Instituto Nacional de Pesquisas da Amazônia – INPA
Programa de Pós-Graduação em Ecologia

# DISPERSÃO DE SEMENTES DE MARANTACEAE: O PAPEL DA HETEROGENEIDADE AMBIENTAL NAS INTERAÇÕES PLANTA-DISPERSOR E NOS PADRÕES DE DISTRIBUIÇÃO DE ERVAS DE SUB-BOSQUE NA AMAZÔNIA CENTRAL

FLÁVIA DELGADO SANTANA

Manaus, Amazonas
Outubro, 2017

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Orientadora: Dra. Flávia Regina Capellotto Costa (INPA)

Tese apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Doutor em Biologia (Ecologia).

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Outubro, 2017

INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

PG·ECO·INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

MINISTÉRIO DA CIÊNCIA, TECNOLOGIA, INOVAÇÕES E COMUNICAÇÕES

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# ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Aos 05 dias do mês de outubro do ano de 2017, às 14:30 horas, no auditório do LBA, Campus II, INPA/ALEIXO. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **William Ernest Magnusson**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **Tânia Margarete Sanaiotti**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **José Manuel Vieira Fragoso**, do Instituto Nacional de Pesquisas da Amazônia - INPA, o(a) Prof(a). Dr(a). **Rodrigo Ferreira Fadini**, da Universidade Federal do Oeste do Pará – UFOPA, o(a) Prof(a). Dr(a). **Marina Correa Cortês**, Universidade Estadual Paulista Júlio de Mesquita Filho – UNESP, tendo como suplentes o(a) Prof(a). Dr(a). Isolde Dorothea Kossmann Ferraz, do Instituto Nacional de Pesquisas da Amazônia - INPA, e o(a) Prof(a). Dr(a). Marina Anciães, do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **TESE DE DOUTORADO** de **FLÁVIA DELGADO SANTANA**, intitulado **"DISPERSÃO DE SEMENTES DE MARANTACEAE: O PAPEL DA HETEROGENEIDADE AMBIENTAL NAS INTERAÇÕES E DISTRIBUIÇÃO DE ERVAS NA AMAZÔNIA CENTRAL"**, orientado pelo(a) Prof(a). Dr(a). Flávia Regina Capellotto Costa, do Instituto Nacional de Pesquisas da Amazônia – INPA.

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO(A)　　☐ REPROVADO(A)

☒ POR UNANIMIDADE　　☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). William Ernest Magnusson　W E Magnusson.

Prof(a).Dr(a). Tânia Margarete Sanaiotti　Tânia Margarete Sanaiotti

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S231 Santana, Flávia Delgado

Dispersão de sementes de Marantaceae: o papel da heterogeneidade ambiental nas interações planta-dispersor e nos padrões de distribuição de ervas de sub-bosque na Amazônia central /Flávia Delgado Santana. --- Manaus: [s.n.], 2017.
117 f.: il.

Tese (doutorado) — INPA, Manaus, 2017.
Orientador: Costa, Flávia Regina Capellotto Costa
Área de concentração: Ecologia

1. Sementes . 2. Marantaceae . 3.Dispersão de sementes . I. Título.

CDD 583

**Sinopse:**
Nessa tese investigou-se o processo de dispersão de sementes em diferentes espécies de Marantaceae em uma paisagem heterogênea. Foi avaliado como ervas com diferentes tipos de sementes diferiam quanto aos grupos de dispersores, limitações de dispersão e estabelecimento e como esses fatores afetam a estrutura das populações e padrões de distribuição nas escalas local e da paisagem.

**Palavras-chave:** múltiplos dispersores, recrutamento, filtros ambientais, padrões de abundância.

*Dedico esse trabalho à Rosamélia e Rogério, pelo amor, apoio e confiança incondicionais.*

# AGRADECIMENTOS

Esse trabalho é COLETIVO em todos os aspectos da minha vida acadêmica e pessoal e é tanta coletividade que certamente vou cometer o lapso de deixar alguém de fora. Aqui nomeados ou não, sou grata a todos de coração <3

Aos financiadores da tese: o Conselho Nacional de Desenvolvimento Científico e Tecnológico, que financiou a bolsa de Doutorado, a bolsa de Doutorado Sanduíche e o projeto de Doutorado (Edital Universal 2013); ao CEMBAM e ao Projeto PELD, pelas ajudas de custo e logística do trabalho de campo.

Agradeço à Família Vegetal por esses longos 6 anos de convivência. Aos "irmãos vegetais" que já estão mundo à fora e deixaram saudades: Thatá, Cadu, Cíntia, Karina, Gabi, Flávio, Fer Coelho, Fer Costa; à velha-guarda remanescente: Juju, Nando, Pri (Sócia), Carol e Carlinha; e aos mais novos: Jeff, Thai, Elis, Loris, Carlito, Éder, Havle. Á Giselle que por tabela é secretaria de todo o lab. e não só da xará. Sou grata por me mostrarem os vários caminhos das pedras da logística de campo e burocracias do INPA, os momentos de café e todas as reuniões com bolo do lab. Muitos de vocês se tornaram amigos da vida, obrigada!

Às pessoas do INPA, do PPG Ecologia, da secretaria da pós-graduação e do CEMBAM. Existem pessoas que simplesmente cumpre as funções que lhe são designadas, outras vão além das amarras burocráticas institucionais e simplesmente querem ajudar quem precisa. Então especialmente sou grata ao sr. Valdir (prefeitura do campus do V8); ao Rubenildo (chefia da DSER) e sua equipe; aos funcionários e guardas da Reserva Ducke; a Val, Ana e Jéssica e demais assistentes da secretaria de pós; a Andresa e Cida do CEMBAM.

Aos amigos queridos de Manaus e do mundo à fora, por tantos momentos de distrações, ajudas, acolhimentos, puxões de orelha... Primeiro agradeço aos colegas e amigos da sala 9: Nando, Cassiano, Pancho e Isa, por compartilharem a impressora, o café, as conversas, as angústias e problemas. Agradeço à Marie-Josée Fortin, ao Nicholas Brooks e aos amigos queridos Tanque e à Kika pelo o acolhimento durante meu período em Toronto. Agradeço ao Alexander Christianini, à Milene, e às companheiras de casa Marielle e Laís por me acolherem tão bem durante meu tempo em Sorocaba. Aos colegas de prédio da pós-graduação e do "Anexo da Ecologia" pelos almoços e cafés compartilhados. Aos amigos queridos, Ana, Camis, Mia, Manô, Mari, Rosinha (gêmula), Juju, Bia, Lis, Gi, Fabrício, Bogão (gêmulo) e Saci, vocês foram especialmente importantes nesse fim de tese. Ao clã de bruxas mais poderoso do universo: xará, Manô, Pri, Fer, Carlota, Nati, obrigada por todos os momentos de caldeirão e feitiços curadores.

Aos colaboradores de trabalho. Os companheiros de campo: Nery, Mariazinha, Célio, Joãozinho, Ronaldo, Cassiano, Arthur, Mari, Thuane, Manô, Pantoja. Aos parceiros de pesquisa e co-autores dos artigos, Fabrício Bacccaro e Alexander Christianini. Ao Marcelo Gordo e ao Trupico pela ajuda com as câmeras-traps lá no começo do trabalho.

À minha família Delgado-Santana, mainha Rosa, painho Rogério, irmã Ayla e irmão Fabinho, agradeço infinitamente por tudo. Ao irmão-primo Tito, minha inspiração acadêmica e também como ser humano. Todos os primos e primas queridos, à dinda Tia Chú e todos o aos tios e tias, avós, pela torcida e envio de energias positivas, muitas vezes sem nem saber direito o que eu faço aqui no meio do mato (i.e. Manaus).

À Cassiano Gatto, companheiro que me convenceu que a Amazônia era um lugar maravilhoso para se pesquisar. Obrigada por tantos anos de convivência, das dores e os prazeres na mistura entre vida pessoal e acadêmica. Certamente você é um co-autor de bastidores dessa tese. Principalmente obrigada por me contagiar com seu olhar de historiador da natureza e por tantas inspirações naturalísticas.

À xará (Flávia Costa), mulher de tantas facetas, mãe, amiga, artista, escritora nas horas vagas (será que tem hora vaga?), pesquisadora e orientadora. Obrigada por trazer elementos de todas as suas facetas para a nossa relação dentro e fora da academia.

Sou grata por ser rodeada de muitas mulheres fortes, grandes amigas e gostaria de dizer que vocês me inspiram, são meu alicerce, minha força. Então minha segunda dedicatória é para todas as mulheres guerreiras do dia-a-dia.

Finalmente, agradeço aos revisores da tese Marina Côrtes, Rodrigo Fadini, José Fragoso, Tânia Sanaiotti e Bill Magnusson cujos comentários e sugestões foram muito construtivos para a versão final do trabalho escrito e certamente melhoraram a qualidade dos manuscritos.

*"Ser capaz, como um rio*
*que leva sozinho*
*a canoa que se cansa,*
*de servir de caminho*
*para a esperança.*

*E de levar do límpido*
*a mágoa da mancha,*
*como o rio que leva*
*e lava.*

*Crescer para entregar*
*na distância calada*
*um poder de canção,*
*como o rio decifra*
*o segredo do chão.*

*Se tempo é de descer,*
*reter o dom da força*
*sem deixar de seguir.*
*E até mesmo sumir*
*para, subterrâneo,*
*aprender a voltar*
*e cumprir, no seu curso,*
*o ofício de amar.*

*Como um rio, aceitar*
*essas súbitas ondas*
*feitas de águas impuras*
*que afloram a escondida*
*verdade das funduras.*

*Como um rio, que nasce*
*de outros, sabe seguir*
*junto com outros sendo*
*e noutros se prolongando*
*e construir o encontro*
*com as águas grandes*
*do oceano sem fim.*

*Mudar em movimento,*
*mas sem deixar de ser*
*o mesmo ser que muda.*
*Como um rio"*

Thiago de Mello (poeta amazonense)

# RESUMO

Investigamos aspectos da dispersão de sementes de quatro espécies de Marantaceae relacionados à complexidade dos múltiplos dispersores e de uma paisagem heterogênea de terra firme na Amazônia Central. No **capítulo 1** comparamos a dispersão de sementes por formigas e grilos entre as espécies de ervas e descobrimos que não há diferença entre o número de sementes removidas por grilos e formigas. Porém grilos removem sementes principalmente no período da noite e tendem a mover as sementes grandes mais longe. Ressaltamos que os grilos, assim como as formigas, podem ter papel importante na dispersão de sementes ariladas. No **capítulo 2** utilizamos o framework de efetividade de dispersão (SDE) para comparar o papel de diferentes grupos de dispersores na dispersão e recrutamento das ervas dentro de uma paisagem heterogênea. Perguntamos especificamente se existia relação entre o modo de dispersão atribuído à erva e a contribuição relativa dos diferentes dispersores à efetividade; como a efetividade de dispersão e assembleia de dispersores mudava com relação ao tipo de ambiente; e se existia uma associação entre os locais com maior efetividade, germinação e recrutamento. Encontramos que a dispersão de sementes é realizada principalmente por invertebrados, muitos deles inesperados. Para três das quatro espécies estudadas houve relação entre a síndrome de dispersão atribuída e o grupo dispersor mais efetivo. Entretanto, entre ambientes diferentes, o segundo dispersor mais efetivo pode contribuir desproporcionalmente para o SDE. Além disso, nem sempre o ambiente com maior SDE é também melhor para a germinação e recrutamento. Portanto, os papéis complementares dos dispersores de sementes à escala local de ervas, combinados com as mudanças no padrão de correspondência da SDE e habitat adequado para o recrutamento, devem ajudar a impulsionar a estrutura da comunidade de ervas de sub-bosque dispersas em animais em ambientes heterogêneos tropicais. No **capítulo 3** investigamos mudanças na estrutura das populações, padrões de abundância e suas relações com luz e hidrologia, para entender processos de limitação de dispersão e de estabelecimento ao longo de uma paisagem. As ervas com diásporos pequenos foram mais restritas a um tipo de ambiente, sugerindo limitação de dispersão e recrutamento mais associados a ambientes mais iluminados. Ervas com diásporos grandes estiveram mais distribuídas na paisagem sugerindo ausência de limitação de dispersão, e com recrutamento fortemente associado à hidrologia. Portanto, o padrão espacial da paisagem das espécies de ervas emerge da combinação de dispersão e limitação de recrutamento que atuando em diferentes escalas espaciais. Nesta tese, demonstramos que o processo de dispersão de sementes das ervas de sub-bosque é muito mais complexo do que considerado anteriormente e envolve inúmeros dispersores de sementes não antes reconhecidos. A condição de tolerância à sombra das espécies estudadas não está relacionada ao tipo de dispersor de sementes como visto anteriormente. A dispersão é um processo importante para permitir que as espécies estudadas ocupem diferentes habitats, no entanto, os filtros ambientais parecem refinar os padrões de abundância ao longo da paisagem heterogênea.

