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KELLY FERNANDES DE OLIVEIRA RIBEIRO

MECANISMOS DE COEXISTÊNCIA DE TRÊS ESPÉCIES CONGENÉRICAS SIMPÁTRICAS EM UMA FLORESTA TROPICAL

COEXISTENCE MECHANISMS OF THREE CONGENERIC SIMPATRIC SPECIES IN A TROPICAL FOREST

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Resumo

Entender os processos ecológicos que promovem a coexistência de espécies arbóreas em ambientes com alta diversidade como as florestas tropicais é um tema central em ecologia de comunidades. Nesses ambientes, os principais mecanismos de coexistência são baseados em processos determinísticos como filtragem ambiental e competição intra- e interespecífica. O objetivo do presente estudo foi investigar principalmente os processos determinísticos utilizando abordagens recentes que avaliam a estrutura espacial das populações e a variação das estratégias funcionais de três espécies arbóreas congenéricas simpátricas em uma floresta tropical sujeita a alagamento periódico (Floresta de Restinga). Em uma parcela de 1 ha, todos os indivíduos pertencentes a três espécies de *Myrcia* (Myrtaceae) foram marcados e mapeados. Também coletamos dados de variáveis ambientais e atributos funcionais dos adultos das espécies estudadas. Encontramos que as espécies são filtradas em diferentes graus para as mesmas manchas ambientais sujeitas a alagamento dentro da parcela, evidenciando que a filtragem ambiental é um importante processo direcionando a distribuição espacial local das espécies estudadas. Não encontramos evidências que sustentassem a competição direta entre as espécies de *Myrcia*, a competição direta entre cada espécie de *Myrcia* e heteroespecíficos, a competição difusa entre as três espécies de *Myrcia* e a atuação da dependência negativa de densidade em cada uma das espécies de *Myrcia*. A tolerância às manchas sujeitas a alagamento pode ser mediada pelo coeficiente alométrico similar entre as três espécies estudadas, enquanto a ausência de competição entre as espécies de *Myrcia* pode ser explicada por diferentes atributos funcionais relacionados à aquisição de recursos (principalmente área foliar, área foliar específica e densidade da madeira). Assim, concluímos que a coexistência das três espécies de *Myrcia* é direcionada pela diferenciação de nicho como resultado de pressões seletivas de competição interespecífica passada.

Palavras-chave: atributos funcionais, competição, dependência negativa de densidade, diferenciação de nicho, biodiversidade, ecologia de comunidades, estrutura espacial, filtragem ambiental, Floresta Atlântica, mecanismos de coexistência, processos ecológicos.

Abstract

Understanding the ecological processes that promote the coexistence of tree species in environments with high diversity such as tropical forests is a central theme in community ecology. In these environments, the main coexistence mechanisms are based on deterministic processes such as environmental filtering and intra- and interspecific competition. The aim of this study was to investigate especially the deterministic processes using recent approaches that assess the spatial structure of populations and the variation in functional strategies of three congeneric sympatric tree species in a tropical forest subject to seasonal flooding (Restinga Forest). In a 1 ha-plot, all individuals belonging to three *Myrcia* (Myrtaceae) species were marked and mapped. We also collected data on environmental variables and functional traits of adults of the species studied. We found that the species are filtered with different degrees to the same environmental patches subject to flooding within the plot, showing that environmental filtering is an important process driving the local spatial distribution of the species studied. We did not find evidence supporting direct competition between the *Myrcia* species, direct competition between each *Myrcia* species and heterospecifics, diffuse competition among the three *Myrcia* species, and the action of negative-density dependence in each of the *Myrcia* species. Tolerance to patches subject to flooding might be mediated by the similar allometric coefficient of the three species studied, while the absence of competition among the *Myrcia* species might be explained by different functional traits related to resource acquisition (mainly leaf area, specific leaf area, and wood density). Thus, our conclusion is that the coexistence of the three *Myrcia* species is driven by niche differentiation as a result of selective pressures of past interspecific competition.

Keywords: functional traits, competition, negative-density dependence, niche differentiation, biodiversity, community ecology, spatial structure, environmental filtering, Atlantic Forest, coexistence mechanisms, ecological processes.

Sumário

Introdução geral

Entender os processos ecológicos que mantêm a alta diversidade de espécies em ambientes naturais, tais como florestas tropicais, é um dos objetivos centrais em ecologia de comunidades (He et al. 1996). Os principais mecanismos de coexistência descritos em florestas tropicais são filtragem ambiental, competição interespecífica (Wright 2002), estocasticidade demográfica (Wiegand et al. 2012) e dependência negativa de densidade (DND; LaManna et al. 2017). Uma das abordagens que tem sido empregada para estudar os mecanismos de coexistência é a avaliação da estrutura espacial das populações vegetais (Getzin et al. 2006, Brown et al. 2013, Yan et al. 2015). A premissa por trás dessa abordagem é que a distribuição no espaço dos indivíduos de espécies sésseis é o resultado de processos ecológicos que ocorreram ao longo da vida dos indivíduos, gerando uma estrutura espacial característica (Wiegand et al. 2007).

Se a distribuição dos indivíduos responder à tolerância ambiental da espécie, *i.e.* filtragem ambiental, a distribuição espacial da população será relacionada às variáveis ambientais (Getzin et al. 2006) e apresentará agregação na escala das manchas de habitat propício (Condit et al. 2000). Além disso, se duas ou mais espécies responderem de maneira distinta ao ambiente abiótico, o estabelecimento dos indivíduos em locais propícios para o desenvolvimento de cada espécie deve causar crescente dissociação no espaço entre as espécies ao longo do desenvolvimento dos indivíduos caso as associações de habitat não se formem logo nos primeiros estágios da vida (Comita et al. 2007). O padrão resultante é a segregação espacial observada entre as árvores grandes (comumente referidas como adultos) das diferentes espécies, em escalas espaciais que variam de acordo com a distribuição dos ambientes propícios (Itoh et al. 2003). Por outro lado, se cada espécie responder de maneira distinta ao ambiente abiótico e as associações de habitat se formarem nos primeiros estágios de vida (Baldeck et al. 2013), o padrão resultante é a segregação espacial entre as espécies desde os primeiros estágios de desenvolvimento dos indivíduos, como observado por Lan et al. (2012) em 38,4% das análises interespecíficas com plantas jovens.

A competição interespecífica ocorre quando espécies interagem via exploração dos mesmos recursos, comumente limitados em ambientes naturais (Wright 2002). Assim, a competição ocorre principalmente em pequenas escalas espaciais que compreendem a vizinhança dos indivíduos (Velázquez et al. 2015). A competição intensa pode levar à morte dos indivíduos da espécie mais fraca competitivamente (Mayfield & Levine 2010). Consequentemente, assim como na filtragem ambiental, deve ocorrer crescente repulsão no espaço entre as espécies competidoras, resultando em segregação espacial dos adultos das diferentes espécies (Itoh et al. 2003). No entanto, a competição interespecífica atua em escalas espaciais menores do que a filtragem ambiental, *i.e.*, na escala em que ocorre a interação ao invés da escala da mancha de habitat propício (Velázquez et al. 2015). Porém, nem sempre a competição resulta na morte do indivíduo da espécies competitivamente mais fraca, podendo ser detectada somente no decréscimo do crescimento ou da fecundidade quando o indivíduo da espécies mais fraca localiza-se próximo a um indivíduo da espécie competitivamente mais forte (Kenkel 1988, Getzin et al. 2008). Assim, é esperada uma redução no tamanho do indivíduo pertencente à espécie competitivamente mais fraca conforme a distância do heteroespecífico mais forte diminui. Por outro lado, o tamanho dos indivíduos de uma espécie deve ser independente da proximidade de indivíduos da outra espécie se elas não competirem (Hubbell et al. 2001, Getzin et al. 2008).

No entanto, a competição direta entre espécies com requisitos ambientais semelhantes pode ser anulada por outros mecanismos, tais como a competição difusa de heteroespecíficos e a dependência negativa da densidade de coespecíficos (DNDC; Chesson 2000), permitindo a coexistência de espécies dentro das mesmas manchas ambientais. Na competição difusa, as interações negativas simultâneas entre muitas espécies promovem a coexistência, suprimindo a vantagem competitiva das espécies mais fortes sobre as mais fracas (Godoy et al. 2017). No entanto, em ambientes severos como a floresta de restinga sazonalmente alagável na Mata Atlântica brasileira, não se espera que a competição interespecífica seja forte, como postulado pela hipótese do gradiente de estresse (He et al. 2013), e outros mecanismos como o DNDC podem ser mais importantes (Kim & Ohr 2020). Além disso, a agregação espacial comumente observada em espécies de florestas tropicais (Condit et al. 2000) pode levar a vários efeitos dependentes da densidade (Uriarte et al. 2005, Zhu et al. 2015a). A DNDC resulta principalmente de dois processos ecológicos distintos: competição intraespecífica e ataque de inimigos naturais espécie-específicos (LaManna et al. 2017). Quando em alta densidade, coespecíficos podem competir intensamente (Tilman 1982, Wright 2002) e promover a atração e a disseminação de inimigos naturais (Janzen 1970, Connell 1971). Assim, as interações negativas coespecíficas são mais fortes do que as interações negativas heteroespecíficas, de forma que uma dada espécie é mais fortemente afetada pela densidade local de coespecíficos do que de heteroespecíficos (Chesson 2000, Zhu et al. 2015a, Liu et al. 2022). Consequentemente, a mortalidade pode aumentar e o crescimento dos indivíduos pode diminuir com o aumento da densidade local de coespecíficos (Hubbell et al. 2001, Getzin et al. 2008, Comita & Hubbell 2009, Comita et al. 2014, Lebrija-Trejos et al. 2014), o que permite o estabelecimento de outras espécies na comunidade (Chesson 2000).

A investigação de estratégias ecológicas intra- e interespecíficas também pode ajudar na distinção entre filtragem ambiental e competição interespecífica. Espécies que ocupam diferentes manchas de habitat devem apresentar características distintas indicando diferentes estratégias de tolerância. Por exemplo, uma base do tronco relativamente maior provém maior apoio e estabilidade mecânica a árvores, indicando uma estratégia mais eficiente de ocupação de manchas de habitat com solo mais instável (Mori et al. 2021). Por outro lado, espécies que usam diferentes recursos devem apresentar características distintas indicando diferentes estratégias de aquisição de recursos, as quais estão relacionadas com o equilíbrio entre crescimento e sobrevivência dos indivíduos. Por exemplo, densidade da madeira comumente apresenta relação negativa com área foliar (Wright et al. 2007), pois espécies com menor densidade da madeira têm maior eficiência hidráulica que permite maior tamanho de folhas, o que requer mais seiva (Wright et al. 2007, Chave et al. 2009). Espécies que investem mais em área foliar apresentam estratégia mais eficiente de captura de luz, enquanto espécies que investem mais em densidade da madeira apresentam estratégia mais eficiente de crescimento e resistência a patógenos (Wright et al. 2004, Chave et al. 2009). A distinção das características de tolerância e aquisição de recursos das espécies pode ainda variar em diferentes escalas espaciais e ocorrer devido a plasticidade em resposta a variação ambiental local ou variabilidade genética interpopulacional (Violle et al. 2012).

De maneira oposta, a coexistência de espécies direcionada por processos estocásticos, propostos por Hubbell (2001) em sua teoria neutra, também tem sido evidenciada em vários estudos (*e.g.*, Wiegand et al. 2012, Wang et al. 2016). A teoria neutra assume que todas as espécies de um mesmo nível trófico são ecologicamente equivalentes em suas taxas demográficas, incluindo especiação e extinção. Assim, a riqueza e a abundância de espécies em uma comunidade dependeriam do equilíbrio a longo prazo entre o desaparecimento e o surgimento de novas espécies na escala regional (Hubbell 2005). Localmente, a coexistência do alto número de espécies em florestas tropicais dependeria de processos aleatórios de chegada de diferentes espécies na comunidade a partir do conjunto regional e de recrutamento estocástico dos novos indivíduos (Hubbell 2001). Assim, o estabelecimento de uma espécie depende dos indivíduos alcançarem um local disponível e se estabelecer antes das demais espécies da comunidade, e não das interações competitivas entre espécies. Dessa forma, o padrão espacial predominante nas populações de espécies arbóreas deve ser associação entre coespecíficos em diferentes fases de desenvolvimento devido à limitação de dispersão (Hubbell 2005), comum em florestas tropicais (Condit et al. 2000). Esse padrão é esperado se as plantas parentais não alterarem o ambiente e influenciarem o estabelecimento de novos indivíduos coespecíficos por sombreamento ou alelopatia (Kobe & Vriesendorp 2021). Outro padrão espacial esperado a partir de processos estocásticos é a independência entre heteroespecíficos, devido à irrelevância das interações entre espécies (Wiegand et al. 2007).

As espécies congenéricas são um bom modelo para examinar os processos ecológicos que mantêm a diversidade nas comunidades porque elas tendem a apresentar nichos semelhantes devido à sua proximidade filogenética (Burns & Strauss 2011, Baraloto et al. 2012). Espécies congenéricas em locais com condições ambientais severas podem revelar padrões espacialmente significativos, pois tais ambientes restringem o crescimento e o estabelecimento das plantas, podem promover divergências na aquisição de recursos entre espécies e alterar resultados competitivos (Muench & Elsey-Quirk 2019). Assim, uma questão intrigante é como três espécies de Myrcia (Myrtaceae) que estão amplamente distribuídas na Mata Atlântica brasileira podem co-ocorrer em floresta de restinga sazonalmente alagável.

Objetivos e expectativas

O objetivo geral do presente estudo é investigar evidências de processos ecológicos que podem estruturar a comunidade arbórea em uma floresta de Restinga com áreas sazonalmente alagáveis. Nossos objetivos específicos foram explorar os processos ecológicos de filtragem ambiental, competição interespecífica e limitação de dispersão, bem como o mecanismo de dependência negativa de densidade de coespecíficos (DNDC), resultante de competição intraespecífica e ataque de inimigos naturais espécie-específicos, como potenciais direcionadores da coexistência das espécies estudadas. Utilizamos como modelo três espécies congenéricas simpátricas e buscamos inferir os processos e mecanismos por meio da estrutura espacial das populações e da variação das estratégias funcionais das espécies.

De acordo com as diferentes hipóteses de coexistência das espécies, temos as seguintes expectativas: (1) Se a filtragem ambiental for o principal mecanismo de coexistência, esperamos que a distribuição de cada espécie seja relacionada a variáveis ambientais distintas, as variáveis ambientais influenciem as interações congenéricas, os adultos congenéricos sejam espacialmente segregados em escalas espaciais maiores que a escala de vizinhança e os atributos funcionais relacionados à tolerância ambiental sejam divergentes entre as três espécies. (2) Se a competição interespecífica for mais importante, os adultos congenéricos devem ser espacialmente segregados na escala de vizinhança, apresentar redução de tamanho em função da proximidade com congenéricos e apresentar convergência dos atributos funcionais relacionados à aquisição de recursos. (3) Se processos estocásticos influenciarem mais fortemente a estrutura espacial das populações, esperamos independência espacial entre indivíduos congenéricos pertencentes à mesma classe de tamanho e ausência de variação interespecífica nos atributos funcionais. Nos casos 1, 2 e 3, esperamos influência da limitação de dispersão (associação espacial entre coespecíficos pequenos e grandes), devido à predominância desse processo em espécies arbóreas tropicais. (4) Se a DNDC for um forte direcionador da coexistência das espécies, esperamos detectar efeitos dependentes de densidade mais fortes entre coespecíficos em relação a heteroespecíficos.

A tese foi dividida em três capítulos que abordam evidências complementares de processos ecológicos e mecanismos que podem direcionar a coexistência das espécies estudadas. O primeiro capítulo foi publicado na revista Ecology and Evolution, e os capítulos dois e três estão redigidos em inglês para publicação em periódicos científicos internacionais. No primeiro capítulo, examinamos a filtragem ambiental, a competição interespecífica direta e a limitação de dispersão por meio da influência de variáveis ambientais sobre o padrão de distribuição espacial das populações das três espécies congenéricas estudadas, a relação espacial entre as classes de tamanho de congenéricos e coespecíficos, a distribuição espacial do tamanho dos indivíduos das três populações e as interações com outras espécies simpátricas da comunidade. No segundo capítulo, investigamos a DNDC e a competição difusa por meio dos efeitos dependentes de densidade na mortalidade e no tamanho dos indivíduos, se esses efeitos são mais fortes em árvores pequenas do que em árvores grandes, e se a mortalidade e o tamanho são influenciados pela heterogeneidade ambiental. No terceiro capítulo, observamos a variação das estratégias funcionais entre as espécies e como essas estratégias variam entre e dentro da mesma espécie em resposta à variação ambiental.

Área de estudo

A Mata Atlântica brasileira apresenta apenas cerca de 12% de sua cobertura original distribuídos em fragmentos (Ribeiro et al. 2009). Devido à alta riqueza de espécies, endemismo e grande pressão antrópica, a floresta ao longo da costa foi classificada como um *hotspot* para conservação da biodiversidade (Myers et al. 2000). Sua maior área contínua preservada inclui o Parque Estadual da Serra do Mar (PESM; 23°34' - 23°17'S e 45°02' - 45°11'O), que recobre a formação montanhosa da Serra do Mar ao longo da costa do estado de São Paulo, sudeste do Brasil, e compreende uma variação altitudinal de 0 m a 1.200 m (Alves et al. 2010). Devido a sua grande extensão (332.000 ha), o PESM é dividido em núcleos administrativos. O Núcleo Picinguaba localiza-se em Ubatuba, litoral norte do estado de São Paulo (Parque Estadual da Serra do Mar 2018), e compreende as fitofisionomias florestais de Restinga, Floresta Ombrófila Densa de Terras Baixas, Floresta Ombrófila Densa Submontana e Floresta Ombrófila Densa Montana (Joly et al. 2012). O clima da região é tropical úmido, com precipitação média anual de 2.634 mm. A precipitação média mensal de outubro a abril (período chuvoso) é > 200 mm e a de maio a setembro (período menos chuvoso ou seco) varia de 80 mm a 160 mm. A temperatura média anual é próxima dos 22ºC, com temperatura média máxima de 30,4ºC em fevereiro e mínima de 12,6ºC em julho (Morelatto & Haddad 2000).

A Floresta de Restinga de Picinguaba ocorre na planície costeira a aproximadamente 10 m de altitude (Alves et al. 2010, Joly et al. 2012). Em geral, essa fitofisionomia apresenta também estratos arbustivo e herbáceo desenvolvidos, e comporta epífitas e trepadeiras (Fernandes & Queiroz 2015). É um tipo de vegetação edáfica, associada aos depósitos arenosos costeiros quaternários, na qual os solos representam papel importante no desenvolvimento florestal (Bonilha et al. 2011) devido a atuação da podzolização resultante das inundações periódicas (Gomes et al. 2007). Na área de estudo, os solos são arenosos, muito ácidos e com teores variáveis de matéria orgânica (Martins 2010). As populações de algumas espécies vegetais são tolerantes ao alagamento, enquanto outras restringem-se às áreas secas devido à limitação fisiológica (Pedroni 2001, Diniz 2009, Oliveira 2011).

No presente estudo, os dados foram coletados em uma parcela permanente de 1 ha instalada na Floresta de Restinga do Núcleo Picinguaba. Parte da floresta é alagada periodicamente, com a presença de cordões arenosos formados entre canais de inundação, os quais influenciam a distribuição das plantas (Diniz 2009, Figura 1A). Essa parcela foi instalada no âmbito do Projeto Temático "Gradiente Funcional" (Biota/FAPESP 03/12595-7), sendo denominada de parcela A, e subdividida em 100 subparcelas de 10 m x 10 m (Figura 1B). Todos os indivíduos arbóreos e palmeiras com diâmetro na altura do peito (DAP, medido à 1,30 m de altura) igual ou maior do que 4,8 cm foram identificados, tiveram seu DAP medido e a sua localização espacial determinada em 2006 (Joly et al. 2012). No primeiro semestre de 2015, foi realizado o quarto censo da parcela no âmbito do Projeto "Processos ecológicos espacialmente estruturados em uma floresta tropical megadiversa - EcoSpace" (Edital Universal CNPq, processo número 459941/2014-3), seguindo o mesmo protocolo utilizado pelo Projeto

Temático. Os dados dos quatro inventários florestais realizados na parcela podem ser obtidos em Florestplots.net.

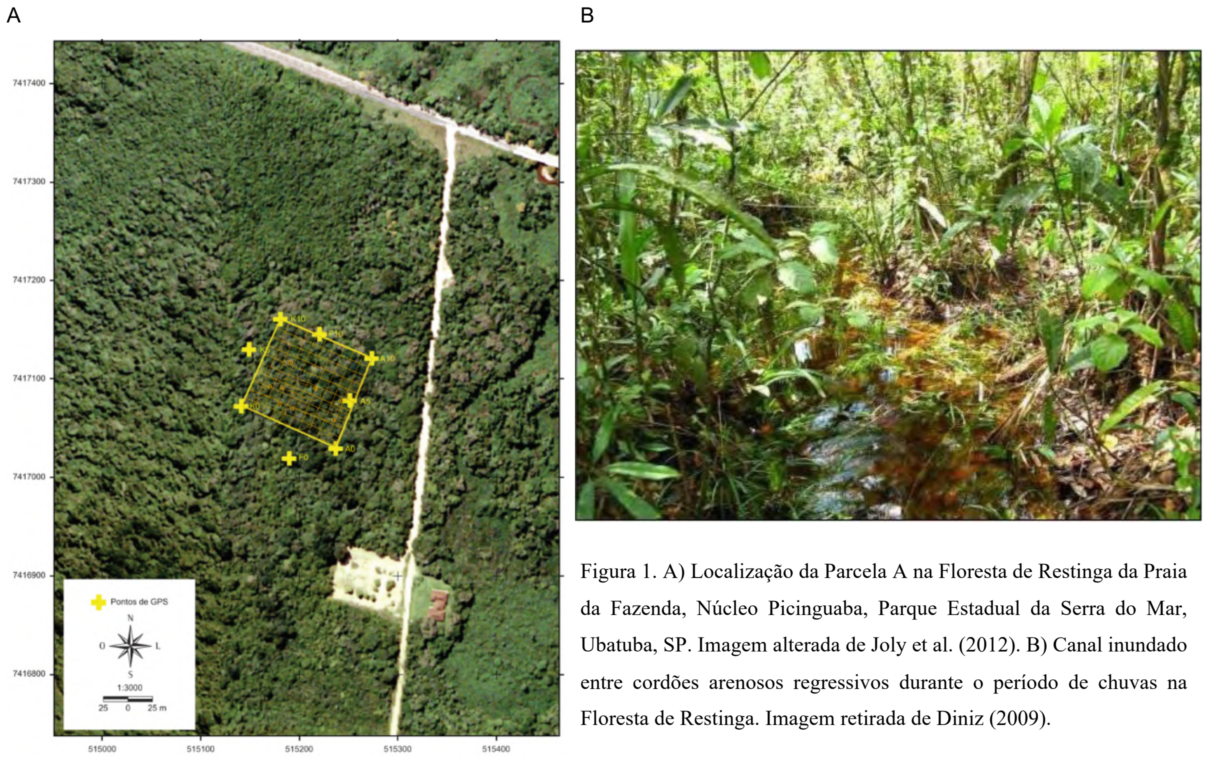

Figura 1. A) Localização da Parcela A na Floresta de Restinga da Praia da Fazenda, Núcleo Picinguaba, Parque Estadual da Serra do Mar, Ubatuba, SP. Imagem alterada de Joly et al. (2012). B) Canal inundado entre cordões arenosos regressivos durante o período de chuvas na Floresta de Restinga. Imagem retirada de Diniz (2009).

Espécies estudadas

As três espécies escolhidas pertencem ao gênero *Myrcia* (Myrtaceae, subfamília Myrtoideae). Myrtaceae apresenta o maior número de espécies em florestas tropicais úmidas (Oliveira-Filho & Fontes 2000), sendo considerada uma família modelo no domínio fitogeográfico da Floresta Atlântica (Lucas & Bünger 2015). No Núcleo Picinguaba, a família é representada por 138 espécies, sendo 28 espécies na Floresta de Restinga. As espécies *M. brasiliensis*, *M. multiflora* e *M. racemosa* representam 2,65% do total de espécies e apresentam 50 ou mais indivíduos com DAP ≥ 4,8 cm na parcela estudada, possibilitando análises espaciais mais consistentes. As espécies estudadas ocorrem predominantemente na Floresta Atlântica, mas podem ser encontradas em todo território brasileiro (Figura 2). Dentre as fitofisionomias encontradas no Núcleo Picinguaba, as espécies ocorrem somente na Floresta de Restinga.

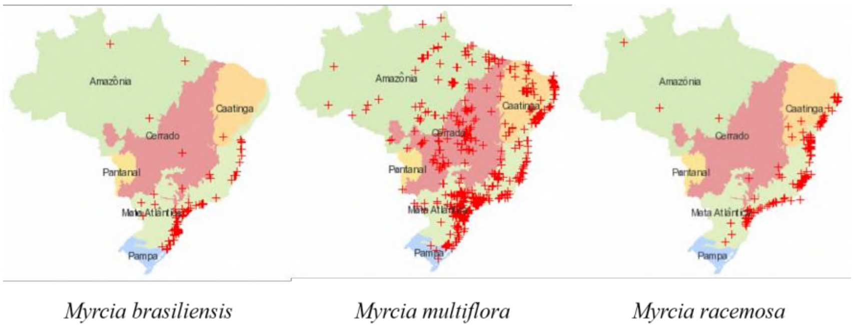

Figura 2. Distribuição geográfica de *Myrcia brasiliensis*, *M. multiflora* e *M. racemosa* no Brasil. Dados obtidos na plataforma speciesLink (2018). Os pontos vermelhos são as coordenadas informadas por coleções biológicas; as regiões com tonalidades diferentes representam os diferentes domínios fitogeográficos do Brasil.

Myrcia brasiliensis Kiaersk (sinonímia *Gomidesia schaueriana* O. Berg) é um arbusto, arvoreta ou árvore que, no estado de São Paulo, foi observada variando de 2 m a 30 m de altura. Tem folhas verdes ou marrons, inflorescência em panículas amarelado-esbranquiçadas a ligeiramente douradas, botões de 4-6 mm de comprimento, e frutos globosos de coloração amarelo, alaranjado e avermelhado a preto com 9-14 mm de diâmetro (Caliari 2013, Figura 3A). Na Floresta de Restinga na Ilha do Mel, Paraná, foi observada florescendo de outubro a janeiro e frutificando de dezembro a junho (Marques & Oliveira 2004). Na Restinga do Parque Estadual da Ilha do Cardoso, São Paulo, o pico de floração ocorre em janeiro e o de frutificação, em maio (Staggemeier et al. 2010).

Myrcia multiflora (Lam.) DC. é uma árvore que, em áreas de Floresta Estacional Semidecídua, capoeira e campo rupestre de Minas Gerais, apresenta altura entre 2 m e 4 m (Morais & Lombardi 2006, Rosa & Romero 2012), enquanto na Restinga de Marambaia, Rio de Janeiro, os indivíduos alcançam até 18 m (Souza et al. 2007). Apresenta caule descamante, folhas discolores com glândulas evidentes, flores pediceladas reunidas em panículas e frutos globosos. Os botões variam de 1,5-3 mm de comprimento, e os frutos são negros e variam de 3,6-6 mm de diâmetro (Morais & Lombardi 2006, Rosa & Romero 2012, Figura 3B). Na Restinga de Marambaia, a espécie apresenta flores de julho a fevereiro, e frutos de outubro a abril (Souza et al. 2007). Já na Restinga da Ilha do Mel, a floração restringe-se aos meses de outubro a janeiro e a frutificação, de dezembro a abril (Marques & Oliveira 2004). Na Restinga do Parque Estadual da Ilha do Cardoso, o pico de floração ocorre em janeiro e o de frutificação, em março (Staggemeier et al. 2010).

Myrcia racemosa (O. Berg) Kiaersk é uma árvore cujos indivíduos localizados na Floresta Ombrófila Densa na Ilha do Mel atingem até 6 m de altura (Lima et al. 2015), enquanto em material examinado em várias regiões do estado do Rio de Janeiro, a espécie atingiu até 8 m de altura (Souza et al. 2007). É caracterizada por apresentar ramos novos, pecíolos, inflorescências e nervura central das faces abaxial e adaxial das folhas densamente cobertos por tricomas. O caule é descamante e as folhas têm ápice longo-acuminado. Os botões têm 2 mm de comprimento, as flores são sésseis ou pediceladas e os frutos são globosos avermelhados com 4,3-6,5 mm de diâmetro (Figura 3C). Na Restinga de Marambaia, floresce de outubro a janeiro e frutifica de janeiro a julho (Souza et al. 2007). Na Restinga do Parque Estadual da Ilha do Cardoso, o pico de floração ocorre em fevereiro e o de frutificação, em julho (Staggemeier et al. 2010).

Figura 3. Ramo fértil das espécies estudadas *Myrcia brasiliensis* (A), *M. multiflora* (B) e *M. racemosa* (C). Imagem de C. Caliari. Disponível em http://143.107.246.248/peic/guiaplanta.php.

Referências bibliográficas

Alves, L. F., Vieira, S. A., Scaranello, M. a., Camargo, P. B., Santos, F. A. M., Joly, C. a., Martinelli, L. A. (2010). Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecology and Management*, *260*(5), 679–691.

Baldeck, C. A., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Valencia, R., … Dalling, J. (2013). Habitat filtering across tree life stages in tropical forest communities. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*, 20130548. doi:https://doi.org/10.1098/rspb.2013.0548

Baraloto, C., Hardy, O. J., Paine, C. E. T., Dexter, K. G., Cruaud, C., Dunning, L. T., Gonzalez, M. A., Molino, J. F., Sabatier, D., Savolainen, V., Chave, J. (2012). Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology*, *100*(3), 690–701.

Baraloto, C., Morneau, F., Bonal, D., Blanc, L., & Ferry, B. (2007). Seasonal water stress tolerance and habitat associations within four neotropical tree genera. *Ecology, 88*(2), 478–489.

Bonilha, R. M., Casagrande, J. C., & Soares, M. R. (2011). Characterization of the Soil Fertility and Root System of Restinga Forests. *Revista Brasileira de Ciência Do Solo*, *36*, 1804–1813.

Brown, C., Burslem, D. F. R. P., Illian, J. B., Bao, L., Brockelman, W., Cao, M., Chang, L. W., Dattaraja, H. S., Davies, S., Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., Huang, J., Kassim, A. R., Lafrankie, J. V., Lian, J., Lin, L., Ma, K., Mi, X., Nathalang, A., Noor, S., Ong, P., Sukumar, R., Su, S. H., Sun, I. F., Suresh, H. S., Tan, S., Thompson, J., Uriarte, M., Valencia, R., Yap, S. L., Ye, W., Law, R. (2013). Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 0502.

Caliari, C. P. (2013). *Estudos em Myrtaceae do Estado de São Paulo: Myrcia seção Gomidesia*. Universidade de São Paulo.

Chapin, F. S. (1991). Integrated Responses of Plants to Stress. *BioScience*, *41*(1), 29–36.

Chapin, F. S., Schulze, E.-D., & Mooney, H. A. (1990). The Ecology and Economics of Storage in Plants. *Annual Review of Ecology and Systematics*, *21*, 423–447.

Chapin, F. S., Autumn, K., & Pugnaire, F. (1993). Evolution of Suites of Traits in Response to Environmental Stress. *The American Naturalist*, *142*, S78–S92.

Chauvet, M., Kunstler, G., Roy, J., & Morin, X. (2017). Using a forest dynamics model to link community assembly processes and traits structure. *Functional Ecology*, 31: 1452–1461.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366. doi:10.1111/j.1461-0248.2009.01285.x

Colmer, T. D., & Voesenek, L. A. C. J. (2009). Flooding tolerance: suites of plant traits in variable environments. *Functional Plant Biology*, *36*, 665–681.

Comita, L. S., Condit, R., & Hubbell, S. P. (2007). Developmental changes in habitat associations of tropical trees. *Journal of Ecology*, *95*(3), 482–492. doi:10.1111/j.1365-2745.2007.01229.x

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

Connell, J. H. (1971). "On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees" in: Den Boer, PJ & Gradwell, GR (eds.) Dynamics of populations. Oosterbeek, the Netherlands: Centre for Agricultural Publishing and Documentation.

Diniz, F. V. (2009). *Composição e estrutura fitossociológica da regeneração natural na floresta de restinga alta em Picinguaba (Parque Estadual da Serra do Mar), município de Ubatuba, SP, Brasil.* Universidade Estadual Paulista.

Endara, M. J., & Coley, P. D. (2011). The resource availability hypothesis revisited: a meta- analysis. *Functional Ecology*, *25*, 389–398.

Fernandes, M. F., & Queiroz, L. P. de. (2015). Floristic surveys of Restinga Forests in southern Bahia, Brazil, reveal the effects of geography on community composition. *Rodriguésia*, *66*(1), 51–73.

Getzin, S., Dean, C., He, F., Trofymow, J. A., Wiegand, K., Wiegand, T. (2006). Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography*, *29*, 671– 682.

Getzin, S., Wiegand, K., Schumacher, J., Gougeon, F. A. (2008). Scale-dependent competition at the stand level assessed from crown areas. *Forest Ecology and Management*, *255*, 2478–2485.

Gomes, F. H., Vidal-torrado, P., Macías, F., Gherardi, B., & Perez, X. L. O. (2007). Solos Sob Vegetação De Restinga Na Ilha Do Cardoso (SP). I - Caracterização e Classificação. *Revista Brasileira de Ciência Do Solo*, *31*, 1563–1580.

Harvey, P. H., Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.

He, F., Legendre, P., LaFrankie, J. V. (1996). Spatial Pattern of Diversity in a Tropical Rain Forest in Malaysia. *Journal of Biogeography*, *23*, 57–74.

