indicates uncertainty about the importance of the fixed terms on the aboveground biomass increment.

5.4.3 Abiotic parameters

Both *G. opposita* and artificial shade strongly buffered soil temperature and PAR at midday (Table S3, Table 4 and Table 5). Comparing to the open microsites, soil temperature was, on average, 34% and 42% lower under *G. opposita* and artificial shade, respectively (Table 6). Regarding PAR, the reduction reached 85% under *G. opposita* and 75% under artificial shade (Table 6).

5.5 Discussion

We found that *G. opposita* has a positive net effect on survival of *T. brasiliensis* seedlings. These results agree with previous experimental studies in the same site (Chapter 4), providing further evidence that the nurse effect of *G. opposita* is consistent. The benefit provided by the artificial shade on seedlings survival indicates that the positive net effect of *G. opposita* on survival of *T. brasiliensis* seedlings is, at least partly, due to the shade provided by *G. opposita* crown. Furthermore, the benefits provided by *G. opposita* and the artificial shade were constant along the entire environmental gradient, contrary to our expectations.

Environmental conditions are critical factors to the net interaction between plants. Theoretical models, collectively known as stress gradient hypothesis (SGH), state that the relative frequency of facilitation and competition will vary inversely across gradients of stress and disturbance, with facilitation being dominant in harsh conditions (Bertness & Callaway 1994; Brooker & Callaghan 1998). We found strong negative effect of the sea

proximity on the survival of *T. brasiliensis* seedlings, confirming our assumption that distance is a good surrogate for stress. However, we did not find any influence of distance on the nurse effect of *G. opposita* and the artificial shade on seedlings survival. These results indicate that the shade-driven facilitation of *G. opposita* on survival of *T. brasiliensis* seedlings was not affected by variation of the environmental conditions here considered. Therefore nurse plants are effective not only in the most severe conditions, but also in a wider range of environmental conditions, which expands the use of nurse plants to restore degraded areas under distinct severity levels.

Shade-driven facilitation by wood species on tree seedlings survival have been experimentally detected in natural systems, such as temperate open woodlands (Callaway 1992; Kitzberger et al. 2001; Baumeister & Callaway 2006) and lake sand dunes (Kellman & Kading 1992), and also in restoring degraded systems (Yang et al. 2010). Shade provided by wood species protects seedlings from lethal temperatures, reduces photoinhibition and improves soil water through the reduction on transpiration losses and the reduction on evaporation of soil moisture (Callaway 1995; Shumway 2000; Yang et al. 2010). Most plants suffer physiological damage at temperatures higher than 50 °C as a consequence of the degradation of enzymes and cell membranes (Larcher 1995). We found that in the hottest period of a summer day, soil temperature reaches more than 60 °C in open microsites, whereas the shade provided by *G. opposita* and the mimic efficiently buffered extreme temperatures below the critical temperature, as well as the overabundant amount of light typical of midday.

The observed positive net effect of *G. opposita* may be the result of other negative and positive interactions besides the positive effects provided by shade. It is possible that *G. opposita* has additional facilitation mechanisms that the mimic does not possess. As observed in coastal dunes, woody adults can also ameliorate the seedling abiotic conditions through, for example, nutrient soil enrichment (Shumway 2000; Joy and Young 2002). On the other hand, it is also possible that *G. opposita* has negative effects on

seedlings survival. Although the roots of adult and seedlings are mostly located at distinct levels of the soil, competition for water and nutrient is possible. Even if negative effects are present, the positive net effect of *G. opposita* on *T. brasiliensis* survival indicates that the facilitative effects are predominant over the potential negative effects. Furthermore, the positive effect of artificial shade on seedlings survival indicates that, at least part of the positive net effect of *G. opposita* is due to shading. Although plant-plant interactions are frequently species-specific (Callaway 1998), the shade-driven facilitation found between *G. opposita* and *T. brasiliensis* may be a widespread nurse effect among woody adults and seedlings of distinct species in coastal shrublands. Accordingly, even with variation on the intensity of net interaction depending on the identity of the interaction species, the better performance of seedlings with adult neighbors in a variety of systems (Callaway 1992; Kellman & Kading 1992; Kitzeberger et al. 2000; Flores & Jurado 2003; Martínez 2003; Gómez-Aparicio et al. 2004; Yang et al. 2010) indicates that the positive net effect of adults on wood seedlings are a widespread phenomenon in harsh environments.