# ABSTRACT

## Seed dispersal of Marantaceae: the role of the habitat heterogeneity on plant-seed disperser interactions and on distribution patterns of understory herb species in the Central Amazonia

We investigated aspects of seed dispersal of four Marantaceae species related to the complexity of multiple dispersers and a *terra firme* heterogeneous landscape in Central Amazonia. In **Chapter 1** we compared seed dispersal by ants and crickets among herb species and found that there is no difference between the number of seeds removed by crickets and ants. However, crickets remove seeds mainly at night and tend to move large seeds further. We emphasize that crickets, like ants, may play an important role in the dispersion of arilate seeds. In **Chapter 2** we used the seed dispersal effectiveness framework (SDE) to compare the role of different disperser groups in the dispersion and recruitment of herbs within a heterogeneous landscape. We specifically asked whether there was a relationship between the seed dispersal assigned to the herb and the relative contribution of the different dispersers to herb SDE; How the SDE and dispersers assemblage changed due to the habitat type; and if there was a match between the SDE, germination and recruitment within habitat types. We found that the seed dispersion is mainly carried out by invertebrates, many of them unexpected. For three of the four species studied there was a relationship between the assigned dispersion syndrome and the most effective group of seed disperser. However, among different habitats, sometimes the second most effective disperser contributed disproportionately to the SDE. In addition, the habitat with higher SDE is not always better for germination and recruitment. Therefore, the complementary roles of seed dispersers at local scale, combined with changes in the match pattern between SDE and the suitable recruitment habitat, should hold the changes in community structure of animal dispersed understory herbs in tropical heterogeneous landscapes. In **Chapter 3** we investigated changes in population structure, patterns of abundance and their relationships with light and hydrology, to understand processes of limitation of dispersion and recruitment along a landscape. Herbs with small diaspores were more restricted to one type of environment, suggesting dispersion limitation and recruitment more associated with more enlightened environments. Herbs with large diaspores were more distributed in the landscape suggesting no dispersion limitation, and with recruitment strongly associated with hydrology. Therefore, the landscape spatial pattern of the herb species emerges from the combination of dispersion and recruitment limitation acting on different spatial scales. In this thesis, we demonstrate that the seed dispersal process of understory herbs is much more complex than previously considered and involves numerous seed dispersers not previously recognized. The shade tolerance condition of the species studied is not related to the type of seed disperser as seen previously. Dispersion is an important process to allow the studied species to occupy different habitats; however, environmental filters seem to refine patterns of abundance along the heterogeneous landscape.

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**Figure 1** – Summary of the main characteristics of the four Marantaceae plant species used in this study. Diaspores are represented in the same scale.

**Figure 2:** Interactions between crickets and seeds of Marantaceae species. A- Trial experiment using M. spicatum seeds that showed that the painted seeds with fluorescent ink did not interfer with the disperser – seed interactions (see also the appendix C for further details). B- Seed removed by female of *Luzaridella sussura* cf, distance = 8 cm; C- male of *Luzarida lata* and *G. altissima* seed; D- *Hygronemobius* sp. and *Luzarida* sp. cf with *I. arouma* seeds; E- *Hygronemobius* sp. cf with *I. arouma* seeds; F- *Phalangopsis* sp. and seed of *G. altissima*.

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**Figure A1:** Number of seeds removed per period of the day according to the pigment color used to paint the seeds. We used seeds of *M. spicatum* for the trial experiment. The trial was performed in one 10 x 100 m plot and in three observation points next to adult individuals of *M. spicatum*, separated by at least 10 m from each other. Each observation point received three seeds without pigmentation, three seeds painted with orange pigmentation and three with yellow pigmentation. Observations were performed for 2 hours in two periods: diurnal, between 8:00 and 16:00 and nocturnal, between 18:30 and 1:00.

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### CAPÍTULO 2

**Figure 1:** Characteristics of the four species of Marantaceae at Reserva Ducke, in Central Amazonia. Predicted seed disperser information from Horvitz (1991).

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(QC) and Quality component (QL) are showed, respectively, on the X- and Y-axes. Seed dispersers were clustered as functional groups and distinguished by the labels. Different colors represent three types of habitats along a topographical gradient. Note scale differences on axes of different plant species.

**Figure 3:** Simulated loss of individuals from different groups of seed dispersers of four species of Marantaceae, and its consequences for Seed Dispersal Effectiveness (SDE). Each dot represents the net change in the SDE value after complete removal of a given group. The black line represents the decline of SDE after random removal of individuals, with 95% CI (in gray). SDE values were log-transformed for presentation.

**Figure 4:** Boxplots showing the relative contribution of each seed disperser group to Seed Dispersal Effectiveness (SDE) of four species of Marantaceae, along a topographical gradient, in Central Amazonia. Graphics showing the median, the 25th and 75th percentiles.

## CAPÍTULO 3

**Figure 1.** Map of the study site in Reserva Florestal Adolpho Ducke (RFAD) and sample design. Surveys of herbs individuals of the four Marantaceae species took place in the 87 plots of 5 m x 100 m represented by colored rectangles which were placed in the main habitat types of the study area: plateau (red); slope (yellow); valley (blue).

**Figure 2.** Characteristics of the four species of Marantaceae at Reserva Ducke, in Central Amazonia. Predicted seed disperser information from Horvitz (1991).

**Figure 3.** Abundance of four herb species across life history stages in the main different microhabitat of study. Life history stages were separated based on individual heights. The line near the middle of the boxplot represents the median, and the bottom and top of the box represents the 25th and 75th percentile, respectively. Extreme data are represented by black points. Plant species are ordered by diaspore size: Large diaspores on above graphs (*Goeppertia altissima* and *Ishchnosiphon arouma*) and; Small diaspores on under graphs (*Monotagma densiflorum* and *Monotagma spicatum*).

**Figure 4.** Influence of environmental factors in the abundance of four herb species across life history stages. HAND is a proxy for “distance from drainage”, Light were measured with canopy scope.  Estimates values are from GLMM models and variable's values were standardized to permit comparisons. Life history stages were separated based on individual heights.  Species are divided according to diaspore size: Large diaspores *Goeppertia altissima* and *Ischnosiphon arouma* and; Small diaspores *Monotagma densiflorum* and *Monotagma spicatum*.

**Figure 5:** Maps showing the spatial associations of life stages within blocks contain the three main habitats at study site (i.e. plateau, slope and valley) distinguished by colors. Symbols type represent the life stages adults, juveniles and seedlings. The symbols size is in accordance with the G* score value, bigger symbols strongest is the spatial association. The colored crosses represent the plots where the species were presented but with the G* score below the average.

# INTRODUÇÃO GERAL

A dispersão de sementes é um dos processos mais importantes no ciclo reprodutivo das espécies vegetais e também um dos mais complexos. O processo de dispersão engloba desde o início da fase reprodutiva, a floração, passando pela maturação dos frutos/sementes, à deposição da semente no sítio final, até o recrutamento e geração de um novo indivíduo reprodutivo (Nathan and Muller-Landau 2000, Wang and Smith 2002). É um processo complexo porque sofre influência de fatores intrínsecos, como fitness e características genéticas do indivíduo, e extrínsecos como condições do ambiente e interações bióticas (Levin et al. 2003). Poucos são os eventos de dispersão que são bem-sucedidos devido a todos esses filtros, no entanto quando realizada, a dispersão de sementes diminui a mortalidade denso-dependente, maximiza o recrutamento de novos indivíduos, viabiliza a colonização de novos ambientes, afetando diretamente a dinâmica da população (Howe and Smallwood 1982, Willson and Traveset 2000).

As espécies vegetais experimentam diferentes níveis de limitação de dispersão e de recrutamento que determinam localmente a composição e distribuição espacial das espécies, e são portanto, processos chave para a manutenção da riqueza nos ambientes tropicais (Hubbell 2001, Chave et al. 2002, Schupp et al. 2002, Hubbell 2005). Portanto, é fundamental entender como as espécies vegetais diferem quanto à capacidade de dispersão e recrutamento e como esses processos são afetados por fatores bióticos e abióticos, afim de melhor compreender a estruturação de comunidades vegetais tropicais.

Dentre as diversas formas de dispersão, a realizada por animais predomina nos ambientes tropicais e é mediada pela presença de estruturas carnosas e nutritivas ofertadas pela planta em troca da dispersão dos seus diásporos (i.e. unidade que é dispersa) (Clark et al. 1999). Estudos das últimas duas décadas têm mostrado que plantas que possuem estruturas carnosas incialmente adaptadas co-evolutivamente para dispersão por um animal específico (i.e. síndrome de dispersão), na realidade, atraem dois ou mais tipos de dispersores de sementes (Vander Wall and Longland 2004, Jordano et al. 2007). Os frugívoros vertebrados são os dispersores principais da maioria das espécies vegetais nos trópicos (Gentry 1982; Fleming e Kress 2011), seguidos pelos invertebrados que são comumente reconhecidos por desempenharem a dispersão secundária dessas espécies vegetais (Roberts and Heithaus 1986, Christianini and Oliveira 2010, Culot et al. 2015). A presença de dois ou mais dispersores no processo de dispersão implica que a distribuição das sementes pós-dispersão é muito mais complexa do que pensada anteriormente e demanda o conhecimento dos padrões de comportamento dos agentes dispersores envolvidos.

As condições ambientais locais afetam o ciclo de dispersão de sementes ao longo de várias etapas. Quando em condições climáticas favoráveis, e considerando que a polinização não é limitante, a reprodução e produção de sementes é maior, tanto na escala do indivíduo quanto na escala da população local (Spiegel and Nathan 2012). Consequentemente, na perspectiva dos frugívoros, quanto maior a mancha de recurso maior a atratividade e taxa de remoção de frutos (García et al. 2011, Moorales et al. 2012). A qualidade do sítio de deposição da semente também varia e depende da predação pós-dispersão, dos requisitos favoráveis à germinação e estabelecimento, além da probabilidade de mortalidade por efeito de densidade (Howe and Miriti 2004). Desse modo, a heterogeneidade das condições ambientais exerce importante papel no ciclo de dispersão de sementes, influenciando a abundância e assembleia de dispersores e modificando o resultado da dispersão de sementes (Gómez-Aparicio et al. 2005, Rother et al. 2015). Porém, ainda são poucos os estudos que avaliam a dispersão de sementes e recrutamento em ambientes tropicais levando em conta a heterogeneidade ambiental.

Diferentes dispersores de sementes contribuem desproporcionalmente no processo de dispersão em decorrência de diferenças na frequência de visitas, na capacidade de carregar os diásporos (i.e., relação entre tamanho corpóreo e tamanho do diásporo) e na chance de depositá-los em microsítios mais favoráveis (Roberts and Heithaus 1986, Clark et al. 2005, Westcott et al. 2005). Consequentemente, a distribuição espacial das sementes irá depender inicialmente do tipo de tratamento dado ao diásporo pelos dispersores (i.e., ingestão ou não) e qual o padrão de movimentação e preferência de habitat desses animais (Cortês and Uriarte 2013, Da Silveira et al. 2016). Os dispersores de sementes são importantes para realizar a manutenção local das populações ou ainda dispersar sementes para outras populações contribuindo para o fluxo gênico via dispersão. Portanto, podem afetar drasticamente tanto a estrutura espacial quanto genética das espécies vegetais (Godoy and Jordano 2001, Jordano et al. 2007). No entanto, conectar a ação de múltiplos dispersores à estruturação das populações vegetais tem sido um dos grandes desafios dos estudos de ecologia de dispersão de sementes nas últimas décadas (García et al. 2007, Spiegel and Nathan 2010, Rother et al. 2016). Uma das razões para isso é a ausência de informações mais completas sobre a identidade dos agentes dispersores envolvidos. Nesse sentido, há necessidade de mais estudos de história natural das interações planta-dispersor.