Hubbell, S. P. (2001). The unified neutral theory of biodiversity and biogeography. New Jersey: Princeton University Press.

Hubbell, SP (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19: 166-172

Lin, L., Comita, L. S., Zheng, Z., & Cao, M. (2012). Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. Journal of Ecology, 100, 905–914.

Itoh, A., Yamakura, T., Ohkubo, T., Kanzaki, M., Palmiotto, P. a., LaFrankie, J. V., Ashton, P. S, Lee, H. S. (2003). Importance of topography and soil texture in the spatial distribution of two sympatric dipterocarp trees in a Bornean rainforest. *Ecological Research, 18*, 307–320.

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

Joly, C. A., Assis, M. A., Bernacci, L. C., Tamashiro, J. Y., Campos, M. C. R., Gomes, J. A., Lacerda, M. A., Santos, F. A. M., Pedroni, F., Pereira, L. S., Padgurschi, M. C. G., Prata, E. M. B., Ramos, E., Torres, R. B., Rochelle, A., Martins, F. R., Alvez, L. F., Vieira, S. A., Martinelli, L. A., Camargo, P. B., Aidar, M. P. M., Eisenlohr, P. V., Simões, E., Villani, J. P., Belinello, R. (2012). Florística e fitossociologia em parcelas permanentes da Mata Atlântica do sudeste do Brasil ao longo de um gradiente altitudinal. *Biota Neotropica*, *12*(1), 0–23.

Kenkel, N C. (1988). Pattern of Self-Thinning in Jack Pine: Testing the Random Mortality Hypothesis. *Ecology,* 69(4), 1017–1024.

Kobe, R. K., & Vriesendorp, C. F. (2011). Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecology Letters, 14(5), 503–510. doi:10.1111/j.1461-0248.2011.01612.x

Kraft, N. J., Valencia, R. & Ackerly, D. D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322: 580-582

Lamanna, J. A., Mangan, S. A., Alonso, A., Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., … Myers, J. A. (2017). Plant diversity increases with the strength of negative density dependence at the global scale. *Science*, 356, 1389–1392.

Lebrija-Trejos, E., Wright, S. J., Hernández, A., & Reich, P. B. (2014). Does relatedness matter? Phylogenetic density-dependent survival of seedlings in a tropical forest. Ecology, 95(4), 940–951.

Lima, D. F., Krasinski, M., Goldenberg, R. (2015). A família Myrtaceae na Ilha do Mel, Paranaguá, Estado do Paraná, Brasil. *Hoehnea*, *42*(3), 497–519.

Lin, L., Comita, L. S., Zheng, Z., & Cao, M. (2012). Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. Journal of Ecology, 100, 905–914.

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, *11*, 995–1003.

Lucas, E. J., Bünger, M. O. (2015). Myrtaceae in the Atlantic forest: their role as a “model” group. *Biodiversity and Conservation*, *24*, 2165–2180.

Marques, M. C. M., Oliveira, P. E. A. M. (2004). Fenologia de espécies do dossel e do sub- bosque de duas Florestas de Restinga na Ilha do Mel, sul do Brasil. *Revista Brasileira de Botânica*, *27*(4), 713–723.

Martins, S. C. (2010). *Caracterização dos solos e serapilheira ao longo do gradiente altitudinal da Mata Atlântica, estado de São Paulo*. Universidade de São Paulo.

Mayfield, M. M. & Levine, J. M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085-1093

Morais, P. O., Lombardi, J. A. (2006). A família Myrtaceae na reserva particular do patrimônio natural da Serra do Caraça, Catas Altas, Minas Gerais, Brasil. *Lundiana*, *7*(1), 3–32.

Morellato, L. P. C., Haddad, C. F. B. (2000). Introduction: The Brazilian Atlantic Forest. *Biotropica*, *32*(4b), 786–792.

Myers, J. A., Harms, K. E. (2011). Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology*, *92*(3), 676–686.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858.

Oliveira-Filho, A. T., Fontes, M. A. L. (2000). Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate1. *Biotropica*, *32*, 793–810.

Oliveira, V. C. (2011). *Sobrevivência, morfo-anatomia, crescimento e assimilação de carbono de seis espécies arbóreas neotropicais submetidas à saturação hídrica do solo*. Universidade Estadual de Campinas.

Parque Estadual da Serra do Mar (2018). Parque Estadual da Serra do Mar. Disponível em: http://www.parqueestadualserradomar.sp.gov.br/pesm/

Pedroni, F. (2001). *Aspectos da estrutura e dinâmica da comunidade arbórea na Mata Atlântica de planície e encosta em Picinguaba, Ubatuba, SP*. Universidade Estadual de Campinas.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, *164*(3), S143–S164.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, *142*, 1141–1153.

Rosa, P. O., Romero, R. (2012). O gênero Myrcia (Myrtaceae) nos campos rupestres de Minas Gerais, Brasil. *Rodriguésia*, *63*(3), 613–633.

Souza, M.C., Morim, M.P., Conde, M.M.S., Menezes, L.F.T. (2007). Subtribo Myrciinae O. Berg (Myrtaceae) na Restinga da Marambaia, RJ, Brasil. *Acta bot. bras.* 21: 49–63.

SpeciesLink. 2018. Disponível em < http://www.splink.org.br>.

Velázquez, E, Paine, CET, May, F & Wiegand, T (2015) Linking trait similarity to interspecific spatial associations in moist tropical forest. *Journal of Vegetation Science* 26: 1068-1079

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., … Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology and Evolution*, 27(4), 244–252. doi:10.1016/j.tree.2011.11.014

Wagg, C., Ebeling, A., Roscher, C., Ravenek, J., Bachmann, D., Eisenhauer, N., Mommer, L., Buchmann, N., Hillebrand, H., Schmid, B., & Weisser, W.W. 2017. Functional trait dissimilarity drives both species complementarity and competitive disparity. *Functional Ecology* 31: 2320–2329.

Wang, X., Wiegand, T., Kraft, N. J. B., Swenson, N. G., Davies, S. J., Hao, Z., … Wolf, A. (2016). Stochastic dilution effects weaken deterministic effects of nichebased processes in species rich forests. *Ecology*, *97*(2), 347–360. doi:10.1890/14-2357.1

Weiner, J. (1990). Asymmetric Competition in Plant Populations. *Tree*, *5*(11), 360–364.

Wiegand, T., Gunatilleke, S., Gunatilleke, N. (2007). Species associations in a heterogeneous Sri Lankan dipterocarp forest. *The American Naturalist*, *170*(4), E77–E95.

Wiegand, T., Huth, A., Getzin, S., Wang, X., Hao, Z., Gunatilleke, C. S. & Gunatilleke, I. N. (2012) Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *Proceedings of the Royal Society B: Biological Sciences* 279: 3312-3320

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J-A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*, 1310–1324.

Wilson, P. G., O'Brien, M. M., Heslewood, M. M., Quinn, C. J. (2005). Relationships within Myrtaceae sensu lato based on a matK phylogeny. *Plant Systematics and Evolution*, *251*, 3–19.

Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(22), 821–827. doi:10.1038/nature02403

Yan, Y., Zhang, C., Wang, Y., Zhao, X., von Gadow, K. (2015). Drivers of seedling survival in a temperate forest and their relative importance at three stages of succession. *Ecology and Evolution*, 1–13.

Zhu, K., Woodall, C., Monteiro, J., Clark, J. (2015). Prevalence and strength of density-dependent tree recruitment. Ecology, 96(9), 2319–2327. doi:10.1890/14-1780.1.sm

Capítulo 1

Ribeiro, K. F. O., Martins, V. F., Wiegand, T., & Santos, F. A. M. (2021). Habitat filtering drives the local distribution of congeneric species in a Brazilian white-sand flooded tropical forest. *Ecology and Evolution*, *11*, 1797–1813. doi:10.1002/ece3.7169

Habitat filtering drives the local distribution of congeneric species in a Brazilian white-sand flooded tropical forest

Running head: Local distribution of congeneric species

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Abstract

The investigation of ecological processes that maintain species coexistence is revealing in naturally disturbed environments such as the white-sand tropical forest, which is subject to periodic flooding that might pose strong habitat filtering to tree species. Congeneric species are a good model to investigate the relative importance of ecological processes that maintain high species diversity because they tend to exploit the same limiting resources and/or have similar tolerance limits to the same environmental conditions due to their close phylogenetic relationship. We aim to find evidence for the action and relative importance of different processes hypothesized to maintain species coexistence in a white-sand flooded forest in Brazil, taking advantage of data on the detailed spatial structure of populations of congeneric species. Individuals of three *Myrcia* species were tagged, mapped, and measured for diameter at soil height in a 1-ha plot. We also sampled seven environmental variables in the plot. We employed several spatial point process models to investigate the possible action of habitat filtering, interspecific competition, and dispersal limitation. Habitat filtering was the most important process driving the local distribution of the three *Myrcia* species, as they showed associations, albeit of different strength, to environmental variables related to flooding. We did not detect spatial patterns, such as spatial segregation and smaller size of nearby neighbours, that would be consistent with interspecific competition among the three congeneric species and other co-occurring species. Even though congeners were spatially independent, they responded to differences in the environment. Last, dispersal limitation only led to spatial associations of different size classes for one of the species. Given that white-sand flooded forests are highly threatened in Brazil, the preservation of their different habitats is of utmost importance to the maintenance of high species richness, as flooding drives the distribution of species in the community.

Keywords: Atlantic Forest, coexistence, community structure, congeneric species, ecological processes, habitat filtering, natural disturbance, *restinga*, spatial point processes

Introduction

Understanding the ecological processes that maintain high species diversity in natural environments, such as tropical forests, is fundamental in community ecology (Leight *et al.*, 2004; Brown, 2014). The main processes maintaining species coexistence in tropical forests are deterministic or stochastic (Chase and Myers, 2011). The deterministic processes of interspecific competition and habitat filtering are based on the species' niche (Wright, 2002). Species that exploit the same limiting resources or that have similar tolerance limits to the same environmental conditions compete intensely (Chesson, 2000), especially in the case of sessile organisms such as trees (Silvertown, 2004). In a two-species model with asymmetric competition, the stronger species exclude the weaker species (Schluter, 2000) or constrains the spatial distribution of the weaker species to less favourable environments (Baraloto *et al.*, 2007). Thus, if these deterministic processes are important forces structuring a community, species coexistence is possible when there is niche partitioning among the species or high environmental heterogeneity that enables species with similar niches to be restricted to somewhat different environments (Silvertown, 2004). On the other hand, according to the neutral theory (Hubbell, 2001), species diversity results from a balance between stochastic emergence and disappearance of species at the regional scale (Hubbell, 2005). Locally, seed arrival in vacant recruitment sites is unpredictable, considering the spatio-temporal variation in availability of space. However, dispersal and recruitment limitation, common in tropical forests (Hubbell *et al.*, 1999), can prevent the most abundant species from occupying all available recruitment sites and thus dominating the community over time (competition exclusion), i.e. "winning-by-forfeit" (Hurtt and Pacala, 1995; Hubbell, 2001).

The ecological processes that act on each individual plant throughout its life determine the arrangement of plants in space, with each process generating a characteristic spatial structure at a given spatial scale (Hubbell *et al.*, 2001). Habitat filtering, for example, is expected to result both in spatial segregation of species with different environmental requirements at spatial scales larger than the size of patches within which the environment is approximately homogeneous (Itoh *et al.*, 2003; Getzin *et al.*, 2006; Table 1) and in spatial association of species with similar environmental requirements at spatial scales smaller than these patch scale (Burns and Strauss, 2011; Table 1). When these species additionally compete within patches, reduced resource availability should result in a decrease in growth rate (Kenkel, 1988), thereby causing nearby neighbours to be smaller than distant trees (Getzin *et al.*, 2008; Table 1). Also, in extreme cases, the stronger competitor can eventually cause mortality of the weaker competitor (Kenkel, 1988), resulting in spatial segregation of competing species at the small neighbourhood scale (say < 5 m; Velázquez *et al.*, 2015; Table 1).

In contrast, if stochastic mechanisms governs community structuring as assumed in the neutral theory, we should observe an approximate independent spatial relationship between species pairs (Volkov *et al.*, 2007; Table 1). Additionally, species distributions should not be related to environmental characteristics, as all species are expected to respond to the environment in a similar way (Hubbell, 2005). Last, dispersal limitation is expected to result in aggregation of seeds and small trees, and in spatial associations of seeds and smaller trees with large trees (Murphy *et al.*, 2017; Table 1).

Even though habitat filtering and dispersal limitation both result in aggregation and spatial association of conspecifics, the former reflects environmental tolerance of species (Kraft et al. 2015) that can lead to species distribution related to local environmental variables, whereas the latter can cause high density of small trees centred on conspecific large trees (Wang *et al.*, 2015). Additionally, the spatial pattern of conspecifics of different sizes can indicate which ecological process has acted more strongly on the population (Comita *et al.*, 2007; Shen *et al.*, 2009). Species-habitat association might change across demographic stages of plant development, possibly resulting in spatial dissociation between size classes. Moreover, species-habitat association is expected to be stronger for large than for small trees (Comita *et al.*, 2007; but see Baldeck *et al.*, 2013). On the other hand, aggregation of conspecifics of different sizes and spatial association between size classes are expected under strong dispersal limitation (Wiegand *et al.*, 2007). However, spatial patterns driven by dispersal limitation may be masked by high mortality of seeds and small trees that occur at high local densities in the neighbourhood of parent trees due to intraspecific competition and the attack of species-specific natural enemies (Comita *et al.*, 2014; Getzin *et al.*, 2014), which is known as conspecific negative-density dependence (CNDD; LaManna *et al.*, 2017).

The investigation of ecological processes that maintain species coexistence is revealing in naturally disturbed environments such as the Brazilian white-sand tropical forest, which is subject to periodic flooding (Eisenlohr *et al.*, 2013). Flooding reduces the amount of oxygen available for roots, and consequently limits plant growth (Oliveira and Joly, 2010) and increases plant mortality (Johnson *et al.*, 2017). The soil moisture gradient thus acts as a selective pressure on plants that can result in niche differentiation among co-occurring species (Werner and Platt, 1976) and different species-habitat associations in the white-sand tropical forest, according to each species' flooding tolerance and local environmental heterogeneity (Baraloto *et al.*, 2007). Additionally, flooding can act as a strong driver of species composition through habitat filtering (Baraloto *et al.*, 2007; Eisenlohr *et al.*, 2013, Oliveira *et al.*, 2014). Therefore, changes in environments subject to flooding, such as those caused by climate change or land use changes, are likely to lead to drastic changes in community structure. These changes include spatial rearrangement or local extinction of species according to their tolerance ranges and the new environmental characteristics (Kraft *et al.*, 2015). Nevertheless, few studies have evaluated the spatial structure of trees in environments with seasonal flooding such as the highly threatened Brazilian white-sand tropical forest (e.g. Baraloto *et al.*, 2007; Oliveira *et al.*, 2014).

Congeneric species are a good model to investigate the relative importance of ecological processes that maintain high species diversity because they tend to exploit the same limiting resources and/or have similar tolerance limits to the same environmental conditions due to their close phylogenetic relationship (Losos, 2008). Therefore, strong interspecific competition within the same tolerable environment should be easily detected, resulting in spatial association between species at the scale of environmental patches (< 30 m) due to habitat filtering and dissociation at the scale of local neighbourhood (< 5 m) due to interspecific competition (Velázquez *et al.*, 2015). However, congeneric species may show niche differentiation due to selective pressures that acts on each one of them at the evolutionary scale, including competition within the same tolerable environment (Wiegand *et al.*, 2007). This “ghost of competition past” results, at present day, in each species specialized in a different environment (Stubbs and Wilson, 2004; Yamada *et al.*, 2005) or in different use of resources within the same tolerable environment (Schluter, 2000). Alternatively, species’ niche may not be important, and so the spatial structure of populations should reflect dispersal limitation and stochasticity (May *et al.*, 2014).

The present study aims to find evidence for the action and relative importance of different ecological processes hypothesized to maintain species coexistence in a tropical forest subject to seasonal flooding, taking advantage of data on the detailed spatial structure of populations of three congeneric species. Specifically, we ask: (1) which environmental variables are associated with the spatial distribution of the different size classes of each species? (2) What is the spatial relationship between congeners in the same size class? (3) Is the size of an individual influenced by the proximity to congeners in the same size class? (4) What is the spatial relationship between small and large conspecific trees? (5) Are the spatial patterns of the three congeners explained by interactions with other co-occurring species? The combination of different spatial patterns will indicate which ecological processes are more important to the maintenance of species coexistence in the white-sand flooded tropical forest (see Table 1).

Material and methods

Study site

The Brazilian Atlantic Forest covers today only about 12% of its original extension and is distributed in fragments (Ribeiro *et al.*, 2009). Because it also presents high species richness and endemism, the forest along the coast was classified as a hotspot for biodiversity conservation (Myers *et al.*, 2000). The vegetation closest to the beach, covering sandy soils, is called *restinga*. It can vary from sparse herbaceous to forest communities (i.e. white-sand tropical forest; Oliveira *et al.*, 2014). The low altitude (< 10 m; Joly *et al.*, 2012) and fairly shallow water table result in periodic flooding, especially during the rainy season. Microtopographic variation forms dry sandy cords between flood channels, which, when dry, hold high quantities of organic matter (Diniz, 2009). While some plant species are flood-tolerant, others are restricted to the sandy cords (Oliveira *et al.*, 2014). Due to their proximity to the beach, *restinga* communities are highly threatened in Brazil by the real estate market (Alho *et al.*, 2002).

In the present study, we collected data in a 1-ha, permanent plot (23° 21’ 22” S and 44° 51’

03” W) installed at a protected white-sand flooded forest in the northern coast of the state of São Paulo, southeastern Brazil. There is a mountain range along the coast and the forest studied was recently formed from the downward movement of some species from the Atlantic Forest of the interior of the state of São Paulo (Eisenlohr *et al.*, 2013; Sanchez *et al.*, 2013). The white-sand forest is composed of dense vegetation with a large proportion of trees in the intermediate stratum (5-10 m height), but light levels are high in the understory due to canopy irregularities. There are also a shrub and an herbaceous stratum, epiphytes and lianas (Joly *et al.*, 2012). The regional climate is tropical humid, with mean annual precipitation of 2634 mm and mean annual temperature around 22 ºC (Morellato *et al.*, 2000). The study plot was divided into 100 subplots of 10 m × 10 m and presents 84 tree and palm species, being Myrtaceae and Fabaceae the richest families, and Myrtaceae, Arecaceae and Euphorbiaceae the most abundant ones (Joly *et al.*, 2012).

Species studied

The three species studied belong to the genus *Myrcia*, family Myrtaceae, subfamily Myrtoideae. Myrtaceae presents the highest number of species in tropical rainforests (Oliveira-Filho and Fontes, 2000) and is considered a characteristic family in the Brazilian Atlantic coastal forest (Lucas and Bünger, 2015). In the study plot, there are 21 Myrtaceae species, seven belonging to *Myrcia* (Joly *et al.*, 2012). The three species studied have 50 or more individuals in the plot (individuals with stem diameter at breast height ≥ 4.8 cm; data from the Functional Gradient Project Biota/FAPESP 03/12595-7 – available upon request).

The three species are not restricted to the white-sand forest and are widely distributed in the Atlantic Forest (Appendix S1). Their fruits have a fleshy pulp with 1-4 seeds and dark-reddish coloration, characteristics attractive to birds (Castro 1998, Pedroni 2001). Fruits of *M. brasiliensis* show a larger diameter (9-14 mm; Caliari 2013) than fruits of *M. multiflora* and *M. racemosa* (3.5-6.5 mm; Morais and Lombardi 2006, Souza et al. 2007, Rosa and Romero 2012). In the study plot, the species occupy different canopy strata. *Myrcia brasiliensis* occupies the first stratum and also occurs as an emergent tree; *M. multiflora* occupies the first and second strata, and *M. racemosa* occupies the first stratum (Pedroni, 2001). The three species increase water absorption in the soil at 50 cm depth and reduce the use of topsoil water (10 cm depth) from the flooded to the dry period. In the dry period, the species show a similar use of water sources, but *M. racemosa* absorves a higher proportion of water at 30-cm depth (Antunes, 2018). The similar water use suggests that the three *Myrcia* species are restricted to similar environments in the periodically flooded white-sand forest studied here, but we lack additional data on between-species variation of functional traits and plant physiological processes to hypothesize whether the species occupy similar niches.

Data collection

Between 2016 and 2017, we marked with individually numbered tags all freestanding stems with diameter at soil height (DSH) ≥ 1.5 mm (minimum size at which taxonomic identification was possible) of the three species studied. We also measured the DSH and mapped the x, y coordinates of all individuals in the study plot. Diameter at soil height was measured above root insertion, at the point where the stem shows an approximated circular shape.

We sampled environmental variables that are likely related to different species requirements in a white-sand flooded tropical forest. Canopy openness, elevation, terrain slope and soil moisture were obtained at a 10 m × 10 m scale, while flooding depth and litterfall depth were measured at a 5 m × 5 m scale. We measured canopy openness, elevation and terrain slope following Rosa *et al.* (2019). Canopy openness was calculated from hemispherical photographs and represents light availability in the understory. Because recent light environment should influence smaller plants and past light environment likely influenced large trees as they were growing (Poorter, 2007), we measured canopy openness at two different times (years 2008 and 2017). Elevation and terrain slope are associated with flooding depth in the study area, with lower flooding depth in higher and steeper patches (Diniz, 2009). Soil moisture was determined as the volumetric soil water content measured at the centre of each subplot at 12-cm depth with a HS2 Hydrosense II sensor (Campbell Scientific, Logan, Utah, USA; Uriarte *et al.*, 2018) and represents soil water availability. We measured flooding depth and litterfall depth at four diagonal points 3.5 m from each corner of the subplots using a graduated stake (Souza and Martins, 2005; Wang and Augspurger, 2006). Flooding depth was measured during the rainy season (January 2017), as flooding can limit plant growth (Oliveira and Joly, 2010) and increase plant mortality (Johnson *et al.*, 2017). Although litterfall is not related to the environmental requirements of plants, it can cause seedling mortality and significantly influence forest regeneration (Gillman, 2016).

In order to determine whether the spatial patterns of the three *Myrcia* species were explained by interactions with other co-occurring species, we selected the species with 30 or more individuals in the study plot (abundant species) from the Functional Gradient Project database to be included in our analysis. We only included abundant species because smaller samples result in too large stochastic effects in the characterization of the spatial structure of populations (Wiegand *et al.*, 2016). The database presents botanical identification, diameter at breast height (DBH) and spatial location (x, y coordinates) of each individual tree or palm with DBH ≥ 4.8 cm (Joly *et al.*, 2012). Our dataset comprised 14 abundant species including the three *Myrcia* species studied (Appendix S2).

Data analysis

Size classes of the three *Myrcia* species

To investigate ecological processes across demographic stages of tree development, we divided the individuals of each of the three *Myrcia* species into three size classes based on DSH and taking into account the minimum number of individuals needed in each class for spatial point pattern analysis ($n \geq 30$, Martins *et al.*, 2018). The smaller size class limit differs between *M. brasiliensis* and the other two species. Small trees were defined as individuals with DSH ≤ 0.2 cm for *M. brasiliensis*, and DSH ≤ 0.5 cm for *M. multiflora* and *M. racemosa*. Medium-sized trees had 0.2 < DSH ≤ 10.0 cm for *M. brasiliensis*, and 0.5 < DSH ≤ 10.0 cm for *M. multiflora* and *M. racemosa*. Large trees were those with DSH > 10.0 cm for the three species. We conducted all the following analyses separately for the three size classes of each of the three species studied.

Analysis 1: Relationship between the distribution of the three *Myrcia* species and environmental variables

To test for species habitat-association across demographic stages of plant development, we first used the variance inflation factor (VIF) to check whether our seven environmental variables were multicollinear (VIF > 10, Zuur *et al.*, 2007). None of them showed multicollinearity, we therefore included all environmental variables in our models. We modelled the intensity function $\lambda_h(x, y)$ at the location (x, y) as a function of the sum of the variables on a log scale. The corresponding log-linear regression model yields:

$$\log(\lambda_h(x, y)) = \beta_0 + \beta_1\, v_1(x, y) + \ldots + \beta_7\, v_7(x, y),$$

where β_0 is the intercept and β_i is the coefficient of the i^{th} environmental variable $v_i(x, \mathrm{y})$ to be estimated (Waagepetersen, 2007), with v_1 being flooding depth, v_2 soil moisture, v_3 terrain slope, v_4 elevation, v_5 litterfall depth, v_6 canopy openness in 2017, and v_7 canopy openness in 2008.

We used the Z value to evaluate the significance and direction of the effect of the different environmental variables on each species' pattern. For a significance level of $\alpha = 0.05$, we have a significant and positive association with a given variable if $Z > 1.96$ (and negative if $Z < -1.96$) and the larger the absolute value of Z, the stronger the association. We considered habitat effects to be strong when $Z \geq |4|$. We fitted $\lambda_h(x, y)$ using maximum likelihood estimation to determine the values of the coefficients β_i (Shen *et al.*, 2009; Wang *et al.*, 2011) in the package "spatstat" (Baddeley *et al.*, 2015) of the software R (R Core Team, 2018).

Analysis 2: Spatial relationship between *Myrcia* species and between each *Myrcia* species and heterospecifics

Here we investigated the spatial relationship between the individuals of two congeners of the same size class. Additionally, we apply the same methods to assess spatial relationships between large trees of each of the three *Myrcia* species and co-occurring abundant species. To this end, we used the bivariate pair correlation function $g_{12}(r)$ as the summary function (Stoyan and Stoyan, 1994) and the null model of spatial independence, in which we fixed the original location of points of pattern 2 and randomized the point pattern of focal species 1. We used two different null models to generate null model patterns of the focal species that conserve its univariate pattern. They are based on the technique of pattern reconstruction (Wiegand *et al.*, 2013) and use a spatially constant intensity function λ (i.e. homogeneous pattern reconstruction) and the intensity function $\lambda_h(x, y)$ (i.e., inhomogeneous pattern reconstruction) describing the environmental dependency of the focal species (Wiegand *et al.*, 2013; Wang *et al.*, 2015).

Positive departures of the observed $g_{12}(r)$ from the homogeneous null model indicate species association (caused by positive interspecific interactions or the location of the two species within the same environmental patches), negative departures indicate species dissociation (caused by negative interspecific interactions such as competition or the location of the two species in different environmental patches), and values within the simulation envelope indicate no significant departure from independence (Wiegand and Moloney, 2014). Departures from the inhomogeneous null model suggest operation of species interactions beyond habitat-association quantified by $\lambda_h(x, y)$ or missing environmental variables (Wiegand and Moloney, 2014).

Analysis 3: Spatial distribution of size between *Myrcia* species and between each *Myrcia* species and heterospecifics

Here we are interested in assessing if the size of an individual of a focal species 1 is influenced by the proximity to congeners of a species 2 in the same size class. Additionally, we search for interactions between large trees of each of the three *Myrcia* species (species 1) and the co-occurring abundant species in the study plot (species 2). For this, we used the bivariate *r*-mark correlation function with our size measure DSH as the quantitative mark. The bivariate *r*-mark correlation function $\kappa_{m.}(r)$ measures in our case the mean size of focal trees of species 1 that have a species 2 neighbour located at distance *r*. This function is normalized by the mean size of all individuals of the focal species 1. Because $\kappa_{m1.}(r)$ is evaluated at different interpoint distances *r*, we can observe how spatial effects on the quantitative mark decline with increasing distance to individuals of species 2 (Wiegand and Moloney, 2014).

In order to generate the null model values representing the absence of interactions for comparison of $\kappa_{m1.}(r)$, we randomly shuffled the size (i.e., DSH) among individuals of the focal species 1; additionally, the original location of all individuals was kept fixed. This “random marking” null model assumes that the size of the focal individuals is independent of the size of nearby individuals of species 2. Positive departures from the observed $\kappa_{m.}(r)$ indicate positive interspecific interactions or both species are located at favourable patches, whereas negative departures indicate negative interspecific interactions such as competition, or location of the two species at unfavourable patches (Wiegand and Moloney, 2014).

In order to separate the effects of environmental heterogeneity and the effects interspecific interactions, we used the local random marking null model. In this variation of the null model, shuffling of the sizes of the focal species 1 is restricted to points separated only up to a given distance

R, which represents an approximated size of environmental patches. By doing this, we can check whether departures from the independent marking null model are caused by environmental heterogeneity. Conversely, departures from the local random marking indicate interspecific interactions within patches (Wiegand and Moloney, 2014). We stipulated $R = 25$ m (one-quarter of the 1-ha plot) for the local random marking null model after testing for different values of R. The selected value corresponds to an approximate patch size where most distance effects disappear. Additionally, $R = 25$ m is large enough to encompass neighbourhood interactions within patches. In all analyses, we considered the influence of species 1 on species 2 and vice-versa.

Significance of spatial patterns against the null models for analysis 2 and 3

In order to determine whether the observed summary functions indicating spatial associations between species ($g_{12}(r)$) and the spatial distribution of size between species ($\kappa_{m1.}(r)$) differed from the expected values under the appropriate null models, we first performed 199 Monte Carlo simulations of the point processes underlying the null models. Then we created global simulation envelopes for the 1-50 m distance interval, considering the critical α value as calculated in the Z test statistics. The global envelopes have the convenient property that the null model can be rejected with the prescribed significance level α if the observed summary function falls at least at one distance bin outside the envelopes (Wiegand *et al.*, 2016).

Analysis 4: Spatial relationship between *Myrcia* conspecifics of different sizes

In order to assess ecological processes driving spatial relationships between *Myrcia* conspecifics of different size classes, we used a suite of alternative point process models that represent competing hypotheses, namely independence, dispersal limitation, habitat filtering, and a combination of dispersal limitation and habitat filtering. In all cases, we fixed the pattern of large trees, and randomized the pattern of small and medium trees according to the point process model used. To conserve the univariate pattern of small and medium trees during the simulations, we again used the technique of pattern reconstruction (Wiegand *et al.*, 2013) with different intensity functions tailored specifically for each point process model.

For the independence hypothesis (lack of small-scale species interactions), we used a spatially constant intensity function λ (i.e. homogeneous pattern reconstruction as in analysis 2). To represent dispersal limitation, we used the intensity function $\lambda_d(x, y)$ given by the superposition of Gaussian kernels with parameter σ around large trees. This creates patterns where the distribution of small and medium trees follows a normal distribution around the large conspecific trees (Wiegand and Moloney, 2014). The value of the parameter σ was fitted. For the habitat association hypothesis, we used the parametric intensity function $\lambda_h(x, y)$ of small trees as in analysis 1. Finally, to represent the combined dispersal limitation and habitat filtering hypothesis, we used the geometric mean of the two intensity functions (i.e. $[\lambda_d(x, y)\ \lambda_h(x, y)]^{0.5}$).

To determine the most parsimonious point process model, given the data, we used model selection based on the Akaike information criterion (AIC) and "synthetic" likelihood functions (Wood, 2010). With this method, we reduced the raw point pattern data to three-point pattern summary functions that quantify the spatial structure of the observed bivariate point patterns, namely $g_{12}(r)$, the bivariate *L*-function $L_{12}(r)$, and the bivariate nearest neighbour distribution function $D_{12}(r)$. We performed 999 simulations of the point process model to obtain the mean and the covariance matrix of these functions for each radius r (in steps of 3 m), given the vector $\boldsymbol{\theta}$ of model parameters. This allows for the construction of the synthetic likelihood to assess model fit. The resulting log-likelihood can then be used to calculate the AIC that balances model fit and model complexity to identify the most parsimonious model (Akaike, 1974; Wiegand and Moloney, 2014). We used here 999 simulations for better estimation of the covariance matrix needed for construction of the likelihood function.

We performed all point pattern analyses with the software *Programita* (Wiegand and Moloney, 2014), which can be accessed at www.programita.org. Estimators of the summary functions and the edge correction used in *Programita* are detailed in Wiegand, Grabarnik, and Stoyan (2016). We used a spatial resolution of 1 m, which is much smaller than the study plot, fine enough to answer our questions, and larger than the mapping error of the data (Wiegand and Moloney, 2004, 2014). We selected a ring width $d = 3$ m in all analyses.

Results

Number of *Myrcia* individuals and distribution of size classes in the plot

Our three focal species showed different abundances and distribution patterns within the plot. *Myrcia racemosa* showed the highest number of individuals in all size classes (n = 574), followed by *M. brasiliensis* (n = 192) and *M. multiflora* (n = 110, Fig. 1). Individuals of all size classes of *M. brasiliensis* were well distributed across the study plot. Small and medium trees of *M. racemosa* were distributed as a decreasing gradient from flooded to drier areas (from northwest to southeast of the plot), and large trees were distributed as a decreasing gradient from north to south of the plot. All size classes of *M. multiflora* occurred only in the flooded area (west part of the plot; Fig. 1 and 2).

Relationship between the distribution of the three *Myrcia* species and environmental variables

Results of this analysis are summarized in Table 2. On overall, the three species occur in similar environments in the plot, that is low flat areas and better-lit patches. For *M. brasiliensis*, small trees were associated to areas with higher canopy openness in 2017 and 2008, while large trees showed associations with lower terrain slope and elevation. However, these associations were weak. All size classes of *M. multiflora* were related to lower terrain slope and elevation. Additionally, small and large

M. multiflora trees were associated with higher soil moisture, small and medium trees were associated with higher canopy openness in 2008, and large trees were related to lower litterfall depth. Elevation was the environmental variable that more strongly influenced the distribution of individuals, especially of medium and large trees. The distribution of small and mainly medium trees of *M. racemosa* was also strongly influenced by lower elevation. Additionally, small trees were strongly related to lower terrain slope, and medium trees, weakly and positively related to canopy openness in 2008, which kept influencing the distribution of large trees, but now in a negative fashion.