In spite of the shade-driven facilitation on seedlings survival, *G. opposita* and the artificial shade had no effect on seedlings growth. Another study conducted in the same site did not detect any influence of *G. opposita* presence on biomass increment of *T. brasiliensis* seedlings either (Chapter 4), indicating a consistent neutral effect of *G. opposita* on growth of *T. brasiliensis* seedlings during the period evaluated in the experiments. Despite the positive effects on microclimate amelioration, shade can have negative effects, limiting light availability for photosynthesis (Callaway 1995). In our study, light was probably not a limiting factor for seedlings under neighbor because the shade provided both by *G. opposita* and mimic were effective around midday, when leaves are exposed to maximum amount of light. Even under shade, light availability is much higher than the compensation point for sun plants, which ranges from 10 to 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Taiz & Zeiger 2002). In fact, the growth under shade was not smaller than that observed in open microsites, suggesting that light was not a limiting resource. The distinct effect of shade-

driven facilitation on seedling performance estimators indicates that conditions and resources that influence survival do not necessarily affect growth (Hastwell & Facelli 2003; Gómez-Aparicio 2009). These considerations should be taken in account when nurse plants are incorporated as tools for restoration plans. However, in spite of the potential costs in terms of biomass production, the use of nurse plants has been considered a promising technique to increase survival in restoration programs since seedlings survival on recovering degraded systems is quite low (Gómez-Aparicio et al. 2004; Rey Benayas et al. 2005; King & Stanton 2008; Gómez-Aparicio 2009; Yang et al. 2010).

Coastal sand dunes are harsh environments where plant establishment and growth are limited by soil moisture, soil nutrients, wind exposure, salt spray and soil salinity (Wilson & Sykes 1999). As observed in arid systems (Holmgren & Scheffer 2001), several studies have been highlighting the role of adult wood species in nucleating the settlement of woody seedling in coastal dunes (Yarranton & Morrison 1974; Joy & Young 2002; Kellman & Kading 2002; Scarano 2002; Chapter 3). The main mechanisms behind this nucleation process are the attraction of dispersers (Joy & Young 2002) and also facilitation mechanisms such as microclimatic amelioration provided by shade, as demonstrated in the present study (see also Kellman & Kading 1992; Shumway 2000), nutrient improvement (Shumway 2000; Joy & Young 2002; Cushman et al. 2010) and reduction in wind speed and sand movement (Martínez 2003). The positive feedback created by the first woody individuals reinforces the woody vegetated state (Figure 3a), which is a key process for the successional transition between herbaceous to woody physiognomies (Yarranton & Morrison 1974; Joy & Young 2002; Scarano 2002; Chapter 3). This positive feedback between woody individuals could be of great value for the success of restoration of shrublands and forests. Accordingly, increasing populations of nurse plants have been considered a promising strategy for restoring degraded woodlands (Gómez-Aparicio et al. 2004; Gómez-Aparicio 2009). However, the dependency on nurse-

plants to make environmental conditions suitable for woody plant establishment implies that the lack of at least some adult woody individuals hinders sustained revegetation (Figure 3b; Holmgren & Scheffer 2001), making the degraded system resilient to restorative change (Suding et al. 2004). Hence, remaining treelets (such as isolated individuals of *G. opposita* used in our experiment) in degraded areas have high restoration value because they can nurse transplanted seedlings used in restoration programs, thus triggering the state transition from an herbaceous state to a shrubland or forest state. Hence, traditional techniques that remove all pre-existent woody vegetation before planting desired species may be a mistaken procedure when the objective is to restore a shrubland or a forest (Gómez-Aparicio 2009).