A maior parte do arcabouço teórico sobre o papel da dispersão na dinâmica e estruturação das populações nos trópicos foi construído a partir dos estudos de espécies arbóreas. No entanto, as espécies herbáceas do sub-bosque representam até 40% da diversidade de plantas na floresta tropical (Gentry e Emmons 1987) e muitas dessas ervas são dispersas por animais. Dessa forma, as ervas são componentes importantes de riqueza e estrutura do sub-bosque de florestas tropicais (Costa 2006). Muitos estudos focam em como as ervas de sub-bosque são estruturadas quanto à gradientes de solos, de umidade e clima em escalas regionais e biogeográficas (Costa et al. 2005, 2012, Costa 2006, Moulatlet et al. 2014, 2015). No entanto, poucos estudos abordaram a forma como a dispersão de sementes influencia a distribuição das ervas de sub-bosque nas escalas locais (Horvitz e Corff 1993, Uriarte et al. 2010, 2011). Dentre as ervas de sub-bosque, as espécies da família Marantaceae são maioria nas florestas da planície amazônica, compondo até 30% do estrato herbáceo (Costa 2006). Além da alta representatividade da família no estrato herbáceo da floresta, as espécies da família Marantaceae possuem sementes ariladas com distintas características como tamanho variado de sementes, contraste de coloração, presença de odor (Carden 1961, Horvitz 1991), que são dispersas por diferentes tipos de animais. A maioria dos estudos de dispersão de sementes de espécies de Marantaceae limitam-se a inferir o papel dos dispersores primários, de acordo com a abordagem de síndromes de dispersão, e quase sempre ignoram os potencias dispersores secundários e seus impactos na dinâmica populacional dessas ervas. Portanto, essa tese espera preencher lacunas a respeito dos múltiplos dispersores de espécies de Marantaceae e integrar tal perspectiva ao estudo das limitações de dispersão e recrutamento das ervas de sub-bosque. Para isso, selecionamos quatro espécies de Marantaceae que possuem baixa taxa de reprodução clonal e características que sugerem dispersão por vertebrados (aves e pequenos mamíferos ou morcego) e por formigas (Horvitz 1991), mas que posteriormente foram classificadas apenas como espécies com sementes grandes (> 0,3 g) e espécies de sementes pequenas (peso < 0,07g), respectivamente (Santana et. al 2016).

Muitos diásporos carnosos de espécies vegetais, uma vez disponíveis no solo, são removidos pela fauna de invertebrados. Formigas, principalmente, removem com frequência diásporos caídos da planta-mãe, ou ainda após dispersão primária (Pizo et al 2005, Christianini et al 2012). A presença parcial ou integral da parte carnosa aumenta a atratividade do diásporo para as formigas e também a chance de dispersão, por outro lado, sementes caídas no solo sem a estrutura carnosa têm mais chance de serem predadas (Horvitz and Schemske

1994, Pizo et al. 2005). As formigas não são os únicos invertebrados atraídos e que consomem a parte carnosa dos diásporos. Frutos carnosos disponíveis no solo das florestas são um importante recurso alimentar tanto para a fauna de vertebrados quanto para invertebrados (Böhning-Gaese et al. 1999, Carnicer et al. 2009, Bottcher et al. 2016). Embora quase nunca sejam feitos experimentos assistidos de remoção de diásporos na superfície do solo, a maioria dos estudos de dispersão secundária assume que a remoção dos diásporos no solo é realizada basicamente por pequenos mamíferos ou formigas. No entanto, grilos por exemplo, geralmente são observados consumindo partes carnosas dos frutos, mas sua capacidade de remover e dispersar diásporos nunca tinha sido efetivamente estudada nas florestas neotropicais. No **primeiro capítulo** dessa tese, realizamos experimentos de remoção utilizando as sementes ariladas de quatro espécies de Marantaceae (cite as espécies) para avaliar o papel dos grilos como potenciais dispersores de sementes de Marantaceae, comparando-os com as formigas.

A contribuição efetiva dos dispersores de sementes varia tanto quantitativamente (i.e. número de sementes dispersas), quanto qualitativamente (tratamento dado à semente pelo frugívoro e qualidade do local de dispersão). Entre os dispersores potenciais de espécies de Marantaceae, por exemplo, é esperado que os vertebrados possam contribuir mais na qualidade da dispersão, uma vez que podem dispersar os diásporos a maiores distâncias. Porém localmente, invertebrados como as formigas, por exemplo, podem depositar os diásporos desproporcionalmente em locais mais favoráveis para o recrutamento, também afetando a qualidade da dispersão. A quantidade e qualidade são componentes da efetividade de dispersão de sementes (SDE – sigla em inglês para Seed Dispersal Effectiveness), que idealmente significa a contribuição do dispersor para que a dispersão do diásporo resulte em um novo indivíduo reprodutivo (Schupp 1993, Schupp et al. 2010). A partir de intensivo monitoramento da remoção de sementes direto da planta-mãe com câmeras-trap e dos experimentos de remoção de sementes no solo, no **segundo capítulo**, nós determinamos os grupos dispersores (vertebrados e invertebrados) mais efetivos para as quatro espécies de Marantaceae e avaliamos como a efetividade de dispersão de cada espécie de erva é afetada pela variação ambiental na escala da paisagem. Nesse capítulo, nós também relacionamos a efetividade de dispersão com taxas de germinação e recrutamento inicial, através de experimentos realizados em campo.

A distribuição espacial dos indivíduos reprodutivos e a forma como ocorre a dispersão (quantidade de sementes dispersas e sua distribuição espacial) dependendo do tipo de dispersor, determina o padrão de dispersão de sementes (Nathan and Muller-Landau 2000). Porém, nem sempre o padrão da dispersão de sementes reflete o padrão de recrutamento (Swamy et al 2011), que irá depender também dos filtros-ambientais que atuam ao longo dos estágios de vida da planta. O recrutamento das plantas pode ser limitado pela dispersão (i.e. produção de sementes e/ou espalhamento das sementes disponíveis), denominado de limitação de dispersão (*sensu* Nathan e Muller-Landau 2000) e/ou pela qualidade do ambiente onde a semente foi depositada (i.e. determinada pelas chances de germinação/estabelecimento que variam em função de taxas de predação e de condições ambientais), processo denominado de limitação de estabelecimento pelo mesmo artigo. A importância desses processos varia tanto no espaço, quanto no tempo e embora cada espécie experimente diferentes níveis de limitação de dispersão e de estabelecimento, os estudos com ervas de sub-bosque mostram que o recrutamento de plântulas está associado com a disponibilidade de luz (Bruna and Kress 2002, Uriarte et al 2010, Horvitz and Schemske 1994). Porém, na maioria dos casos, esses padrões foram encontrados para espécies cujo recrutamento é conhecidamente associado a dinâmica de clareiras ou em paisagens modificadas (mas veja Horvitz, 1991). No **terceiro capítulo** dessa tese, a partir da amostragem e mapeamento dos indivíduos das quatro espécies estudadas na escala de uma paisagem de floresta, avaliamos a estrutura das populações e os padrões de abundância, para entender como limitação de dispersão e de estabelecimento afetam os padrões espaciais na escala da paisagem.

## OBJETIVOS

### Objetivo Geral

Essa tese teve como objetivo principal investigar qual o papel da dispersão de sementes realizada por diferentes dispersores e dos fatores ambientais no recrutamento e estruturação populacional de marantáceas.

### Objetivos específicos

A tese possui três objetivos específicos que são apresentados nos três capítulos a seguir:

**Capítulo 1:** Avaliar a importância relativa de diferentes grupos de dispersores de sementes (i.e. grilos e formigas) de Marantaceae;

**Capítulo 2:** Avaliar o efeito de múltiplos dispersores na efetividade de dispersão das Marantaceae ao longo de um gradiente topográfico;

**Capítulo 3:** Determinar os papeis da limitação de dispersão e de estabelecimento para espécies de Marantaceae com diásporos de diferentes tamanhos, através da perspectiva de múltiplos dispersores de sementes.

# CAPÍTULO 1

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Santana, F. D.; Baccaro, F. B.; Costa, F. 2016. Busy nights: high seed dispersal by crickets in a Neotropical forest. *The American Naturalist* 188(5):E126

## Abstract

Among invertebrates, ants are the most abundant and probably the most important seed dispersers in both temperate and tropical environments. Crickets, also abundant in tropical forests, are omnivores and commonly attracted to fruits on the forest floor. However, their capability to remove seeds has only been reported once. We compared Marantaceae seed removal by crickets and ants to assess the role of crickets as secondary seed dispersers in Amazonia. Crickets dispersed an equivalent number of seeds and tended to disperse larger seeds further compared with ants. However, seed removal by crickets occur mostly at night, suggesting that removal of arillate seeds by crickets on the tropical forest floor is probably being overlooked or wrongly attributed to other invertebrate groups. One potential consequence of seed dispersal by crickets may be a change in the local spatial distribution of arillate-seed species, due to lower aggregation around ant nests.

## Introduction

Diplochory, is a complex multistage seed dispersion process that relies on two or more dispersal agents (Willson and Traveset 2000; Vander Wall et al. 2005*b*). Plants that display fleshy diaspores have their dispersal capability enhanced, given the possible presence of animals as dispersal vectors in subsequent phases of diplochory (Jordano et al. 2007, Travesset et al. 2014). In tropical forests, more than 80% of woody plants are primarily dispersed by frugivore vertebrates (Gentry 1982), and in most cases, also followed by a second movement of seeds by invertebrates (secondary seed dispersal). Secondary seed dispersal by invertebrates is one of the described types of diplochory (Vander Wall and Longland 2004, Christianini and Oliveira 2009, García-Robledo and Kuprewicz 2009). The combination of multiple biotic dispersers results in complementary processes, given that each vector disperse different numbers of seeds for different distances and to different micro-habitats (Beckman and Rogers 2013). Ultimately, the differences in the quantity and distance of seeds dispersed by multiple vectors is reflected in the shape and scale of the seed spatial distribution, or seed shadow (Horvitz and Le Corff 1993; Clark et al. 2005; Cortês and Uriarte 2012). Disentangling the effects of multiple disperser agents is a challenge for seed dispersal ecologists and essentially depends on our natural history knowledge of what organisms remove the seeds and how they do so.

As primary dispersers, frugivore vertebrates are key to structure plant recruitment at different scales, in addition to promoting the colonization of new environments due to the capacity for dispersing seeds further (>100m) from the source (Fragoso 1997; Jordano 2007). Occasionally, dispersed diaspores remain in the vicinity of the parent plant, or reach the floor with the fleshy part intact, partially consumed or in vertebrate feces (Jordano and Schupp 2000; Christianini and Oliveira 2009). Those dispersed diaspores become available to the invertebrate community that can either prey on or act as secondary seed dispersers, causing a rearrangement of the vertebrate seed shadows (Vander Wall et al. 2005*a*). Secondary seed dispersal influence plant population and recruitment at local scales enhancing the chances of plant to escape from predators and to reach best microsites for seedling establishment (Vander Wall and Longland 2004). Among invertebrate dispersal agents, ants are important primary seed dispersers in both temperate and tropical environments. Myrmechocore plants are common in arid zones (Bond et al. 1991; Giladi 2006; Boulay et al. 2007) and as herbs in tropical forests (Horvitz 1981). However, for most tropical vegetation, ants act mainly as secondary dispersers of diaspores primarily dispersed by frugivore vertebrates (Pizo et al. 2005; García-Robledo and Kuprewicz 2009; Santana et al. 2013). Seeds bearing lipid-rich arils, a highly attractive structure, enhances the removal of seeds by ants on the forest floor (Bieber et al. 2013; Santana et al. 2013). In the last three decades, an increasing number of post-dispersal seed removal studies have highlighted the impact of invertebrates in the second phase of seed dispersal.

Given the diversity and abundance of invertebrates on tropical forests floor, it is possible that other invertebrate groups also act as secondary seed dispersers, and some studies already pointed to New Zealand weta, slugs, and crickets as such (Dutie et al. 2006, Türke et al. 2012; Sidhu and Datta 2015). Large-bodied orthopterans called weta (Anostostomatidae) can disperse seeds by endozoochory and enhance seed germination after gut passage (King et al. 2011). Crickets (Orthoptera: Grylloidea) are considered to be omnivores and are commonly attracted to fallen leaves, fruits rich in glucids, and seeds (Szinwelski et al. 2015), but their role as seed dispersers is still poorly explored (but see Sidhu and Datta, 2015). The low frequency of records of crickets in seed removal may reflect a bias towards observation periods, given that crickets are mostly active at night (Desutter-Grandcolas 1995), and most seed removal experiments with direct observations of invertebrate-seed interactions focus on diurnal trials. Even so, crickets have been observed interacting with fruits on the floor of tropical forest (Christianini and Oliveira 2010, Bieber et al 2013), but in such interactions, they did not remove seeds.