Spatial relationship between *Myrcia* species

Although the three *Myrcia* species occur in similar environments in the plot, we found no spatial associations indicating habitat filtering to the same favourable patches, or spatial dissociation as evidence of interspecific competition. The same size class of the species studied were, in most cases, spatially independent, i.e. the observed $g_{12}(r)$ fell within the simulation envelopes of the null model of independence. The only exception was medium trees of *M. multiflora* and *M. racemosa*, which were spatially associated (Appendix S3). This association could be explained by a shared habitat association of the two congener species, as $g_{12}(r)$ fell within the simulation envelopes when we used the parametric intensity function $\lambda_h(x, y)$ to generate the null model patterns (Fig. 3).

Spatial distribution of size between *Myrcia* species

We also found no evidence of interspecific competition in relation to the size of the three species. The sizes of trees were in most cases not influenced by the presence of nearby congeners of the same size class, as indicated by results of the independent marking null model. The only exception was medium-sized trees of *M. racemosa*, which showed smaller DSH near individuals of *M. brasiliensis* (< 6 m) and of *M. multiflora* (< 13 m). However, this effect was caused by systematic size differences caused by unfavourable environmental conditions, as the observed $\kappa_{m1.}(r)$ fell within the simulation envelopes of the local random marking null model (Fig. 4).

Spatial relationship and spatial distribution of size between each *Myrcia* species and heterospecifics

The distribution of the individuals in the largest size class of the three *Myrcia* species was spatially independent from the distribution of the individuals belonging to each of the 11 abundant species in the plot ($n \geq 30$). Additionally, size of the larger *Myrcia* trees was independent from the distance of nearby abundant heterospecifics. All abundant species occur in both flooded and dry areas of the plot, and include five Myrtaceae species, from which three belong to *Myrcia* (Appendix S2).

Spatial relationship between *Myrcia* conspecifics of different sizes

Only *M. multiflora* showed spatial associations between different size classes, which were best explained by dispersal limitation for small trees in relation to large trees, and combination of dispersal limitation and habitat filtering for medium size trees in relation to large trees (Table 3). For *M. brasiliensis* and *M. racemosa*, small and medium trees were spatially independent of large trees, but for the small-large tree combination of *M. racemosa*, the habitat filtering model received similar support as the independence model (Table 3). The parameter σ that resulted in the best fit for the models of dispersal limitation was 20 m for *M. brasiliensis*, 9 m for *M. multiflora*, and 15 m for *M. racemosa*.

Discussion

In this study, habitat filtering was the most important process driving the local distribution of three *Myrcia* species in a white-sand flooded tropical forest, as species distribution showed associations, albeit of different strength, to environmental variables. We did not detect spatial patterns that are consistent with interspecific competition between the three species studied and between each *Myrcia* species and other co-occurring species in the plot, i.e. spatial segregation and smaller size of nearby neighbours. Additionally, the three *Myrcia* were spatially independent, but responded to differences in the environment. Last, dispersal limitation only led to spatial associations of different size classes for one species studied. Like our results, many studies on topo-edaphic variation in tropical forests (e.g. Baldeck *et al.*, 2012), including flooded areas (Baraloto *et al.*, 2007; Oliveira *et al.*, 2014), have shown that habitat filtering is an important ecological process driving community structure.

Relationship between the distribution of the three *Myrcia* species and environmental variables

The distribution of the three congeneric species showed somewhat similar associations to environmental variables, which is expected due to their close phylogenetic relationship (Losos, 2008). In general, the distribution of the three *Myrcia* species was related to lower elevation and terrain slope, and higher canopy openness. Flooding is expected to be more frequent, last for a longer time, and/or reach higher depths at lower parts of the study plot due to periodic water table flood (Diniz, 2009). As shown in Fig. 2, the lower part of the study plot does present higher soil moisture and flooding depth. Therefore, we believe elevation is a good surrogate for flooding at the study site. Additionally, we detected relationships between the distribution of small and large trees with higher soil moisture for *M. multiflora*, which reinforces our hypothesis that the three congeneric species occur predominantly in patches subject to flooding within the plot.

We probably found no further relationships between species distribution and flooding depth and/or soil moisture because both variables were measured only once and may thus not be able to capture flooding seasonality properly. The distribution of the three congeneric species was also restricted to better-lit patches, where individuals are likely to show higher survival probability, growth rate and fecundity (Dahlgren and Ehrlén, 2009). Interestingly, we were able to detect the influence of temporal changes in the light environment on the distribution of different size classes of the three *Myrcia* species. Although smaller trees were correlated with recent and/or past light environment (canopy openness in 2017 and 2008, respectively), large trees were correlated only with the past light environment, which probably reflects more closely the conditions of the time when plants were smaller.

Myrcia brasiliensis, which is well distributed in the study plot, showed weak associations to the environmental variables. Conversely, the other two species, whose distributions follow a flood-dry gradient, showed stronger associations to elevation. For the three species, environmental requirements shifted across demographic stages of plant development, as also observed for other species (e.g. Comita *et al.*, 2007). For *M. brasiliensis*, the light environment was important for small trees (Poorter, 2007), while large trees no longer depended on light, as the species occupies the first canopy stratum and also occurs as an emergent tree (Valladares *et al.*, 2016). As individuals grow in better-lit environments, some become restricted to patches subject to flooding. On the other hand, *M. racemosa* showed an opposite pattern, whereby smaller trees get restricted to patches subject to flooding and later on development the past light environment becomes detectable on the distribution of large trees. The shift in environmental requirements likely explains the change in distribution from small and medium trees (flood-dry gradient) to large trees (from northwest to southeast of the plot) for *M. racemosa*. *Myrcia multiflora* showed an intermediate pattern, with species distribution restricted to patches subject to flooding from early to late development, and light influencing the distribution of small and medium trees.

Even though flooding is the most important environmental characteristic driving species distribution in the plot, the fundamental niche of the three *Myrcia* species potentially encompasses a much wider variation of conditions than the environments of the study site, as the species occur in different vegetation types and are not restricted to areas subject to flooding at the geographic scale (Appendix S1). Thus, in the white-sand forest studied, the species can use the most common environmental condition (niche position, Marino *et al.*, 2019) and patches subject to flooding may work as areas of refuge from strong competitors and/or natural enemies (Baraloto *et al.*, 2007), which drives the species' realized niche. The same reasoning may apply to other species in the community, because most occur in both flooded and dry patches within the study plot (Appendix S2). We suggest future studies should evaluate flood tolerance of the different species of the community and the presence of natural enemies to better understand the spatial distribution constraint in a gradient of soil moisture in flooded forests.

Spatial relationship and spatial distribution of size between *Myrcia* species and between each *Myrcia* species and heterospecifics

The overall association of the three *Myrcia* species to patches subject to flooding let us expect spatial association between congeners. Nevertheless, only medium trees of *M. multiflora* and *M. racemosa* were spatially associated due to the same habitat-association. All other congener pairs showed independence, as well as pairs between the three focal *Myrcia* species and the abundant species in the plot. Interestingly, the abundant species include other *Myrcia* and Myrtaceae species, and so our results suggest that plant-plant interactions, even among closely related species, are not the main drivers structuring of our white-sand tropical forest community. It is possible that the three focal *Myrcia* species preferentially use areas subject to flooding in the plot as a refuge from natural enemies such as pathogens, which are important mortality agents of tropical plant species (Terborgh, 2012; Comita *et al.*, 2014).

Spatial independence between species has been frequently shown for tropical tree species (Wiegand *et al.*, 2012; Wang *et al.*, 2016). One explanation is that positive and negative interactions between species cancel each other's effects out, resulting in spatial patterns that appear overall to be independent (Punchi-Manage *et al.*, 2015). Also, according to the stochastic dilution hypothesis, independence should be more common in more species rich forests due to the large variability in the identity of neighboured trees that inhibit the detection of the spatial arrangement of plants directed by interactions between species (Wang *et al.*, 2016).

The apparent spatial independence between congeners (and between *Myrcia* and other heterospecifics) is in line with the independence between tree size and distance between species when we considered environmental heterogeneity in our analysis (i.e. local random marking null model). The evaluation of plant performance in greenhouse experiments and functional traits related to resource acquisition could help to elucidate whether our three focal *Myrcia* species use resources differently, as expected by niche differentiation of sympatric species with similar environmental requirements due to strong competition in the past (Connell, 1980).

Spatial relationship between *Myrcia* conspecifics of different sizes

Even though dispersal limitation is common in tropical forests (Hubbell, 2005) and habitat filtering is expected to influence species distribution in naturally disturbed environments (Baraloto *et al.*, 2007), we found that the combination of these two processes only best explained the observed spatial associations between small/medium and large trees of *M. multiflora.* Dispersal limitation drives the initial spatial relationship between small and large *M. multiflora* trees and, as small trees grow into medium sized trees, habitat filtering gains an importance for this species, which was also indicated by the stronger associations (i.e. higher Z values) of medium and large trees to environmental variables. Note that we estimated for *M. multiflora* the smallest width of the kernel function (σ = 9 m *vs*. 15 m and 20 m for the other two congeners) of the dispersal limitation model. Although it is consistent with species height (occupation in different canopy strata), we cannot exclude the possibility that the size of our plot is too small to allow for the detection of the effects of dispersal limitation for *M. racemosa* and especially *M. brasiliensis*, which shows the largest tree height, fruit diameter and width of the kernel function ($\sigma = 20$ m) among the three species studied. Because larger fruits can be dispersed by larger animals (Janson, 1983; Wheelwright, 1985), which have larger home ranges (Kelt and Van Vuren, 2001), seeds of *M. brasiliensis* are likely to be dispersed further from parent plants relative to the other two congeners and thus show lower dispersal limitation (Seidler and Plotkin, 2006). Therefore, a larger study site would be needed to detect spatial patterns consistent with dispersal limitation at larger spatial scales.

Spatial independence between small and large trees was also found by Getzin, Wiegand, and Hubbell (2014) on Barro Colorado Island, Panama. The authors suggested that this pattern could result from habitat-association masked by unpredictable dispersal events created by disperser movement behaviour or from the uncoupling of the positive association of trees expected from dispersal limitation due to high mortality of seeds and early developmental stages caused by conspecific negative-density dependence (CNDD). Because CNDD is widespread in tropical forests (LaManna *et al.*, 2017), a future project is to address whether CNDD of the three *Myrcia* species uncouples the spatial distribution patterns of trees from the seed deposition patterns. Additionally, some studies have shown that phylogenetically related neighbours increase mortality of a focal species (Bagchi *et al.* 2010; Metz *et al.* 2010; Paine *et al.* 2012; Zhu *et al.* 2015), so our three *Myrcia* species could show phylogenetic density dependence. Last, we still lack knowledge on how flooding may affect CNDD, which is especially important in the face of future environmental changes.

Conclusions

In this study, we employed several spatial point process models to simultaneously investigate important ecological processes that are hypothesized to maintain species coexistence in tropical forests, i.e. habitat filtering, interspecific competition, and dispersal limitation. Using data from congeneric species as a model in a naturally disturbed environment, we demonstrated that habitat filtering to areas subject to flooding is the most important ecological process driving the local distribution of these species in a white-sand flooded tropical forest. In this type of vegetation, there seems to be a clear division of tree species into either flood-tolerant or flood-intolerant (Oliveira *et al.*, 2014). However, climate change and other anthropic pressures can affect species coexistence by providing new habitat conditions and so understanding how habitat filtering acts in forests subject to flooding potentially aids mitigation plans of environmental changes (Kraft *et al.*, 2015). Given that *restinga* is highly threatened in Brazil (Alho *et al.*, 2002), the preservation of its different habitats is of utmost importance to the maintenance of high species richness and functional strategies.

Data accessibility

The data are available from Knowledge Network for Biocomplexity (KNB) repository at https://doi.org/10.5063/X928QD.

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References

Akaike, H. (1974). A New Look at the Statistical Model Identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723. doi:10.1109/TAC.1974.1100705

Alho, C. J. R., Schneider, M., and Vasconcellos, L. A. (2002). Degree of threat to the biological diversity in the Ilha Grande State Park (RJ) and guidelines for conservation. *Brazilian Journal of Biology*, *62*(3), 375–385. doi:10.1590/S1519-69842002000300001

Antunes, C. M. N. (2018). *Responses of coastal dune forests to groundwater changes: insights from mediterranean and tropical ecosystems*. Universidade Estadual de Campinas.

Baddeley, A., Rubak, E., and Turner, R. (2015). Spatial Point Patterns: Methodology and Applications with R. Chapman and Hall/CRC Press, London. http://www.crcpress.com/Spatial-Point-Patterns-Methodology-and-Applications-with-R/Baddeley-Rubak-Turner/9781482210200/

Bagchi, R., Swinfield, T., Gallery, R. E., Lewis, O. T., Gripenberg, S., Narayan, L., and Freckleton, R. P. (2010). Testing the Janzen-Connell mechanism: Pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters*, *13*(10), 1262–1269. doi:10.1111/j.1461-0248.2010.01520.x

Baldeck, C. A., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Valencia, R., … Dalling, J. W. (2012). Soil resources and topography shape local tree community structure in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20122532. doi:10.1098/rspb.2012.2532

Baldeck, C. A., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Valencia, R., … Dalling, J. (2013). Habitat filtering across tree life stages in tropical forest communities. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*, 20130548. doi: 10.1098/rspb.2013.0548

Baraloto, C., Morneau, F., Bonal, D., Blanc, L., and Ferry, B. (2007). Seasonal water stress tolerance and habitat associations within four neotropical tree genera. *Ecology*, *88*(2), 478–489. doi:10.1890/0012-9658(2007)88[478:SWSTAH]2.0.CO;2

Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, *41*, 8–22. doi:10.1111/jbi.12228

Burns, J. H., and Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences*, *108*(13), 5302–5307. doi:10.1073/pnas.1116085108

Caliari, C. P. (2013). *Estudos em Myrtaceae do Estado de São Paulo: Myrcia seção Gomidesia*. Universidade de São Paulo.

Castro, S. L. R. (1998). *Ecologia do tié-sangue, Ramphocelus bresilius (Aves: Emberezidae: Thraupinae), no Parque Estadual da Serra do Mar, Núcleo Picinguaba, Ubatuba, SP*. Universidade Estadual Paulista, Rio Claro.

Chase, J. M., and Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2351–2363. doi:10.1098/rstb.2011.0063

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.*, *31*, 343–366. doi:10.1146/annurev.ecolsys.31.1.343

Comita, L. S., Condit, R., and Hubbell, S. P. (2007). Developmental changes in habitat associations of tropical trees. *Journal of Ecology*, *95*(3), 482–492. doi:10.1111/j.1365-2745.2007.01229.x

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Beckman, N., and Zhu, Y. (2014). Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*, *102*, 845–856. doi:10.1111/1365-2745.12232

Connell, J. H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, *35*, 131–138. doi:10.2307/3544421

Dahlgren, J. P., and Ehrlén, J. (2009). Linking environmental variation to population dynamics of a forest herb. *Journal of Ecology*, *97*(4), 666–674. doi:10.1111/j.1365-2745.2009.01504.x

Diniz, F. V. (2009). *Composição e estrutura fitossociológica da regeneração natural na floresta de restinga alta em Picinguaba (Parque Estadual da Serra do Mar), município de Ubatuba, SP, Brasil.* Universidade Estadual Paulista.

Eisenlohr, P. V., Alves, L. F., Bernacci, L. C., Padgurschi, M. C. G., Torres, R. B., Prata, E. M. B., … Joly, C. A. (2013). Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. *Biodiversity and Conservation*, *22*(12), 2767–2783. doi:10.1007/s10531-013-0553-x

Getzin, S., Dean, C., He, F., Trofymow, J. A., Wiegand, K., and Wiegand, T. (2006). Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography*, *29*, 671–682. doi: 10.1111/j.2006.0906-7590.04675.x

Getzin, S., Wiegand, T., and Hubbell, S. P. (2014). Stochastically driven adult-recruit associations of tree species on Barro Colorado Island. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1790), 20140922–20140922. doi:10.1098/rspb.2014.0922

Getzin, S., Wiegand, K., Schumacher, J., and Gougeon, F. A. (2008). Scale-dependent competition at the stand level assessed from crown areas. *Forest Ecology and Management*, *255*, 2478–2485. doi:10.1016/j.foreco.2008.01.007

Gillman, L. N. (2016). Seedling mortality from litterfall increases with decreasing latitude. *Ecology*, *97*(2), 530–535. doi:10.1890/14-2019

Hubbell, S.P. (2001). The Unified Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Hubbell, S. P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, *19*, 166–172. doi:10.1111/j.0269-8463.2005.00965.x

Hubbell, S. P., Ahumada, J. A., Condit, R., and Foster, R. B. (2001). Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research*, *16*, 859–875. doi:10.1046/j.1440-1703.2001.00445.x

Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condite, R., Wechsler, B., … Loo de Lao, S. (1999). Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. *Science*, *283*(5401), 554–557.

Hurtt, G. C., and Pacala, S. W. (1995). The consequences of recruitment limitation: Reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology 176*, 1–12.

Itoh, A., Yamakura, T., Ohkubo, T., Kanzaki, M., Palmiotto, P. A., LaFrankie, J. V., … Lee, H. S. (2003). Importance of topography and soil texture in the spatial distribution of two sympatric dipterocarp trees in a Bornean rainforest. *Ecological Research*, *18*, 307–320. doi:10.1046/j.1440-1703.2003.00556.x

Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science 219*, 187–189.

Joly, C. A., Assis, M. A., Bernacci, L. C., Tamashiro, J. Y., Campos, M. C. R., Gomes, J. A. M. A., … Belinello, R. (2012). Florística e fitossociologia em parcelas permanentes da Mata Atlântica do sudeste do Brasil ao longo de um gradiente altitudinal. *Biota Neotropica*, *12*(1), 123–145. doi: 10.1590/S1676-06032012000100012

Johnson, D. J., Condit, R., Hubbell, S. P., and Comita, L. S. (2017). Abiotic niche partitioning and negative density dependence drive tree seedling survival in a tropical forest. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1869). doi:10.1098/rspb.2017.2210

Kelt, D. A., and Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *The American Naturalist, 157*, 637–645.

Kenkel, N. C. (1988). Pattern of Self-Thinning in Jack Pine : Testing the Random Mortality Hypothesis. *Ecology*, *69*(4), 1017–1024.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., and Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*, 592–599. doi:10.1111/1365-2435.12345

LaManna, J. A., Mangan, S. A., Alonso, A., Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., … Myers, J. A. (2017). Plant diversity increases with the strength of negative density dependence at the global scale. *Science*, *356*, 1389–1392.

Leigh, E. G., Davidar, P., Dick, C. W., Puyravaud, J. P., Terborgh, J., Ter Steege, H., and Wright, S. J. (2004). Why do some tropical forests have so many species of trees? *Biotropica*, *36*(4), 447–473. doi:10.1111/j.1744-7429.2004.tb00342.x

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, *11*, 995–1003. doi:10.1111/j.1461-0248.2008.01229.x

Lucas, E. J., and Bünger, M. O. (2015). Myrtaceae in the Atlantic forest: their role as a ‘model’ group. *Biodiversity and Conservation*, *24*, 2165–2180. doi:10.1007/s10531-015-0992-7

Marino, N. A. C., Céréghino, R., Gilbert, B., Petermann, J. S., Srivastava, D. S., de Omena, P. M., … Farjalla, V. F. (2019). Species niches, not traits, determine abundance and occupancy patterns: A multi-site synthesis. *Global Ecology and Biogeography, 29*, 295–308. doi:10.1111/geb.13029

Martins, V. F., Seger, G. D. S., Wiegand, T., and Santos, F. A. M. (2018). Phylogeny contributes more than site characteristics and traits to the spatial distribution pattern of tropical tree populations. *Oikos*, 1–12. doi:10.1111/oik.05142

May, F., Huth, A., and Wiegand, T. (2014). Moving beyond abundance distributions: neutral theory and spatial patterns in a tropical forest. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20141657. doi:10.1098/rspb.2014.1657

Metz, M. R., Sousa, W. P., and Valencia, R. (2010). Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. *Ecology 91*, 3675-3685. doi: 10.1890/08-2323.1

Morais, P. O., and Lombardi, J. A. (2006). A família Myrtaceae na reserva particular do patrimônio natural da Serra do Caraça, Catas Altas, Minas Gerais, Brasil. *Lundiana*, *7*(1), 3–32.

Morellato, L. P. C., Talora, D. C., Takahasi, A., Bencke, C. C., Romera, E. C., and Zipparro, V. B. (2000). Phenology of Atlantic Rain Forest Trees: A Comparative Study. *Biotropica*, *32*(4b), 811–823.

Murphy, S. J., Wiegand, T., and Comita, L. S. (2017). Distance-dependent seedling mortality and long-term spacing dynamics in a neotropical forest community. *Ecology Letters*, *20*(11), 1469–1478. doi:10.1111/ele.12856

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858. doi:10.1038/35002501

Oliveira, A. A., Vicentini, A., Chave, J., Castanho, C. D. T., Davies, S. J., Martini, A. M. Z., … Souza, V. C. (2014). Habitat specialization and phylogenetic structure of tree species in a coastal Brazilian white-sand forest. *Journal of Plant Ecology*, *7*(2), 134–144. doi:10.1093/jpe/rtt073

Oliveira, V. C., and Joly, C. A. (2010). Flooding tolerance of *Calophyllum brasiliense* Camb. (Clusiaceae): morphological, physiological and growth responses. *Trees - Structure and Function*, *24*, 185–193. doi:10.1007/s00468-009-0392-2

Oliveira-Filho, A. A. T., and Fontes, M. A. L. (2000). Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. *Biotropica*, *32*(4), 793–810.

Paine, C. E. T., Norden, N., Chave, J., Forget, P. M., Fortunel, C., Dexter, K. G., and Baraloto, C. (2012). Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecology Letters*, *15*, 34–41. doi:10.1111/j.1461-0248.2011.01705.x

Pedroni, F. (2001). *Aspectos da estrutura e dinâmica da comunidade arbórea na Mata Atlântica de planície e enconsta em Picinguaba, Ubatuba, SP*. Universidade Estadual de Campinas.

Poorter, L. (2007). Are Species Adapted to Their Regeneration Niche, Adult Niche, or Both? *The American Naturalist*, *169*(4), 433–442. doi:10.1086/512045

Punchi-Manage, R., Wiegand, T., Wiegand, K., Getzin, S., Huth, A., Gunatilleke, C. V. S., and Gunatilleke, I. A. U. N. (2015). Neighborhood diversity of large trees shows independent species patterns in a mixed dipterocarp forest in Sri Lanka. *Ecology*, *96*(7), 1823–1834. doi: 10.1890/14-1477.1

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., and Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, *142*, 1141–1153. doi:10.1016/j.biocon.2009.02.021

Rosa, P. O., and Romero, R. (2012). O gênero Myrcia (Myrtaceae) nos campos rupestres de Minas Gerais, Brasil. *Rodriguésia*, *63*(3), 613–633. doi:10.1590/S2175-78602012000300011

Rosa, L. B. G., Sampaio, M. B., and Martins, V. F. (2019). Local spatial variation in the population dynamics of two tree species in a region of Atlantic Rainforest, SE Brazil. *Revista Brasileira de Botanica*, *42*(4), 671–680. doi:10.1007/s40415-019-00563-w

Sanchez, M., Pedroni, F., Eisenlohr, P. V., and Oliveira-Filho, A. T. (2013). Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, southeastern Brazil, from near sea level to 1000m of altitude. *Flora*, *208*, 184–196. doi:10.1016/j.flora.2013.03.002

Schluter, D. (2000). Ecological Character Displacement in Adaptive Radiation. *The American Naturalist*, *156*, S4–S16. doi:10.1086/303412

Seidler, T. G., and Plotkin, J. B. (2006). Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, *4*(11), 2132–2137. doi:10.1371/journal.pbio.0040344

Shen, G., Yu, M., Hu, X.-S., Mi, X., Ren, H., Sun, I.-F., and Ma, K. (2009). Species-area relationships explained by the joint effects of dispersal limitation and habitat heterogeneity. *Ecology*, *90*(11), 3033–3041. doi:10.1890/08-1646.1

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology and Evolution*, *19*(11), 605–611. doi:10.1016/j.tree.2004.09.003

Souza, A. F., and Martins, F. R. (2005). Spatial variation and dynamics of flooding, canopy openness, and structure in a Neotropical swamp forest. *Plant Ecology*, *180*, 161–173. doi:10.1007/s11258-004-7811-7

Souza, M. C., Morim, M. P., Conde, M. M. S., and Menezes, L. F. T. (2007). Subtribo Myrciinae O. Berg (Myrtaceae) na Restinga da Marambaia, RJ, Brasil. *Acta Bot. Bras.*, *21*(1), 49–63. doi:10.1590/S0102-33062007000100006

Stoyan, D., and Stoyan, H. (1994). Fractals, Random Shapes and Point Fields. John Wiley and Sons, Chichester.

Stubbs, W. J., and Wilson, J. B. (2004). Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, *92*(4), 557–567. doi:10.1111/j.0022-0477.2004.00898.x

Terborgh, J. (2012). Enemies maintain hyperdiverse tropical forests. *American Naturalist*, *179*(3), 303–314. doi:10.1086/664183

Uriarte, M., Muscarella, R., and Zimmerman, J. K. (2018). Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change Biology*, *24*(2), e692–e704. doi:10.1111/gcb.14000

Valladares, F., Laanisto, L., Niinemets, Ü., and Zavala, M. A. (2016). Shedding light on shade: ecological perspectives of understorey plant life. *Plant Ecology and Diversity*, *9*(3), 237–251. doi:10.1080/17550874.2016.1210262

Velázquez, E., Paine, C. E. T., May, F., and Wiegand, T. (2015). Linking trait similarity to interspecific spatial associations in a moist tropical forest. *Journal of Vegetation Science*, *26*, 1068–1079. doi:10.1111/jvs.12313

Volkov, I., Banavar, J. R., Hubbell, S. P., and Maritan, A. (2007). Patterns of relative species abundance in rainforests and coral reefs. *Nature*, *450*, 45–49. doi:10.1038/nature06197

Waagepetersen, R. P. (2007). An estimating function approach to inference for inhomogeneous Neyman-Scott processes. *Biometrics*, *63*(252–258). doi:10.1111/j.1541-0420.2006.00667.x

Wang, X., Wiegand, T., Kraft, N. J. B., Swenson, N. G., Davies, S. J., Hao, Z., … Wolf, A. (2016). Stochastic dilution effects weaken deterministic effects of nichebased processes in species rich forests. *Ecology*, *97*(2), 347–360. doi:10.1890/14-2357.1

Wang, X., Wiegand, T., Swenson, N. G., Wolf, A. T., Howe, R. W., Hao, Z., … Yuan, A. Z. (2015). Mechanisms underlying local functional and phylogenetic beta diversity in two temperate forests. *Ecology*, *96*(4), 1062–1073. doi:10.1890/14-0392.1.sm

Wang, X., Wiegand, T., Wolf, A., Howe, R., Davies, S. J., and Hao, Z. (2011). Spatial patterns of tree species richness in two temperate forests. *Journal of Ecology*, *99*(6), 1382–1393. doi:10.1111/j.1365-2745.2011.01857.x

Wang, Y. H., and Augspurger, C. (2006). Comparison of seedling recruitment under arborescent palms in two Neotropical forests. *Oecologia*, *147*(3), 533–545. doi:10.1007/s00442-005-0279-x

Werner, P. A., and Platt, W. J. (1976). Ecological Relationships of Co-Occurring Goldenrods (Solidago compositae). *The American Naturalist*, *110*(976), 959–971.

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

Wiegand, T., He, F., and Hubbell, S. P. (2013). A systematic comparison of summary characteristics for quantifying point patterns in ecology. *Ecography*, *36*, 92–103. doi:10.1111/j.1600-0587.2012.07361.x

Wiegand, T., Huth, A., Getzin, S., Wang, X., Hao, Z., Gunatilleke, C. V. S., and Gunatilleke, I. A. U. N. (2012). Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1741), 3312–3320. doi:10.1098/rspb.2012.0376

Wiegand, T., and Moloney, K. A. (2004). Rings, circles, and null-models for point pattern analysis in ecology. *Oikos*, *104*, 209–229. doi:10.1111/j.0030-1299.2004.12497.x

Wiegand, T., and Moloney, K. A. (2014). Handbook of Spatial Point Pattern Analysis in Ecology. CRC Press, Boca Raton.

Wiegand, T., Grabarnik, P., and Stoyan, D. (2016). Envelope tests for spatial point patterns with and without simulation. *Ecosphere*, *7*(6), e01365. doi:10.1002/ecs2.1365

Wiegand, T., Gunatilleke, S., Gunatilleke, N., and Okuda, T. (2007). Analyzing the spatial structure of a Sri Lankan tree species with multiple scales of clustering. *Ecology*, *88*(12), 3088–3102. doi:10.1890/06-1350.1

Wood, S. N. (2010). Statistical inference for noisy nonlinear ecological dynamic systems. *Nature*, *466*, 1102–1104. doi:10.1038/nature09319

Wright, S. J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, *130*, 1–14. doi:10.1007/s004420100809

Yamada, T., Suzuki, E., Yamakura, T., and Tan, S. (2005). Tap-root depth of tropical seedlings in relation to species-specific edaphic preferences. *Journal of Tropical Ecology*, *21*, 155–160. doi:10.1017/S0266467404002238

Zhu, Y., Comita, L. S., Hubbell, S. P., and Ma, K. (2015). Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. *Journal of Ecology*, *103*, 957–966. doi:10.1111/1365-2745.12414

Zuur, A., Ieno, E. N., and Smith, G. M. (2007). Analyzing Ecological Data. Springer-Verlag, New York.

Table 1. Expectations for different ecological processes driving local species distribution. The analyses employed in this study and the results for three size classes of three *Myrcia* species sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil, are also shown. The neighbourhood scale (up to some 10 m) represents direct species interactions, the patch scale represents approximately homogeneous (suitable or less suitable) environments, whereas the community scale (100 m – tens of km) comprises several patches.

Questions/Ecological process driving species distribution	Expectation for different ecological processes				Analysis	Results		
	Species have different environmental requirements and do not compete	Species have the same environmental requirements and do not compete	Species have the same environmental requirements and compete	Species patterns according to neutral theory		*M. brasiliensis*	*M. multiflora*	*M. racemosa*
Which environmental variables are associated with the spatial distribution of the different size classes of each species?	Congeners distribution is related to different environmental variables, especially in large trees	Congeners distribution is related to the same environmental variables, especially in large trees	Congeners distribution is related to the same environmental variables, especially in large trees	No relationship between species distribution and environmental variables	Log-linear regression model	Small trees: relationship to higher canopy openness in 2017 and 2008 Large trees: relationship to lower terrain slope and elevation	Small trees: relationship to lower terrain slope and elevation, and higher soil moisture and canopy openness in 2008 Medium trees: relationship to lower terrain slope and elevation, and higher canopy openness in 2008 Large trees: relationship to lower terrain slope, elevation, and litterfall height, and higher soil moisture	Small trees: relationship to lower elevation and terrain slope Medium trees: relationship to lower elevation, and higher canopy openness in 2008 Large trees: relationship to lower canopy openness in 2008
What is the spatial relationship between congeners in the same size class?	Spatial segregation of congeners at the patch scale, especially for large trees	Spatial association of congeners at the scale of suitable patches, especially for large trees	Spatial association of congeners at the patch scale, especially for large trees, and tendency to segregation at the neighbourhood scale	Spatial independence of congeners in all size classes	$g_{12}(r)$ with pattern reconstruction of species 1 with spatially constant intensity λ for the independence null model, and with the parametric λ_h(x,y) for testing environmental filtering	Spatial independence of congeners in all size classes	Spatial independence of congeners in all size classes	Spatial independence of congeners in all size classes
Is the size of an individual influenced by the proximity to congeners in the same size class?	No influence of nearby congeners on tree size	No influence of nearby congeners on tree size	Negative influence of nearby congeners on tree size	No influence of nearby congeners on tree size	$\kappa_{m1.}(r)$ with the null models of regular random marking for a general analysis and local random marking for specific test of environmental filtering	No influence of nearby congeners on tree size	No influence of nearby congeners on small and large trees. Medium trees was influenced by less favourable environmental conditions	No influence of nearby congeners on small and large trees. Medium trees was influenced by less favourable environmental conditions
What is the spatial relationship between small and large conspecific trees?	Spatial association of small and large trees due to habitat filtering and/or dispersal limitation	Spatial association of small and large trees due to habitat filtering and/or dispersal limitation	Spatial association of small and large trees due to habitat filtering and/or dispersal limitation	Spatial association of small and large trees due to dispersal limitation	A suit of competing point process models to distinguish among independence and association due to dispersal limitation and/or shared habitat associations	Spatial independence of conspecifics in all size classes	Spatial association small and large trees due to dispersal limitation; spatial association of medium and large trees due to the combination of dispersal limitation and habitat filtering	Spatial independence of conspecifics in all size classes
Are the spatial patterns of the three congeners explained by interactions with other co-occurring species?	Spatial segregation between each *Myrcia* species and heterospecifics at the patch scale for large trees	Spatial association between each *Myrcia* species and heterospecifics at the scale of suitable patches for large trees	Spatial association between each *Myrcia* species and heterospecifics at the patch scale for large trees, and tendency to segregation at the neighbourhood scale	Spatial independence between each *Myrcia* species and heterospecifics in all size classes	$g_{12}(r)$ with pattern reconstruction of species 1 with spatially constant intensity λ for the independence null model, and with the parametric λ_h(x,y) for testing environmental filtering	Spatial independence between each *Myrcia* species and heterospecifics in all size classes	Spatial independence between each *Myrcia* species and heterospecifics in all size classes	Spatial independence between each *Myrcia* species and heterospecifics in all size classes

Table 2. Results of species-habitat association analysis using log-linear regression models for different size classes three *Myrcia* species sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. Bold indicates significant species-habitat association. *$p < 0.05$, **$p < 0.01$, *** $p < 0.001$.