However, in most of the cases there are not enough remaining wood individuals in the degraded areas. In these situations, artificial structures that simulate the beneficial effects of nurse plants could be a simple alternative to allow the establishment of the first wood individuals in restoration plans (Rey Benayas 2005; Badano et al. 2011). In our study, we showed that artificial shade provides the same beneficial net effect of *G. opposita*, improving the survival of seedlings of a tree species common in coastal dunes from southeast Brazil. Therefore, in the absence of remaining vegetation, artificial shade are an effective, cheap alternative to increase the establishment of transplanted seedlings to degraded coastal dunes since they can trigger the positive feedback among woody species and the shift of the system from a barren or herbaceous state to a state dominated by wood species.

5.6 Implications for Practice

- In restoration of shrubland or forest coastal dunes mature pre-existent woody individuals should be kept to increase, via shade-driven facilitation, the establishment of transplanted seedlings.

- In the absence of such remaining nurse plants, their beneficial effect on seedlings can be replaced by artificial shading.

5.7 Acknowledgments

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Tables and Figures

Table 1. Model selection results for survival of *Ternstroemia brasiliensis* seedlings. The models are general linear mixed models (GLMM) with binomial errors and proportion of surviving seedlings after one year as response. Presence of neighbor (NE), distance from the seashore (DI), and their interaction (NE:DI) are the fixed variables, and block is the random variable. The selected model ($\Delta AIC < 2$) is in bold.

<i>Models</i>	<i>Predicted terms included</i>		<i>K</i>	<i>AIC</i>	ΔAIC
	<i>Fixed</i>	<i>Random</i>			
M1	NE+DI+NE:DI	1+NE Block	15	301.5	3.0
M2	NE+DI	1+NE Block	11	298.5	0.0
M3	NE	1+NE Block	9	301.1	2.6
M4	DI	1+NE Block	9	339.3	40.7
M5	-----	1+NE Block	7	342.3	43.8

Table 2. Fixed parameters of the best model for survival of *Ternstroemia brasiliensis* seedlings under three neighbor treatments (beneath *Guapira opposita*, beneath artificial shade provided by a mimic of *G. opposita* shade, and no neighbor control) and three distances from the seashore (I- closest; III – farthest). The model includes the effect of neighbor and distance from the sea as fixed variables, and block as random variable (see model M2 Table 1).

<i>Parameter description</i>	<i>Estimate</i>	<i>SE</i>
Intercept (neighbor control and distance I)	-3.53	0.37
<i>G. opposita</i>	0.73	0.32
Artificial shade	0.73	0.30
Distance II	2.43	0.36
Distance III	2.59	0.36

Table 3. Model selection results for increment in aboveground biomass of *Ternstroemia brasiliensis* seedlings. The models are linear mixed models (LMM) with presence of neighbor (NE), distance from the seashore (DI), and their interaction (NE:DI) as the fixed variables, and block as the random variable. The selected models ($\Delta AIC < 2$) are in bold.

<i>Predicted terms included</i>					
<i>Models</i>	<i>Fixed</i>	<i>Random</i>	<i>K</i>	<i>AIC</i>	<i>ΔAIC</i>
M1	NE+DI+NE:DI	1 Block	11	834.9	7.2
M2	NE+DI	1 Block	7	829.3	1.5
M3	NE	1 Block	5	827.8	0.0
M4	DI	1 Block	5	830.5	2.7
M5	-----	1 Block	3	828.1	0.3

Table 4. Model selection results for soil temperature. The models are linear mixed models (LMM) with presence of neighbor (NE) as the fixed variable, and block as the random variable. The selected model ($\Delta AIC < 2$) is in bold.