During fieldwork at central Amazonia, frequent interactions between crickets and Marantaceae arillate seeds came to our attention, raising questions about the implications of those interactions on the seed shadow and plant spatial structure. In this study, we compared seed removal by crickets and ants to measure their potential role as secondary seed dispersers of Marantaceae species in Central Amazonia. The study aimed to answer the following questions: 1) Do ants and crickets differ in the number and size of seeds that they remove? 2) Do crickets remove more seeds at night compared to ants? 3) Does the distance of seed removal by ants and crickets differ?

## Material and Methods

*Study Area*

The study was carried out in *Reserva Ducke*, a 10,000 ha (10 km x 10 km) protected area 26 km north of Manaus - Brazil (02º 55’-03º 01’ S, 59º53’-59º59’ W) in central Amazonia. The site is covered by *terra firme* tropical moist forest with a 30 - 37 meters tall canopy. The heterogeneous landscape in *Reserva Ducke* is formed by moderately rugged terrain generating a soil gradient from high percentages of clayey yellow latosol on the upland areas (plateau) towards less clayey red-yellow soils on slopes until the wet and sandy podzol soils on the valleys with small perennial streams (Chauvel et al. 1987). Mean annual temperature is 26°C and annual rainfall ca. 2400 mm with a monthly maximum of ~330 mm in March, and a minimum in August, with <100 mm (Marques-Filho et al. 1981). The site is subdivided by an 8 x 8 km grid system for long-term ecological studies, with trails spaced by 1 km.

The present study was carried out in nine 10 x 100 m plots, within a 2 x 2 km portion of the grid. Three plots were placed on each of the main topographical microhabitats, plateaus, slopes and valleys. Although possible seed dispersal variation related with topography is not the main focus of this study, the plot distribution aimed to cover the natural habitat heterogeneity, and to avoid any bias in ants and cricket’s distribution.

*Plant species*

Marantaceae is the most conspicuous group within the understory herb community of *Reserva Ducke* representing 36.5 percent of the total herb cover, with 22 species (Costa 2006).

The diaspores of Marantaceae species are characterized by a seed bearing a lipid-rich aril that are mainly dispersed by ants and birds (Horvitz 1991). We choose four Marantaceae species with contrasting primary dispersal syndromes and seed mass: *Goeppertia altissima* (dispersed by birds) and *Ischnosiphon arouma* (dispersed by unknown vertebrate) produce large seeds (>0.3 g) while *Monotagma densiflorum* and *Monotagma spicatum* (both dispersed by ants) produce small seeds (< 0.07 g) (fig. 1). Vertebrate frugivores were observed only once, when a thrush-like Schiffornis (*Schiffornis turdina*) was manipulating *G. altissima* seeds (unpublished data). The total number of seeds per infrutescence differ greatly among species and ranges from 3-10 seeds in *I. arouma*, 7-40 seeds in *G. altissima*, 15-40 seeds in *M. densiflorum* and 30-70 in *M. spicatum*. However, there is a gradual maturation in the seeds within the infrutescence and just a few become available for dispersal at the same time (F. Santana personal observation).

### *Seed Removal Experiments*

We collected mature seeds directly from the infrutescence of several individuals (10-20) aiming to use them in removal experiments. In each plot, seeds were placed directly on the ground, in three observation points next to adult individuals of the focal species, separated by at least 10 m from each other. In the absence of adult individuals in the plot, seeds were placed at random locals respecting the minimum distance of 10 m. The number of seeds per observation point was standardized for each species and ranged between two and five, based on variable abundance of seeds between different species. Observations were performed for 2 hours, in two periods: diurnal, between 8:00 and 17:00 and nocturnal, between 18:30 and 1:00 in all plots. To facilitate visualization during night trials, all seeds were painted with a solution of fluorescent pigment powder diluted in acetone (Reiter et al. 2005) the day before the experiment. A previous experiment showed that painted seeds did not affect how they were treated by ants and crickets (figs. 2*A* and A1). Observation points were constantly monitored by an observer that took notes of all interactions between invertebrates and seeds. In a seed removal event, the invertebrate was followed until the deposition of the seed in the ground, or the animal reached the nest (in the case of ants), or where the seeds were lost from sight. The measurement of removal distance was between the observation point and the last known location of the seed at the end of 2 hours of the experiment. One specimen of each ant and cricket species involved in the seed removal was collected whenever possible. We also used images of the seed removal events to help in the identification of species in the cases when it was not possible to collect a specimen.

### *Statistical Analysis*

We used generalized linear mixed models (GLMM) available in the package "*gamlss*" in R 3.2.3 (R Core Team 2015), to answer our three questions. The fixed effects in the models were: disperser agent (ant or cricket), seed weight (representing the mean weight value of each plant species as presented in table 1) and period of the day (day or night). In model 1, we evaluated whether the number of seeds removed was explained by the dispersal agent, the mean weight of seeds and their interaction. In model 2, we evaluated whether the number of seeds removed was explained by the dispersal agent, the period of the day and their interaction. In model 3, we evaluated whether the distance of seed removal was explained by the dispersal agent, the mean weight of seeds and their interaction. We fitted GLMMs, based on the best AIC, with Poisson error distribution for models 1 and 2, and Gamma error distribution for model 3. Data analysed in this manuscript are deposited in PPPBio, Meta Cat Repository: https://ppbiodata.inpa.gov.br/metacatui/#view/PPBioAmOc.56.6 (Santana and Costa 2016).

## Results

We used 648 seeds of the four Marantaceae species in the removal experiments and 21% (n = 136) of those seeds were removed by ants and crickets. Besides ants and crickets, 5 seeds were removed by other invertebrates such as cockroaches (n = 4) and spiders (n=1) but those records were not included in data analyses. Seed removal was performed by 16 ant and 6 cricket species (table B1). The removal behaviour of ants varied according to the species, being basically of two types: i) seed removal followed by the aril consumption out of the nest performed by ant species that recruit to food source, such as *Pheidole* and *Solenopsis*; and ii) seed removal to the nest by solitary foragers of *Ectatomma* and *Pachycondyla* species. Cricket species varied greatly in morphology and body size (fig. 2), but their behaviours toward seeds were remarkably similar. Generally, crickets removed seeds, then consumed the aril (fig. 2*C-F* and video C1, available online), and the predation of seed after removal was observed in only a single event.

Among crickets, *Luzarida lata* removed most of the seeds, followed by *Luzaridella* sp. Crickets and ants were sometimes seen simultaneously at the same observation point during the experiments and, in some events, they removed the same seed at different times. The crickets' maximum dispersal distance was 80 cm, which was around half the maximum distance observed for seeds dispersed by ants (fig. 3*A*).

Ants and crickets removed seeds of all four studied plant species (fig. 3*B*) and the proportion of removal events was approximately the same, around 56.6% (n = 77) by ants and 43.4% (n = 59) by crickets (X-squared = 36, df = 30, p-value = 0.208). Seed removal was not, however, evenly distributed among plant species. Based on the median values, ants removed more seeds of *M. densiflorum* (small seed) and *I. arouma* (large seed), while crickets removed seeds of *G. altissima* (large) and *M. spicatum* (small seed) (fig. 3*B*).

Seed weight influenced seed removal and both disperser groups tended to remove more small seeds (table 1, model 1, fig. D1-*A*). There was a tendency for crickets to remove larger seeds more frequently than ants (fig 1D); however, the interaction between seed weight and crickets was not significant (table 1). Crickets removed more seeds at night compared to ants (fig. 3*C*). Indeed, the time of day was an important effect for explaining the number of seeds removed (table 1, model 2) by each disperser group (fig. D1-*B*). On average, ants removed seeds for longer distances (mean = 39.31 cm, range = 2 - 226 cm) than crickets (mean = 13.83 cm, range = 3 - 80 cm) (fig. 3*D*). However, distance of seed removal by crickets and ants also differed according to the plant species and seed size (table 1, model 3, fig. D1-*C*), ants moved small seeds further than crickets and crickets moved large seeds further than ants (fig. 3*D*).

## Discussion

Crickets are known predators of fallen leaves, fruits and seeds (Szinwelski et al. 2015) and records of seed removal by crickets are rare and involving one particular species (Sidhu and Datta (2015). However, to our knowledge, the role of assemblages of crickets acting as secondary seed dispersers has not been reported. Our study showed that crickets consume only the aril of arillate seeds and abandon the seed in another location, acting as secondary dispersers. Crickets removed the same amount of seeds than ants of all four studied Marantaceae species, indicating that seed removal by crickets on the forest floor is common. The number of seeds removed by crickets was not affected by seed weight for the studied species, but crickets removed larger seeds further than ants.

The role of crickets as seed dispersers remains little explored or is largely unknown. The New Zealand weta is the only orthopteran group widely recognized as seed dispersers (Dutie et al. 2006). However, wetas consume the entire seed and some of them escape from the gut passage in conditions to germinate (Dutie et al. 2006). In a recent report, Sidhu and Datta (2015) showed that the Indian cricket *Brachytrupes* sp. was responsible for approximately 30% of secondary seed removal. Seeds removed by crickets were buried underground and had higher germination rate when compared to seeds found by rodents, which acted as seed predators (Sidhu and Datta 2015). Our data suggest that at least six crickets species act as dispersers, removing seeds from the surface of the leaf-litter after they fall directly from the parent plant. Sidhu and Datta (2015) used in their experiments seeds with the aril removed, and therefore they were not able to observe aril consumption as shown here. Consumption of the aril can be can be considered a benefit for plant species with fleshy diaspores when this activity decrease seed attack by fungi and pathogens (Ohkawara and Akino 2005).

Our study shows that there is a temporal partitioning of seed removal by ants and crickets. Although some ant species of Ectatomminae and Ponerinae subfamilies forage more actively at night (Pizo et al. 2005; Santana et al. 2013), most of the species that interacted with the seeds during this study were more frequently observed during the day. Conversely, we recorded a higher occurrence of crickets during nocturnal seed removal experiments. Therefore, increasing the number of experiments for direct observation of seed removal by invertebrates in the nocturnal period will probably generate a better picture of the role of crickets in seed dispersal of arillate seeds.

On average, crickets did not transport seeds further than ants. However, there was an indication that large seeds of *G. altissima* and *I. arouma* were removed greater distances by crickets (fig. 3*D*). These results suggest that crickets may affect the local seed distribution of herb species that produce seeds too heavy to be carried by ants (Gómez et al. 2005), changing their dispersal kernel. Body size of crickets may vary 16 mm among species and around 5 mm within the same species during their life cycle (Mews and Sperber, 2008; Gorochov, 2014), so their effects on dispersal distance may be more variable than we report here. Invertebrates such as ants and crickets act at local scales (mean radius < 5 m) and their seed removal distances, even if apparently small, represent enough escape from under parent´s canopy for herbs that are mostly around 1 m high (except for *I. arouma* that averages 2 m high). For some plant species, habitat quality where seeds arrive is more important than dispersal distance *per se* (Shupp et al. 2010), especially in patchier environments such as tropical forests.

Besides distance *per se*, ants and crickets disperse seeds differently. It is known that in the ant-seed interaction, the final destination of the seed tends to be the ant nest (Leal et al. 2007; Servigne and Detrain 2008) resulting in plant recruitment concentrated around nests (Horvitz and Schemske 1994; Passos and Oliveira 2002). This generates an aggregated spatial pattern at small-scales. The impacts of seed aggregation were not specifically explored for our studied species, however aggregated seed dispersal may in some cases be responsible for increases in denso-dependent mortality caused by spread of pathogens (Spiegel and Nathan, 2010, Beckman and Rogers 2013). Crickets, however, forage individually and have an errant behaviour, resulting in a multi-directionally scattered seed shadow, which may be advantageous in decreasing the negative effects of seed aggregation. However, ant nests may provide a better germination site (Passos and Oliveira, 2002), so the consequences of the combination of ant and cricket dispersal for plant recruitment should still be examined. As seen here, crickets may have a complementary role on the dispersal process of vertebrate and ant-dispersed species, potentially modifying spatial population patterns.