M. brasiliensis	Estimate	Std. Error	z Value	*M. multiflora*	Estimate	Std. Error	z Value	*M. racemosa*	Estimate	Std. Error	z Value
	Small trees				Small trees				Small trees		
(Intercept)	-5.51	13.70	-0.40	(Intercept)	70.70	21.29	3.32***	(Intercept)	77.23	6.75	11.44***
Flooding depth	-0.01	0.02	-0.42	Flooding depth	0.00	0.02	0.04	Flooding depth	0.00	0.01	-0.14
Soil moisture	0.05	0.03	1.92	**Soil moisture**	**0.09**	**0.04**	**2.53***	Soil moisture	-0.01	0.01	-0.45
Terrain slope	-0.16	1.19	-0.13	**Terrain slope**	**-5.01**	**1.89**	**-2.65****	**Terrain slope**	**-2.04**	**0.61**	**-3.34*****
Elevation	-0.43	1.31	-0.33	**Elevation**	**-8.03**	**2.09**	**-3.84*****	**Elevation**	**-7.99**	**0.65**	**-12.24*****
Litterfall depth	0.04	0.05	0.85	Litterfall depth	0.00	0.07	0.02	Litterfall depth	0.04	0.02	1.84
Canopy openness 2017	**0.10**	**0.05**	**2.02***	Canopy openness 2017	0.02	0.08	0.23	Canopy openness 2017	-0.05	0.03	-1.93
Canopy openness 2008	**0.08**	**0.04**	**2.29***	**Canopy openness 2008**	**0.11**	**0.05**	**2.09***	Canopy openness 2008	0.03	0.02	1.38
	Medium trees				Medium trees				Medium trees		
(Intercept)	-0.89	16.50	-0.05	(Intercept)	171.92	33.27	5.17***	(Intercept)	50.38	7.28	6.92***
Flooding depth	0.02	0.02	1.35	Flooding depth	0.03	0.02	1.50	Flooding depth	0.00	0.01	-0.23
Soil moisture	0.01	0.03	0.26	Soil moisture	0.02	0.04	0.50	Soil moisture	-0.02	0.01	-1.23
Terrain slope	1.96	1.41	1.39	**Terrain slope**	**-11.96**	**2.72**	**-4.40*****	Terrain slope	-1.08	0.67	-1.60
Elevation	-0.64	1.57	-0.41	**Elevation**	**-18.18**	**3.39**	**-5.36*****	**Elevation**	**-5.38**	**0.70**	**-7.71*****
Litterfall depth	-0.02	0.06	-0.40	Litterfall depth	-0.01	0.07	-0.20	Litterfall depth	0.00	0.03	-0.18
Canopy openness 2017	-0.03	0.06	-0.49	Canopy openness 2017	0.12	0.07	1.60	Canopy openness 2017	-0.02	0.03	-0.66
Canopy openness 2008	0.09	0.05	1.95	**Canopy openness 2008**	**0.26**	**0.06**	**4.54*****	**Canopy openness 2008**	**0.06**	**0.02**	**3.03*****
	Large trees				Large trees				Large trees		
(Intercept)	22.95	12.62	1.82	(Intercept)	83.07	20.09	4.13***	(Intercept)	7.68	13.10	0.59
Flooding depth	0.00	0.02	-0.20	Flooding depth	0.01	0.02	0.69	Flooding depth	0.02	0.01	1.53
Soil moisture	0.04	0.02	1.51	**Soil moisture**	**0.08**	**0.04**	**2.24***	Soil moisture	0.03	0.03	1.25
Terrain slope	**-2.57**	**1.15**	**-2.23***	**Terrain slope**	**-4.25**	**1.78**	**-2.38***	Terrain slope	0.23	1.09	0.21
Elevation	**-2.92**	**1.21**	**-2.42***	**Elevation**	**-8.86**	**1.97**	**-4.51*****	Elevation	-1.13	1.24	-0.91
Litterfall depth	0.02	0.04	0.52	**Litterfall depth**	**-0.17**	**0.07**	**-2.34***	Litterfall depth	0.04	0.04	0.91
Canopy openness 2017	0.03	0.05	0.64	Canopy openness 2017	-0.08	0.07	-1.11	Canopy openness 2017	-0.08	0.05	-1.58
Canopy openness 2008	0.02	0.04	0.65	Canopy openness 2008	0.03	0.05	0.64	**Canopy openness 2008**	**-0.11**	**0.05**	**-2.28***

Table 3. Akaike's information criterion values for four competing hypothesis explaining spatial relationships at distance r = 1–50 m between small and large trees, and between medium and large trees of conspecifics of three *Myrcia* species sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. Bold indicates the best fitted model. Bold face indicates the most parsimonious model(s).

Conspecifics interactions	Independence	Association due to dispersal limitation	Association due to habitat filtering	Association due to the combination of dispersal limitation and habitat filtering	
Intensity function	$\lambda_1(x,y)$	$\lambda_d(x,y)$	$\lambda_h(x,y)$	$\sqrt{\lambda_d \cdot \lambda_h}$	Fitted value of σ
M. brasiliensis					
Large x Small trees	**-158.58**	-152.78	-144.56	-146.9	20m
Large x Medium trees	**-119.88**	-85.48	-107.06	-89.7	20m
M. multiflora					
Large x Small trees	-121.28	**-179.66**	-144.78	-158.6	9m
Large x Medium trees	-106.12	-150.42	-159.78	**-162.16**	9m
M. racemosa					
Large x Small trees	**-159.58**	95.52	-159.74	-142.3	15m
Large x Medium trees	**-171.90**	-130.62	-163.84	-159.6	15m

Figure 1. Distribution of individuals of different size classes of three *Myrcia* species in a 1-ha plot of white-sand flooded forest, southeastern Brazil. For size thresholds, please see the text.

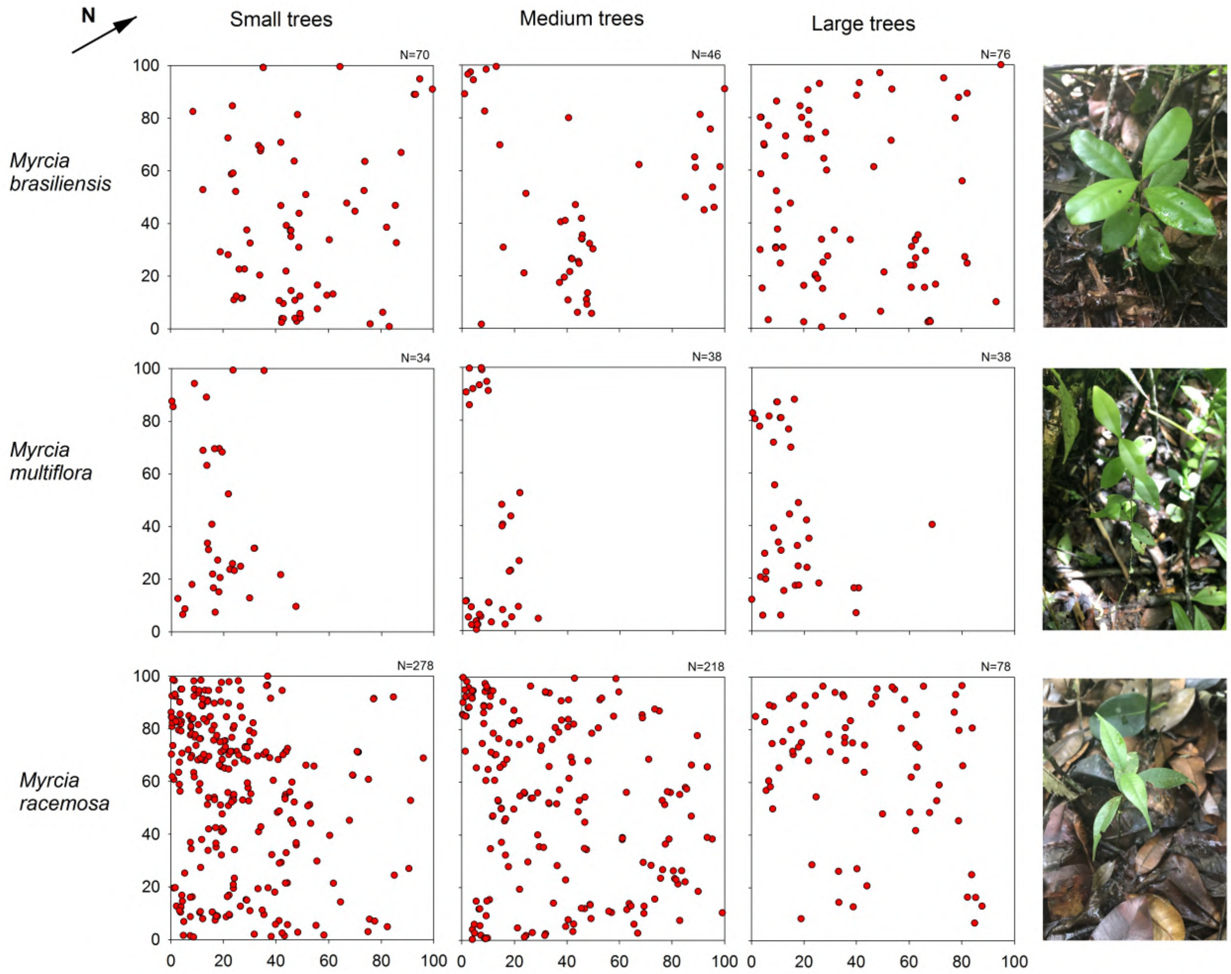


Figure 2. Maps of environmental variables measured in a 1-ha plot of white-sand flooded forest, southeastern Brazil.

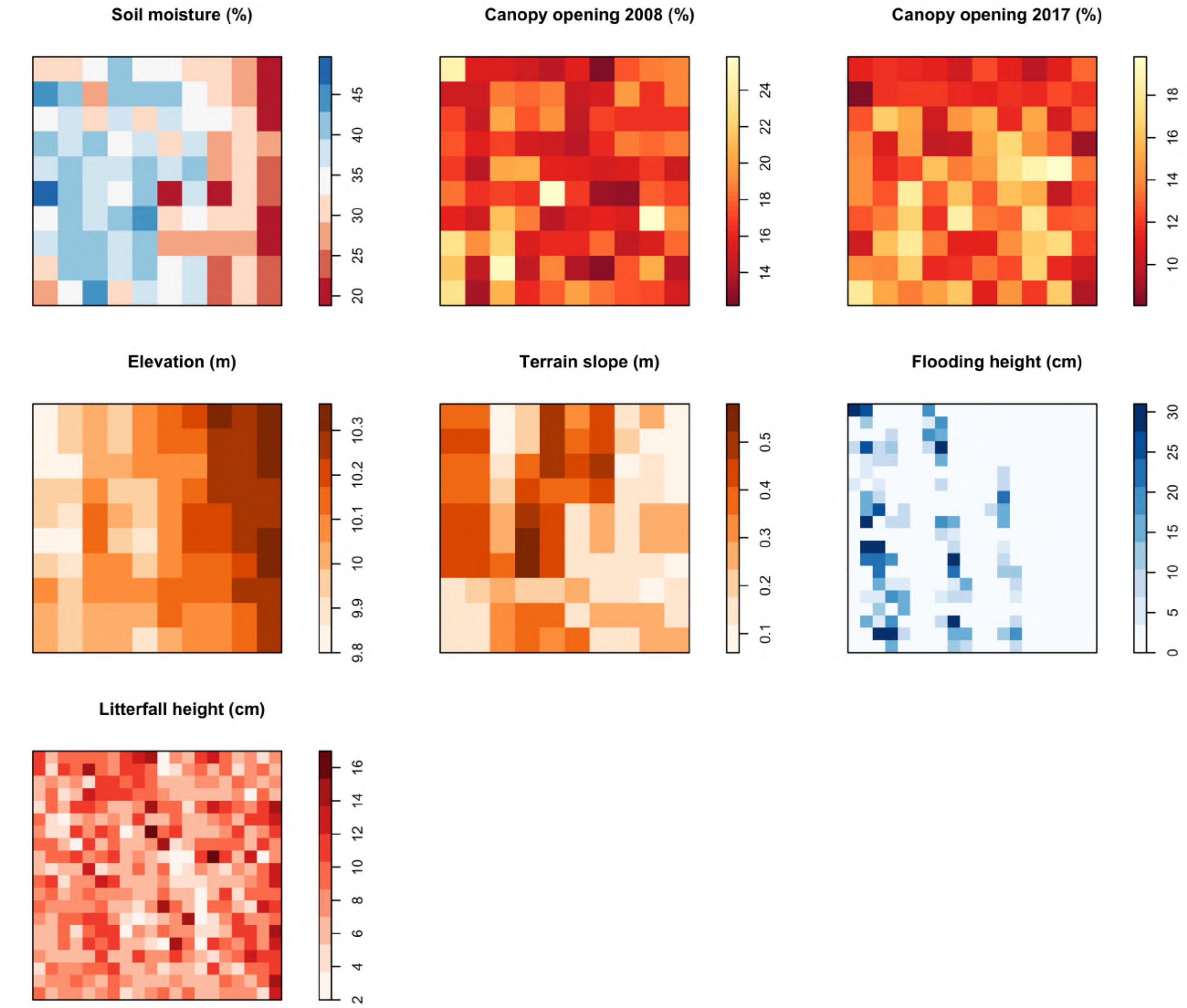


Figure 3. Spatial relationship, as measured by the bivariate pair correlation function $g_{12}(r)$, between medium trees of *Myrcia multiflora* and *M. racemosa* (pairwise) sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. The spatial relationship was compared to a null model representing large-scale habitat association. The observed $g_{12}(r)$ is represented by closed circles, the mean $g_{12}(r)$ of 199 simulations by grey solid lines, and the global simulation envelope at $\alpha = 5\%$ by dotted lines. The black horizontal line at $g_{12}(r) = 1$ is the expectation for spatial independence between congeners.

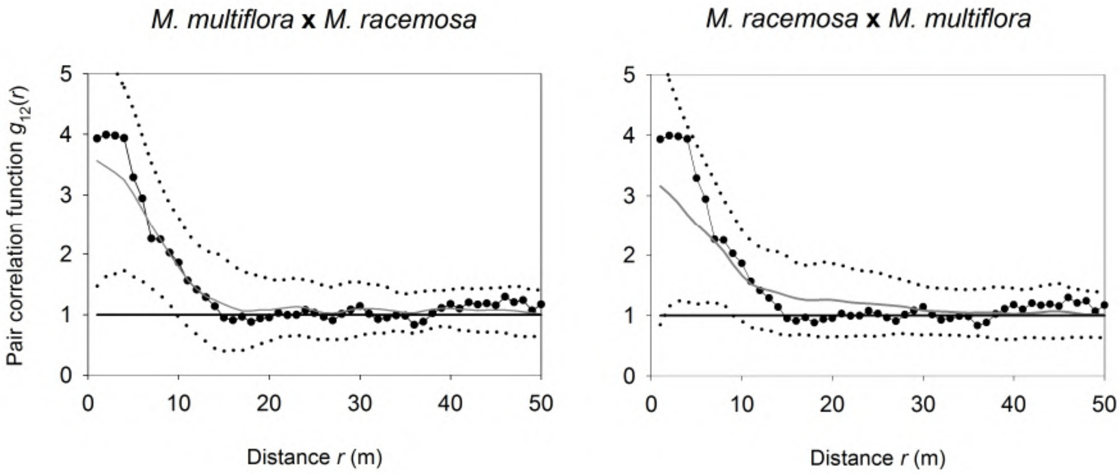
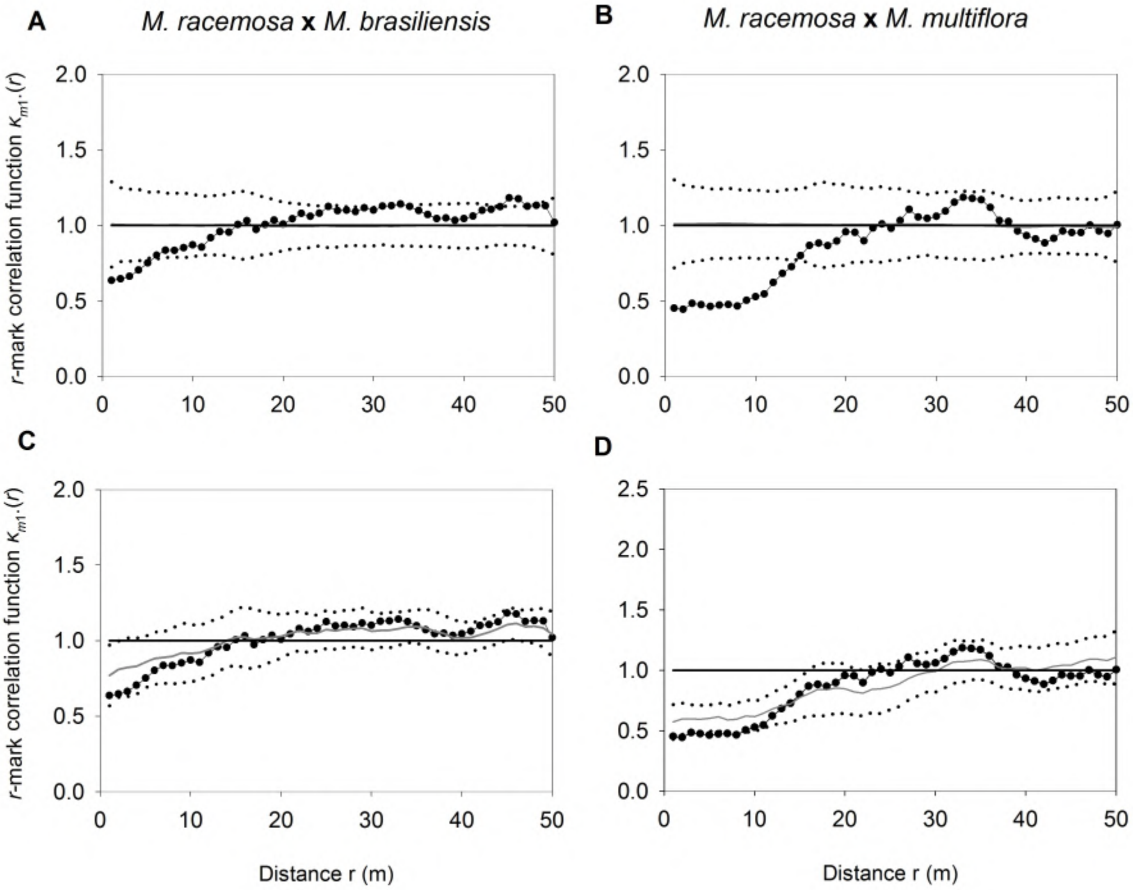
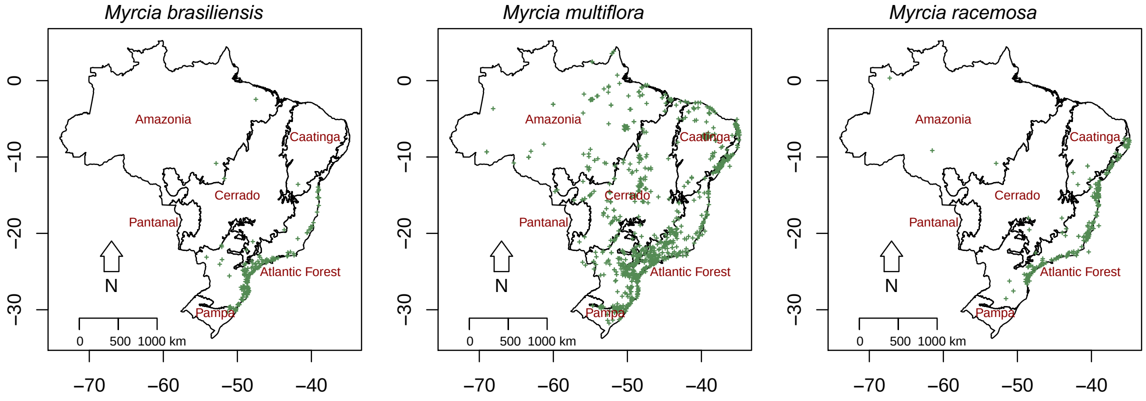


Figure 4. Mean stem diameter at soil height (DSH), as measured by the bivariate *r*-mark correlation function $\kappa_{m1.}(r)$, between medium trees of *Myrcia racemosa* in relation to *M. brasiliensis* and *M. multiflora* (pairwise) sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. The mean DSH was compared to the independent marking null model (A and B) and to the local random marking null model with $R = 25$ m (C and D). The observed $\kappa_{m1.}(r)$ is represented by closed circles, the mean $\kappa_{m1.}(r)$ of 199 simulations by grey solid lines, and the global simulation envelope at $\alpha = 5\%$ by dotted lines. The horizontal line at $\kappa_{m1.}(r) = 1$ is the expectation for independence between DSH and distance between congeners.



Appendix S1. Geographical distribution of *Myrcia brasiliensis*, *M. multiflora* and *M. racemosa* in Brazil. Data obtained from the speciesLink platform (2019). The green crosses are the coordinates reported by biological collections; the delimited regions represent the different phytogeographical domains in Brazil.

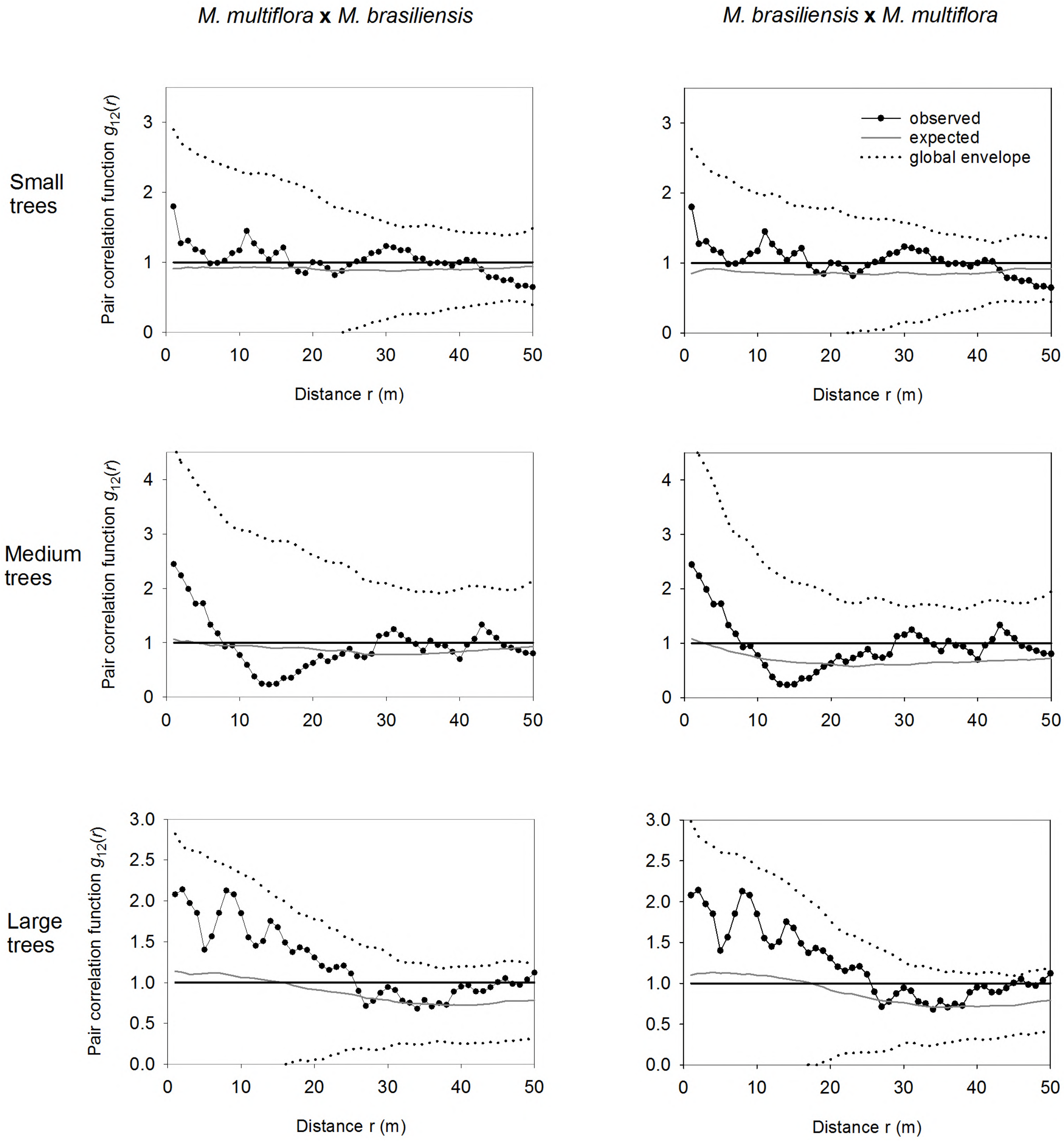


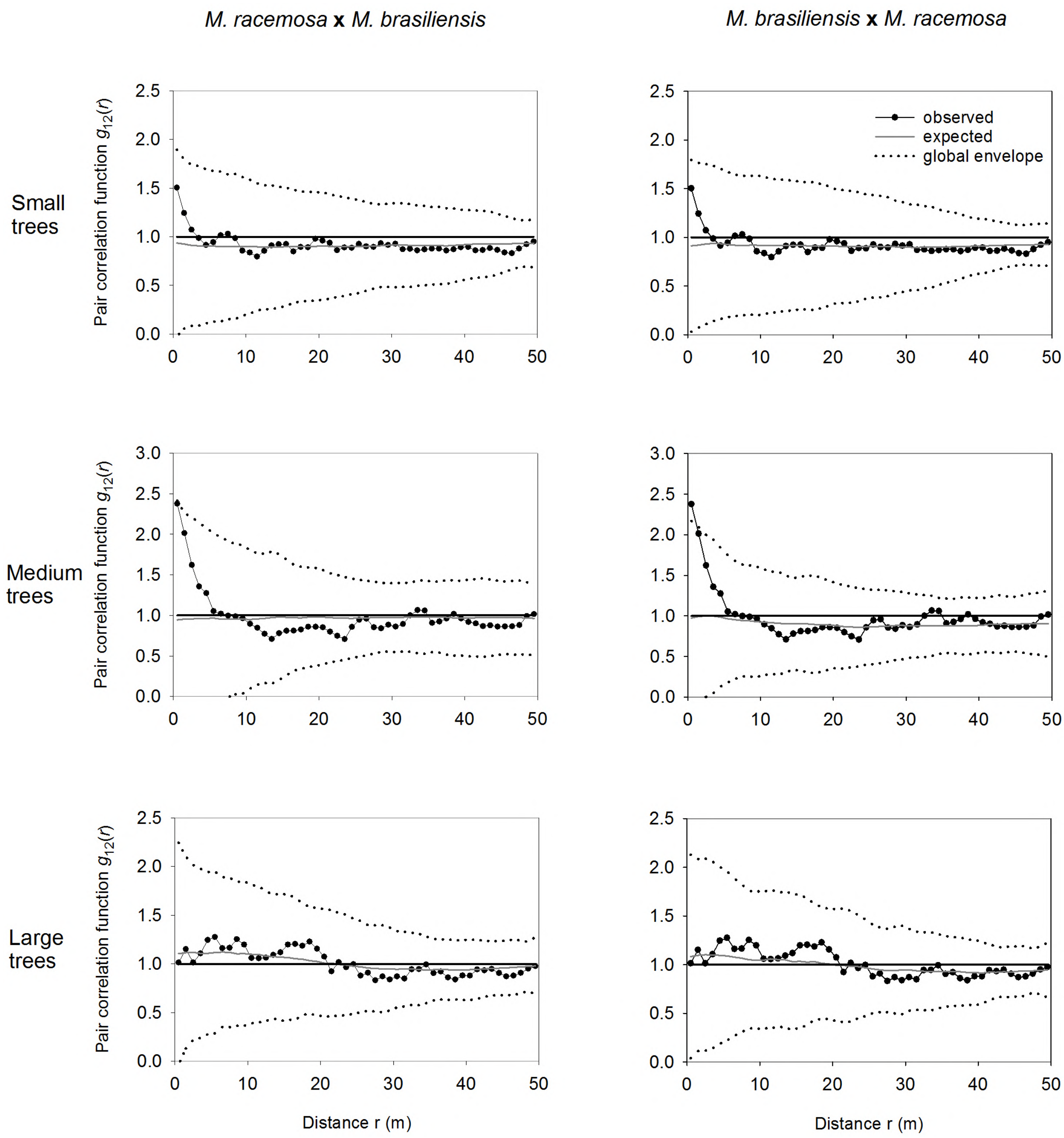
Appendix S2. Tree and palm species, their abundance and occurrence in dry, flooded or both environments in a 1-ha plot of white-sand flooded forest, southeastern Brazil. Bold indicates abundant species (> 30 individuals). Environment indicates that all individuals of each species were located in exclusively flooded, dry or both subplots (10 x 10 m).