<i>Predicted terms included</i>					
<i>Models</i>	<i>Fixed</i>	<i>Random</i>	<i>K</i>	<i>AIC</i>	<i>ΔIAC</i>
M1	NE	1 Block	5	280.3	0.0
M2	-----	1 Block	3	427.8	147.5

Table 5. Model selection results for PAR. The models are linear mixed models (LMM) with presence of neighbor (NE) as the fixed variable, and block as the random variable. The selected model ($\Delta AIC < 2$) is in bold.

<i>Predicted terms included</i>					
<i>Models</i>	<i>Fixed</i>	<i>Random</i>	<i>K</i>	<i>AIC</i>	<i>ΔIAC</i>
M1	NE	1 Block	5	592.4	0.0
M2	-----	1 Block	3	876.0	283.6

Table 6. Soil temperature and PAR (mean $\pm$ 1 SE) in the noon period on 23 December, 2012, in control (open microsites), under *Guapira opposita* crown, and under artificial shade provided by shade mimic.

	<i>Control</i>	<i>G.opposita</i>	<i>Shade mimic</i>
Temperature (°C)	63.7 $\pm$ 0.73	42.1 $\pm$ 0.93	36.8 $\pm$ 0.93
PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	2000 $\pm$ 13	297 $\pm$ 18	492 $\pm$ 18

Figure 1. Neighbor treatment implemented to investigate if shading is the mechanism behind the nurse effect of the tree species *Guapira opposita* on survival of *Ternstroemia brasiliensis* seedlings at coastal dune vegetation, São Paulo, Brazil. A) Beneath *G. opposita* canopy; B) Beneath artificial shade provided by a mimic of *G. opposita* shade; and C) Control with no neighbor and no shading. In the three levels of neighbor treatment it is possible to see the seedlings of *Ternstroemia brasiliensis* with their metallic tags. All other plants in a 0.5 m radius were regularly clipped.

Figure 2. Proportion of surviving seedlings of *Ternstroemia brasiliensis* at three distances from the seashore and three levels of neighbor treatment. The estimates are based on the selected model, which includes neighbor treatment and distance from the seashore as fixed variables, and block as random variable (see model M2 in Table 1). Circles linked by lines represent treatments from the same block. Dashed lines represent blocks where seedlings had better performance in control, and solid lines represent blocks where seedlings had better performance with neighbor (*Guapira opposita* or artificial shade).

Figure 3. Alternative stable states for coastal sand dunes in which both states are reinforced by positive feedbacks. a) Wood state. In this situation, the presence of adult woody individuals improves the environmental conditions, decreases the mortality of seedlings and also attracts dispersers, thus reinforcing the wood vegetated state; b) Herbaceous state typical of degraded areas. In this situation, the harsh conditions due to the absence of vegetation cause high mortality of the woody seedlings and do not attract dispersers, thus reinforcing the herbaceous state. Therefore, restoration plans should keep pre-existent, mature wood individuals to increase the establishment of transplanted seedlings, attract propagules to degraded coastal dunes, and, possibly, trigger the positive feedback between woody species and a system shift from herbaceous to wood state. Furthermore, in the absence of remaining nurse plants, the beneficial effect of adult woody plants can be partially replaced by artificial shading.

Supplementary material

Table S1. Results of random component model selection for survival of *Ternstroemia brasiliensis* seedlings. The models are general linear mixed models (GLMM) with binomial errors and proportion of surviving seedlings as response. Presence of neighbor (NE), distance from the seashore (DI), and their interaction (NE:DI) are the fixed variables, and block is the random variable. The random intercept and slope model (1+NE | Block) was compared with the random intercept model (1| Block). The selected model ($\Delta AIC < 2$) is in bold.