Our results show that crickets remove similar amounts of arillate seeds than ants, suggesting that the removal of arillate seeds by crickets on the tropical forest floor is being overlooked or wrongly attributed to other invertebrate groups. Given that interactions between crickets and seeds involved more than one species and the high diversity and abundance of cricket' species in Neotropical forests (Desutter-Grandcolas 1992), it is possible that additional cricket and plant species interactions will be identified, especially if nocturnal experiments become a common practice.

## Acknowledgements

The authors acknowledge Jacques Delabie, Alexander Christianini and the two anonymous referees for their valuable comments and suggestions that enriched the manuscript and also Fernando Figueiredo and Cassiano Gatto for data analyses suggestions. We thank Maria Águida and Nery Garcia their assistance during seed removal observations. Sincere thanks to Lúciene Gimaque for cricket species identification. This study was supported by Brazil's National Council for Scientific and Technological Development (CNPq), grant number 478908 / 2012-1. Flavia Santana received a PhD. scholarship from Brazil's National Council for Scientific and Technological Development (CNPq)

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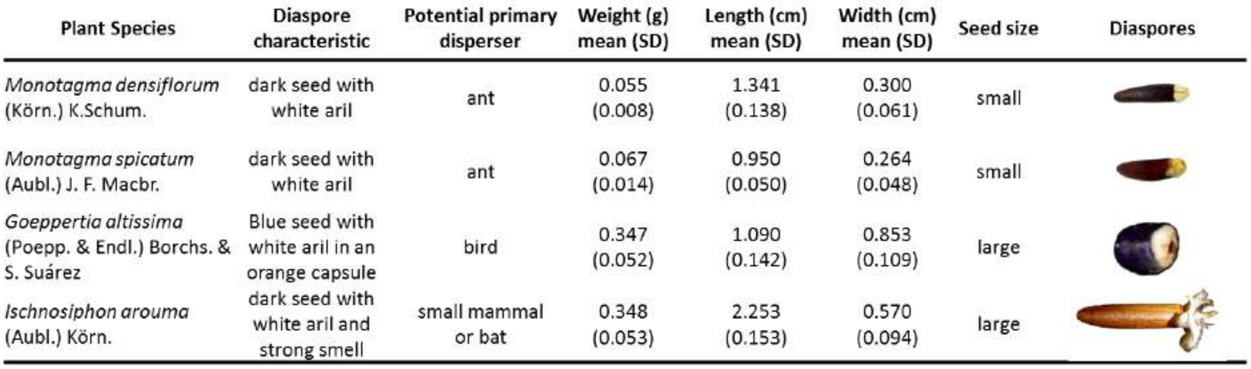
## List of Tables

**Table 1:** Summary of the generalized linear mixed models comparing seed removal by ants and crickets in an Amazonian forest

| **Table 1: Summary** | **Coefficient B** | **Pr(>\|t\|)** |
|---|---|---|
| MODEL 1 | | |
| (Intercept) | 1.17 | < 0.01 ** |
| disperser | -0.54 | 0.04* |
| weigth | -5.03 | 0.01 * |
| disperser:weigth | 1.77 | 0.17 |
| MODEL 2 | | |
| (Intercept) | 5.82 | 0.001*** |
| disperser | -4.92 | 0.001*** |
| period | -3.41 | 0.001*** |
| disperser:period | 2.79 | 0.001*** |
| MODEL 3 | | |
| (Intercept) | 6.35 | 0.001*** |
| disperser | -2.10 | 0.001*** |
| weigth | -13.18 | 0.001*** |
| disperser:weigth | 7.81 | 0.001*** |

**Note:** Plant species was set as random factor in all models.

## List of Figures



| Plant Species | Diaspore characteristic | Potential primary disperser | Weight (g) mean (SD) | Length (cm) mean (SD) | Width (cm) mean (SD) | Seed size | Diaspores |
|---|---|---|---|---|---|---|---|
| *Monotagma densiflorum* (Körn.) K.Schum. | dark seed with white aril | ant | 0.055 (0.008) | 1.341 (0.138) | 0.300 (0.061) | small | |
| *Monotagma spicatum* (Aubl.) J. F. Macbr. | dark seed with white aril | ant | 0.067 (0.014) | 0.950 (0.050) | 0.264 (0.048) | small | |
| *Goeppertia altissima* (Poepp. & Endl.) Borchs. & S. Suárez | Blue seed with white aril in an orange capsule | bird | 0.347 (0.052) | 1.090 (0.142) | 0.853 (0.109) | large | |
| *Ischnosiphon arouma* (Aubl.) Körn. | dark seed with white aril and strong smell | small mammal or bat | 0.348 (0.053) | 2.253 (0.153) | 0.570 (0.094) | large | |

**Figure 1** – Summary of the main characteristics of the four Marantaceae plant species used in this study. Diaspores are represented in the same scale.

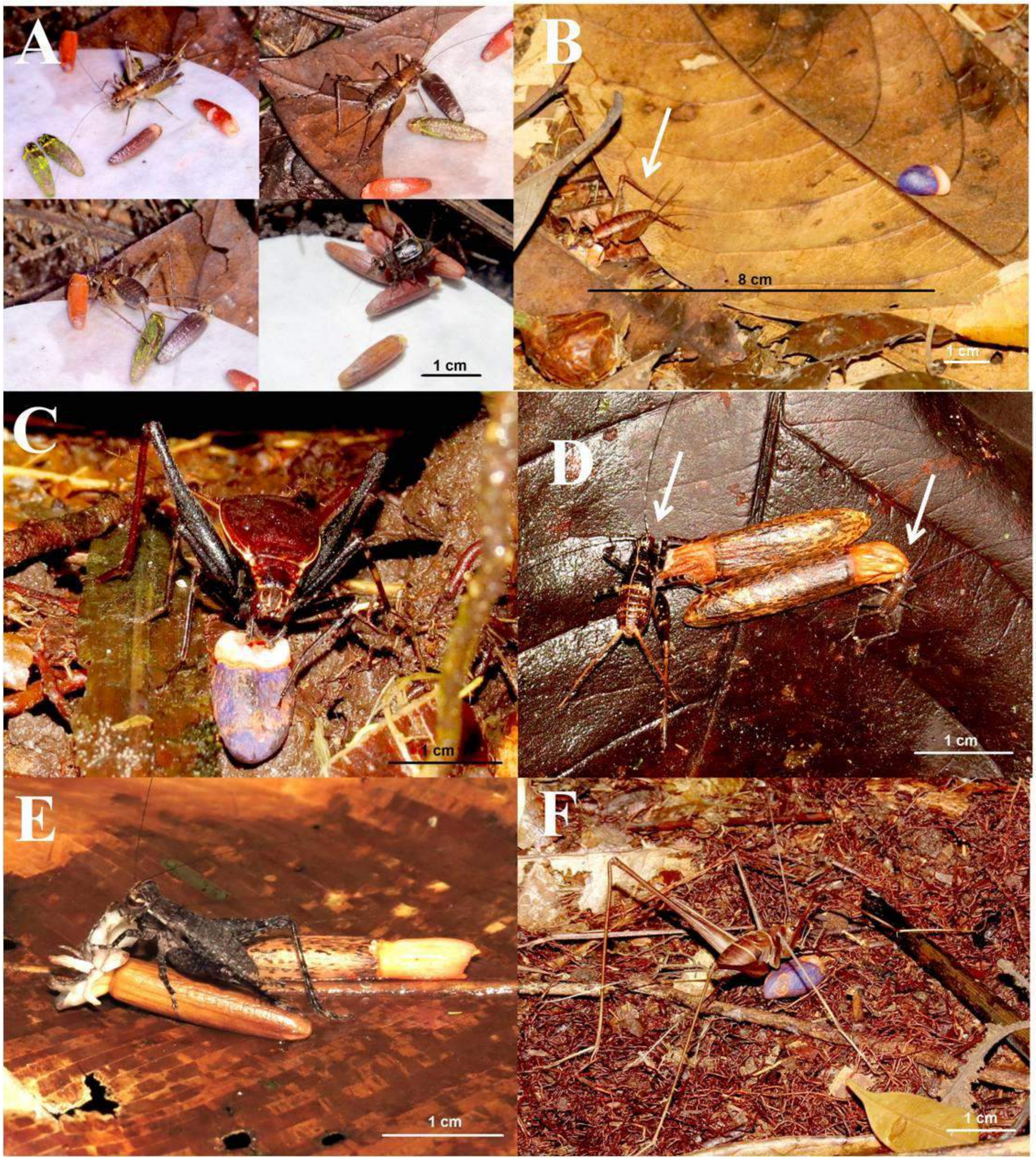


**Figure 2:** Interactions between crickets and seeds of Marantaceae species. A- Trial experiment using M. spicatum seeds that showed that the painted seeds with fluorescent ink did not interfer with the disperser – seed interactions (see also the appendix C for further details). B- Seed removed by female of *Luzaridella sussura* cf, distance = 8 cm; C- male of *Luzarida lata* and *G. altissima* seed; D- *Hygronemobius* sp. and *Luzarida* sp. cf with *I. arouma* seeds; E- *Hygronemobius* sp. cf with *I. arouma* seeds; F- *Phalangopsis* sp. and seed of *G. altissima*.

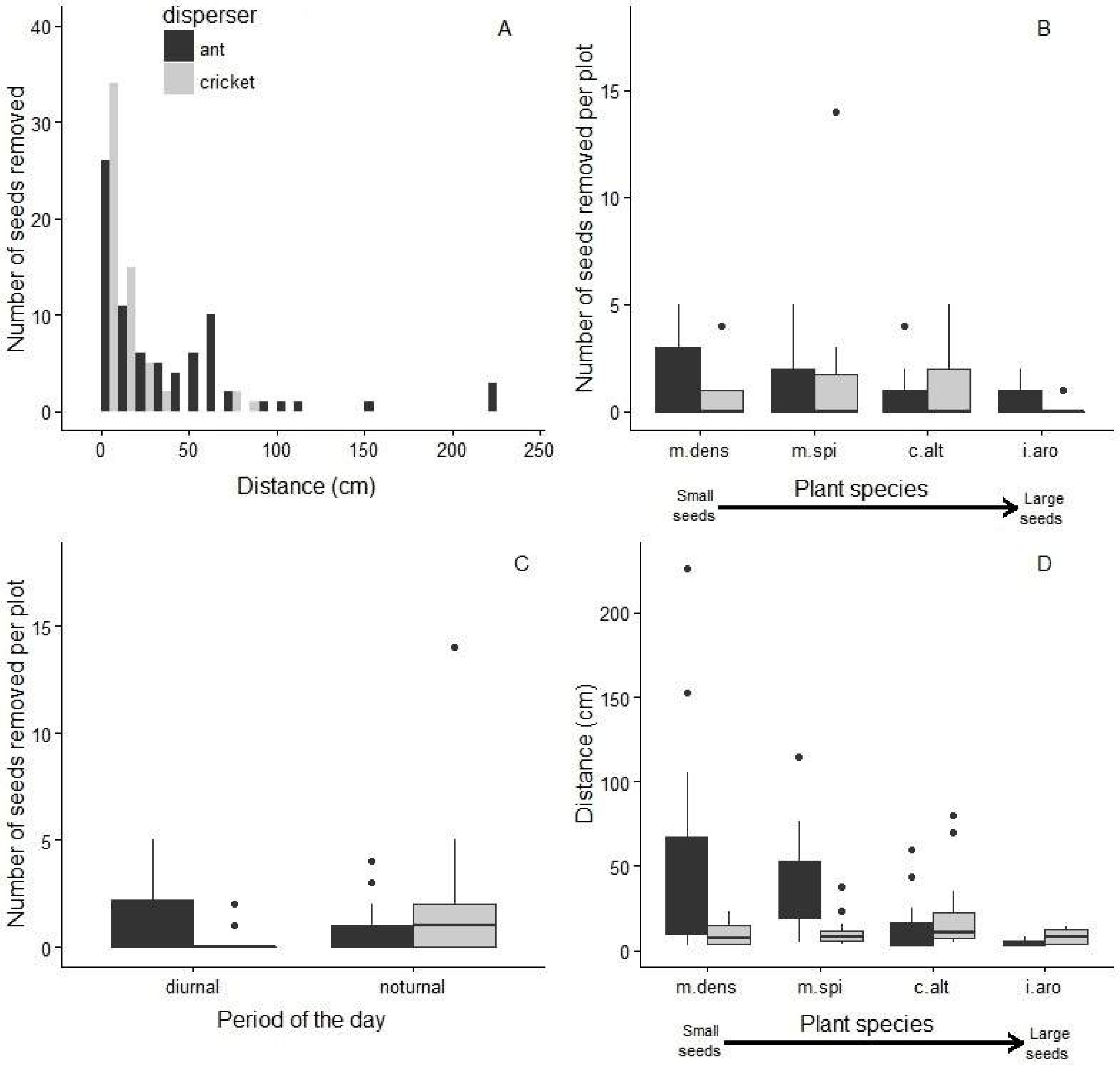


**Figure 3:** Seed dispersal by ants and crickets in the Amazonian forest. A – Range of seed removal distances; B – number of seeds removed per plot among plant species; C – Differences in number of seeds removed during each period; D - Variation in seed removal distance among plant species; The line near the middle of the boxplot represents the median, and the bottom and top of the box represents the 25th and 75th percentile, respectively. Extreme data are represented by black points. Plant species are ordered by seed mean weight values.