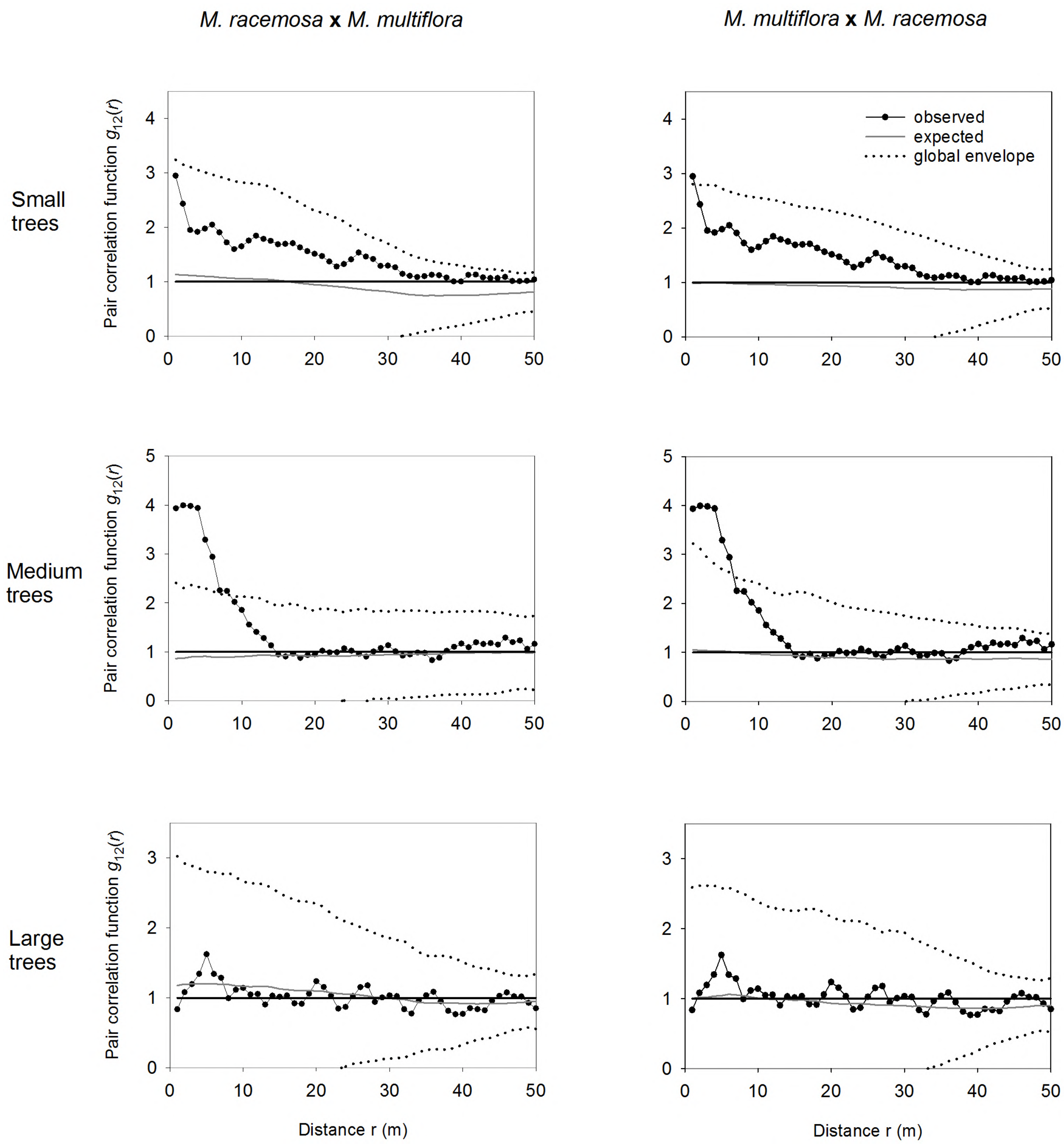
Family	**Species**	**Abundance**	**Environment**
Annonaceae	*Guatteria australis*	3	both
Annonaceae	***Guatteria* sp. 4**	**41**	both
Aquifoliaceae	*Ilex integerrima*	7	both
Araliaceae	***Schefflera angustissima***	**31**	both
Arecaceae	***Euterpe edulis***	**142**	both
Bignoniaceae	***Jacaranda puberula***	**78**	both
Celastraceae	***Maytenus littoralis***	**51**	both
Celastraceae	*Maytenus* sp.	9	both
Chrysobalanaceae	*Hirtella hebeclada*	2	both
Clusiaceae	***Garcinia gardneriana***	**36**	both
Clusiaceae	*Kielmeyera petiolaris*	26	both
Elaeocarpaceae	*Sloanea guianensis*	7	both
Erythroxylaceae	*Erythroxylum* sp.	6	both
Euphorbiaceae	***Alchornea triplinervia***	**67**	both
Fabaceae	*Andira fraxinifolia*	23	both
Fabaceae	*Inga edulis*	3	both
Fabaceae	*Inga subnuda*	20	both
Lacistemataceae	*Lacistema lucidum*	5	both
Lacistemataceae	*Lacistema pubescens*	4	both
Lauraceae	*Aniba viridis*	2	both
Lauraceae	*Nectandra oppositifolia*	26	both
Malpighiaceae	*Byrsonima ligustrifolia*	2	both
Melastomataceae	*Miconia prasina*	1	both
Meliaceae	***Guarea macrophylla subsp. tuberculata***	**71**	both
Myristicaceae	*Virola bicuhyba*	3	both
Myrtaceae	*Calyptranthes lucida*	4	both
Myrtaceae	*Eugenia astringens*	9	both
Myrtaceae	*Eugenia brasiliensis*	12	both
Myrtaceae	*Eugenia fusca*	5	both
Myrtaceae	***Eugenia verticillata***	**41**	both
Myrtaceae	*Marlierea obscura*	5	both
Myrtaceae	***Marlierea tomentosa***	**33**	both
Myrtaceae	***Myrcia brasiliensis***	**77**	both
Myrtaceae	***Myrcia multiflora***	**49**	both
Myrtaceae	***Myrcia racemosa***	**152**	both
Nyctaginaceae	*Guapira opposita*	25	both
Peraceae	***Pera glabrata***	**248**	both
Phyllanthaceae	*Hieronyma alchorneoides*	5	both
Primulaceae	*Myrsine venosa*	24	both
Proteaceae	*Euplassa cantareirae*	19	both
Proteaceae	*Roupala montana var. brasiliensis*	3	both
Rubiaceae	*Faramea pachyantha*	15	both
Rubiaceae	*Genipa infundibuliformis*	5	both
Sapindaceae	*Cupania oblongifolia*	3	both
Sapindaceae	*Matayba elaeagnoides*	3	both
Urticaceae	*Coussapoa microcarpa*	5	both
Anacardiaceae	*Tapirira guianensis*	9	flooded
Apocynaceae	*Aspidosperma* sp.	3	flooded
Apocynaceae	*Tabernaemontana laeta*	1	flooded
Aquifoliaceae	*Ilex theezans*	6	flooded
Araliaceae	*Oreopanax capitatus*	1	flooded
Arecaceae	*Astrocaryum aculeatissimum*	4	flooded
Chrysobalanaceae	*Couepia venosa*	2	flooded
Clusiaceae	*Calophyllum brasiliense*	9	flooded
Clusiaceae	*Clusia criuva subsp. parviflora*	1	flooded
Fabaceae	*Abarema brachystachya*	3	flooded
Fabaceae	*Balizia pedicellaris*	1	flooded

Fabaceae	*Fabaceae* sp. 4	1	flooded
Fabaceae	*Inga* sp.	1	flooded
Fabaceae	*Lonchocarpus cultratus*	2	flooded
Fabaceae	*Ormosia arborea*	4	flooded
Fabaceae	*Swartzia simplex var. grandiflora*	3	flooded
Fabaceae	*Tachigali denudata*	1	flooded
Lauraceae	*Ocotea rariflora*	1	flooded
Melastomataceae	*Miconia dodecandra*	1	flooded
Melastomataceae	*Miconia rigidiuscula*	3	flooded
Melastomataceae	*Miconia* sp.	1	flooded
Melastomataceae	*Miconia* sp. 1	1	flooded
Melastomataceae	*Miconia* sp. 3	1	flooded
Moraceae	*Sorocea jureiana*	2	flooded
Myrtaceae	*Calyptranthes concinna*	12	flooded
Myrtaceae	*Eugenia badia*	1	flooded
Myrtaceae	*Eugenia copacabanensis*	1	flooded
Myrtaceae	*Eugenia handroana*	3	flooded
Myrtaceae	*Eugenia monosperma*	1	flooded
Myrtaceae	*Eugenia mosenii*	1	flooded
Myrtaceae	*Eugenia speciosa*	3	flooded
Myrtaceae	*Marlierea racemosa*	1	flooded
Myrtaceae	*Marlierea spectabilis*	1	flooded
Myrtaceae	*Myrcia spectabilis*	4	flooded
Myrtaceae	*Myrtaceae* sp. 10	1	flooded
Myrtaceae	*Syzygium jambos*	6	flooded
Primulaceae	*Myrsine coriacea*	5	flooded
Rosaceae	*Prunus myrtifolia*	1	flooded
Rubiaceae	*Amaioua intermedia*	13	flooded
Rubiaceae	*Posoqueria latifolia*	7	flooded
Sapindaceae	*Cupania vernalis*	1	flooded
Sapotaceae	*Chrysophyllum flexuosum*	1	flooded
Theaceae	*Laplacea fruticosa*	2	flooded
Urticaceae	*Cecropia glaziovii*	1	flooded
Annonaceae	*Guatteria* sp.	2	dry
Aquifoliaceae	*Ilex dumosa*	1	dry
Elaeocarpaceae	*Sloanea hirsuta*	1	dry
Euphorbiaceae	*Margaritaria nobilis*	2	dry
Lamiaceae	*Vitex cymosa*	1	dry
Lauraceae	*Endlicheria paniculata*	1	dry
Lauraceae	*Persea willdenovii*	1	dry
Melastomataceae	*Miconia latecrenata*	22	dry
Monimiaceae	*Mollinedia schottiana*	1	dry
Moraceae	*Ficus insipida*	1	dry
Moraceae	*Sorocea hilarii*	1	dry
Myrtaceae	*Campomanesia guaviroba*	1	dry
Myrtaceae	*Eugenia multicostata*	1	dry
Myrtaceae	*Marlierea sylvatica*	1	dry
Myrtaceae	*Myrcia pubipetala*	3	dry
Myrtaceae	*Myrcia splendens*	3	dry
Myrtaceae	*Psidium cattleianum*	1	dry
Olacaceae	*Heisteria silvianii*	1	dry
Polygonaceae	*Coccoloba glaziovii*	4	dry
Rubiaceae	*Coussarea meridionalis var. porophylla*	1	dry

Appendix S3. Spatial relationship, as measured by the bivariate pair correlation function $g_{12}(r)$, between individuals in the same size class of three *Myrcia* species (pairwise) sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. The observed $g_{12}(r)$ is represented by closed circles, the mean $g_{12}(r)$ of 199 pattern reconstruction simulations of the point pattern underlying the independence null model by grey solid lines, and the global simulation envelope at $\alpha = 5\%$ by dotted lines. The location of the first species was randomized while the location of the second species was kept fixed. The black horizontal line at $g_{12}(r) = 1$ is the expectation for spatial independence between congeners without large-scale habitat association.




M. racemosa x M. brasiliensis
M. brasiliensis x M. racemosa
Small trees
Medium trees
Large trees
Pair correlation function g12(r)
observed
expected
global envelope
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
10
20
30
40
50
Distance r (m)


M. racemosa **x** *M. multiflora*
M. multiflora **x** *M. racemosa*
Small trees
Medium trees
Large trees
Pair correlation function $g_{12}(r)$
observed
expected
global envelope
0
1
2
3
4
5
0
10
20
30
40
50
Distance r (m)

Capítulo 2

Environmental heterogeneity, but not negative density-dependence and diffuse competition, influences mortality and size of congeneric trees in a seasonally flooded tropical forest

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Abstract

Species coexistence within the same environmental patches should be possible if direct competition is overridden by other mechanisms such as diffuse competition and conspecific negative density-dependence (CNDD). Congeneric species are a suitable model for examining ecological processes because they tend to show similar niches due to their close phylogenetic relatedness. This study aims to find evidence of diffuse competition and CNDD by examining the spatial structure of mortality and size in three *Myrcia* species. We conducted a population census of the three species in 1-ha plot of white-sand flooded forest in southeast Brazil, where the species co-occur in seasonally flooded patches. One year later, we checked all previously sampled individuals to record mortality. The individuals of each species were divided into small and large trees based on diameter at soil height. We additionally used forest inventory data available for a period of ~10 yr to analyze mortality of large trees and to assess the effects of large heterospecifics on the species studied. We analyzed spatial patterns of mortality and size for small and large trees of each *Myrcia* species separately and for their joined pattern in relation to the neighborhood densities of conspecifics (small and large trees), congenerics (small and large trees) and heterospecifics (large trees). We compared observed patterns to those expected under null models of independent marking. Overall, the mortality and size of the species and of their joined pattern were independent of the density of conspecifics, congenerics, and heterospecifics. Few exceptions were explained by environmental heterogeneity. Thus, we did not find evidence of the action of diffuse competition and CNDD on the species studied. Our results reinforce the importance of habitat filtering to the structuring of the community studied. Our contribution consists of discarding the investigated mechanisms and suggesting an alternative hypothesis for the coexistence of the *Myrcia* species, i.e. niche differentiation.

Keywords: environmental filtering, flooding, interspecific competition, intraspecific competition, niche theory, tropical forest.

Introduction

A central issue in community ecology is to understand the ecological processes that promote the coexistence of tree species in megadiverse tropical forests (Brown 2014). The main mechanisms promoting coexistence are niche-based processes, such as environmental filtering and interspecific competition (Wright 2002). According to niche theory, species with similar environmental requirements compete within suitable patches or differ in resource acquisition (Kraft et al. 2015, Wagg et al. 2017).

Nevertheless, direct competition between species with similar environmental requirements might be overridden by other mechanisms such as diffuse competition from heterospecifics and conspecific negative density-dependence (CNDD; Chesson 2000), allowing species to coexist within the same environmental patches. In diffuse competition, simultaneous negative interactions among many species promote coexistence by suppressing the competitive advantage of stronger species over weaker ones (Godoy et al. 2017). However, in harsh environments such as the white-sand flooded tropical forest in the Brazilian Atlantic Forest, interspecific competition is not expected to be strong, as postulated by the stress-gradient hypothesis (He et al. 2013), and other mechanisms such as CNDD may be more important (Kim & Ohr 2020). In addition, the commonly observed spatial aggregation of species in tropical forests (Condit et al. 2000) can lead to several density-dependent effects (Uriarte et al. 2005, Zhu et al. 2015a).

In the stabilizing CNDD mechanism, negative conspecific interactions are stronger than negative heterospecific interactions and therefore a given species is more strongly negatively affected by local conspecific densities than by local heterospecific densities (Chesson 2000, Zhu et al. 2015a, Liu et al. 2022). Several mechanisms can lead to such pattern, for example, locally high conspecific densities can result in strong intraspecific competition for resources (Tilman 1982) as well as in the attraction and spread of species-specific natural enemies (Janzen 1970, Connell 1971). Consequently, mortality might increase with increasing conspecific densities and growth might decrease in patches with higher conspecific densities (Hubbell et al. 2001, Comita & Hubbell 2009, Comita et al. 2014), which should allow the establishment of other species in the community (Chesson 2000).

Small plants are especially susceptible to density-dependent mortality factors (Comita et al. 2014) due to high initial seedling densities resulting from limited seed dispersal (Comita & Hubbell 2009) combined with a high susceptibility to natural enemies (Janzen 1970, Mangan et al. 2010, Terborgh 2012). Additionally, small plants might suffer strong asymmetric competition from large trees (Wright 2002, Lin et al. 2012). Differences among species in susceptibility to natural enemies may be related to the degree of adaptation to the local environment, i.e., species at the edge of their environmental tolerance may be more vulnerable to the attack of natural enemies (Comita et al. 2010). Also, species occurring in harsh environments may show a trade-off between environmental tolerance and susceptibility to natural enemies. In the white-sand flooded tropical forest, the seasonal flooding requires trees to adapt for prolonged inundation (Johnson et al. 2017). Additionally, high soil moisture may increase the susceptibility of plants to pathogens and herbivores (Swinfield et al. 2012).

Congeneric species are a suitable model to examine the ecological processes that maintain diversity in communities because they tend to show similar niches due to their close phylogenetic relatedness (Burns & Strauss 2011, Baraloto et al. 2012). Looking at congeneric species is especially revealing in harsh environments that restrict plant growth and establishment because such harsh environments may promote divergence in resource acquisition among species and change competitive outcomes (Muench & Elsey-Quirk 2019). Thus, an intriguing question is how three *Myrcia* species (Myrtaceae) that are widely distributed in the Brazilian Atlantic Forest can co-occur in patches subject to flooding in a white-sand tropical forest (Ribeiro et al. 2021).

This study aims to find evidence of the mechanisms that act at the neighborhood scale and maintain diversity in communities, namely diffuse competition and CNDD, by examining the spatial structure of populations of three congeneric tropical tree species. After assessing aggregation and spatial associations of different size classes, our specific questions are: (1) is mortality higher in areas with high local densities of conspecifics and heterospecifics? (2) Are individuals smaller in areas with high local densities of conspecifics and heterospecifics? (3) Are density-dependent effects stronger for small trees than for large ones? (4) Are mortality and plant size influenced by environmental heterogeneity? Since the white-sand flooded tropical forest in southeastern Brazilian is subject to periodic flooding patches, we expect to detect weaker density-dependent effects of heterospecifics relative to conspecifics as well as stronger effects on small trees relative to large trees, indicating that CNDD is a stronger driver of species coexistence in the Brazilian white-sand flooded forest than diffuse competition, especially in small plants.

Material and methods

Study site and species studied

This study was conducted in a permanent 1-ha plot of white-sand flooded forest in southeast Brazil (23°21′S and 44°51′W). Part of the plot is seasonally flooded due to the exposure of the water table, which influences the distribution of plant species (Diniz 2009). The distribution of our three study species, *Myrcia brasiliensis*, *M. multiflora,* and *M. racemosa,* is associated with areas subject to seasonal flooding in the plot (Ribeiro et al. 2021), even though the three species are widely distributed in the Brazilian Atlantic Forest. This indicates that the three *Myrcia* species occur in the harsh environment of the white-sand flooded tropical forest at the edge of their environmental tolerance. A detailed description of the study site and species studied can be found in Ribeiro et al. (2021).

Data collection

Between July 2016 and February 2017, we conducted a population census of our three species studied in the plot. We checked all previously sampled individuals between October 2017 and February 2018 to record mortality. To assess the effects of heterospecifics on mortality and size of the three *Myrcia* species, we used forest inventory data collected in 2015 in the study plot, available at ForestPlots.net (Lopez-Gonzales et al. 2011). The heterospecifics comprise 110 species and 1586 trees with a diameter at breast height (DBH) ≥ 4.8 cm.

Data analysis

Size classes

The individuals of the three *Myrcia* species were divided into small and large trees based on diameter at soil height (DSH) and taking into account adequate numbers of surviving and dead individuals for spatial point pattern analysis. Small trees are defined as individuals with DSH ≤ 10.0 cm (small and medium size classes in Ribeiro et al. 2021) and large trees are those with DSH > 10.0 cm (large size class in Ribeiro et al. 2021). Due to the small number of large dead trees sampled ~1 yr after our population census (please see Figure 1), we performed spatial point patterns analyses of mortality for large trees in a ~10 yr period (2005-2015). For this, we used forest inventory data available at ForestPlots.net (Lopez-Gonzales et al. 2011), which included trees with DBH ≥ 4.8 cm.

We assessed the effects on mortality and size of each *Myrcia* species separately in relation to the density of conspecifics (small and large trees) and heterospecifics (large trees). We also assessed density-dependent effects on the joined pattern of the three *Myrcia* species because congeners can show symmetric competition and share natural enemies due to their close phylogenetic relatedness (Liu et al. 2012, Godoy et al. 2014). We hereafter refer to the set of individuals of the three *Myrcia* species as congenerics.

Spatial distribution pattern of size classes

To test if each size class of the three *Myrcia* species and their joined congeneric pattern showed an aggregated distribution pattern at the moment of our population census (2016-2017), we used the univariate pair correlation function $g_{11}(r)$, which can be interpreted as a normalized neighborhood density. The $g_{11}(r)$ calculates the average number of neighbours within a ring with radius *r* (and width *dr*) centered at a focal point of the pattern, divided by the intensity λ of the point pattern in the study area (the number of individuals divided by area). We used a ring width of $dr = 5$ m and compared the observed $g_{11}(r)$ to pointwise simulation envelopes, being the 5th lowest and highest values expected under 199 simulations the null model of complete spatial randomness (CSR). The expectation under CSR is $g_{11}(r) = 1$ and departures above the pointwise simulation envelopes indicate aggregation at distance *r* (Wiegand & Moloney 2014).

To test if small (pattern 2) and large (pattern 1) trees of the three *Myrcia* species and their joined congeneric pattern were spatially associated, we used the bivariate pair correlation function $g_{12}(r)$, which is analogous to the univariate function, but now the $g_{12}(r)$ calculates the average number of neighbours of pattern 2 within a ring with radius *r* centered at a focal point of pattern 1, divided by the intensity λ_2 of point pattern 2 in the study area. For the calculation of $g_{12}(r)$, we fixed the location of pattern 1 points and randomized pattern 2 points following a CSR null model. The expectation under the null model is $g_{12}(r) = 1$ and departures above the simulation envelope indicate spatial association of small and large trees (Wiegand & Moloney 2014).

Density-dependent effects on mortality

To test if mortality of individuals of pattern 1 (given by small or large trees of the three *Myrcia* species, or by their joined congeneric pattern) was higher in areas with high local densities of individuals of pattern 1, we used the univariate function dd_1 for a binary mark of pattern 1 ($d1$: "dead" or $s1$: "alive"). The function dd_1 is the ratio

$$dd_1(r) = \lambda_1 g_{d1,1}(r) / \lambda_1 g_{s1,1}(r)$$

of the neighbourhood densities $\lambda_1 g_{d1,1}(r)$ and $\lambda_1 g_{s1,1}(r)$ of pattern 1 at distance *r* of dead and surviving individuals of pattern 1, respectively. The $g_{d1,1}(r)$ and $g_{s1,1}(r)$ are the partial pair correlation functions giving the aggregation of points of pattern 1 (i.e., with marks "surviving" and "dead"; $s1+d1$) around points with the mark "dead" ($d1$) and "surviving" ($s1$), respectively. The λ_1 is the intensity of individuals of pattern 1 (i.e., number of individuals divided by the area of the plot). Thus, the function dd_1 measures density effects on mortality: it quantifies how many more individuals surround on average dead individuals compared with surviving individuals, and therefore estimates the strength and direction of the density-dependent effects on mortality (Jacquemyn et al. 2010).

To test the influence of a second pattern 2 (given by conspecific, congeneric, or heterospecific large trees) on the mortality of individuals of pattern 1 (as defined above), we used the bivariate function dd_2

$$dd_2(r) = \lambda_2 g_{d1,2}(r) \; / \; \lambda_2 g_{s1,2}(r)$$

that is analogous to the univariate function, but now the density of individuals of pattern 2 is determined around dead individuals of pattern 1 (i.e., $\lambda_2 g_{d1,2}(r)$) and surviving individuals of pattern 1 (i.e., $\lambda_2 g_{s1,2}(r)$). The λ_2 is the intensity of individuals of pattern 2 (i.e., number of individuals divided by the area of the plot). The function dd_2 therefore measures density effects of a second pattern on the mortality of individuals of the focal pattern: it quantifies how many more individuals of pattern 2 surround on average dead individuals of the focal pattern 1 compared with surviving individuals of the focal pattern 1.

To identify significant density-dependent effects, we compared the summary functions dd_1 and dd_2 to values expected under the "global" independent marking null model (as opposed to the corresponding "local" null model - see below in "Effects of environmental heterogeneity on mortality and size"), in which the marks "dead" and "alive" are randomly shuffled among individuals of the focal pattern while keeping the original location of the individuals fixed (Wiegand & Moloney 2014). If the observed values are above the simulation envelope, density-dependent effects are negative, i.e. mortality is higher in areas with high local densities of individuals, while values below the simulation envelope indicate positive density-dependent effects, i.e. survival is higher in areas with high local densities of individuals.

Density-dependent effects on size

To determine if the size of the individuals of pattern 1 (i.e., small or large trees of the three *Myrcia* species, or their joined congeneric pattern) was correlated with the density of nearby individuals of pattern 1, we used the univariate non-cumulative density correlation function $C_{m1,g11}(r)$ (Fedriani et al. 2015) with diameter at soil height (DSH) as the quantitative mark representing plant size. The non-cumulative density correlation function $C_{m1,g11}(r)$ is the standard Pearson cross-correlation coefficient between the sizes m_{1i} of individuals i of pattern 1 and the corresponding density $\lambda_1 g_{1i,1}(r)$ of individuals of pattern 1 at distance r around individuals i. Thus, $C_{m1,g11}(r)$ is given by:

$$C_{m1,g11}(r) = \frac{\sum_i [m_{1i} - \mu_1]\left[\lambda_1 g_{1i,1}(r) - \lambda_1 g_{1,1}(r)\right]}{\sqrt{\sum_i [m_{1i} - \mu_1]^2}\sqrt{\sum_i \left[\lambda_1 g_{1i,1}(r) - \lambda_1 g_{1,1}(r)\right]^2}}$$

where m_i is the DSH of the focal individual i, μ_1 is the mean DSH of individuals of pattern 1, $\lambda_1 g_{1i,1}(r)$ is the density of points of pattern 1 at distance r of the focal individual i of pattern 1, $g_{1i,1}(r)$ is the "local" univariate pair correlation function of individual i of pattern 1, and $g_{1,1}(r)$ is the common univariate pair correlation function of pattern 1 at distance r of pattern 1 (the average of $\lambda_1 g_{1i,1}(r)$ over all individuals i of the focal pattern). The function $C_{m1,g11}(r)$ is normalised by the product of the standard deviations of the marks m_{1i} and the local pair correlation functions ($\sigma_{m_{1i}}\sigma_{g_{i,1}}$).

To test the influence of pattern 2 (i.e., conspecific, congeneric, or heterospecific large trees) on the size of individuals of pattern 1 (as defined as above), we used the corresponding bivariate function $C_{m1,g12}(r)$

$$C_{m1,g12}(r) = \frac{\sum_i [m_{1i} - \mu_1]\left[\lambda_2 g_{1i,2}(r) - \lambda_2 g_{1,2}(r)\right]}{\sqrt{\sum_i [m_{1i} - \mu_1]^2}\sqrt{\sum_i \left[\lambda_2 g_{1i,2}(r) - \lambda_2 g_{1,2}(r)\right]^2}}$$

that is analogous to the univariate function, but now the size of the individuals of pattern 1 is correlated with the density of nearby individuals of pattern 2. The $\lambda_2 g_{1i,2}(r)$ is the density of points of pattern 2 at distance r of the focal individual i of pattern 1, $g_{1i,2}(r)$ is the "local" bivariate pair correlation function of individual i of pattern 1, and $g_{1,2}(r)$ is the common bivariate pair correlation function of pattern 2 at distance r of pattern 1 (the average of $\lambda_2 g_{1i,2}(r)$ over all individuals i of the focal pattern). The function $C_{m1,g12}(r)$ is normalised by the product of the standard deviations of the marks m_{1i} and the local pair correlation functions $(\sigma_{m_{1i}}\sigma_{g_{i,2}})$.

To identify significant density-dependent effects, we compared the summary functions $C_{m1,g11}(r)$ and $C_{m1,g12}(r)$ to values expected under the independent marking null model, in which DSH values are randomly shuffled among individuals of the focal pattern while keeping the original location of the individuals fixed (Fedriani et al. 2015). If the observed values are above the simulation envelope, density-dependent effects are positive, i.e. trees are larger in areas with high local densities of individuals, while values below the simulation envelope indicate negative density-dependent effects, i.e. trees are smaller in areas with high local densities of individuals.

Effects of environmental heterogeneity on mortality and size

In order to tease apart the effects of environmental heterogeneity and density-dependence on mortality and size, we compared the summary functions $dd(r)$ and $C_{m,g}(r)$ to values expected under the local independent marking null model. In this variation, the marks are shuffled only among individuals closer than a given distance R, representing an approximate size of environmental patches. If the summary functions now fall inside the simulation envelopes, previous departures can be attributed to higher or lower densities of individuals within more or less favorable patches, respectively. Conversely, departures from the local null model indicate density-dependent effects within environmentally similar patches (Wiegand & Moloney 2014). We used $R = 25$ m (a quarter of the plot) for the local null model.

Significance of patterns against a null model

To determine whether the observed values differed from the expectation according to the appropriate null model at a given distance r, we constructed pointwise simulation envelopes containing 95% of the values of the summary functions calculated during 199 Monte Carlo simulations (Jacquemyn et al. al 2010, Fedriani et al. 2015). Then, to accept or reject the null model for the entire 0-50 m-distance interval, we used global simulation envelopes to correct for the effect of pointwise multiple testing. In global envelopes, the significance level α of the test is valid for an entire given distance interval and not only for one distance r as for the pointwise test (Wiegand et al. 2016). We performed the spatial point pattern analyses using the *Programita* software (Wiegand & Moloney 2014), available at www.programita.org. Estimators and edge correction of $g(r)$ are detailed in Wiegand et al. (2016). In all analyses, we used a 1-m spatial resolution, which is much smaller than the plots, fine enough to answer our questions, and larger than the mapping error of the data (Wiegand & Moloney 2014).

Results

Myrcia racemosa was three times more abundant than *M. brasiliensis* and five times more abundant than *M. multiflora*. The three *Myrcia* species showed a higher number of small than large trees, with *M. racemosa* showing the largest difference in the proportion between size classes. While 14-20% of small trees of the three species died in a ~1-yr period, only one large tree (*M. racemosa*) died in the same period. Among the three species studied, *M. brasiliensis* showed the highest mortality of small trees. When we considered the ~10-yr period between forest inventories, mortality of trees with DBH ≥ 4.8 cm were as follows: 11% for *M. brasiliensis*, 29% for *M. multiflora*, and 7% for *M. racemosa* (Figure 1). Small trees of *M. multiflora* and *M. racemosa* showed similar DSH and were larger than small trees of *M. brasiliensis*. Considering large trees, DSH was larger for *M. brasiliensis* and smaller for *M. racemosa*. For *M. brasiliensis* and *M. multiflora,* mortality occurred predominately in the smallest individuals in the small size class, whereas for *M. racemosa*, dead trees showed more variable DSH both in the small and large size classes (Figure 2).

Both small and large trees of the three *Myrcia* species were aggregated. For *M. brasiliensis*, small trees were aggregated up to 25 m and large trees up to 9 m, and the size classes did not show spatial association. Small and large trees of *M. multiflora*, *M. racemosa*, and the joined pattern of the three *Myrcia* species were aggregated up to 25-40 m, and the size classes showed strong spatial association up to 35-40 m (Figure 3).

Overall, the mortality and size of the three focal *Myrcia* species and of their joined pattern were independent of the density of conspecifics, congenerics, and heterospecifics, with the few exceptions we describe in the following. The neighborhood density of heterospecifics up to 1 m resulted in positive effects on survival of large trees of the joined pattern of the three *Myrcia* species (Table 1; Appendix S1). The size of small trees of *M. racemosa* was negatively correlated with the neighborhood density of small conspecifics up to 16 m. On the other hand, the size of small trees of *M. racemosa* was positively correlated with the neighborhood density of heterospecifics between 15 m and 44 m. Last, the size of small trees of the joined pattern of the three *Myrcia* species showed a negative correlation with the neighborhood density of small congenerics between the distances of 6 m and 12 m, and a positive correlation with the neighborhood density of heterospecifics between the distances of 14 m and 24 m (Table 1; Appendix S2). However, all the cases described were completely explained by environmental heterogeneity (the summary functions fell inside the envelopes when we used the local independent marking null model) (Table 1; Appendix S1; Appendix S2).

Discussion

In this study, we searched for evidence of mechanisms of species coexistence by means of diffuse heterospecific competition and/or CNDD using as a model three *Myrcia* species that are widely distributed in the Brazilian Atlantic Forest and coexist in a white-sand flooded forest by sharing the same habitat within the forest (Ribeiro et al. 2021). Even though many studies showed the effects of diffuse competition and CNDD on community structuring (Comita et al. 2014, Zhu et al. 2015a), our refined spatial analysis showed that mortality and size of the three *Myrcia* species were basically independent of the local densities of conspecifics, congeners, and heterospecifics. Thus, we did not find the expected evidence of the action of diffuse competition and/or CNDD on the spatial patterns of the species studied. The few exceptions where we found effects of neighborhood densities on plant mortality and size were completely explained by environmental heterogeneity. This result agrees with a previous study that showed that the three *Myrcia* species show habitat association in the white-sand flooded tropical forest (Ribeiro et al. 2021).

We expected diffuse competition to be weaker than CNDD in the study site, as proposed by the stress-gradient hypothesis (He et al. 2013). Nevertheless, the absence of CNDD was not expected, especially for aggregated small trees that are positively associated with conspecific large trees, which are reported to suffer strong CNDD (e.g., Harms et al. 2000, Comita et al. 2009, 2010, 2014, Bagchi et al. 2014, Lebrija-Trejos et al. 2014). Seedlings are highly susceptible to mortality factors (Comita et al. 2014), with density-responsive natural enemies being their main mortality agents in tropical forests (Mangan et al. 2010, Terborgh 2012, Bagchi et al. 2014, Forrister et al. 2019). Because the three *Myrcia* species are at the edge of their environmental tolerance in the white-sand flooded forest studied, and due to the trade-off between environmental tolerance and susceptibility to natural enemies, we expected high density-dependent mortality caused by the attack of natural enemies (Comita et al. 2010, Swinfield et al. 2012). Nevertheless, we did not find density-dependent effects even on the joined pattern of the three *Myrcia* species, which likely share natural enemies due to their close phylogenetic relatedness (Liu et al. 2012). Seedling-seedling competition is considered weak (Wright 2002, Paine et al. 2008, Terborgh 2012) because seedlings are too small to interact through the acquisition of resources. However, competition among large trees and negative effects of large trees on the availability of resources to small trees have been previously reported (Comita et al. 2010, Lebrija-Trejos et al. 2014). Alternatively, and similarly to our results, some studies found evidences of neutral processes in white-sand tropical vegetation (Silva et al. 2015, Silva et al. 2019) and neutral effects among adults and of adults on seedlings (Queenborough et al. 2007, Kobe & Vriesendorp 2011, Zhu et al. 2015b, Wang et al. 2016).

Competition may become stronger as trees grow and thus play a more important role in community structuring (Comita et al. 2010). Although mortality is an extreme effect of competition among large trees (Getzin et al. 2008), we also did not find evidence of size decrease with increasing densities of neighbours. This result reinforces that diffuse competition and CNDD are not the main drivers of the coexistence of our three *Myrcia* species. Uriarte et al. (2004) found a similar result for most species studied in Barro Colorado Island, Panama, and suggested that environmental heterogeneity greatly influences tree growth. The comparison between the results of our two null models showed that the departures from simulation envelopes of the null model that does not constrain environmental effects disappeared once the effect of habitat was considered in approximation. This suggests that environmental heterogeneity is more important than neighborhood interactions in driving the mortality and growth of the three *Myrcia* species. Additionally, interspecific competition between species pairs (i.e. direct competition) might be more important than diffuse competition (Wiegand et al. 2007), especially between closely related species (Cavender-Bares et al. 2009). Nevertheless, a previous study showed no signatures of interspecific competition in the spatial patterns between pairs of *Myrcia* species, and between each *Myrcia* species and the most abundant species of the white-sand flooded forest studied (Ribeiro et al. 2021).

The lack of neighborhood effects found here might have different explanations. First, for some species, density-dependent mortality during germination may be sufficiently strong to thin out seedlings to levels below which neighborhood effects are not detectable (Harms et al. 2000, Comita & Hubbell 2009). Second, more recently, some studies have shown that signatures of spatial processes are often very weak in species-rich forests (Fortunel et al. 2018). This may be explained by neutrality in neighborhood interactions, as predicted by the neutral theory (Hubbell 2001), or by demographic heterogeneity in the biotic neighborhood, as proposed in the dilution hypothesis (Wiegand et al. 2012, Wang et al. 2016). Third, ecological processes that produce opposite effects, such as interspecific competition and facilitation, may cancel each other out, resulting in an overall lack of neighborhood effects (McGill 2010, Punchi-Manage et al. 2015). Forth, the sample sizes of some of our analyses are relatively low, which can cause wider simulation envelopes. However, most results for the joined congeneric patterns and for the most abundant species *M. racemosa* were non-significant. Finally, and especially important for the species studied here, are interspecific trait differences that might lead to differences in resource acquisition (Adler et al. 2013). Thus, although species occur in the same habitat, they may avoid competition by using different resources (Reynolds et al. 2003). Experimental, observational, and analytical approaches could help elucidate the drivers of the lack of neighborhood effects in the Brazilian white-sand flooded forest.

In summary, our results reinforce the importance of habitat filtering to community structuring in white-sand flooded tropical forests as found by Ribeiro et al. (2021) and suggest that the abiotic environment exerts a strong pressure for closely related species to differentiate. This makes the processes that maintain and contribute to species coexistence in harsh environments even more intriguing. Thus, our findings contribute to a deeper understanding of the mechanisms that act at the neighborhood scale in the study site by discarding the investigated mechanisms, CNDD and diffuse competition, and suggesting an alternative hypothesis for the coexistence of the species studied, i.e. niche differentiation.

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References

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters*, *16*(10), 1294–1306. doi:10.1111/ele.12157

Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., Freckleton, R. P., Lewis, O. T. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, *506*, 85–88.

Baraloto, C., Hardy, O. J., Paine, C. E. T., Dexter, K. G., Cruaud, C., Dunning, L. T., Gonzalez, M. A., Molino, J. F., Sabatier, D., Savolainen, V., Chave, J. (2012). Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology*, *100*(3), 690–701.

Brown, J. H. (2014). Why are there so many species in the tropics? Journal of Biogeography, 41, 8–22. doi:10.1111/jbi.12228

Burns, J. H., Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. Proceedings of the National Academy of Sciences, 108(13), 5302–5307. doi:10.1073/pnas.1116085108

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*(7), 693–715. doi:10.1111/j.1461-0248.2009.01314.x

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.*, *31*, 343–366. doi:10.1146/annurev.ecolsys.31.1.343

Comita, L. S., Hubbell, S. P. (2009). Local neighborhood and species’ shade tolerance influence survival in a diverse seedling bank. Ecology, 90(2), 328–334.