<i>Predicted terms included</i>					
<i>Models</i>	<i>Fixed</i>	<i>Random</i>	<i>K</i>	<i>AIC</i>	<i>ΔIAC</i>
M1	NE+DI+NE:DI	1+NE Block	15	301.5	0.0
M2	NE+DI+NE:DI	1 Block	10	344.0	67.3

Table S2. Results of random component model selection for increment of aboveground biomass of *Ternstroemia brasiliensis* seedlings. The models are linear mixed models (LMM) with presence of neighbor (NE), distance from the seashore (DI), and their interaction (NE:DI) as the fixed variables, and block as the random variable. The random intercept and slope model (1+NE | Block) was compared with the random intercept model (1|Block). The selected model ($\Delta AIC < 2$) is in bold.

<i>Predicted terms included</i>					
<i>Models</i>	<i>Fixed</i>	<i>Random</i>	<i>K</i>	<i>AIC</i>	<i>ΔIAC</i>
M1	NE+DI+NE:DI	1+NE Block	16	862.4	4.8
M2	NE+DI+NE:DI	1 Block	11	857.6	0.0

Table S3. Results of random component model selection for soil temperature. The models are linear mixed models (LMM) with presence of neighbor (NE) as the fixed variable, and block as the random variable. The random intercept and slope model (1+NE | Block) was compared with the random intercept model (1| Block). The selected models ($\Delta AIC < 2$) are in bold.

<i>Models</i>	<i>Predicted terms included</i>		<i>K</i>	<i>AIC</i>	<i>ΔIAC</i>
	<i>Fixed</i>	<i>Random</i>			
M1	NE	1+NE Block	10	277.0	0.1
M2	NE	1 Block	5	276.9	0.0

Figure S1. Random effects and their 95% interval on survival of *Ternstroemia brasiliensis* seedlings in the three levels of neighbor treatment (control, under *Guapira opposita* and under artificial shade) in each experimental block. The estimates are based on the selected model, which includes neighbor presence (NE) and distance from the seashore (DI) as the fixed variables and the block, including both intercept and slope component, as the random variable (model M2 in Table 1 from main text.) Sub-blocks are ordered from bottom to top according to increasing random effect for control level. The resulting pattern of the random effects for *G. opposita* and artificial shade reinforces our conclusion that the selected model, which allows correlation of the random effects for control, *G. opposita*, and artificial shade, is suitable.

Capítulo 6

Considerações finais

6.1 Considerações finais

Uma das conclusões gerais obtidas através desta tese é que a facilitação entre plantas é uma interação relevante entre árvores da restinga. Os padrões de associação espacial positiva entre adultos e jovens de distintas espécies (Capítulo 3) é, pelo menos parcialmente, explicado por mecanismos de facilitação via sombreamento promovido pela copa da espécie-berçário (Capítulos 4 e 5). Apesar dos experimentos serem restritos a um par de espécies, é provável que o efeito de planta-berçário via sombreamento seja generalizado para outros pares de espécies arbóreas, dada a estrutura de copa sombreadora típica desta forma de vida em sua fase adulta. De fato, considerando que no capítulo 3 foram incluídos indivíduos de diferentes espécies, a associação espacial positiva registrada entre árvores sugere que tal padrão esteja muito mais relacionado a uma característica comum da forma de vida, ao invés de uma característica particular ao par de espécies usado como modelo nos experimentos de campo.

Se uma árvore adulta aumenta o desempenho de outra árvore jovem que se estabelece em sua redondeza, e se essa interação positiva se mantém ao longo do tempo, isso sustentaria um ciclo de retroalimentação positiva em que a presença de árvores levaria à manutenção e até predomínio desta forma de vida ao longo do tempo. Tal ciclo positivo de retroalimentação entre árvores é condizente com o padrão, encontrado na própria área de estudo e em outras restingas arbustivas (como a formação aberta de *Clusia* do Rio de Janeiro; Araujo 1992), em que muitas de espécies lenhosas estão distribuídas em uma matriz predominantemente herbácea. Uma vez estabelecido os primeiros indivíduos arbóreos isolados, o ciclo de retroalimentação entre árvores propiciaria a formação de núcleos de vegetação lenhosa, como as moitas de diferentes tamanhos observadas na restinga arbustiva.