## Supplementary Material

### Appendix A: Trial experiment to test the effect the of painted seeds on seed removal

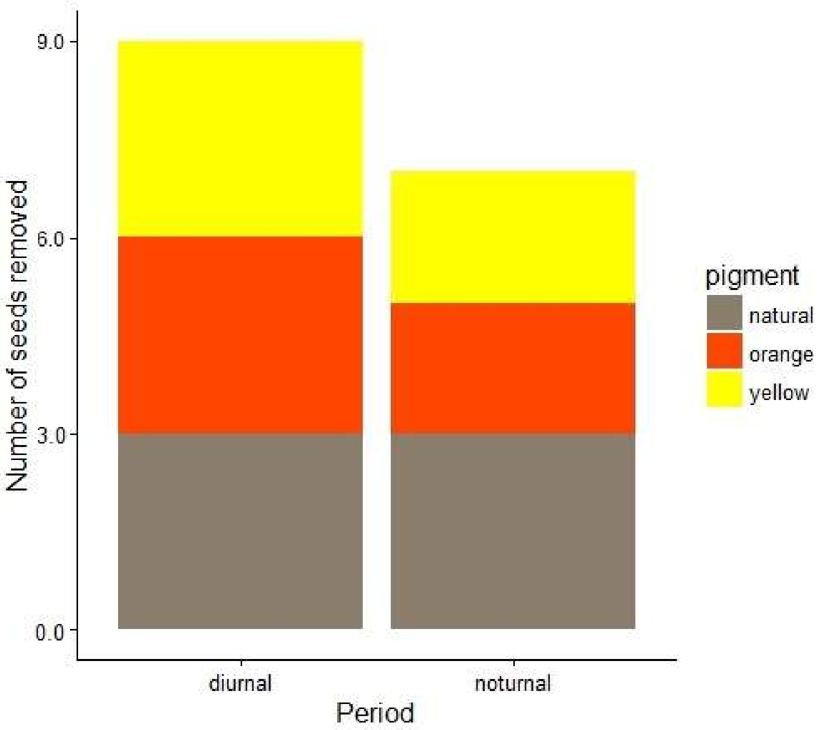


**Figure A1:** Number of seeds removed per period of the day according to the pigment color used to paint the seeds. We used seeds of *M. spicatum* for the trial experiment. The trial was performed in one 10 x 100 m plot and in three observation points next to adult individuals of *M. spicatum*, separated by at least 10 m from each other. Each observation point received three seeds without pigmentation, three seeds painted with orange pigmentation and three with yellow pigmentation. Observations were performed for 2 hours in two periods: diurnal, between 8:00 and 16:00 and nocturnal, between 18:30 and 1:00.

### Appendix B: Species of ants and crickets that removed Marantaceae seeds

**Table B1: Dispersal agent species' list**

| ANTS | | N* | CRICKETS | | N* |
|---|---|---|---|---|---|
| Family | Formicidae | | Family | Phalangopsidae | |
| Subfamily | Ectatomminae | | Subfamily | Luzarinae | |
| | *Ectatomma edentatum* | 3 | | *Luzarida lata* | 6 |
| | *Ectatomma lugens* | 8 | | *Luzarida* sp. | |
| Subfamily | Myrmicinae | | | *Luzaridella sussura cf.* | 1 |
| | *Atta sexdens* | 3 | | *Luzaridella* sp. | |
| | *Pheidole biconstricta* | 4 | Subfamily | Phalangopsinae | |
| | *Pheidole embolopyx* | 2 | | *Phalangopsis* sp. | |
| | *Pheidole sp.4* | 1 | Family | Trigonidiidae | |

|  |  |  |  |  |
|---|---|---|---|---|
|  | *Pheidole sp.5* | 5 | Subfamily | Nemobiinae |
|  | *Pheidole sp.12* | 1 |  | *Hygronemobius* sp. |
|  | *Pheidole sp.24* | 2 |  |  |
|  | *Pheidole sp.25* | 2 |  |  |
|  | *Pheidole sp.60* | 1 |  |  |
|  | *Trachymyrmex cornetzi cf.* | 3 |  |  |
| Subfamily | Ponerinae |  |  |  |
|  | *Mayaponera constricta* | 3 |  |  |
|  | *Neoponera apicalis* | 4 |  |  |
|  | *Odontomachus caelatus* | 12 |  |  |
|  | *Pachycondyla crassinoda* | 5 |  |  |

**Note:** *number of removal events where the collection of a specimen was possible. Most of the cricket's identification was made by photos of seed removal events.

## Appendix C: Cricket interaction with Marantaceae seeds

**Video C1:** Screenshot from a video (video C1, available online) showing two events of seed removal by crickets. First event: a cricket removes seeds of *Monotagma spicatum*. Second event, a cricket removes *Ischnosiphon arouma* seed.

## Appendix D: Partial contribution of the fixed effects in GLMM models

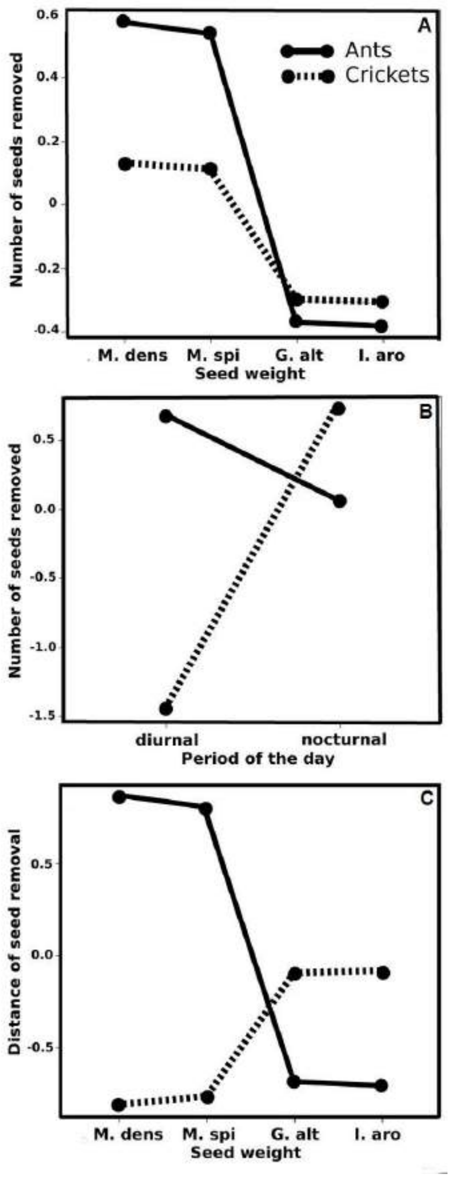


**Figure D1:** Interaction between fixed effects and their partial contribution in the explanation of the dependent variable. A – model 1: interaction between seed disperser and mean weight of seeds by number of seed removed; B - model 2: interaction between seed disperser and period when seed removal occurred by number of seeds removed; C - model 3: interaction between seed disperser and mean weight of seeds by distance of seed removal.

# CAPÍTULO 2

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Santana, F. D., Christianini, A.V.; Baccaro, F. B.; Costa, F. 2016. Multiple dispersers system do matter for dispersal effectiveness of Marantaceae species along environment gradient in Central Amazonia. *Manuscrito em preparação para a Ecological Monographs*

# Abstract

A large proportion of tropical plants rely on multiple seed dispersers which differ in their contribution to seed dispersal effectiveness (SDE). Each seed disperser is expected to behave differently on space and time scales, and it is probable that the effects of their dispersal behaviors vary across environments. In tropical systems, the number of frugivores species and, therefore, the higher number of possible interactions diaspore-seed dispersers, increase the complexity in predict outcomes from seed dispersal effects on plant’s recruitment. Therefore, is necessary to understand the relative contribution of multiple dispersers to SDE across different habitats to enhance our ability to disentangle the connections between seed dispersal and recruitment patterns in plant population dynamics. Here, we focused in four Marantaceae species to investigate patterns and consequences of seed dispersal across plants with a potentially rich and varied set of dispersers. Marantaceae species produce lipid-rich arilate seeds mainly dispersed primarily by birds and secondarily by ants. We asked: (1) whether differences of seed dispersal effectiveness and the relative contribution of seed dispersers were related to the assigned dispersal syndromes; (2) how SDE of herbs changes in relation to habitat type and to distinct groups of seed dispersers; (3) when seed germination and recruitment success were coupled across habitats. We found a high diversity of seed dispersers interacting with the four species, including birds, ants, crickets, cockroaches, spiders, crabs and grasshoppers. Although the highest SDE position were consistently to the same disperser group between the habitat types, the second most effective disperser changed and had a disproportionally impact in SDE changes within the habitat types. Habitat filters played the major role in determining germination and seedling recruitment irrespectively of the SDE for most of the species. Therefore, the complementary roles of seed dispersers at local scale of herbs, combined with the changes in match pattern of SDE and suitable habitat for recruitment should help in drive the community structure of animal-dispersed understory herbs in tropical heterogeneous environments.

**Key words:** lipid-rich arilate seeds, multiple seed dispersers, invertebrate seed dispersers, habitat heterogeneity

# Introduction

As all sessile organisms, plant distribution patterns should be a result of the interplay between the ability to disperse to new environments and the biotic and abiotic interactions within habitats. In sexually reproducing plants, the seed dispersal phase is particularly important to determine how the interaction between dispersers and local habitat filters will affect both demographic and community patterns in heterogeneous landscapes (Eriksson and Erlhén 1992, Willson and Traveset 2000, Beckman and Rogers 2013, Robledo-Arnuncio et al. 2014). The fate of dispersed seeds depends not only on how far they go from parental plants to escape density-dependence mortality (Janzen 1970, Comita et al. 2014), but on the quality of the environment where they land and how often they are deposited (Hampe et al. 2008, Cortês and Uriarte 2013). This could be particularly important in systems where habitat conditions change across spatial scales, such as in soil-driving environmental gradients in the Amazonia (Costa et al. 2005, Jones et al. 2006, Uriarte et al. 2011). A big challenge in seed dispersal ecology is to find out what combinations of seed dispersers, dispersal distances and final seed environments will provide appropriate recruitment opportunities (Levin et al. 2003, Howe and Miriti 2004, Beckman and Rogers 2013).

In the last decades, the studies of seed dispersal in tropical environments have shown that most plant species with zoochoric fruits rely on more than one seed disperser species. The combinations of multiple disperser species may affect the recruitment of new plant individuals playing roles in phase I (primary seed dispersal) and phase II (secondary seed dispersal) of the seed dispersal process (Nathan and Muller-Landau 2000, Vander Wall and Longland 2004). Each seed dispersal agent is expect to behave differently on space and time scales, and it is probable that the effects of their post-consumption behavior vary across environments (Calviño-Cancela 2002, Cortês and Uriarte 2013). Therefore, it is crucial to understand how effective the seed disperser agents are in the context of the heterogeneous landscapes, where species may be unevenly distributed. However, most of the studies that investigated seed dispersal effectiveness focused on relatively simple systems with small species richness of dispersers or worked with small group of seed dispersers  (Schupp et al. 2010). In the complex and hyperdiverse tropical systems, the number of frugivores species and therefore, the higher number of possible interactions between diaspora (i.e. unit of dispersal) and different dispersal species are expected to increase the complexity of seed dispersal effects on plant recruitment.