Comita, L. S., Muller-Landau, H. C., Aguilar, S., Hubbell, S. P. (2010). Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. *Science*, *329*(5989), 330–332. doi:10.1126/science.1190772

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Zhu, Y. (2014). Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*, *102*, 845–856. doi:10.1111/1365-2745.12232

Condit, R., Ashton, P. S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Yamakura, T. (2000). Spatial patterns in the distribution of tropical tree species. Science, 288, 1414–1418. doi:10.1126/science.288.5470.1414

Connell, J. H. (1971). "On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees" in: Den Boer, PJ & Gradwell, GR (eds.) Dynamics of populations. Oosterbeek, the Netherlands: Centre for Agricultural Publishing and Documentation.

Diniz, F. V. (2009). *Composição e estrutura fitossociológica da regeneração natural na floresta de restinga alta em Picinguaba (Parque Estadual da Serra do Mar), município de Ubatuba, SP, Brasil.* Universidade Estadual Paulista.

Fedriani, J.M., Wiegand, T., Calvo, G., Suárez-Esteban, A., Jácome, M., Zywiec, M., Delibes, M. (2015). Unravelling conflicting density- and distance-dependent effects on plant reproduction using a spatially explicit approach. *Journal of Ecology* 103: 1344–1353.

Forrister, D. L., Endara, M. J., Younkin, G. C., Coley, P. D., Kursar, T. A. (2019). Herbivores as drivers of negative density dependence in tropical forest saplings. *Science*, *363*(6432), 1213–1216. doi:10.1126/science.aau9460

Fortunel, C., Lasky, J. R., Uriarte, M., Valencia, R., Wright, S. J., Garwood, N. C., Kraft, N. J. B. (2018). Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest. Ecology, 99(10), 2272–2283. doi:10.1002/ecy.2441

Getzin, S., Wiegand, K., Schumacher, J., Gougeon, F. A. (2008). Scale-dependent competition at the stand level assessed from crown areas. *Forest Ecology and Management*, *255*, 2478–2485.

Godoy, O., Kraft, N. J. B., Levine, J. M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. Ecology Letters, 17(7), 836–844. doi:10.1111/ele.12289

Godoy, O., Stouffer, D. B., Kraft, N. J. B., & Levine, J. M. (2017). Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. Ecology, 98(5), 1193–1200. doi:10.1002/ecy.1782

Harms, K. E., Wright, S. J., Calderón, O., Hernández, A., Herre, E. A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature, 404(6777), 493–495. doi:10.1038/35006630

He, Q., Bertness, M. D., Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters*, *16*(5), 695–706. doi:10.1111/ele.12080

Hubbell, S. P., Ahumada, J. A., Condit, R., Foster, R. B. (2001). Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research*, *16*, 859–875.

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

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

Johnson, D. J., Condit, R., Hubbell, S. P., Comita, L. S. (2017). Abiotic niche partitioning and negative density dependence drive tree seedling survival in a tropical forest. Proceedings of the Royal Society B: Biological Sciences, 284(1869). doi:10.1098/rspb.2017.2210

Kim, D., Ohr, S. (2020). Coexistence of plant species under harsh environmental conditions: An evaluation of niche differentiation and stochasticity along salt marsh creeks. Journal of Ecology and Environment, 44(1). doi:10.1186/s41610-020-00161-y

Kobe, R. K., Vriesendorp, C. F. (2011). Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecology Letters, 14(5), 503–510. doi:10.1111/j.1461-0248.2011.01612.x

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology, 29, 592–599. doi:10.1111/1365-2435.12345

Lebrija-Trejos, E., Wright, S.J., Hernández, A., Reich, P.B. (2014). Does relatedness matter? Phylogenetic density-dependent survival of seedlings in a tropical forest. *Ecology* 95: 940–951.

Lin, L., Comita, L.S., Zheng, Z., Cao, M. (2012). Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *Journal of Ecology* 100: 905–914.

Liu, X., Liang, M., Etienne, R. S., Wang, Y., Staehelin, C., Yu, S. (2012). Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest. Ecology Letters, 15(2), 111–118. doi:10.1111/j.1461-0248.2011.01715.x

Liu, H., Xie, F., Shi, H., Shu, X., Zhang, K., Zhang, Q., & Dang, H. (2022). Disentangling the effects of biotic neighbors and habitat heterogeneity on seedling survival in a deciduous broad-leaved forest. Forest Ecology and Management, 519(June), 120339. doi:10.1016/j.foreco.2022.120339

Lopez-Gonzalez, G., Lewis, S.L., Burkitt, M., Phillips, O.L. (2011). ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. *Journal of Vegetation Science* 22: 610–613. doi: 10.1111/j.1654-1103.2011.01312.x

Lucas, E. J., Bünger, M. O. (2015). Myrtaceae in the Atlantic forest: their role as a "model" group. *Biodiversity and Conservation*, *24*, 2165–2180.

Mangan, S. A., Schnitzer, S. A., Herre, E. A., MacK, K. M. L., Valencia, M. C., Sanchez, E. I., Bever, J. D. (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, *466*(7307), 752–755. doi:10.1038/nature09273

McGill, B. J. (2010). Towards a unification of unified theories of biodiversity. Ecology Letters, 13, 627–642. doi:10.1111/j.1461-0248.2010.01449.x

Muench, A., Elsey-Quirk, T. (2019). Competitive reversal between plant species is driven by species-specific tolerance to flooding stress and nutrient acquisition during early marsh succession. *Journal of Applied Ecology*, (r), 1–12. doi:10.1111/1365-2664.13458

Paine, C. E. T., Harms, K. E., Schnitzer, S. A., Carson, W. P. (2008). Weak competition among tropical tree seedlings: Implications for species coexistence. Biotropica, 40(4), 432–440. doi:10.1111/j.1744-7429.2007.00390.x

Punchi-Manage, R., Wiegand, T., Wiegand, K., Getzin, S., Huth, A., Gunatilleke, C. V. S., Gunatilleke, I. A. U. N. (2015). Neighborhood diversity of large trees shows independent species patterns in a mixed dipterocarp forest in Sri Lanka. Ecology, 96(7), 1823–1834. doi:10.1890/14-1477.1

Queenborough, S. A., Burslem, D. F. R. P., Garwood, N. C., Valencia, R. (2007). Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. Ecology, 88(9), 2248–2258. doi:10.1890/06-0737.1

Reynolds, H. L., Packer, A., Bever, J. D., Clay, K. (2003). Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology, 84(9), 2281–2291. doi:10.1890/02-0298

Ribeiro, K. F. O., Martins, V. F., Wiegand, T., Santos, F. A. M. (2021). Habitat filtering drives the local distribution of congeneric species in a Brazilian white-sand flooded tropical forest. Ecology and Evolution, 11, 1797–1813. doi:10.1002/ece3.7169

Silva, J. L. A., Souza, A. F., Jardim, J. G., & Goto, B. T. (2015). Community assembly in harsh environments: The prevalence of ecological drift in the heath vegetation of South America. Ecosphere, 6(7). doi:10.1890/ES14-00548.1

Silva, J. L. A., Souza, A. F., & Santiago, L. S. (2019). Traits uncover quasi-neutral community assembly in a coastal heath vegetation. Journal of Plant Ecology, 12(4), 703–712. doi:10.1093/jpe/rtz007

Swinfield, T., Lewis, O. T., Bagchi, R., Freckleton, R. P. (2012). Consequences of changing rainfall for fungal pathogen-induced mortality in tropical tree seedlings. Ecology and Evolution, 2(7), 1408–1413. doi:10.1002/ece3.252

Terborgh, J. (2012). Enemies maintain hyperdiverse tropical forests. *American Naturalist*, *179*(3), 303–314. doi:10.1086/664183

Tilman, D. (1982). *Resource competition and community structure*. Monogr. Pop. Biol. 17. Princeton: Princeton University Press

Uriarte, M., Condit, R., Canham, C. D., Hubbell, S. P. (2004). A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology*, *92*(2), 348–360. doi:10.1111/j.0022-0477.2004.00867.x

Uriarte, M., Hubbell, S. P., John, R., Condit, R., Canham, C. D. (2005). Neighbourhood effects on sapling growth and survival in a neotropical forest and the ecological equivalence hypothesis. In D. Burslem, M. Pinard, & S. Hartley (Eds.), Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity. Cambridge University Press.

Wagg, C., Ebeling, A., Roscher, C., Ravenek, J., Bachmann, D., Eisenhauer, N., Mommer, L., Buchmann, N., Hillebrand, H., Schmid, B., Weisser, W. W. (2017). Functional trait dissimilarity drives both species complementarity and competitive disparity. Functional Ecology, 31, 2320–2329. doi:10.1111/1365-2435.12945

Wang, X., Wiegand, T., Kraft, N. J. B., Swenson, N. G., Davies, S. J., Hao, Z., Howe, R., Lin, Y., Ma, K., Mi, X., Su, S. H., Sun, I. F., Wolf, A. (2016). Stochastic dilution effects weaken deterministic effects of niche-based processes in species rich forests. Ecology, 97(2), 347–360. doi:10.1890/14-2357.1

Wiegand, T., Grabarnik, P., Stoyan, D. (2016). Envelope tests for spatial point patterns with and without simulation. Ecosphere 7: e01365.

Wiegand, T., Gunatilleke, S., Gunatilleke, N. (2007). Species associations in a heterogeneous Sri Lankan dipterocarp forest. *The American Naturalist*, *170*(4), E77–E95.

Wiegand, T., Huth, A., Getzin, S., Wang, X., Hao, Z., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N. (2012). Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *Proceedings of the Royal Society B: Biological Sciences* 279: 3312–3320.

Wiegand, T., Moloney, K. A. (2014). *Handbook of Spatial Point Pattern Analysis in Ecology*. Boca Raton: CRC Press.

Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.

Zhu, K., Woodall, C., Monteiro, J., Clark, J. (2015a). Prevalence and strength of density-dependent tree recruitment. *Ecology*, *96*(9), 2319–2327. doi:10.1890/14-1780.1.sm

Zhu, Y., Comita, L. S., Hubbell, S. P., Ma, K. (2015b). Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. Journal of Ecology, 103, 957–966. doi:10.1111/1365-2745.12414

Table 1. Density-dependent effects on mortality and size of three *Myrcia* species and their joined congeneric pattern. Individuals were sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. We compared the observed summary functions to expected values under the independent marking null model (global) and the local independent marking null model (local), which accounts for possible effects of environmental heterogeneity on plant mortality and size. The distances at which the observed summary functions departure from the global simulation envelopes are shown; (+) and (-) are positive and negative departures, respectively; no departures are represented by n.d.

Effects on	Focal pattern	Interactions with	Summary function	Species							
				M. brasiliensis		*M. multiflora*		*M. racemosa*		Joined pattern	
				Global	Local	Global	Local	Global	Local	Global	Local
Mortality	Small conspecifics	Small conspecifics	$dd_1(r)$	nd	nd	nd	nd	nd	nd		
		Large conspecifics	$dd_2(r)$	nd	nd	nd	nd	nd	nd		
		Large heterospecifics	$dd_2(r)$	nd	nd	nd	nd	nd	nd		
	Large conspecifics	Large conspecifics	$dd_1(r)$	nd	nd	nd	nd	nd	nd		
		Large heterospecifics	$dd_2(r)$	nd	nd	nd	nd	nd	nd		
	Small congenerics	Small congenerics	$dd_1(r)$							nd	nd
		Large congenerics	$dd_2(r)$							nd	nd
		Large heterospecifics	$dd_2(r)$							nd	nd
	Large congenerics	Large congenerics	$dd_1(r)$							nd	nd
		Large heterospecifics	$dd_2(r)$							**(-) 0-1 m**	nd
Size	Small conspecifics	Small conspecifics	$C_{m1,g11}(r)$	nd	nd	nd	nd	**(-) 0-16 m**	nd		
		Large conspecifics	$C_{m1,g12}(r)$	nd	nd	nd	nd	nd	nd		
		Large heterospecifics	$C_{m1,g12}(r)$	nd	nd	nd	nd	**(+) 15-44 m**	nd		
	Large conspecifics	Large conspecifics	$C_{m1,g11}(r)$	nd	nd	nd	nd	nd	nd		
		Large heterospecifics	$C_{m1,g12}(r)$	nd	nd	nd	nd	nd	nd		
	Small congenerics	Small congenerics	$C_{m1,g11}(r)$							**(-) 6-12 m**	nd
		Large congenerics	$C_{m1,g12}(r)$							nd	nd
		Large heterospecifics	$C_{m1,g12}(r)$							**(+) 14-24 m**	nd
	Large congenerics	Large congenerics	$C_{m1,g11}(r)$							nd	nd
		Large heterospecifics	$C_{m1,g12}(r)$							nd	nd

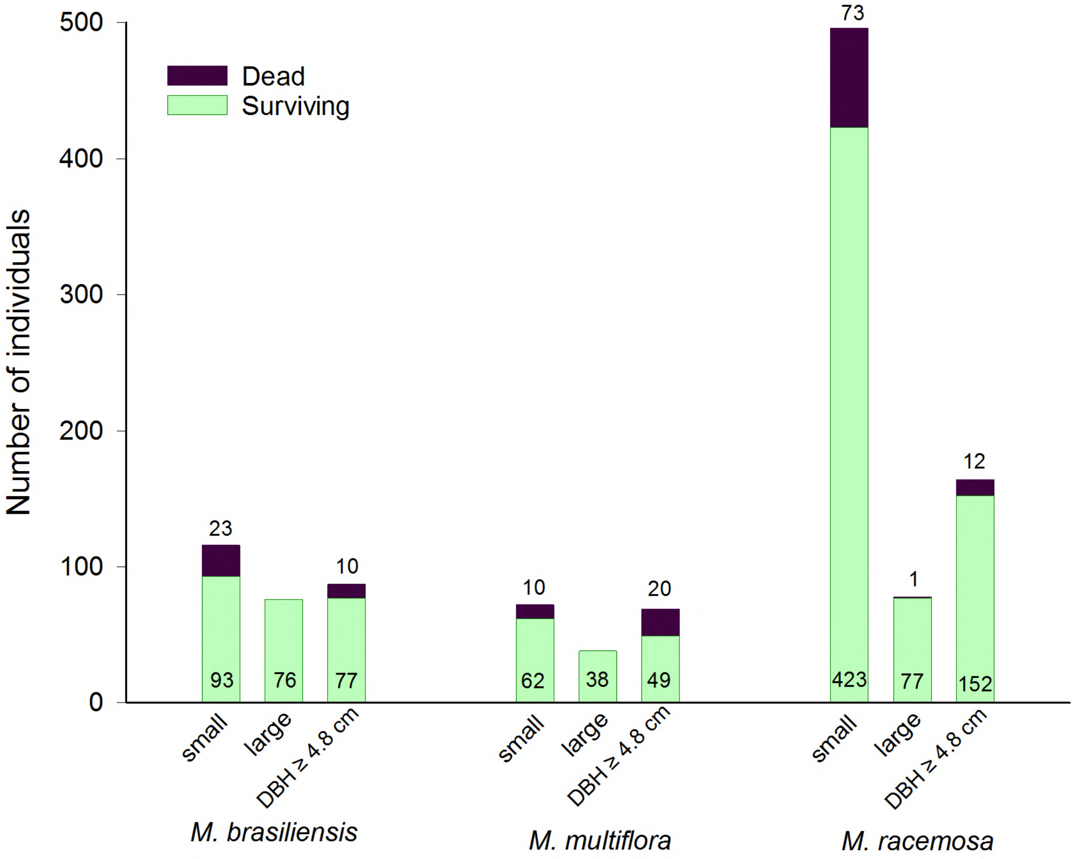


Figure 1. Number of surviving and dead individuals of three *Myrcia* species sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. Mortality of small and large individuals was recorded after a 1-yr period; mortality of individuals with DBH ≥ 4.8 cm was recorded after a 10-yr period.

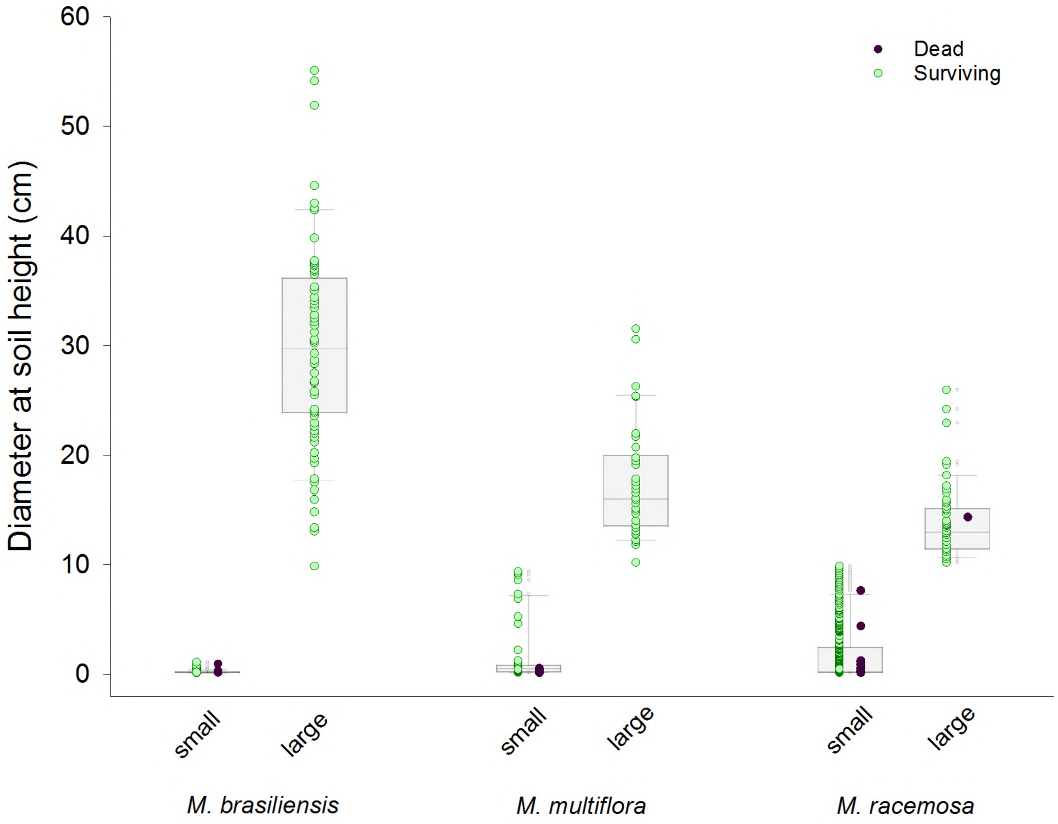


Figure 2. Diameter at soil height (DSH) of surviving and dead individuals of small and large trees of three *Myrcia* species sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. Mortality of small and large individuals was recorded after a 1-yr period.

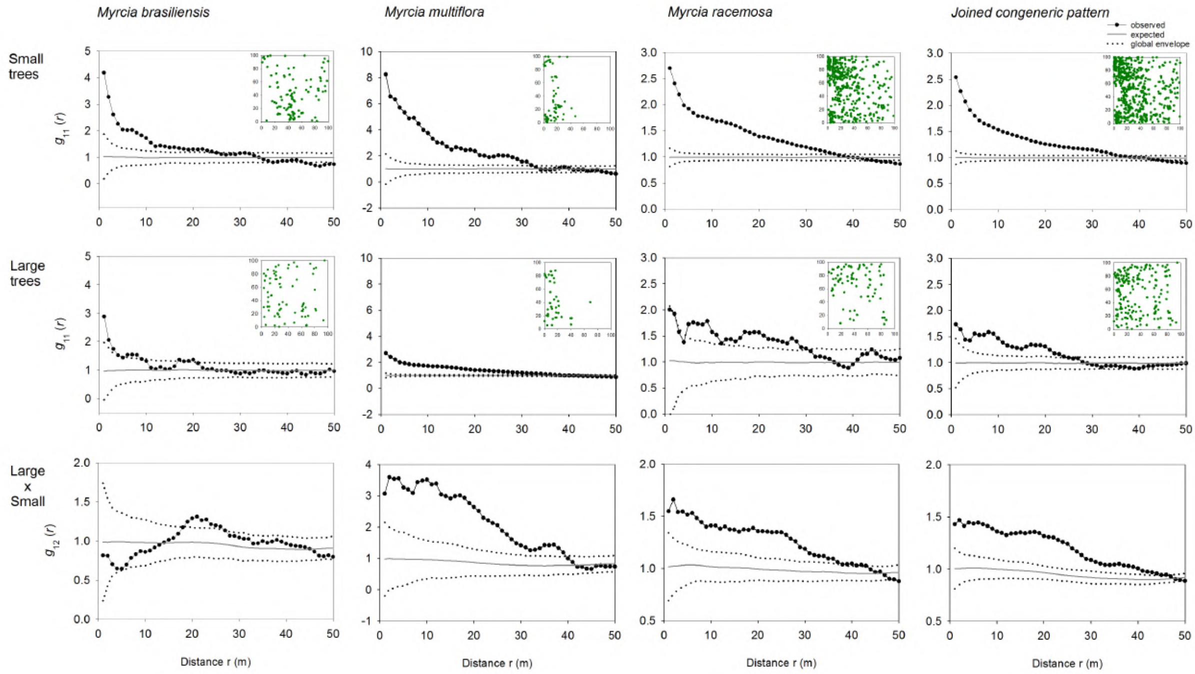
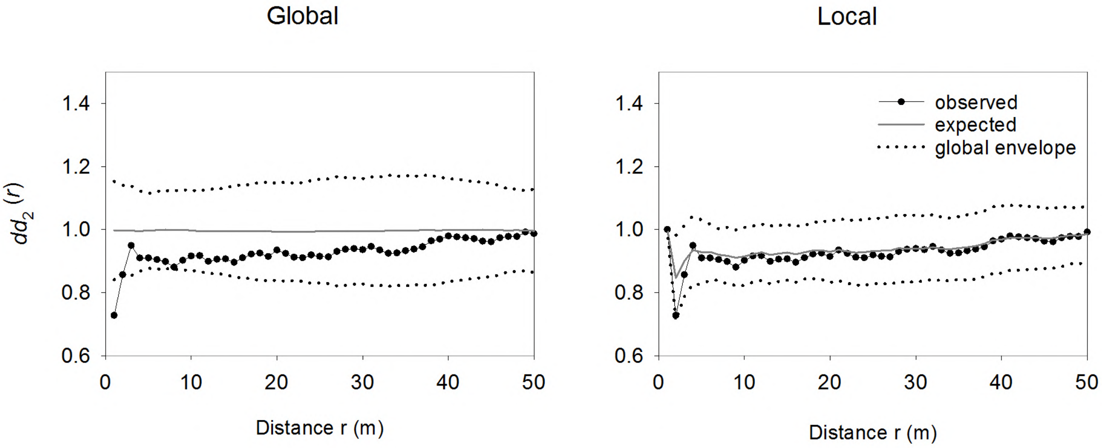


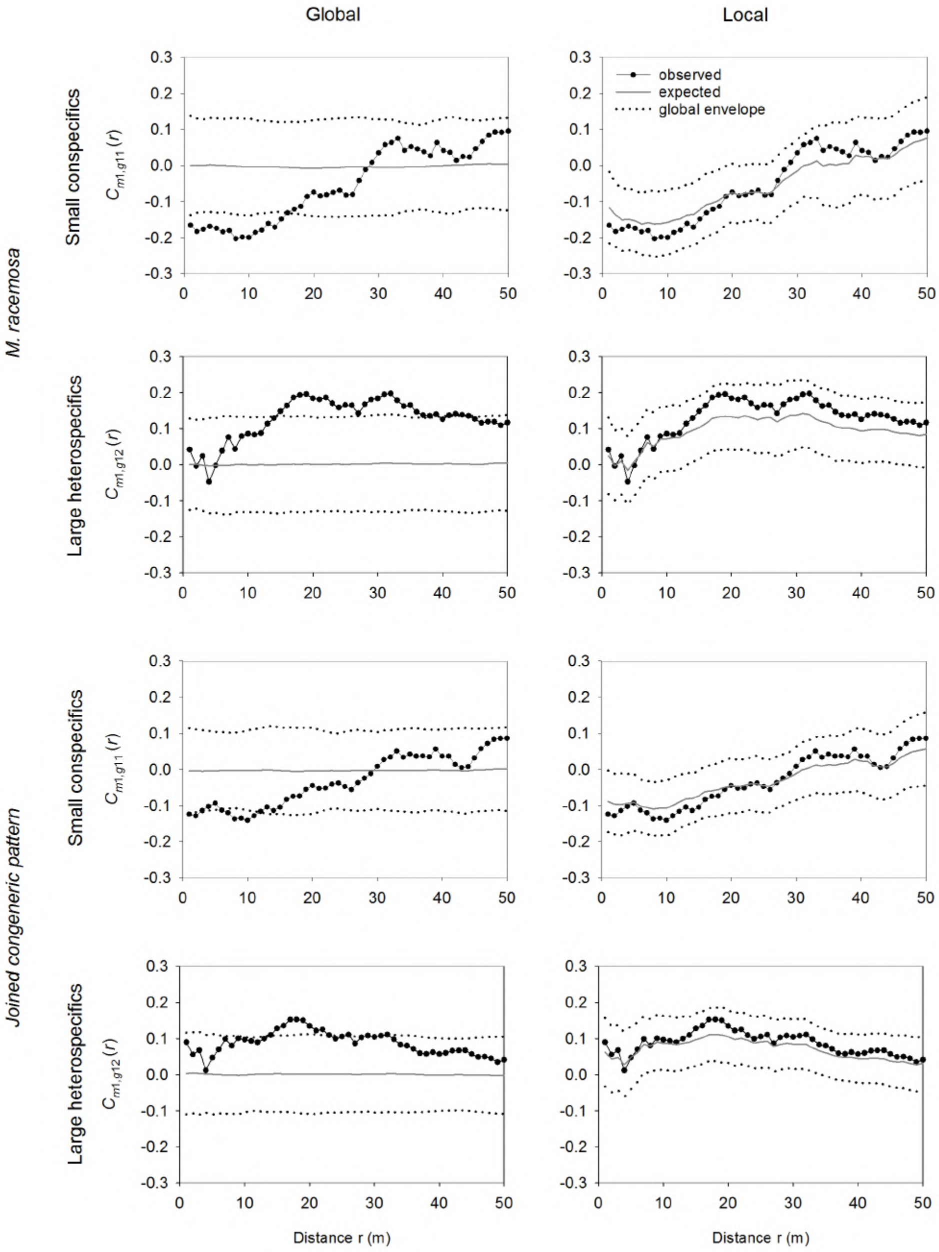
Figure 3. Uni- and bivariate spatial patterns of small and large trees of three *Myrcia* species and their joined congeneric pattern in a 1-ha plot of white-sand flooded forest, southeastern Brazil. The observed pair correlation functions $g_{11}(r)$ and $g_{12}(r)$ (dots) were compared to global simulation envelopes (dashed lines) under the complete spatial randomness null model.

Supplementary material

Appendix S1. Density-dependent effects of large heterospecifics on the mortality of large trees of the joined pattern of three *Myrcia* species, as measured by dd_2. Trees were sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. The observed $dd_2(r)$ (dots) was compared to global envelopes of the “global” independent marking null model (dashed line) and of the local independent marking null model, which accounts for possible effects of environmental heterogeneity on plant mortality.



Appendix S2. Density-dependent effects on size of *Myrcia* species, as measured by the density correlation function $C_{m,g}(r)$. The $C_{m,g}(r)$ was calculated for the effects of small trees of *Myrcia racemosa* and of large heterospecifics on the size of small trees of *M. racemosa*, and for the effects of small trees of the joined pattern of three *Myrcia* species and of large heterospecifics on the size of small trees of the joined congeneric pattern. Trees were sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. The observed density correlation function (dots) was compared to the global simulation envelopes of the "global" independent marking null model (dashed lines) and the local independent marking null model, which accounts for possible effects of environmental heterogeneity on plant size.



Capítulo 3

Coexistence driven by differentiation and plasticity of local strategies in a Brazilian white-sand flooded tropical forest

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Abstract

Understanding the mechanisms structuring diverse communities in natural environments is one of the major interests in community ecology. According to niche theory, species coexistence within the same environmental patch with harsh physical conditions is possible when species exploit the same resources differently to avoid competitive exclusion, i.e., show niche differentiation in resource acquisition. Thus, we aimed to investigate evidence of intra- and interspecific variation in strategies related to tolerance and resource acquisition of three *Myrcia* species. We collected data in a permanent 1-ha plot installed in the white-sand seasonally flooded forest in southeastern Brazil. We selected the species *M. brasiliensis*, *M. multiflora*, and *M. racemosa* co-occur in seasonally flooded areas. To evaluate the species strategies in the study plot, we measured traits to characterise different local strategies, and to compare the species strategies in the study plot and at the wider geographic scale where the species occur, we compiled data from databases and literature. We used six environmental variables to characterise the environment in the study plot. We investigated the relationship among measured traits and among environmental variables, whether strategies related to resource acquisition and tolerance differ among species, whether the three *Myrcia* species show different local strategies associated with the environment in the study plot, and whether there are differences in strategies of each *Myrcia* species between the study plot and the wider geographic scale where the species occur. We observed divergence in local strategies of tolerance and resource acquisition among species indicating coexistence at small spatial scales mediated by habitat filtering and interspecific competition. Contrary to expectations, the strategies of the three species in the study plot were similar to other areas where the species occur but with divergent responses of local strategies to environmental variation. In summary, our study allows us to suggest that the coexistence of *M. brasiliensis* with *M. multiflora* and *M. racemosa* is based on a divergence of local strategies. In addition, the coexistence of *M. multiflora* and *M. racemosa*, which present a convergence of strategies compared to *M. brasiliensis*, should be driven by the plasticity of local strategies associated with environmental variation. In this way, we proposed how species with similar environmental requirements coexist in a forest with severe flooding conditions.

Keywords: Atlantic forest, congeneric species, environmental filtering, functional traits, restinga.

Introduction

Understanding the mechanisms structuring diverse communities in natural environments is one of the major interests in community ecology (Brown 2014). The main coexistence mechanisms described in tropical forests are niche-based habitat filtering and interspecific competition (Wright 2002). According to niche theory, species with similar resource requirements compete intensely within the same environmental patch so that the superior species excludes the inferior one in a given combination of resources and conditions. Thus, coexistence in diverse communities is possible when species exploit same resources in different ways or to occupy different environmental patches, i.e. show niche differentiation (Chauvet et al. 2017, Wagg et al. 2017).

Habitat filtering is expected to be a more important coexistence mechanism in harsh environments due to strong environmental constraints that allow only tolerant species to survive (Chapin et al. 1993, Reich et al. 2003). In seasonally flooded forests, environmental harshness occurs due to the low amount of oxygen available for roots and soil podzolisation resulting from flooding (Gomes et al. 2007). The edaphic conditions drive tree species distribution (Diniz 2009, Ribeiro et al. 2021).

Congeneric species are a good model to study coexistence because they tend to exploit the same resources in similar habitats (Losos 2008, Wiens et al. 2010) due to their shared evolutionary history (Baraloto et al. 2012). Therefore, the coexistence of congeneric species driven by habitat filtering to the same environmental patches would only be possible in the absence of interspecific competition, so that the species show niche differentiation in resource acquisition. However, resource partitioning among species can also occur if they show intraspecific plasticity of strategies that can provide divergent resource acquisition (Callaway et al. 2003, Adler et al. 2013).

Intraspecific plasticity of strategies that can provide divergent resource acquisition enables a given species to exploit the same resources in different environmental patches or to exploit the same resources differently in the same patches, thus avoiding interspecific competition (Callaway et al. 2003, Kim & Ohr 2020). In the case of the three *Myrcia* species in the white-sand seasonally flooded forest, intraspecific plasticity should result in divergent resource acquisition strategies among species in patches subject to flooding, where the three species mostly co-occur (Ribeiro et al. 2021), relative to patches that are not seasonally flooded. We assume that intraspecific variation in local strategies within the 1-ha plot is not subject to natural selection due to pollen- and seed-mediated gene flow among environmental patches. In addition, strategies that can provide divergence of resource acquisition should differ among the three species in patches subject to flooding, enabling species coexistence is such environment, according to niche theory (Chauvet et al. 2017, Wagg et al. 2017). Alternatively, species can coexist neutrally without presenting different strategies (Hubbell 2001).

The different intra- and interspecific strategies that can provide divergent resource acquisition affect the balance between growth and survival. For example, higher leaf area and specific leaf area increase light capture efficiency; wood density is positively associated with growth and pathogen resistance, and higher relative growth rate is associated with increasing efficiency in the acquisition and allocation of soil water and nutrients (Wright et al. 2004, Chave et al. 2009, Pérez-Harguindeguy et al. 2013). Displacement of flowering and fruiting periods among species can also be understood as difference in interspecific strategies, since such displacement prevents competition for pollinators and seed dispersers, reduce pollen deposition in different species, and ensures fecundation and establishment. Thus, the species show different reproductive period. Alternatively, the facilitation hypothesis predicts that overlapping flowering or fruiting periods may provide a higher pollination and dispersal rate due to higher number of flowers and fruits available that attract a higher number of pollinators and seed dispersers. Thus, the species show same reproductive period (Staggemeier et al. 2010).