A influência das condições ambientais sobre a importância e intensidade da facilitação entre árvores (capítulo 4) dá indicações de que a facilitação entre árvores é também um processo chave para entendermos a variação fisionômica encontrada sobre os

cordões arenosos ao longo do gradiente mar-interior. Nós encontramos evidências de que a facilitação entre árvores aumenta com a redução do estresse ambiental, ou seja, o potencial ciclo de retroalimentação positiva entre árvores é regulado pelas condições ambientais. Sob condições muito severas, a melhoria nas condições ambientais decorrente da presença de um vizinho não atende às tolerâncias mínimas exigidas pela espécie alvo e, como resultado, o saldo das interações é neutro ou até negativo, caso interações competitivas continuem presentes (ver Figura 7 do Capítulo 4). Como consequência, árvores isoladas que eventualmente se estabeleçam nesses ambientes sob estresse extremo não são capazes de iniciar um núcleo de colonização lenhosa e permanecem isoladas nesta fisionomia relativamente estável dominada pelo estrato herbáceo (Figura 1A). Em condições ambientais mais amenas, a facilitação tende a predominar o saldo das interações (Figura 1B). Neste cenário, árvores isoladas potencialmente desencadeiam o ciclo de retroalimentação positiva entre árvores, resultando na formação de núcleos de espécies lenhosas. Tal efeito é intensificado com a redução no estresse (Figura 1C). Mas então, sob condições ambientais favoráveis, o ciclo de retroalimentação positiva levaria ao predomínio da estrutura arbórea e formação de uma floresta?

Figura 1. Representação esquemática das fisionomias vegetais de restinga sobre cordões arenosos e do saldo final da interação entre árvores adultas e jovens ao longo do gradiente praia-interior. A) Mais próximo ao mar, onde os níveis de estresse são mais intensos, não há efeito de planta-berçário entre árvores, o que resulta em uma vegetação predominantemente herbácea. B) Em níveis intermediários de estresse, a vegetação ainda é predominantemente herbácea mas árvores isoladas são capazes de iniciar núcleos de vegetação lenhosa uma vez que funcionam como planta-berçário de outras árvores. C) Em áreas mais distantes do mar, os níveis de estresse são ainda menores, intensificando o efeito de planta-berçário entre árvores, o que resulta em núcleos de vegetação lenhosa cada vez maiores e consequente predomínio do estrato arbóreo.

Processo similar é sugerido por alguns autores para explicar sucessão primária em gradientes lacustres semelhantes aos ambientes costeiros (Cowles 1899, Yarranton & Morrison 1974). Yarranton & Morrison (1974) sugerem que, durante a sucessão primária de planícies arenosas, espécies lenhosas colonizadoras se estabelecem na vegetação aberta típica dos estágios iniciais de sucessão. Essas espécies melhoram as condições ambientais sob suas copas e funcionam como núcleos de colonização de espécies lenhosas tardias. Esses núcleos de vegetação se expandem continuamente até coalescerem e formarem uma floresta. No entanto, essas conclusões estão apoiadas na premissa de que o gradiente espacial de fisionomias observado atualmente representa a seqüência de estágios que ocorrem no tempo (cronoseqüência). Para que tal premissa seja válida é preciso pressupor que os diferentes estágios observados diferem apenas em idade e que

cada estágio foi submetido ao mesmo histórico de condições abióticas e bióticas. Dada a improbabilidade de tais premissas, casos clássicos de inferências sucessionais obtidas a partir de cronosequência são fortemente questionados (Johnson & Miyanishi 2008). Isso não significa que esteja descartado a potencial importância da facilitação como processo chave na sucessão de restingas, mas que simplesmente não podemos pressupor que a substituição de uma fisionomia aberta por uma floresta represente a inevitável trajetória da sucessão primária na restinga. Ainda menos confiável é a suposição de que a floresta que se encontra no final do gradiente espacial representa o estágio sucessional final da vegetação herbáceo-arbustiva adjacente.