The seed dispersal effectiveness (SDE) framework was proposed to evaluate the importance of dispersal agents, through a combination of quantitative (QC) and qualitative (QL) components of the seed dispersal process (Schupp 1993). This approach is especially useful in the context of systems with multiple seed dispersal species. It is expected that multiple dispersal agents will differ in their relative contribution to SDE of plants once they have different QC and QL values (Schupp et al. 2017). For example, seed dispersers species with differences in body size and diet preferences may differ in QC due to their frequency of visits or amount of seeds handling in plant-disperser interactions (Jordano and Schupp 2000, Rother et al. 2015). The seed dispersers species behavior and forage habitat preferences, in turn, leads to differences in the qualitative component, which may consider the treatment gave to the seed (i.e. ingestion), distance of seed dispersal and/or local of seed deposition (Spiegel and Nathan 2012). By considering the habitat heterogeneity, another scale of complexity is added to the SDE framework, and therefore can change the relative contribution of seed dispersers for plant species (Spiegel and Nathan 2012, Rother et al. 2016). Locally, within a habitat type, the most frequent seed disperser may be more important for SDE given the amount of seeds dispersed which could reach a good microsite. However, if the likelihood of recruitment of a plant species increases in a different type of habitat (Spiegel and Nathan 2007), it is possible that less frequent seed dispersers with bigger foraging area would increase the distance of seed dispersal event and therefore the SDE (Uriarte et al. 2011, Larsen and Burns 2012, Wotton and Kelly 2012). Therefore, it is possible that within the SDE would exist a tradeoff between QC and QL components, which must affect plant population differently within and across types of habitats.

The understanding of seed dispersal effectiveness across different habitats may enhance our ability to disentangle the connections between seed dispersal and recruitment patterns in plant population dynamics (Wang and Smith, 2002). It is therefore necessary to integrate the complexity of the interactions with the complexity of habitats into the SDE framework. It has been generally suggested that the diversity of disperser species implies in complementary roles and even synergic outcomes to the distribution and recruitment of the plants species (Pérez-Ramos et al. 2013, Camargo et al. 2016, Culot et al. 2017). But the increased number of disperser-plant interactions in the tropics may not necessarily enhance the benefits for plants, given the presence of redundant roles in the systems (Rother et al. 2016). As shown by Zamora (2000), functional equivalence between seed disperser species is observed when different dispersers produce similar effects on the seed dispersal outcome. On the other hand, the same species could differ in seed dispersal outcome when acting in different habitat types. Therefore, to better understand when multiples seed disperser species in the plant-disperser interactions are functional equivalent or complementary we should consider the landscape heterogeneity perspective in seed dispersal processes (Culot et al. 2015, Rother et al. 2016).

Diaspore characteristics are the base for the classification system of dispersal syndromes and have been largely used to assign potential seed dispersers to plant species (Herrera 1992), but we already recognize the existence of multiple dispersers of most seed dispersal systems (Levin et al. 2003, Gove et al. 2007, Camargo et al. 2016). In this study, we focused in Marantaceae, a group of common understory herbs whose species are known by having infrutescence shapes and colors that suggest adaptations for two main groups of seed dispersers, birds and ants (Carden 1961, Horvitz 1991). All Marantaceae produce lipid-rich arillate seeds, which is a good indication that those seeds are also attractive to many other animals, such as crickets (Santana et al. 2016). When infrutescences reaches the mature stage, they dry and the capsules open exposing the mature seeds. Those seeds not dispersed directly from the infrutescence naturally fall from the dried capsules and become available in the forest floor. Therefore, it is quite possible that those herbs are dispersed by a larger variety of dispersers, foraging on the plant itself and on the ground, than observed in previous studies (but see Santana et al. 2016). Additionally, those herbs form an important stratum of the forest understory (Gentry and Emmons 1987, Costa 2006), in which a large proportion of frugivores animals is found, but at the same time, where we still understand poorly the dynamics of plant-animal interactions. All those characteristics provide the opportunity to investigate patterns and consequences of seed dispersal across plants with a potentially rich and varied set of dispersers. Considering the complexity of a multiple seed dispersers systems in the context of a topographic gradient which forms a heterogeneity landscape we aimed to comparatively address the follow questions for the group of understory herb species: 1) Are the differences in seed dispersers SDE and their relative contribution corresponding to the assigned dispersal syndromes? 2) How predicted changes in frugivores assemblages and environmental conditions influence seed dispersal effectiveness? 3) Are the success of seed germination and recruitment coupled across habitats?

## Methods:

### Study site

The study was conducted at Reserva Ducke, a protected area in Central Amazonia north of the city of Manaus (02º 55’-03º 01’ S, 59º53’-59º59’ W), consisting in a 10,000 ha (10 x10 km) of *terra firme* tropical moist forest with a 30 - 37 meters closed canopy (Ribeiro et al. 1999). The mean annual temperature is 26°C and annual rainfall ca. 2400 mm with a monthly maximum of ~330 mm in March, and a minimum in August, with <100 mm (Marques-Filho et al. 1982). The terrain is rugged and crossed by a dense drainage network, creating topographic and soil gradients that originate a heterogeneous landscape even in the scale of a few hundred meters. The upland areas, the plateaus, present a clayed soil (yellow latosol) transitioning to less clayey red-yellow soils on slopes until sandy podzols in the valleys. Seed removal experiments were conducted in 9 plots (10 x 100 m) evenly distributed in 3 blocks of plots to cover the environmental gradient represented by the three main habitats: plateaus, slopes and valleys. This topo-hydrologic gradient structure plant (Costa 2006, Schietti et al. 2014) and animal assemblages, such as birds (Cintra and Naka 2012, Menger et al. 2017), ants (Oliveira et al. 2009) and cockroaches (Tarli et al. 2014). For the camera trap monitoring, we expanded the area for out of the plots and used the 5 km by 3 km grid on the southeast portion of the reserve.

### Plant species

The Marantaceae family at Reserva Ducke is represented by 22 species, being the most conspicuous group in the understory herb community with 36.5 percent of the total herb cover (Costa 2006). Four species of Marantaceae (*Goeppertia altissima*, *Ischnosiphon arouma*, *Monotagma densiflorum* and *Monotagma spicatum*, Fig. 1) were chosen based on their differences in reproductive structures (i.e. seed size and color contrasts within infrutescences), the low frequency of clonal reproduction (F. Costa personal information) and their contrasting distribution patterns along the topographic-hydrologic gradient. All the studied herbs are found in the three main habitats of Reserva Ducke, however their differ in abundance of seedlings, juveniles and adult stages along the topo-hydrological gradient. Populations of *I. arouma* and *M. spicatum* are associated with valleys, while *G. altissima* is mainly associated with the clay soils in plateau habitats. *M. densiflorum* is more homogeneously distributed, but with some tendency to occur more in sandy slopes (Santana et al. unpublished manuscript.). Reproductive individuals of these species were observed in the three main habitats (plateau, slope and valley) except for *G. altissima*, for which we did not found any reproductive adult at valleys during the study period (Santana et al. unpublished data).

### Seed removal by vertebrates

To register seed removal by vertebrates, several reproductive individuals of each plant species were monitored by cameras-traps (Bushnell Trophy Can HD). The cameras were programed to monitor 24 hours per day, working in a stand-by mode and triggered by movement and temperature. Overall 36 individuals of the four studied herb species were monitored by camera-traps during three consecutively reproductivity years. The total of observations hours varied between the herb individuals and habitat types, for detailed monitoring effort (please see Appendix S1:Table S1). We considered as an independent visit if photos/videos were taken with more than 5 minutes of difference. At each visit, we registered the duration, the identity of the animal and the number of seeds touched or ingested. The monitored individuals were selected based on the high amount of seeds available in the infrutescence and the conditions of the surrounding area (completely closed understory was avoided because of high interference of leaves in the camera scan field). Whenever possible, individuals were chosen to cover all the three main habitats (plateaus, slopes and valleys). The camera-traps were kept monitoring a reproductive individual until all the seeds were gone or after three months without any record of seed consumption during the fruiting seasons of Dec/2014 until May/2015 (N = 8 cameras), from Jan/2016 until June/2016 (N = 14 cameras) and from Dec/2016 until Mar/2017 (N = 14 cameras). In the fruit season of 2015 the camera-traps were programed to take 3 sequential photos. In the 2016 and 2017 fruit seasons the camera-traps were programed to record 3 sequential videos of 10 seconds each and an interval of 5 seconds between them.

### Seed removal on the ground

To record the invertebrate fauna interacting with fallen seeds we performed seed removal trials. Seed removal experiments were performed for each plant species during their respective fruit season in two years, from December 2014 until May of 2015 and from January of 2016 until June of 2016, in the nine plots described above. We collected arilate seeds directly from mature infrutescences of several mother plants (10-20) within the study area and used in the experiments. All the seeds were painted with a solution of fluorescent pigment powder diluted in acetone (Reiter et al. 2005) the day before the experiment to facilitate visualization during night trials when a UV flashlight were used. A previous study showed that painted seeds did not affect how invertebrates such as ants and crickets interacted with then (Santana et al. 2016). In each plot, seeds were placed directly on the ground, in three observation points next to adult individuals of the focal species, separated by at least 10 m. In the absence of adult individuals in the plot, seeds were placed at random respecting the minimum distance of 10 m. The number of seeds per observation point was standardized for each plant species and ranged based on variable abundance of seeds available at the forest floor (F. Santana personal observation). The total amount of seeds of each herb species used per year of experiment in the 9 plots was: *G. altissima* (N = 54), *I. arouma* (N = 54), *M. densiflorum* (N = 81), *M. spicatum* (N = 135). The experiments were conducted for 2 hours and repeated in two periods of the day in each plot, resulting in 4 hours of seed removal observation per plot each year. Observations during the diurnal period were between 8:00 and 17:00, and in the nocturnal period between 18:30 and 1:00. The three observation points were simultaneously monitored by two observers that took notes of all invertebrates-arilate seeds interactions. In a seed removal event, the invertebrate was followed until the displacement of the seed in the ground, in the ant nest, or the seeds were lost from sight. The measurement of removal distance was taken between the observation point and the last known location of the seed. The experiments of seed removal totalized 72 hours of observation per herb species per year. One specimen of each invertebrate species involved in the seed removal was collected whenever possible. We also used photographic images of the seed removal events to help in the identification of species in the cases when it was not possible to collect a specimen. Both vouchers and photos were sent to specialists to refine the identification at the lowest taxonomic level. Vouchers were deposited in the Entomological Collection of the Universidade Federal do Amazonas.

### Rates of seed germination and early seedling recruitment

We performed seed addition experiments and monitored seedling establishment to infer potential seed fate after dispersal. A previous study showed that Marantaceae seeds have a dormancy of 7-12 months and suggested that the removal of aril from seed did not affect germination rate (Horvitz and Schemske 1994). The experiments started in May/2015, a moment of fruiting season when it was possible to find all the studied species reproducing. Seeds of each species were collected from several individuals and the amount of seeds available for the experiment varied between species. Seed sowing and monitoring were conducted in six of the nine plots described above, meaning two replicates per habitat type. In each plot we delimited a sub-plot of 80 x 50 cm using a plastic mesh with 120 holes, each 5 cm diameter and evenly spaced, fixed in the ground. The seeds of the studied species were sown in each hole following a randomized distribution. The available number of seeds per studied species per sub-plot was: *G. altissima* (N = 26-27), *I. arouma* (N = 13-15), *M. densiflorum* (N = 40-42) and *M. spicatum* (N = 36-40).

For data analyses, we used the cumulative germination rate, which consisted in the number of seeds that germinated from May/2015 to Mach/2017. We also used the probability of early recruitment of seedlings, represented by the proportion of seedlings alive from May 2016 to March 2017. The seed germination and recruitment were monitored every 3 months.

### Quantitative and qualitative components of seed dispersal effectiveness

The SDE was estimated for each species-habitat combination through the multiplication of quantitative (QC) and qualitative (QL) components described below.