Because the distribution of three *Myrcia* species is driven by habitat filtering to the same environmental patches in the white-sand seasonally flooded forest (Ribeiro et al. 2021) and due to shared evolutionary history, the species should show similarity of strategies that provide higher tolerance, such as those that promote colonisation, establishment, support, and mechanic stability, and which are influenced by fruit and seed size, allometry, and stem form (Muller-Landau 2010, Mori et al. 2021). Fruit and seed size affect dispersal via disperser movement behaviour and the consequent seed arrival in habitats with suitable conditions for the species (Seidler & Plotkin 2006). Additionally, fruit and seed size affect the establishment of individuals through stored resources in seeds that aid the survival and recruitment of young seedlings (Moles & Westoby 2004, Bruelheide et al. 2018). Regarding allometry and stem form, larger relative stem base should provide greater mechanical support for trees in flooded areas (Mori et al. 2021).

Although the three *Myrcia* species show habitat association to seasonally flooded patches in the white-sand seasonally flooded forest in southeastern Brazil, they are widely distributed throughout the Brazilian Atlantic forest (Ribeiro et al. 2021). Therefore, it is appropriate to compare the amplitude of strategies that can provide higher tolerance and divergent resource acquisition among species at the wider geographic scale where the species occur and explore amplitude variation of strategies driven by coexistence mechanisms at a local scale. The plasticity of local strategies with displaced and/or reduction of strategy (niche amplitude) sampled at the wider geographic scale may allow species coexistence by reducing the competition with each species occupying a distinct niche position (Callaway et al. 2003, Kim & Ohr 2020). For example, because larger seeds can present a higher tolerance, the three *Myrcia* species may show larger seeds in the white-sand seasonally flooded. Intraspecific variation in strategies at different spatial scales may occur due to plasticity or interpopulation genetic variability (Violle et al. 2012), which is an interesting topic for further research.

Here we aimed to investigate evidence of intra- and interspecific variation in strategies that can provide higher tolerance and divergent resource acquisition of the three *Myrcia* species. We questioned: (1) do strategies differ among the species in the white-sand seasonally flooded forest plot? (2) Do the species show plasticity in strategies associated with environmental variables within the plot? (3) Are there differences in strategies of each species between the study plot and the wider geographic scale where the species occur? Within the study plot, as the species are driven by habitat filtering to the same environmental patches and shared an evolutionary history, we expect that the three *Myrcia* species show similarity of strategies that can provide higher tolerance, commonly associated to larger fruits and seeds, and larger relative stem base. Conversely, the three species should show different resource acquisition strategies that result in the absence of interspecific competition, commonly associated to different relative growth rate, leaf and wood traits, and possibly flowering and fruiting patterns. We also expect divergence of local strategies associated with environmental variation of within the white-sand seasonally flooded forest plot, enabling each of the three species to exploit different resources in seasonally flooded patches. Last, we expect smaller and displaced values of local strategies in study plot compared to amplitude of strategies at wider geographic scale, and different niche positions among three *Myrcia* species in study plot.

Material and methods

Study site

We collected data in a permanent 1-ha plot installed at the white-sand flooded forest, *i.e., Restinga* forest, of the State Park "Parque Estadual da Serra do Mar", municipality of Ubatuba, southeastern Brazil. The *Restinga* vegetation is the set of plant communities distributed as a mosaic and associated with quaternary coastal sand deposits and coastal rock environments (Oliveira et al. 2014). Therefore, the *Restinga* is considered an edaphic vegetation, in which soils play an important role in plant development (Bonilha et al. 2011). The regional climate is tropical humid (Morelatto & Haddad 2000). In the study plot (23° 21' S and 44° 51' W), the *Restinga* is a forest physiognomy with 84 tree and palm species, being Myrtaceae and Fabaceae the richest families, and Myrtaceae, Arecaceae, and Euphorbiaceae the most abundant ones (Joly et al. 2012). The plot is partially flooded during the rainy season (Joly et al. 2012).

Species studied

The family Myrtaceae shows the highest species richness in tropical rainforests (Oliveira-Filho & Fontes 2000) and is represented by seven genera in the study plot, with the genus *Myrcia* (subfamily Myrtoideae) showing six species (Sanchez et al. 2013). We selected the tree species *M. brasiliensis* Kiaersk (synonym *Gomidesia schaueriana* O. Berg), *M. multiflora* (Lam.) DC., and *M. racemosa* (O. Berg) Kiaersk, for which a previous population study showed that, despite their wide geographic distribution, they occur associated with seasonally flooded areas in the study plot (Ribeiro et al. 2021). At the geographic scale, the three *Myrcia* species are predominantly distributed in the Brazilian

Atlantic Rainforest but may also be found throughout the Brazilian territory, from ombrophilous forests to grasslands (Sobral et al. 2015). As with all species of the subfamily Myrtoideae, the three species studied have bisexual flowers (Wilson et al. 2005). The pollination is performed predominantly by bees and occasionally by Diptera for *M. multiflora* and *M. racemosa* (Fidalgo & Kleinert 2009). The three species show fruits attractive to birds, which act as the main seed dispersers (Castro 1998, Pedroni 2001).

Despite some similarities of the three *Myrcia* species, studies conducted in different regions of Brazil show that the species differ in maximum tree height, vegetative traits such as stem and leaves, flower and fruit traits, and reproductive period, as shown in Table 1. Within the study plot, Ribeiro et al. (2021) showed that *M. brasiliensis* is widely distributed, *M. multiflora* occurs predominantly in the portion that is seasonally flooded, and *M. racemosa* is the most abundant *Myrcia* species and occurs most densely in the seasonally flooded area.

Data collection

Local strategies

In order to evaluate the strategies of the three *Myrcia* species in the study plot (as shown in table 2), we measured all individuals for height (H) and diameter at soil height (DSH) between 2016 and 2017 (details in Ribeiro et al. 2021). For individuals taller than 2.5 m, we examined monthly the presence of flowers (flower buds and flowers in anthesis) and fruits (immature and mature) between March 2017 and March 2019 in order to determine the flowering and fruiting period of the three species. We used binoculars for the observation of reproductive structures when necessary. Individuals shorter than 2.5 m were not included in phenological observations because we did not observe such individuals reproducing during the population census. In early 2019, we randomly collected three fruits from 10 adults of *M. brasiliensis* and *M. racemosa*, and from two adults of *M. multiflora* that were reproductively active at that moment. For each fruit, we measured the length (FL), width (FW), and the number of seeds. Then, we manually extracted the seeds from the fruits, dried in an oven for three days at 58ºC, and measured, for each seed, the length (SL), width (SW), and mass (SM). We also measured the length and width of seeds collected in seed traps. These seeds were sampled monthly for three years (August 2016 to July 2019) in 60 traps randomly distributed in the study plot (a total of seed traps 2160 samples). The samples were dried for three days at 58ºC, and the dry seeds were identified to the species level by comparison with seeds collected directly from adults of each species. We raffled ten samples containing *Myrcia* species seeds and measured one seed per sample. For *M. multiflora*, we selected ten samples collected in seed traps located more than 10 m away from individuals of *Calyptranthes* sp., as fruits and seeds of the latter are very similar to seeds of *M. multiflora*.

For individuals that were reproductively active between March 2017 and February 2018, we collected leaf and wood traits distributed in random locations covering flooded and non-flooded areas (as shown in table 2). These data were collected for 11 adults of each *M. brasiliensis* and *M. racemosa*, and eight adults of *M. multiflora*, as there were not more individuals of the latter species large enough for the collection of stem baguettes. To quantify specific leaf area (SLA), we randomly collected one branch exposed directly to the sun per individual, using a pruner on an extension pole in February 2018. We digitalized three leaves per branch, converted the digitalized images into binary images, and obtained the leaf area (LA) through the threshold-based pixel count measurement with the ImageJ program, available at https://imagej.nih.gov/ij/index.html. Subsequently, the leaves were dried in an oven for three days at 58ºC and weighed in a digital scale to obtain the dry mass. The SLA was given by LA / dry mass (Pérez-Harguindeguy et al. 2013). We calculated the mean of the three leaves to obtain one SLA value for each adult. To obtain wood density (WOOD), we removed one stem baguette per individual at 1.20-m height with an increment borer also in February 2018. We then calculated WOOD as the dry mass of the wood sample divided by the water mass displaced by the wood core volume (Chave 2005). For this, we used a digital scale and a Becker with water to calculate the mass of water displaced by the volume of the collected baguette. Subsequently, we used an oven for drying the baguettes for three days at 58ºC and a digital scale to obtain the dry mass.

For the same 11 adults of each *M. brasiliensis* and *M. racemosa*, and eight adults of *M. multiflora* that we collected leaf and wood traits, we calculated the relative growth rate as $\mathrm{RGR} = (\mathrm{DBH}_{t2} - \mathrm{DBH}_{t1}) / \mathrm{DBH}_{t1}$ (Pérez-Harguindeguy et al. 2013), where DBH is the diameter at breast height measured in 2006 (t_1) and 2015 (t_2) in forest inventories conducted in the study plot (data available in ForestPlots.net). We also calculated the allometric coefficient as $\mathrm{AC} = \ln(\mathrm{H}) / \ln(\mathrm{DSH})$ (Mori et al. 2021) and the stem-form coefficient as $\mathrm{SFC} = \mathrm{DSH} / \mathrm{DBH}$ to identify the form of the stem base. To calculate SFC, we used the DBH measured in 2015 to match more closely the DSH measured in our population census.

In order to compare the strategies that can provide divergent resource acquisition and higher tolerance of the three *Myrcia* species in the study plot and at the wider geographic scale where the species occur, we compiled data from TRY (Kattge et al. 2020), Neotropical Tree Community (TreeCo; http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start), ForestPlots.net (https://www.forestplots.net/), and Knowledge Network for Biocomplexity (KNB; https://knb.ecoinformatics.org/) databases and literature. The databases contain information from 14 Brazilian areas (municipalities or states) and the data available corresponds to the value per individual, the maximum value obtained at a given area, or the average value for an area.

Environmental variables

We used six environmental variables measured by Ribeiro et al. (2021) at a 10 x 10 m scale to characterize the environment in the study plot. The variables are associated with seasonal flooding (flooding depth, soil moisture, elevation, and terrain slope), and with light availability in the understory (canopy openness) and forest regeneration (litterfall depth). Details can be found in Ribeiro et al. (2021).

Data analysis

To investigate whether strategies that can provide higher tolerance and divergent resource acquisition among the three *Myrcia* species in the study plot, we performed an analysis of variance (ANOVAs) with *a posteriori* Tukey's (Zar 2010) tests for each of the variables measured (table 2), except for reproductive period. We also performed a principal component analysis (PCA) for each *Myrcia* species to assess the relationship among LA, SLA, WOOD, AC, SFC, RGR measured in the same individuals (trait PCA), and to assess the relationship among environmental variables in study plot (habitat PCA) (Zuur et al. 2007). Although the species are filtered for the same environment (Ribeiro et al. 2021), we performed the PCA with the environmental variables data obtained where the individuals used to collect the traits are located. We analysed the frequency of flowering and fruiting (*i.e.*, the number of individuals in a given reproductive phenophase per month) of the three *Myrcia* species using circular statistics. We calculated the mean angle ($\bar{a}$), which indicates the month with the central tendency of the phenophase; the length of the mean vector (r), which represents the concentration of each phenophase, and the circular standard deviation of each phenophase. For calculating these parameters, the months are converted into angles at regular intervals of 30º, being January 15º and December 345º (Zar 2010). To evaluate the seasonality of flowering and fruiting of each species, we used the Watson uniformity test (U^2), which is recommended when the population sample is grouped and not unimodal (Zar 2010). To compare the seasonal flowering and fruiting patterns among the three *Myrcia* species, we used the Watson-Williams test (F) recommended for multisamples (Zar 2010). We analysed data using the R Statistical Environment (R Core Team 2014).

To investigate whether the three *Myrcia* species show plasticity in strategies associated to the environmental variation within the study plot and whether the strategies differ among the species in seasonally flooded patches, we conducted multiple linear regressions between the first trait PCA axis and each environmental variable as a predictor (Zuur et al. 2009, Lebrija-Trejos et al. 2010). For the regressions, we standardised the predictor variables by subtracting the mean and dividing the result by the standard deviation to enable a direct comparison of the relative importance of local strategies. We log-transformed the environmental variables before standardisation (Fortunel et al. 2018).

To investigate whether there are differences in strategies of each *Myrcia* species between the study plot and the wider geographic scale where the species occur, we produced a graph with the strategies displayed at the *Restinga* forest and data compiled from other sites. The graph enables comparative visual inspections between two data groups and among species.

Results

Fruit and seed size (FL, FW, SL, and SW) differed among the three species, with *M. brasiliensis* showing the largest fruits and *M. multiflora* the smallest, whereas *M. racemosa* showed the largest seeds and *M. multiflora* showed the smallest. Seed mass (SM) was similar between *M. brasiliensis* and *M. multiflora*, whose seeds were lighter in weight relative to *M. racemosa* (Tukey's test p <000.1, Figure 1). *Myrcia brasiliensis* had more than one seed per fruit (1-4), while the other two species had only one seed.

The three species showed similar stem-form coefficient (SFC) and relative growth rate (RGR). *Myrcia multiflora* and *M. racemosa* showed similar wood density and allometric coefficient, which were higher than for *M. brasiliensis*. *Myrcia brasiliensis* and *M. racemosa* showed similar leaf area (LA), which was higher than for *M. multiflora*. However, *M. multiflora* showed similar specific leaf area (SLA) to the other two species, while *M. racemosa* showed higher SLA than *M. brasiliensis* (Tukey's test p <000.1, Figure 1). The first trait PCA axis explained 36.7% of the variation in strategies among the three species in the study plot. *Myrcia brasiliensis* showed higher light capture efficiency (represented by LA), whereas *M. multiflora* and *M. racemosa* similarly invest more in growth, pathogen resistance, and mechanic stability (represented by WOOD and AC; Figure 2A) However, *M. multiflora* and *M. racemosa* showed greater variation of the second axis traits (SFC and RGR), although they have little influence on the difference between species. The habitat PCA showed habitat overlap of the three species with first axis explaining 44.2% of the environmental variation among the three species in the study plot. The elevation is inversely proportional to soil moisture, terrain slope and flooding depth, and canopy openness is inversely proportional to flooding depth (Figure 2B).

The three *Myrcia* species showed seasonal flowering and fruiting in the two monitored years, except for the fruiting of *M. brasiliensis*, which was unseasonal in the first year. All species showed flowering overlap in January, whereas fruiting was not overlapped among the species, occurring from January to April, and more variable between years for the same species than the flowering period (Table 3).

The three *Myrcia* species showed plasticity in strategies associated with environmental variation within the study plot and differed in their strategies in seasonally flooded patches. *Myrcia brasiliensis* responded to higher elevations with higher light capture efficiency (LA in the first trait PCA axis; R=0.42, p=0.04). *Myrcia multiflora* showed higher investment in growth, pathogen resistance, and mechanic stability (WOOD and AC in the first trait PCA axis) in areas with higher soil moisture (R=0.74, p=0.01) and terrain slope (R=0.57, p=0.05). On the other hand, *M. racemosa* showed lower investment in growth, pathogen resistance, and mechanic stability in areas with higher soil moisture (R=0.40, p=0.05; Figure 3).

The values of traits measured for each *Myrcia* species in the study plot and other areas where the species occur are within the same range (Figure 4). Additionally, given one trait, the species with the highest, the intermediate, and the lowest values are the same in the study plot and in other areas. Thus, there is no difference in traits of the *Myrcia* species between the study plot and the wider geographic scale where the species occur as we observed by the visual inspection of the graphs.

Discussion

In this study, we investigated evidence of intra- and interspecific variation in strategies that can provide higher tolerance and divergent resource acquisition of three *Myrcia* species that show habitat association to the same seasonally flooded patches in a 1-ha plot of white-sand seasonally flooded forest in southeastern Brazil. Within the seasonally flooded patches, the three species do not show spatial patterns consistent with interspecific competition (Ribeiro et al. 2021). Here, we found that the species differ in their strategies that can provide higher tolerance and divergent resource acquisition in the study plot. Even though differences of fruit and seed size, commonly associated to tolerance, were not expected because the three species co-occur within the same seasonally flooded patches, our results showing different strategies of resource acquisition reinforce the previous finding that interspecific competition (Ribeiro et al. 2021) is not an important driver of coexistence of the three *Myrcia* at small spatial scales. We also found that the species show plasticity in strategies associated with environmental variation within the study plot and differ in their strategies in seasonally flooded patches, which might also promote coexistence. Because the three *Myrcia* species are widely distributed throughout the Brazilian Atlantic forest (Ribeiro et al. 2021), we additionally compared strategies displayed by each species in the white-sand seasonally flooded forest and at the wider geographic scale where the species occur. Contrary to expectations, the strategies did not differ between the study plot and other areas where the species occur.

We evaluated strategies that can provide higher tolerance commonly associated to fruit and seed size, seed mass, stem form coefficient (SFC), and allometric coefficient (AC). Although the three *Myrcia* species differed in their fruit and seed traits, SFC was similar among the species, and *M. multiflora* and *M. racemosa* showed similar AC. Because the species are filtered to seasonally flooded patches in the study plot, it is likely that SFC and AC play a more important role in the occupation of such environmentally harsh patches than fruit and seed traits, as both SFC and AC are related to tree mechanical stability (Mori et al. 2021). Moreover, fruit and seed traits affect colonisation and establishment (Moles & Westoby 2004, Bruelheide et al. 2018), whose resulting spatial distribution patterns might be overridden by other ecological processes that act during the lifetime of individual trees (Levine & Murrell 2003). On the other hand, fruit and seed traits may show a long-lasting effect on the abundance of large trees, as shown for grass species (Padullés et al. 2022). The larger seeds of *M. racemosa* might promote higher survival and establishment of young seedlings (Moles & Westoby

2004), and allow the observed highest species abundance in seasonally flooded patches in comparison to the other two *Myrcia* species. Conversely, *M. multiflora* is the less abundance and more restricted to seasonally flooded patches among the three *Myrcia* species (Ribeiro et al., 2021) and has the smallest seed.

We evaluated resource acquisition strategies commonly associated to wood density (WOOD), leaf area (LA), specific leaf area (SLA), relative growth rate (RGR), allometric coefficient (AC), and reproduction period. WOOD is usually negatively related with LA (Wright et al. 2007), as our trait PCA showed for the three *Myrcia* species in the study plot. The negative relationship occurs because species with lower WOOD show higher hydraulic efficiency that supports larger leaves that require more sap (Wright et al. 2007, Chave et al. 2009). Among the three species here studied, *M. brasiliensis* invest more in light capture efficiency (represented by LA), whereas both *M. multiflora* and *M. racemosa* invest more in growth, pathogen resistance, and mechanic stability (represented by AC in addition to WOOD). Although the latter two species show high similarity, *M. racemosa* has a higher photosynthetic performance, as represented by higher values of SLA in the ANOVA. Therefore, there is divergence in resource acquisition strategies among the three species, suggesting that there is not interspecific competition among them (Adler et al. 2013). This result agrees with a previous study that used the spatial structure of *Myrcia* populations in the study plot, and showed no spatial dissociation between species pairs and no decrease of tree size with increasing proximity of congeners, which indicate no interspecific competition (Ribeiro et al. 2021).

Wood density is often a phylogenetically conserved trait and varies little among species of the *Myrcia* genus (Chave et al. 2006). However, all three species here studied showed lower wood density than the mean for the genus (Chave et al. 2006), and *M. multiflora* and *M. racemosa* that occur exclusively and more abundantly in the flooded area, respectively, presented higher wood density than *M. brasiliensis*, probably reflecting the strong selective pressure act on plants differentiation in harsh environments of seasonal flooding. Also, *M. multiflora* and *M. racemosa* showed higher allometric coefficients, indicating more mechanical stability in seasonally flooded areas (Mori et al. 2021) compared to *M. brasiliensis*.

The overlapping flowering period of the three *Myrcia* species was also observed by Fidalgo & Kleinert (2009) and Talora & Morellato (2000) in the study area. Because the species share pollinator bee species (Fidalgo & Kleinert 2009), they might either compete for pollinators according to the competition hypothesis or show a higher pollination rate due to the attraction of a higher number of pollinators according to the facilitation hypothesis (Staggemeier et al. 2010). The pollen as a characteristic floral resource of Myrtaceae species (Silva & Pinheiro 2007, Fidalgo & Kleinert 2009) is available in large quantities with the overlapping flowering which allow more attraction of pollinators. This strategy supports the facilitation hypothesis to coexistence of the three *Myrcia* species studied that predict the absence of competition for pollinators. The same seems true for seed dispersers, as the fruiting period did not overlap among the species (Staggemeier et al. 2010).

Different fruiting periods for *M. multiflora* and *M. racemosa* were also found by Talora & Morellato (2000) in the same area, but the authors observed shorter fruiting periods than we did. Inter-annual variation in reproductive phenology is commonly observed and might reflect biotic and abiotic environmental variation along time (Engel & Martins 2005).

In our study plot, lower elevation, higher soil moisture, higher terrain slope and higher flooding depth are correlated and indicate seasonally flooded patches. Indeed, the three *Myrcia* species showed plasticity and interspecific differences in their strategies associated with elevation, soil moisture, and terrain slope. As in Ribeiro et al. (2021), we probably did not find responses to flooding depth because this variable was measured only once and may thus not be able to capture flooding seasonality properly. Considering the first trait PCA axis (WOOD-LA), *M. brasiliensis* and *M. multiflora* showed lower LA and higher WOOD associated with higher flooding, while *M. racemosa* showed the opposite association. Additionally to higher growth and pathogen resistance provided by higher WOOD, it is also related to higher hydraulic safety due to very thick-walled fibres, and lower efficiency in water transport and release during transpiration (Chave et al. 2009). Therefore, higher investment in WOOD should work well in environments with high water availability, as found here for *M. brasiliensis* and *M. multiflora*, and for other tree species studied by Xu et al. (2021) in flooded areas. Nevertheless, *M. racemosa* associated with flooding in an opposite fashion. In this case, lower investment in WOOD in flooded areas can maximize water transport without the costs of trunk thickening. Overall, the species *M. multiflora* and *M. racemosa* showed similar strategies, so the differentiation associated with environmental variables indicate a means of avoiding competition and coexist in flooded areas. Thus, future studies evaluating local strategies of species in flooded and non-flooded areas would help better explain this selective pressure from harsh habitats.

In the white-sand tropical forest, the seasonal flooding requires trees to adapt for prolonged inundation (Johnson et al. 2017). Thus, due to harsh physical conditions in the study area, we expected to observe different species strategies in comparison with wider geographic scale where the species occur. Although the species showed plasticity associated with environmental variation, the seasonal flooding do not act as a selective pressure differentiating *Myrcia* species in the studied plot from other areas. Working in a white-sand forest in southeast Brazil, we found evidence of divergence of local strategies driven by habitat filtering and interspecific competition, besides the plasticity of local strategies. However, it is relevant to consider the observational, short-term, and small-scale nature of the data, so that future studies involving these factors will contribute to the understanding of the results obtained in this study.

In summary, our study allows us to suggest that the coexistence of *M. brasiliensis* with *M. multiflora* and *M. racemosa* is based on a divergence of local and general strategies. In addition, the coexistence of *M. multiflora* and *M. racemosa*, which present a convergence of strategies compared to *M. brasiliensis*, should be driven by the plasticity of local strategies associated with environmental variation. In this way, we proposed how species with similar environmental requirements coexist in a forest with severe flooding conditions.

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References

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. Ecology Letters, 16(10), 1294–1306. doi:10.1111/ele.12157

Baraloto, C., Hardy, O. J., Paine, C. E. T., Dexter, K. G., Cruaud, C., Dunning, L. T., Gonzalez, M. A., Molino, J. F., Sabatier, D., Savolainen, V., & Chave, J. (2012). Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology*, *100*(3), 690–701.

Bonilha, R. M., Casagrande, J. C., & Soares, M. R. (2011). Characterization of the Soil Fertility and Root System of Restinga Forests. *Revista Brasileira de Ciência Do Solo*, *36*, 1804–1813.

Brown, J. H. (2014). Why are there so many species in the tropics? Journal of Biogeography, 41, 8–22. doi:10.1111/jbi.12228

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., … Jandt, U. (2018). Global trait–environment relationships of plant communities. Nature Ecology and Evolution, 2(12), 1906–1917. doi:10.1038/s41559-018-0699-8

Caliari, C. P. (2013). *Estudos em Myrtaceae do Estado de São Paulo: Myrcia seção Gomidesia.* Universidade de São Paulo.

Callaway, R. M., Pennings, S. C., & Richards, C. L. (2003). Phenotypic plasticity and interactions among plants. Ecology, 84(5), 1115–1128.

Castro, S. L. R. (1998). *Ecologia do tié-sangue, Ramphocelus bresilius (Aves: Emberezidae: Thraupinae), no Parque Estadual da Serra do Mar, Núcleo Picinguaba, Ubatuba, SP*. Universidade Estadual Paulista, Rio Claro.

Chapin, F. S., Autumn, K., & Pugnaire, F. (1993). Evolution of Suites of Traits in Response to Environmental Stress. *The American Naturalist*, *142*, S78–S92.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., & Zanne, A.E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

Chave, J. (2005). Measuring wood density for tropical forest trees a field manual for the CTFS sites. Disponível em: http://www.edb.ups- tlse.fr/equipe1/chave/wood- density- protocol.pdf

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Hans Steege, T. E. R., & Webb, C. O. (2006). Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecological Applications, 16(6), 2356–2367. doi:10.1890/1051-0761(2006)016[2356:RAPVOW]2.0.CO;2

Chauvet, M., Kunstler, G., Roy, J., & Morin, X. (2017). Using a forest dynamics model to link community assembly processes and traits structure. *Functional Ecology* 31: 1452–1461.

Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35: 131–138.

Diniz, F. V. (2009). Composição e estrutura fitossociológica da regeneração natural na floresta de restinga alta em Picinguaba (Parque Estadual da Serra do Mar), município de Ubatuba, SP, Brasil. Universidade Estadual Paulista.

Engel, V. L., & Martins, F. R. (2005). Reproductive phenology of Atlantic forest tree species in Brazil: An eleven year study. *Tropical Ecology*, *46*(1), 1–16.

Fernandes, M. F., & Queiroz, L. P. de. (2015). Floristic surveys of Restinga Forests in southern Bahia, Brazil, reveal the effects of geography on community composition. *Rodriguésia*, *66*(1), 51–73.

Fidalgo, A. D. O., & Kleinert, A. D. M. P. (2009). Reproductive biology of six Brazilian Myrtaceae:-is there a syndrome associated with buzz-pollination? *New Zealand Journal of Botany*, *47*(4), 355–365. doi:10.1080/0028825x.2009.9672712

Fortunel, C., Lasky, J. R., Uriarte, M., Valencia, R., Wright, S. J., Garwood, N. C., & Kraft, N. J. B. (2018). Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest. *Ecology*, *99*(10), 2272–2283. doi:10.1002/ecy.2441

Gomes, F. H., Vidal-torrado, P., Macías, F., Gherardi, B., & Perez, X. L. O. (2007). Solos Sob Vegetação De Restinga Na Ilha Do Cardoso (SP). I - Caracterização e Classificação. *Revista Brasileira de Ciência Do Solo*, *31*, 1563–1580.

Hofhansl, F., Chacón-Madrigal, E., Brännström, Å., Dieckmann, U., & Franklin, O. (2021). Mechanisms driving plant functional trait variation in a tropical forest. Ecology and Evolution, 1–15. doi:10.1002/ece3.7256

Joly, C. A., Assis, M. A., Bernacci, L. C., Tamashiro, J. Y., Campos, M. C. R., Gomes, J. A., Lacerda, M. A., Santos, F. A. M., Pedroni, F., Pereira, L. S., Padgurschi, M. C. G., Prata, E. M. B., Ramos, E., Torres, R. B., Rochelle, A., Martins, F. R., Alvez, L. F., Vieira, S. A., Martinelli, L. A., Camargo, P. B., Aidar, M. P. M., Eisenlohr, P. V., Simões, E., Villani, J. P., & Belinello, R. (2012).

Florística e fitossociologia em parcelas permanentes da Mata Atlântica do sudeste do Brasil ao longo de um gradiente altitudinal. *Biota Neotropica*, *12*(1), 0–23.

Johnson, D. J., Condit, R., Hubbell, S. P., & Comita, L. S. (2017). Abiotic niche partitioning and negative density dependence drive tree seedling survival in a tropical forest. Proceedings of the Royal Society B: Biological Sciences, 284(1869). doi:10.1098/rspb.2017.2210

Kattge, J, Boenisch, G, Diaz, S, et al. (2020) TRY plant trait database - enhanced coverage and open access. Glob Change Biol. 26: 119-188. https://doi.org/10.1111/gcb.14904

Kim, D., & Ohr, S. (2020). Coexistence of plant species under harsh environmental conditions: An evaluation of niche differentiation and stochasticity along salt marsh creeks. Journal of Ecology and Environment, 44(1). doi:10.1186/s41610-020-00161-y

Kraft, N. J., Valencia, R. & Ackerly, D. D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* **322**: 580-582

Lebrija-Trejos, E., Pérez-GarcíA, E. A., Meave, J. A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology, 91(2), 386–398. doi:10.1890/08-1449.1

Levine, J. M., & Murrell, D. J. (2003). The Community-Level Consequences of Seed Dispersal Patterns. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 549–574. doi:10.1146/annurev.ecolsys.34.011802.132400

Lima, D. F., Krasinski, M., & Goldenberg, R. (2015). A família Myrtaceae na Ilha do Mel, Paranaguá, Estado do Paraná, Brasil. *Hoehnea*, *42*(3), 497–519.

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, *11*, 995–1003.

Marques, M. C. M., & Oliveira, P. E. A. M. (2004). Fenologia de espécies do dossel e do sub- bosque de duas Florestas de Restinga na Ilha do Mel, sul do Brasil. *Revista Brasileira de Botânica*, *27*(4), 713– 723.

Moles, A. T., & Westoby, M. (2004). Seedling survival and seed size: A synthesis of the literature. Journal of Ecology, 92(3), 372–383. doi:10.1111/j.0022-0477.2004.00884.x

Morais, P. O., & Lombardi, J. A. (2006). A família Myrtaceae na reserva particular do patrimônio natural da Serra do Caraça, Catas Altas, Minas Gerais, Brasil. *Lundiana*, *7*(1), 3–32.

Morellato, L. P. C. & Haddad, F. C. B. (2000). Introduction: The Brazilian Atlantic Forest. *Biotropica*, *32*(4b), 786–792.

Mori, G. B., Poorter, L., Schietti, J., & Piedade, M. T. F. (2021). Edaphic characteristics drive functional traits distribution in Amazonian floodplain forests. *Plant Ecology*, *222*(3), 349–360. doi:10.1007/s11258-020-01110-4

Muench, A, & Elsey-Quirk, T. (2019). Competitive reversal between plant species is driven by species-specific tolerance to flooding stress and nutrient acquisition during early marsh succession. *J Appl Ecol*. 2019; 00: 1–12.

Muller-Landau, H. C. (2010). The tolerance-fecundity trade-off and the maintenance of diversity in seed size. Proceedings of the National Academy of Sciences of the United States of America, 107(9), 4242–4247. doi:10.1073/pnas.0911637107

Oliveira-Filho, A. T., & Fontes, M. A. L. (2000). Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate1. *Biotropica*, *32*, 793–810.

Padullés Cubino, J., Axmanová, I., Lososová, Z., Večeřa, M., Bergamini, A., Bruelheide, H., … Chytrý, M. (2022). The effect of niche filtering on plant species abundance in temperate grassland communities. Functional Ecology, 36(4), 962–973. doi:10.1111/1365-2435.13994

Pedroni, F. (2001). *Aspectos da estrutura e dinâmica da comunidade arbórea na Mata Atlântica de planície e encosta em Picinguaba, Ubatuba, SP*. Universidade Estadual de Campinas.

Pérez-Harguindeguy, N., Díaz, A. Garnier, E.,Lavorel, S., Poorter, H., Jaureguiberry, P., Bret- Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E.J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., van der Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, V., Conti, G., Staver, A. C., Aquino, S., & Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany, 61*, 167–234.

R Core Team (2014). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. URL http://www.R-project.org/.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, *164*(3), S143–S164.

Ribeiro, K. F. O., Martins, V. F., Wiegand, T., & Santos, F. A. M. (2021). Habitat filtering drives the local distribution of congeneric species in a Brazilian white-sand flooded tropical forest. Ecology and Evolution, 11, 1797–1813. doi:10.1002/ece3.7169

Rosa, P. O., & Romero, R. (2012). O gênero Myrcia (Myrtaceae) nos campos rupestres de Minas Gerais, Brasil. *Rodriguésia*, *63*(3), 613–633.

Sanchez, M., Pedroni, F., Eisenlohr, P. V., & Oliveira-Filho, A.T. (2013). Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, southeastern Brazil, from near sea level to 1000m of altitude. *Flora* 208: 184–196.

Seidler, T. G., & Plotkin, J. B. (2006). Seed dispersal and spatial pattern in tropical trees. PLoS Biology, 4(11), 2132–2137. doi:10.1371/journal.pbio.0040344

Silva, A. L. G. da, & Pinheiro, M. C. B. (2007). Biologia floral e da polinização de quatro espécies de Eugenia L. (Myrtaceae). Acta Botanica Brasilica, 21(1), 235–247. doi:10.1590/s0102-33062007000100022

Sobral, M., Proença, C., Souza, M., Mazine, F., & Lucas, E. (2015). Myrtaceae in Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. Disponível em: <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB10672>.

Souza, M.C., Morim, M.P., Conde, M.M.S., & Menezes, L.F.T. (2007). Subtribo Myrciinae O. Berg (Myrtaceae) na Restinga da Marambaia, RJ, Brasil. *Acta bot. bras.* 21: 49–63.