Um modelo alternativo ao modelo sucessional tem sido proposto para explicar a dinâmica das fisionomias da restinga (Scarano et al. 2004). Neste modelo é proposto que as fisionomias de restinga, dentre elas a restinga arbustiva, representam estágios em equilíbrio estável, de maneira que as propriedades da comunidade vegetal, como diversidade e cobertura vegetal, devem manter-se dinamicamente estáveis em uma ampla escala temporal (Scarano et al. 2004). No caso da restinga arbustiva, de acordo com este modelo, é esperado que algumas moitas de vegetação lenhosa aumentem de tamanho, que outras se retraiam, e que o saldo final da área coberta por moitas lenhosas seja relativamente constante. Por outro lado, no modelo sucessional é esperado que a vegetação herbácea seja gradativamente substituída por uma vegetação predominantemente lenhosa. De acordo com este modelo, no estágio intermediário (correspondente à restinga arbustiva) seria esperado que as moitas de espécies lenhosas se expandissem ao longo do tempo até coalescerem e formarem uma fisionomia florestal.

Em ambos os modelos de dinâmica, sucessional ou estável, a facilitação entre árvores é considerada um processo chave para explicar as alterações temporais na vegetação de planície costeira (Cowles 1899; Yarranton & Morrison 1974; Scarano et al. 2004). No modelo sucessional, a manutenção da interação positiva entre árvores levaria ao predomínio do estrato arbóreo. No modelo de dinâmica estável, a facilitação é

considerada chave para a formação das moitas e eventual expansão. Então, como o mesmo processo chave poderia levar a previsões tão diferentes? O que a presente tese e outros trabalhos que investigaram interações entre espécies em planície costeira encontraram foi um efeito de planta-berçário entre espécies lenhosas, ou seja, efeito positivo de indivíduos adultos sobre o desempenho de indivíduos mais jovens (Kellman & Kading 1992, Joy & Young 2002). No entanto, pouco se sabe sobre o saldo da interação na outra direção, ou seja, será que a presença da plântula tem algum efeito sobre o adulto (Figura 2)? Além disso, será que a facilitação entre adulto e plântula se mantém ao longo do desenvolvimento ontogenético da plântula, ou é apenas restrita a esse estágio de vida (Figura 2)? As respostas a essas perguntas nos parecem fundamentais para esclarecer qual dos modelos propostos melhor explica a dinâmica da vegetação de restinga. No modelo de sucessão espera-se que, ao longo do desenvolvimento ontogenético das espécies, as interações mantenham-se positivas ou no mínimo neutras e que o efeito de planta-berçário continue presente mesmo com a expansão da moita. Por outro lado, no modelo de dinâmica estável, espera-se que, em algum momento do desenvolvimento da moita, o ciclo de retroalimentação positiva entre árvores seja interrompido, cessando o crescimento da moita e eventualmente fragmentando-a. Isso poderia acontecer porque o efeito do adulto sobre a plântula muda para negativo conforme a plântula se desenvolve ou porque, após crescer, a antiga plântula afeta negativamente sua planta-berçário levando-a à morte. Em ambos os casos, o resultado seria a interrupção do desenvolvimento da moita.

Figura 2. Interações bidirecionais entre árvores ao longo do desenvolvimento ontogenético dos indivíduos. Nesta tese, identificamos um efeito de planta-berçário, ou seja, o indivíduo adulto facilita o desempenho do indivíduo jovem. No entanto, pouco se sabe sobre o saldo da interação no sentido inverso, ou seja, o efeito da plântula sobre o adulto e como essas interações se comportam ao longo do desenvolvimento ontogenético dos indivíduos. Essas questões são fundamentais para entendermos a dinâmica da vegetação de restinga, com implicações para o entendimento da sucessão primária e para a restauração de áreas degradadas de restinga.