Staggemeier, V. G., Diniz-Filho, J. A. F., & Morellato, L. P. C. (2010). The shared influence of phylogeny and ecology on the reproductive patterns of Myrteae (Myrtaceae). Journal of Ecology, 98, 1409–1421. doi:10.1111/j.1365-2745.2010.01717.x

Staggemeier, V. G., Diniz-Filho, J. A. F., Zipparro, V. B., Gressler, E., de Castro, E. R., Mazine, F., … & Morellato, L. P. C. (2015). Clade-specific responses regulate phenological patterns in Neotropical Myrtaceae. *Perspectives in Plant Ecology, Evolution and Systematics*, *17*(6), 476–490. doi:10.1016/j.ppees.2015.07.004

Talora, D. C., & Morellato, P. C. (2000). Fenologia de espécies arbóreas em floresta de planície litorânea do sudeste do Brasil. Revista Brasileira de Botânica, 23(1), 13–26. doi:10.1590/S0100-84042000000100002

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., … Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. Trends in Ecology and Evolution, 27(4), 244–252. doi:10.1016/j.tree.2011.11.014

Wagg, C., Ebeling, A., Roscher, C., Ravenek, J., Bachmann, D., Eisenhauer, N., Mommer, L., Buchmann, N., Hillebrand, H., Schmid, B., & Weisser, W.W. (2017). Functional trait dissimilarity drives both species complementarity and competitive disparity. *Functional Ecology* 31: 2320–2329.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J-A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., & Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*, 1310–1324.

Wilson, P. G., O'Brien, M. M., Heslewood, M. M., & Quinn, C. J. (2005). Relationships within Myrtaceae sensu lato based on a matK phylogeny. *Plant Systematics and Evolution*, *251*, 3–19.

Wright, S. J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia, 130, 1–14. doi:10.1007/s004420100809

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., & Villar, R. (2004). The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., … Wright, S. J. (2007). Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. Annals of Botany, 99(5), 1003–1015. doi:10.1093/aob/mcl066

Xu, M., Zheng, L. T., He, D., Chen, H. Y. H., & Yan, E. R. (2021). Microenvironment filtering and plant competition jointly structure trait distributions across co-occurring individuals. Ecological Indicators, 129, 107893. doi:10.1016/j.ecolind.2021.107893

Zar, J. H. (2010). Biostatistical Analysis. New Jersey: Prentice-Hall.

Zuur, A.F., Ieno, E.N. & Smith, G.M. (2007) Analysing Ecological Data. New York: Springer.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. Smith. (2009). Mixed effects models and extensions in ecology with R . New York: Springer.

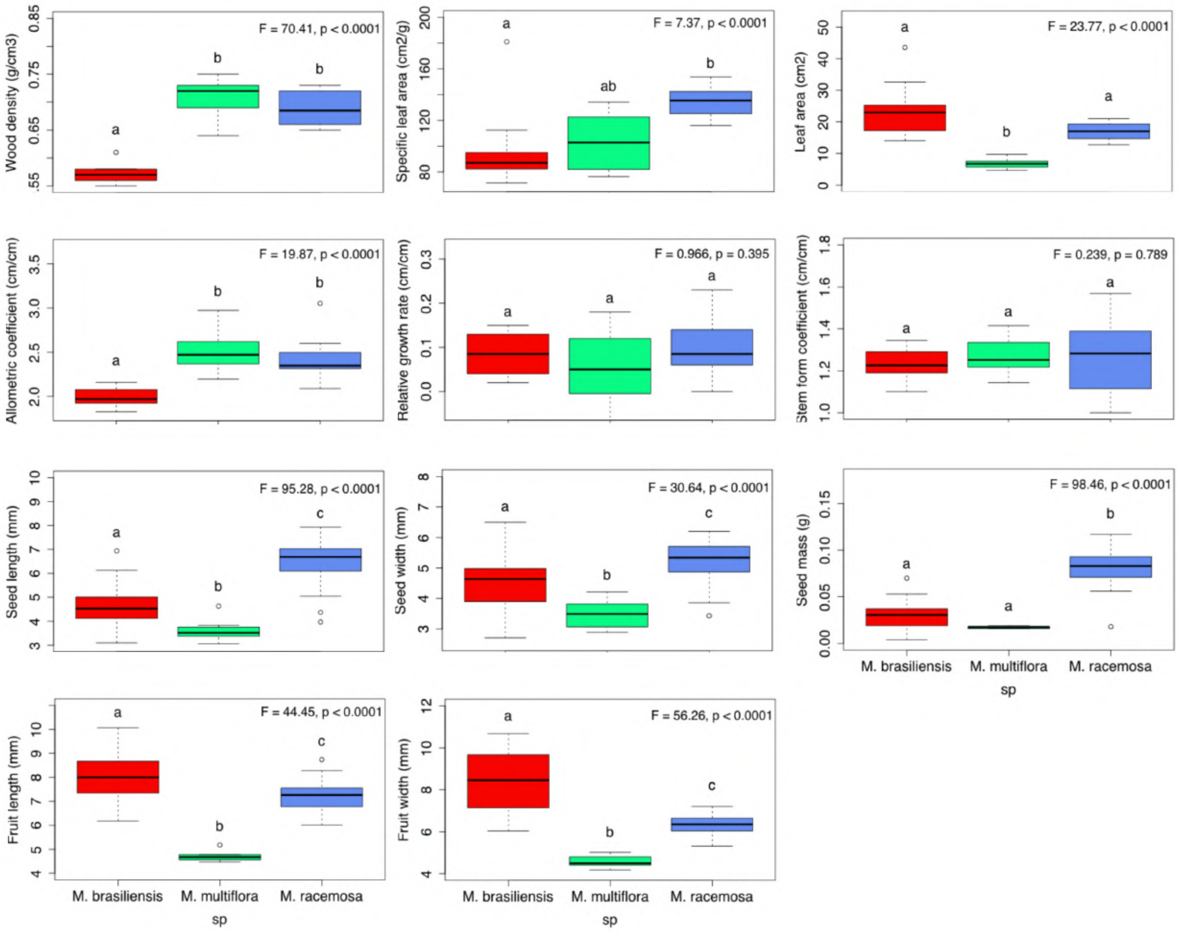

Figure 1. One-way ANOVA evaluating differences in wood density, specific leaf area, leaf area, relative growth rate, allometric coefficient, stem-form coefficient, fruit length, fruit width, seed length, seed width, and seed mass among three *Myrcia* species sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. Different letters indicate statistical difference ($p<0.05$) among species according to Tukey's test.

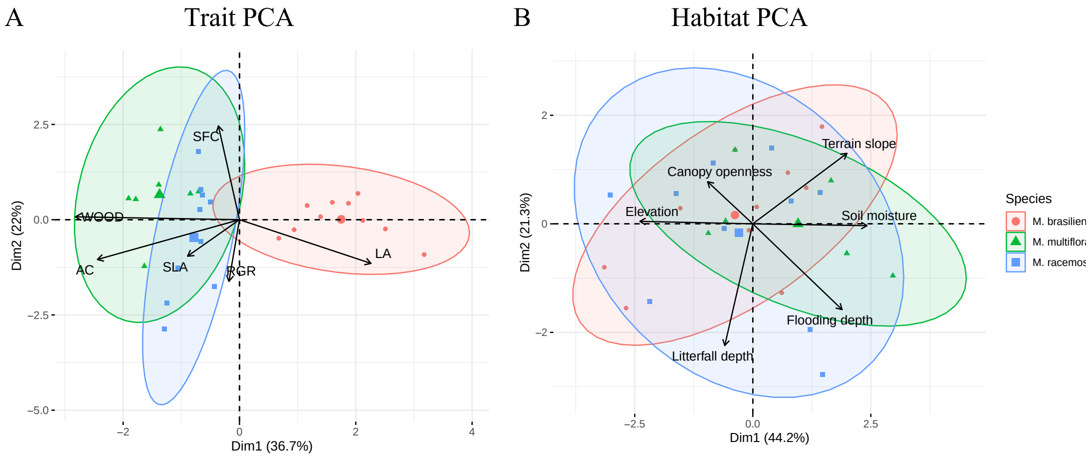

Figure 2. Principal component analysis (PCA-A) of leaf area (LA), specific leaf area (SLA), wood density (WOOD), relative growth rate (RGR), allometric coefficient (AC), and stem-form coefficient (SFC), and principal component analysis (PCA-B) of environmental variables that characterize the point where the individuals of three *Myrcia* species were sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. The size of the symbols indicates contribution of individuals in the analysis.

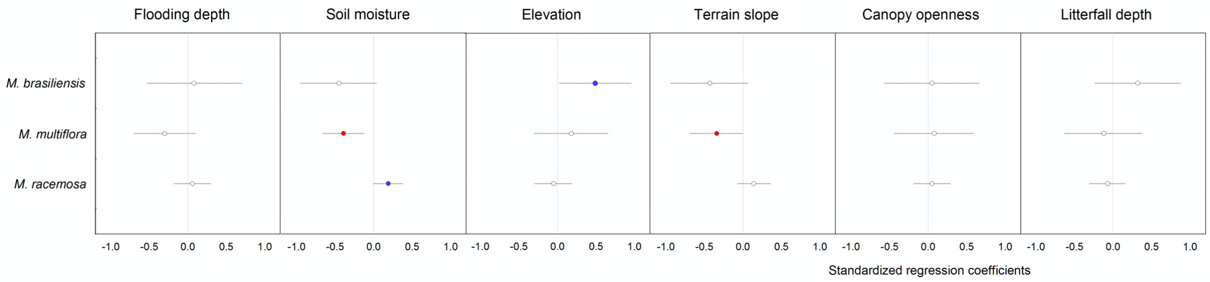

Figure 3. Multiple linear regression coefficients between the first trait PCA axis in Fig. 1 and standardized environmental variables, indicating environmentally-driven, plastic local strategies of three *Myrcia* species sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil. Circles show the medians of the coefficients and the lines indicate 95% credible intervals. Blue circles indicate positive effects ($p \leq 0.05$) and red circles indicate negative effects ($p \leq 0.05$).

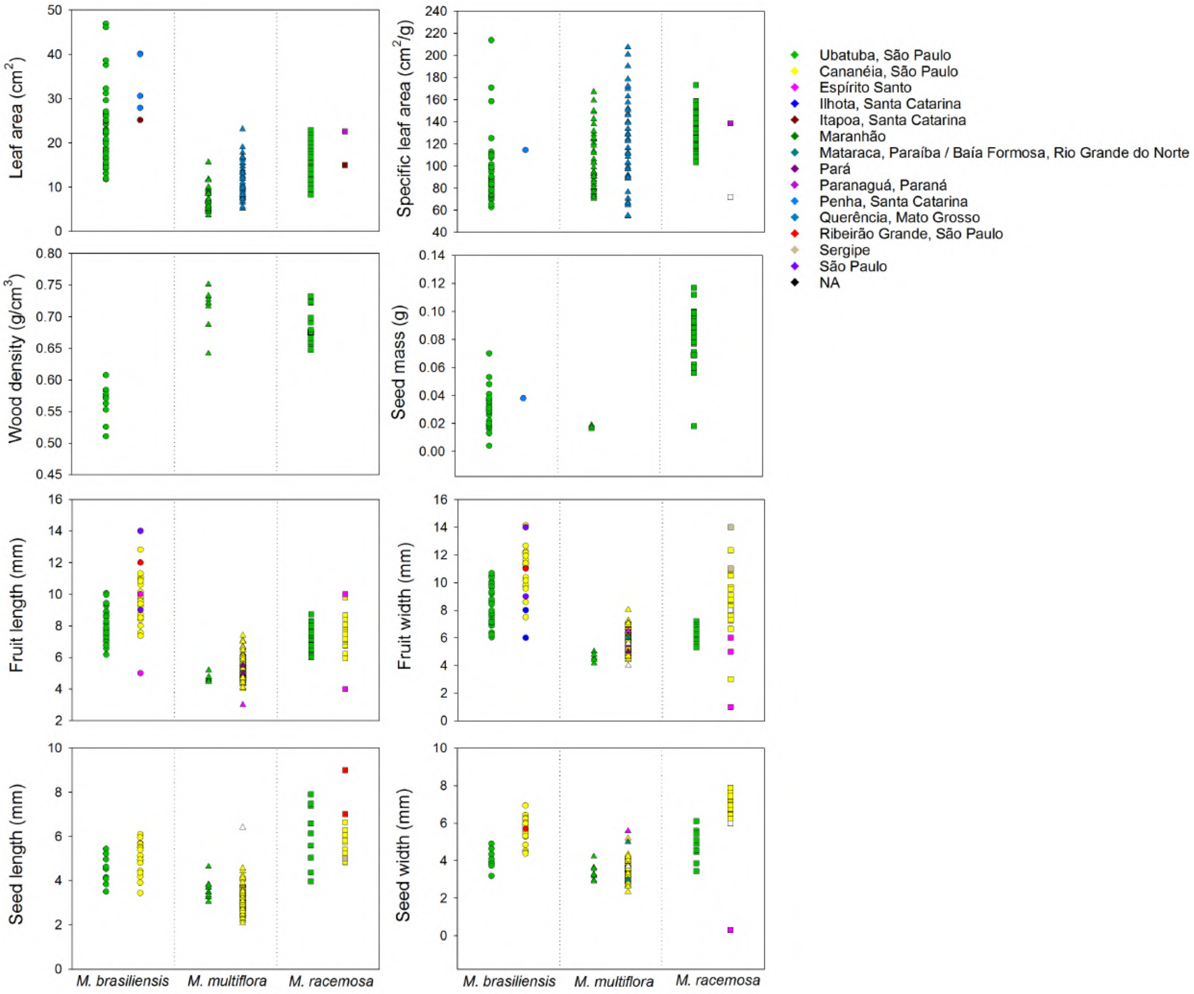

Figure 4. Traits of three *Myrcia* species sampled in a 1-ha plot of white-sand flooded forest, southeastern Brazil (green symbols), and in other Brazilian areas. Data from other Brazilian areas was compiled from databases and the literature.

Table 1. Review of published studies that observed the traits of *Myrcia* species.

Traits		***M. brasiliensis***		***M. multiflora***		***M. racemosa***	
Height	Maximum (m)	30		2-4	18	6	8
	Locality	State of São Paulo		Seasonal Semideciduous Forest, *capoeira*, and rupestrian field of the state of Minas Gerais	*Restinga* of Marambaia, state of Rio de Janeiro	Dense Ombrophilous Forest in Ilha do Mel, state of Paraná	State of Rio de Janeiro
	Reference	Caliari (2013)		Morais & Lombardi (2006), Rosa & Romero (2012)	Souza et al. (2007)	Lima et al. (2015)	Souza et al. (2007)
Trichomes	Local	New branches, petioles and flowers, especially the hypanthium, covered with simple trichomes; leaves and peduncles with simple, but sparse, trichomes		New branches, petioles, stalk and abaxial faces of the leaves sparsely covered with trichomes		New branches, petioles, inflorescences, and central rib of the abaxial and adaxial faces of the leaves densely covering	
	Reference	Lima et al. (2015)		Lima et al. (2015)		Souza et al. (2007), Lima et al. (2015)	
Stem	Aspect			Outer bark laminated and defoliating into small thin blades, with a whitish to pinkish coloration		Outer bark laminated and defoliating into papyraceous, grayish, lichenized blades, with green spots	
	Reference			Souza et al. (2007), Lourenço et al. (2012)		Souza et al. (2007)	
Leaves	Colour	Green or brown		Discolored			
	Shape	Slightly acuminate, acute or obtuse apex		Acuminate apex		Long-acuminate apex	
	Other traits			Evident glands			
	Reference	Boeger et al. (2004), Caliari (2013)		Souza et al. (2007), Lima et al. (2015)		Souza et al. (2007), Lima et al. (2015)	
Inflorescence	Type	Panicle		Panicle		Panicle	
	Colour	Yellowish-whitish to slightly golden					
	Reference	Caliari (2013), Lima et al. (2015)		Morais & Lombardi (2006), Souza et al. (2007) Rosa & Romero (2012), Lima et al. (2015)		Souza et al. (2007), Lima et al. (2015)	
Flower buds	Length (mm)	4-7		1.5-3		2	
	Reference	Caliari (2013)		Morais & Lombardi (2006), Rosa & Romero (2012)		Souza et al. (2007)	
Flower	Type	Sessile or pedicellate		Pedicellate		Sessile or pedicellate	
	Reference	Lima et al. (2015)		Morais & Lombardi (2006), Rosa & Romero (2012)		Lima et al. (2015)	
Fruit	Shape	Globular		Globular		Globular	
	Diameter (mm)	9-14		3.6-6		4.3-6.5	
	Colour	Yellow, orange, reddish, or black		Black		Red	
	Reference	Caliari (2013)		Morais & Lombardi (2006), Rosa & Romero (2012)		Lima et al. (2015)	
Flowering	Period	November to March	September to December	November to February	December to January	Twice a year from December to January and from August to September	January to April
	Locality	White-sand flooded forest here studied	Semideciduous forest	White-sand flooded forest here studied	White-sand flooded forest here studied	White-sand flooded forest here studied	White-sand flooded forest here studied
	Reference	Fidalgo & Kleinert (2009)	Bauer et al 2014	Fidalgo & Kleinert (2009)	Talora & Morellato (2000)	Talora & Morellato (2000)	Fidalgo & Kleinert (2009)
Fruiting	Period	December to June	January to July	January to February		Twice a year from October to December and from May to June	
	Locality	White-sand flooded forest in Ilha do Mel, state of Paraná	Semideciduous forest	White-sand flooded forest here studied		White-sand flooded forest here studied	
	Reference	Marques & Oliveira (2004)	Bauer et al 2014	Talora & Morellato (2000)		Talora & Morellato (2000)	

Table 2. Traits measured for three *Myrcia* species sampled in a 1-ha plot of white-sand forest, southeastern Brazil. The ecological strategy indicated by each trait was obtained from Wright et al. (2004), Chave et al. (2009), Pérez-Harguindeguy et al. (2013), and Mori et al. (2021).

Trait	**Abbreviation**	**Strategy type**	**Ecological strategy**	**Unit**
Wood density	WOOD	Resource acquisition	Allocation to growth and pathogen resistance	g/cm^3
Leaf area	LA		Light capture efficiency	cm^2
Specific leaf area	SLA		Leaf economics-resource capture	cm^2/g
Relative growth rate	RGR		Resource capture and allocation efficiency	cm/cm
Reproductive period	-		Competition for pollinators and dispersers	-
Fruit length	FL	Tolerance	Dispersion distance and colonization	mm
Fruit width	FW		Dispersion distance and colonization	mm
Seed length	SL		Establishment	mm
Seed width	SW		Establishment	mm
Seed mass	SM		Establishment	g
Stem form coefficient	SFC		Support and mechanic stability	cm/cm
Allometric coefficient	AC	Resource acquisition and Tolerance	Growth strategy and mechanic stability	cm/cm

Table 3. Flowering and fruiting patterns of three *Myrcia* species in two study years in a 1-ha plot of white-sand flooded forest, southeastern Brazil.

	Flowering 1st year	Flowering 2nd year	Fruiting 1st year	Fruiting 2nd year
Myrcia brasiliensis				
Observations (N)	30	219	21	213
Mean angle ($\bar{a}$)	16°	13°	93°	10°
Mean month	Jan	Jan	Apr	Jan
Length of mean vector (r)	1.00	0.88	0.04	0.21
Circular standard deviation	5°	29°	143°	101°
Watson test (U^2)	2.488	10.229	0.062	1.951
Watson test (p)	< 0.01	< 0.01	> 0.10	< 0.01
Periodicity	seasonal	seasonal	unseasonal	seasonal
Myrcia multiflora				
Observations (N)	10	98	7	104
Mean angle ($\bar{a}$)	18°	18°	95°	65°
Mean month	Jan	Jan	Apr	Mar
Length of mean vector (r)	0.99	0.89	0.61	0.15
Circular standard deviation	9°	28°	57°	111°
Watson test (U^2)	0.816	4.790	0.266	0.674
Watson test (p)	< 0.01	< 0.01	< 0.025	< 0.01
Periodicity	seasonal	seasonal	seasonal	seasonal
Myrcia racemosa				
Observations (N)	20	363	54	344
Mean angle ($\bar{a}$)	15°	15°	65°	38°
Mean month	Jan	Jan	Mar	Feb
Length of mean vector (r)	1.00	0.87	0.41	0.23
Circular standard deviation	0	30	76	98
Watson test (U^2)	1.728	16.644	0.918	2.831
Watson test (p)	< 0.01	< 0.01	< 0.01	< 0.01
Periodicity	seasonal	seasonal	seasonal	seasonal
Watson-Williams test (F)	0.965	1.277	10.733	7.695
Watson-Williams test (p)	0.387	0.280	< 0.0001	0.0005

Considerações finais

Entender os processos ecológicos que promovem a coexistência de espécies arbóreas em ambientes megadiversos como as florestas tropicais é um tema central em ecologia de comunidades (He et al. 1996). Esse tema ganha maior relevância em ambientes com condições severas de alagamento, cujas alterações decorrentes de mudanças climáticas e uso da terra podem desestruturar a comunidade arbórea (Kraft et al. 2015). Em florestas tropicais, os principais mecanismos de coexistência são baseados em processos determinísticos como filtragem ambiental e competição intra- e interespecífica (Wright 2002), processos estocásticos associados à dispersão de sementes (Wiegand et al. 2012), e dependência negativa de densidade de coespecíficos (DNDC), resultante de competição intraespecífica e ataque de inimigos naturais espécie-específicos (LaManna et al. 2017). Neste estudo, nós investigamos principalmente os processos determinísticos utilizando abordagens recentes que avaliam a estrutura espacial das populações (Getzin et al. 2006, Brown et al. 2013, Yan et al. 2015) e a variação das estratégias funcionais (Hofhansl et al. 2021) de três espécies arbóreas congenéricas simpátricas em uma floresta de restinga sazonalmente alagável.

Ao avaliarmos a influência de variáveis ambientais sobre o padrão de distribuição espacial das populações das três espécies congenéricas estudadas, observamos que as espécies são filtradas em diferentes graus para as mesmas manchas ambientais sujeitas a alagamento dentro da parcela. Assim, evidenciamos que o alagamento não impõe restrições a ocupação das espécies estudadas e que a filtragem ambiental na floresta sazonalmente alagável é um dos mais importantes processos direcionando a distribuição espacial local das espécies estudadas (Ribeiro et al. 2021). As associações ambientais similares são esperadas em espécies que apresentam uma grande proximidade filogenética, como é o caso de espécies congenéricas, devido à potencial similaridade dos requisitos ambientais (Losos 2008).

A coexistência das três espécies congenéricas estudadas nas áreas sujeitas a alagamento sugere que outros processos ecológicos mantenedores de diversidade podem estar atuando em uma escala espacial menor do que a das manchas ambientais, como limitação de dispersão, competição intra- e interespecífica e o ataque de inimigos naturais espécie-específicos, os quais ocorrem em pequenas escalas espaciais (Wright 2002). Ao avaliarmos a relação espacial entre as classes de tamanho de congenéricos e coespecíficos, encontramos evidências de limitação de dispersão apenas para uma das espécies estudadas e apenas entre as classes de tamanho menores e a classe de tamanho maior. Assim, a limitação de dispersão direciona a relação espacial inicial entre indivíduos menores e maiores da espécie, mas, conforme as árvores crescem, a filtragem ambiental se torna mais importante (Ribeiro et al. 2021). Para confirmar nossa inferência, estudos que avaliem a distribuição espacial da chuva de sementes e a relação com as primeiras classes de tamanho seriam fundamentais.

A distribuição espacial do tamanho dos indivíduos das três espécies congenéricas estudadas e as interações com outras espécies da comunidade indicam que não há competição direta entre as três espécies, e entre cada uma delas e as espécies mais abundantes da comunidade (Ribeiro et al. 2021). Então, avaliamos os efeitos dependentes de densidade na mortalidade e no tamanho dos indivíduos, se esses efeitos são mais fortes em árvores pequenas do que em árvores grandes, e se a mortalidade e o tamanho são influenciados pela heterogeneidade ambiental. Embora muitos estudos mostrem evidências de competição difusa e DNDC na estruturação de comunidades (Comita et al. 2014, Zhu et al. 2015), não encontramos evidências que sustentassem a atuação desses mecanismos mantenedores de diversidade nas três espécies estudadas. Porém, novamente encontramos que a mortalidade e o tamanho dos indivíduos respondem à variação ambiental dentro da parcela de floresta de restinga sazonalmente alagável.

As relações espaciais independentes entre coespecíficos, congenéricos e heteroespecíficos indicam que os indivíduos das espécies estudadas não interagem entre si e com outras espécies, de forma a alterar seu arranjo espacial. Isso sugere que a ocupação e a coocorrência das espécies na floresta de restinga são determinadas principalmente pela tolerância das três espécies congenéricas estudadas às condições de alagamento. Para avaliar essa hipótese, estudos futuros podem investigar os padrões de distribuição espacial de outras espécies congenéricas e, mais amplamente, considerar todas as espécies da comunidade.

Para entendermos porquê as três espécies congenéricas estudadas não competem dentro das mesmas manchas de habitat, nós observamos a variação das estratégias funcionais entre as espécies e como essas estratégias variam entre e dentro da mesma espécie em resposta à variação ambiental na parcela de floresta de restinga sazonalmente alagável. A tolerância às manchas sujeitas a alagamento pode ser mediada pelo coeficiente alométrico similar entre as três espécies estudadas, enquanto a ausência de competição entre as espécies pode ser explicada por diferentes atributos funcionais comumente associados a aquisição de recursos (principalmente área foliar, área foliar específica e densidade da madeira). Além disso, embora não tenhamos observado distinção na variação dos atributos entre a área de estudo e outras áreas de ocorrência, as espécies apresentaram plasticidade nas estratégias funcionais dentro da parcela, a qual poderia contribuir para a coexistência das espécies nas mesmas manchas de habitat. No entanto, os dois gráficos da PCA mostram que o ambiente varia mais do que os valores de uma dada característica. Ou seja, as espécies não respondem à totalidade da variação ambiental observada na área de estudo.

Na parcela de 1ha estudada na floresta de restinga, a qual apresenta variação ambiental relacionada ao alagamento periódico, pudemos observar uma amplitude de resposta dos indivíduos das três espécies de Myrcia que nos permitiram inferir determinados processos ecológicos atuando sobre as populações. A partir dos nossos resultados, sugerimos que a coexistência das três espécies congenéricas estudadas é direcionada pela diferenciação de nicho como resultado de pressões seletivas de competição interespecífica passada.

Referências bibliográficas

Brown, C., Burslem, D. F. R. P., Illian, J. B., Bao, L., Brockelman, W., Cao, M., Chang, L. W., Dattaraja, H. S., Davies, S., Gunatilleke, C. V. S., Gunatilleke, I. A. U. N., Huang, J., Kassim, A. R., Lafrankie, J. V., Lian, J., Lin, L., Ma, K., Mi, X., Nathalang, A., Noor, S., Ong, P., Sukumar, R., Su, S. H., Sun, I. F., Suresh, H. S., Tan, S., Thompson, J., Uriarte, M., Valencia, R., Yap, S. L., Ye, W., Law, R. (2013). Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 0502.

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Beckman, N., and Zhu, Y. (2014). Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. Journal of Ecology, 102, 845–856. doi:10.1111/1365-2745.12232

Getzin, S., Dean, C., He, F., Trofymow, J. A., Wiegand, K., Wiegand, T. (2006). Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography*, *29*, 671–682.

He, F., Legendre, P., LaFrankie, J. V. (1996). Spatial Pattern of Diversity in a Tropical Rain Forest in Malaysia. *Journal of Biogeography*, *23*, 57–74.

Hofhansl, F., Chacón-Madrigal, E., Brännström, Å., Dieckmann, U., & Franklin, O. (2021). Mechanisms driving plant functional trait variation in a tropical forest. Ecology and Evolution, (December 2020), 1–15. doi:10.1002/ece3.7256

Kraft, N. J., Valencia, R. & Ackerly, D. D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. Science 322: 580-582

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology, 29, 592–599. doi:10.1111/1365-2435.12345

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters, 11, 995–1003.

Ribeiro, K. F. O., Martins, V. F., Wiegand, T., Santos, F. A. M. (2021). Habitat filtering drives the local distribution of congeneric species in a Brazilian white-sand flooded tropical forest. Ecology and Evolution, 11, 1797–1813. doi:10.1002/ece3.7169

Wiegand, T., Huth, A., Getzin, S., Wang, X., Hao, Z., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N. (2012). Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *Proceedings of the Royal Society B: Biological Sciences* 279: 3312–3320.

Wright, S.J. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.

Yan, Y., Zhang, C., Wang, Y., Zhao, X., von Gadow, K. (2015). Drivers of seedling survival in a temperate forest and their relative importance at three stages of succession. *Ecology and Evolution*, 1–13.

Zhu, K., Woodall, C., Monteiro, J., Clark, J. (2015). Prevalence and strength of density-dependent tree recruitment. Ecology, 96(9), 2319–2327. doi:10.1890/14-1780.1.sm

Anexos

Anexo 1. Cadastro no SISGEN

Ministério do Meio Ambiente
CONSELHO DE GESTÃO DO PATRIMÔNIO GENÉTICO
SISTEMA NACIONAL DE GESTÃO DO PATRIMÔNIO GENÉTICO E DO CONHECIMENTO TRADICIONAL ASSOCIADO

Comprovante de Cadastro de Acesso
Cadastro nº A477A36

A atividade de acesso ao Patrimônio Genético, nos termos abaixo resumida, foi cadastrada no SisGen, em atendimento ao previsto na Lei nº 13.123/2015 e seus regulamentos.

Número do cadastro:	**A477A36**
Usuário:	**UNICAMP**
CPF/CNPJ:	**46.068.425/0001-33**
Objeto do Acesso:	**Patrimônio Genético**
Finalidade do Acesso:	

☑ **Pesquisa Científica** ☐ **Bioprospecção** ☐ **Desenvolvimento Tecnológico**

Espécie

Impossibilidade de identificação

Título da Atividade:	**Estudos da diversidade biológica da Floresta Atlântica**

Equipe

FLAVIO ANTONIO MAES DOS SANTOS	**UNICAMP**
Valéria Forni Martins	**UFSCar**
Luciana Ferreira Alves	**UCLA**
Leonardo Dias Meireles	**USP**
Kelly Fernandes de Oliveira Ribeiro	**UNICAMP**
Lucas Benedito Gonsales Rosa	**UFSCar**
Mauricio Bonesso Sampaio	**Prefeitura de Maringá**
Leon Vieira Amaral	**UNICAMP**

Anete Pereira de Souza	**UNICAMP**
Talita Soares Reis	**UNICAMP**

Parceiras Nacionais

45.358.058/0001-40 / FUNDACAO UNIVERSIDADE FEDERAL DE SAO CARLOS

Resultados Obtidos

Divulgação de resultados em meios científicos ou de comunicação

Identificação do meio onde foi divulgado:	**Ecology and Evolution 5: 1919-1931 (2015)**
Identificação do meio onde foi divulgado:	**capítulo de livro: Fitossociologia no Brasil (201**
Identificação do meio onde foi divulgado:	**Resumo: 53rd Annual Meeting of the Associati**
Identificação do meio onde foi divulgado:	**Resumo: XII Congresso de Ecologia do Brasil (**
Identificação do meio onde foi divulgado:	**Resumo: 5th Workshop of Seed Ecology (2016)**
Identificação do meio onde foi divulgado:	**Resumo: XXIV Congresso de Iniciação Científic**
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Identificação do meio onde foi divulgado:	**Oecologia Australis 22 (no prelo) (2018)**
Identificação do meio onde foi divulgado:	**Tese de Doutorado UNICAMP (2015)**
Identificação do meio onde foi divulgado:	**Tese de Mestrado UNICAMP (2015)**
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Identificação do meio onde foi divulgado:	**Applications in Plant Sciences 1 (11): 1300055 (**

Identificação do meio onde foi divulgado:	**9th Annual Meeting of the Association for Trop**
Identificação do meio onde foi divulgado:	**Brazilian Journal of Botany, v. 42, p. 1-10, 2019**
Identificação do meio onde foi divulgado:	**62nd Annual Symposium of the Internation Ass**
Identificação do meio onde foi divulgado:	**VI Semana dos Estudantes de Biologia da UFS**
Identificação do meio onde foi divulgado:	**XXV Congresso de Iniciação Científica (CIC) e**
Identificação do meio onde foi divulgado:	**Tese de mestrado UFSCar (2018)**
Identificação do meio onde foi divulgado:	**Tese de mestrado UNICAMP (2016)**
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Identificação do meio onde foi divulgado:	**Phillips, O.L.,...ForestPlots.net. Taking the puls**
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Identificação do meio onde foi divulgado:	**MAZINE, FIORELLA F. ; Meireles, Leonardo Dia**
Identificação do meio onde foi divulgado:	**Resumo: 64o Congresso Nacional de Botanica,**
Identificação do meio onde foi divulgado:	**Resumo: 11 th Intecol Congress, Ecology: Into**
Identificação do meio onde foi divulgado:	**Martins, V.F.; Bispo, R.L.B. & Loiola, P.P. A cas**

Identificação do meio onde foi divulgado: **Resumo: VIII SemeBio (Semana dos Estudante**

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Identificação do meio onde foi divulgado: **Martins, V.F.; Costa, R.C.; Virillo, C.B.; Wiegan**

Identificação do meio onde foi divulgado: **DE CAMPOS GORGULHO PADGURSCHI, MAÍR**

Data do Cadastro: **11/06/2018 15:59:21**

Situação do Cadastro: **Concluído**

Conselho de Gestão do Patrimônio Genético
Situação cadastral conforme consulta ao SisGen em **10:10** de **13/01/2022**.

SISTEMA NACIONAL DE GESTÃO
DO PATRIMÔNIO GENÉTICO
E DO CONHECIMENTO TRADICIONAL
ASSOCIADO - **SISGEN**

Anexo 2. Declaração de direitos autorais

Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **Mecanismos de coexistência de três espécies congenéricas simpátricas em uma floresta tropical**, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 14 de dezembro 2022

Assinatura : ___________________________________
Nome do(a) autor(a): **Kelly Fernandes de Oliveira Ribeiro**
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