Uma das maneiras de testar as diferentes previsões geradas pelos modelos sucessionais e estável é através de experimentos de longo prazo em que o saldo das interações seja acompanhado durante o desenvolvimento ontogenético dos indivíduos envolvidos. Dada as complicações logísticas decorrentes do extenso tempo de vida de árvores, um método alternativo seria avaliar o saldo das interações de indivíduos alvo de diferentes tamanhos (pressupondo que idade e tamanho estejam relacionados). Além da avaliação das interações entre pares de espécies ao longo do tempo, também seria interessante ampliar a escala de observação e acompanhar a formação e evolução das moitas de vegetação lenhosa e também as possíveis modificações temporais nas fisionomias de restinga. Considerando que tais processos ocorrem em uma escala de tempo incompatível com a carreira de um pesquisador, uma alternativa para responder tais questões seria o uso de fotografias aéreas. Para muitas localidades existem fotos aéreas tomadas há muitos anos, às vezes décadas, que poderiam ser comparadas com fotos atuais. Ao classificar as fitofisionomias de imagens com diferentes idades poderíamos testar, dentro de uma perspectiva de modelos multiestados, qual a probabilidade de transição entre fisionomias e se esta depende da distância do mar ou de qualquer outro substituto de intensidade de estresse. Segundo os resultados obtidos nesta

tese, seria esperado maior probabilidade de transição de fisionomias abertas para fisionomias mais fechadas (predominadas por indivíduos lenhosos) quanto menor a intensidade de estresse. Além disso, poderíamos avaliar se a evolução temporal de expansão/retração das moitas de vegetação lenhosa da restinga arbustiva corresponde às previsões do modelo sucessional ou de estabilidade dinâmica.

Além dos avanços teóricos, os resultados obtidos nesta tese também apresentam implicações práticas para a restauração de restingas. Se o objetivo é restaurar uma fisionomia arbustivo-arbórea, o uso de indivíduos lenhosos maduros como plantas-berçário tem grande potencial para otimizar o processo de restauração ao aumentar a probabilidade de sobrevivência das mudas transplantadas. Os resultados do capítulo 5 indicam que o efeito de planta-berçário via sombreamento é o mesmo ao longo do gradiente ambiental, ou seja, a intensidade do efeito de planta berçário independe das condições ambientais. Por outro lado, no capítulo 4 encontramos que o efeito facilitador de árvores adultas é mais intenso sob menor estresse. O que explicaria a diferença nestes resultados? Ambos os experimentos foram conduzidos no mesmo trecho do gradiente praia-interior, porém foram realizados em períodos diferentes. Diferenças nas condições ambientais entre os diferentes períodos como, por exemplo, quantidade de chuva, poderiam gerar esses conflitos? Outra questão: o experimento do capítulo 5 foi conduzido por um período mais curto do que o experimento do capítulo 4. Será que o efeito das condições abióticas sobre o saldo das interações seria evidente caso prolongássemos o experimento descrito no capítulo 4? De qualquer forma, em ambos os experimentos vimos que o desempenho das mudas é muito pior sob maior estresse. Logo, técnicas que minimizem o estresse (como por exemplo, adição de substrato que aumente a retenção de água e disponibilidade de nutrientes), no mínimo, reduziriam a mortalidade por estresse e possivelmente aumentariam o efeito positivo das plantas-berçário sobre as mudas transplantadas. No entanto, é fundamental entender se a interação inicialmente positiva entre adulto e plântula é mantida ao longo do desenvolvimento dos indivíduos, para

somente então compreendermos o efeito a longo prazo do uso de plantas-berçário. Se o ciclo de retroalimentação positiva entre árvores for mantido ao longo do tempo, o uso de plantas-berçário poderia desencadear a transição do estado degradado para o estado dominado por espécies lenhosas. Projetos de recuperação de áreas degradadas de restinga que incorporem plantas-berçário são então ótimas oportunidades para testar a efetividade desta técnica ainda pouco explorada, assim como para acompanhar o comportamento das interações entre os indivíduos ao longo do tempo.

6.2 Bibliografia

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