*Quantitative component* (QC): the product of number of visits per hour by number of arillate seeds ingested or removed per visit. Within each plant species, the QC was calculated for each seed disperser species in each of habitat type. For the data from camera-trap monitoring, we considered each plant individual as the independent unit and the sequential videos of 10 seconds in an interval of 5 minutes as a visit event. Seed removal event were considered when seed dispersers were observed touching, manipulating and/or ingesting a seed. However, as we set cameras to record three sequential videos, the interval between videos (5 sec) in the same visit event generate a lack of information about the interactions during this time gap. To overcome this and estimate the number of interactions during the full visit (10 sec + 5 sec + 10 sec + 5 sec + 10 sec), we did the calculations in two steps for each vertebrate species recorded. First, in each independent visit we calculated the mean number of interactions per second, considering the videos of 10 seconds, per vertebrate disperser. Second, we multiplied the average of interactions per second of 10 seconds videos by the total (40 sec).

For the seed removal experiments, we considered each observation station (N= 3) as an independent unit within the nine plots. Seed removal were counted each time that a seed was removed for a distance greater than 5 cm for each invertebrate species.

*Qualitative component* (QL): we used the seed removal distance (m) as the main sub-component of dispersal quality, combined with survivorship probability (sp), (see below) and the germination probability (gp), as a surrogate for the chance of a dispersed seed becoming a seedling. Within each plant species, the QL was calculated for each seed disperser species in each of habitat type, as QL = m x sp x gp. Since we did not have observational data of removal distances for vertebrate disperser species, we used a modified allometric equation (Schoener 1968) to estimate the size foraging area based on body mass when dispersers were birds (for detailed information please see Appendix S2). For the seed removal experiments, we considered the removal events per observation station, and calculated the mean seed removal distance by seed disperser species per habitat type. The probability of a seed surviving the interaction with the potential disperser species (i.e. not be preyed on) was attributed as follow: good disperser = 0.9; intermediate disperser = 0.5; bad disperser = 0.1. These values were based on the available information of food habits at the minimal taxonomic level of seed dispersers. For both vertebrates and invertebrates groups we attributed the values based on the diet information available in the literature. However, for ants we used information at guilds level, for example, within ant group, carnivorous ants were considered as good dispersers (Horvitz 1981, Passos and Oliveira 2002). Attini ants were considered bad dispersers (Christianini and Galetti 2007), with higher probability of seed predation (90%), and others generalists ants species were considered intermediate dispersers. In the case of crickets, all were considered intermediate dispersers. This is a conservative classification, given the rarity of seed predation of Marantaceae seeds by these insects (Santana et al. 2016). Others invertebrates such as cockroaches, crabs and spiders were considered as intermediate dispersers, while grasshoppers were classified as bad dispersers.

### Data Analyses

We calculated the value of effectiveness (SDE = QC x QL) for each herb species/seed disperser species combination per habitat. These values were latter averaged to be presented by herb species/disperser taxonomic group: ants, birds, cockroaches, crabs, crickets, grasshoppers and spiders (Appendix S3:TableS3). We decided to cluster the seed disperser species into taxonomic groups because the uncertain identity of almost 70% of the seed disperser species, and because most variation in SDE values were between groups than within groups. The SDE landscapes were built with the R code available at (http://pedroj.github.com/effectiveness/).

To test the relative contribution of each disperser group on the overall SDE of each herb species, we created an analytic procedure analogous to species extinctions or species-removal simulations (Fonseca and Ganade 2001). These simulations tested whether and how the removal of individuals belong to a give disperser group would affect the SDE of the herb species. We first summed the SDE values from all groups interacting with a given herb species. This was the total SDE value for each herb species. We than sequentially removed individuals of a given disperser group at a time and computed the remaining overall SDE. After the removal of all individuals of a given group, we start the process for other group using all the data available (i.e. all individuals from all species). After the rarefaction procedure, we calculated the mean SDE value after the removal of each disperser group, and their respective 95% confidence intervals (based on 999 permutations with replacement). The observed changes in SDE after the removal of a disperser group are informative by themselves, but to investigate if they were greater than expected by chance, we contrasted those scenarios to null models where individuals were randomly removed. The SDE and their respective 95% confidence intervals for each number of individuals in the assemblage were estimated by 999 randomizations with replacement. Finally, we plotted the null model scenario and the overall SDE after the removal of each disperser group. Each SDE group values were plotted along the x axis representing the total number of individuals after the focal group removal. Simulations were made in R 3.2.3 (R Core Team 2016).

To determine how the SDE of each herb species was influenced by seed dispersal groups, habitat and their interactions, we used generalized linear models (GLM) using the package gamlss in R 3.2.3 (R Core Team 2016). First, we did a model selection based on AIC for find the best family of error distribution that adjusted the predictor variables using the function fitDist. We fit the GLM with Gumbel error distribution for *G. altissima* and *M. densiflorum* models, Logistic error distribution for *I. arouma* model and Reverse Gumbel error distribution for *M. spicatum*. To understand the importance of seed dispersal events until first year of recruitment we calculated the transition probabilities associated to each habitat and disperser group. We summed the proportional amount of seeds that were removed from the plant (vertebrates), and removed from the ground (invertebrates). At each stage sequence (i.e germination and 1-year survivor rates) we calculated the probabilities of transitions. We compared the probabilities rates between habitat types for each herb species.

## Results:

### Seed disperser assemblages

We documented a large diversity of seed dispersers associated to our four studied herb species. Camera-trap monitoring effort was of 12,774 hours (Appendix S1:Table S1), while the observations of seed removal by invertebrates on the ground totalized 72 hours per herb species. The whole assemblage of seed dispersers was composed by 75 morphospecies: *G. altisima* (32), *I. arouma* (17), *M. densiflorum* (24) and *M. spicatum* (32). Most of the seed removal events were recorded on the ground, by invertebrates (n=70 morphospecies). The registered interactions between invertebrates and arilate seeds consisted in seed removal, while seed predation was observed just once by a cricket. Five bird species were recorded in the camera-traps removing seeds of *G. altissima*, the only herb species attended by vertebrates during this study (Appendix S3:Table S3), with *Psophia crepitans* as the most important seed disperser. Contrary to expectations, no vertebrate interactions were recorded for *I. arouma*, despite the intensive monitoring with camera-trap.

At least three different groups of seed dispersers composed the seed disperser assemblages of each of the studied herbs. In general, our results show high concordance between expected seed dispersal syndrome and the most effective seed disperser. For the species assigned as ornithocoric (*G. altissima*), the group of the birds had the highest SDE value and for those assigned as myrmecochoric (*M. densiflorum* and *M. spicatum*), ants had also the highest SDE values. However, contrary to our expectation, the herb *I. arouma*, which was assigned as vertebrate dispersed, had crickets as the dispersers with highest SDE (Fig. 2).

SDE differed significantly among the species with assigned vertebrate-dispersed syndromes, which presented its lowest (*I. arouma*) and highest (*G. altissima*) values (Fig. 2a and 2b). Given the presence of frugivore birds that had a higher contribution to the QL component, the SDE of *G. altissima* presented the highest amplitude of values compared to the other herbs (Fig. 2a). In the opposite, *I. arouma* had both low frequency of interactions and short distances of seed dispersal, presenting the lowest values of effectiveness (Fig. 2b). Even though, within the *I. arouma* SDE landscape the higher variability in the QL was played by the crickets.  Both species assigned as myrmecochores, *M. densiflorum* and *M. spicatum*, had similar values of SDE, but the relative contribution of QC and QL differ. *M. spicatum* was more variable in terms of frequency of seed removal, affecting mostly the QC, while the differences between the seed dispersers interactions within *M. densiflorum* were leaded by the higher variation in the QL of seed dispersal.

We found a disproportional role of the main disperser group for all species, except *I. arouma*. By far the presence of birds among the seed dispersers of *G. altissima* is responsible to increase the SDE above all other species. The removal of birds from the seed dispersal assemblage made the effectiveness decline significantly fast, even if there were few birds interacting (N = 5). Similarly, the removal of ants from the seed dispersal assemblages of *M. densiflorum* and *M. spicatum* caused a significant decline in the SDE values (Fig. 2). In general, compared to crickets, ants were not effective dispersers of herbs with an assigned vertebrate syndrome. For *I. arouma* the removal of crickets decreased significantly its SDE (Fig. 2B), even if these were not the expected main dispersers according to this plant dispersal syndrome.

The disperser assemblages varied across herb species and habitats, but as a general pattern, the most effective seed disperser group played consistently as main disperser in all habitats for most studied species (Fig. 3). Considering the different habitat types, there was, however, some complementarity in the contribution of seed disperser groups within the dispersion assemblies, which affected the local SDE. Particularly for *G. altissima* and *I. arouma*, we observed that the role of the second most effective disperser groups changed between habitats types (Fig.3). For *G. altissima*, ants were the most effective dispersers in plateaus and slopes after birds (Fig. 2a and 3a), but in the valleys, where we did not have reproductive adults monitored by camera traps, crickets were the main dispersers during seed removal experiments. Cockroaches had the second place for *I. arouma* SDE in plateaus and valleys, whilst ants were more effective in the slopes. Ants had a significant value as the most effective seed disperser of *M. densiflorum* and *M. spicatum* at all habitats. The SDE of *M. densiflorum* were slightly higher in the valleys, compared to the SDE of *M. spicatum* that was highest SDE in the plateau, in both cases, given a singular morphospecies with disproportional SDE value (Fig. 3a and 3c).

In addition, our results show that the number of the seed disperser groups per habitat type does not necessarily increase the dispersal effectiveness. For example, both *I. arouma* and *M. densiflorum* had high diversity of dispersers groups in the valleys, although these major number of groups only increased SDE for *M. densiflorum* (Figs. 1b, 1c, 3b, 3c).  For *G. altissima* and *M. spicatum*, effectiveness was higher in slopes and plateaus, respectively, regardless the number of seed dispersers groups (Fig. 1a, 1d, 3a, 3d). However, when we asked if the SDE of the studied species was related with the habitat type and disperser group, we found that indeed SDE changes depended on the combination of the type of habitat and the disperser group for the herbs with assigned vertebrate-disperser syndrome (Table 3). In the case of *G. altissima*, the SDE the valley differed from the other habitats because were considerably lower and was only played by crickets (fig. 1 and table 3). The SDE of the herbs *M. densiflorum* and *M. spicatum,* were not related with habitat type nor disperser group. Although there is a higher variability in SDE values within the ant group (Fig. 3 C and D), the mean value of SDE for ants is not different from the other disperser groups and did not change between habitats within *M. densiflorum* and *M. spicatum*.

Seed germination and herb early recruitment success between habitat types

Germination initiated seven months after seed sowing. Seed germination rate was low for all but *G. altissima*, whose seeds germinated more than 60% in plateaus and slopes (Tab. 2). The mean of SDE and germination or recruitment rates were coupled (i.e. higher values of SDE associated to higher recruitment success) within a habitat type only for *G. altissima* (Table 2). For *I. arouma,* higher dispersal effectiveness was associated with higher seed germination in the plateaus, while the lowest effectiveness and germination were in the valleys. Both *M. densiflorum* and *M. spicatum*, which have ants as the most effective disperser group, had a decoupled pattern between the mean of SDE and both germination and recruitment rates. The SDE of *M. densiflorum* and *M. spicatum* was higher in the plateau for both, while germination and recruitment were higher in the valleys for those herbs (Figs 1, 3 and Table 2). Generally, the best habitat for germination and recruitment was matched for the herb species, except for *I. aroma*. However, we did not observe seedling survivors of *I. arouma* in plateaus and valleys, and of *M. densiflorum* and *M. spicatum* in the plateaus. The habitat filter still highly affecting recruitment success, irrespectively of the amount of seeds germinated for all out of *G. altissima*.

## Discussion

Our study revealed many unexpected animals dispersing the seeds of Marantaceae, which increased the complexity of seed dispersal process of these herbs. One out of all animal groups played the overall role as the most effective seed disperser group, though not always in accordance with the expected dispersal syndrome. At the habitat scale, the effectiveness of the main seed disperser group changed, and in some cases, the activity of the second most effective dispersers had significant contributions to SDE. There was considerable variation on QC and QL within herb species across habitat types. In addition, we found that the effectiveness of seed dispersal might not reflect the best chance for the seed germination and seedling recruitment, which depends considerably on environmental filters.

Seed dispersal effectiveness differed largely between the four species of Marantaceae, but mainly between herbs with big and small seeds. We observed a large diversity of invertebrates acting as dispersers. Although most species in tropical forests are mainly dispersed by vertebrates and usually invertebrates have afterwards a secondary role in the dispersal process (Kaufmann et al. 1991, Passos and Oliveira 2002, Camargo et al. 2016), for plants with small seeds such as herbs, the effectiveness of seed dispersal may depend largely on invertebrates as observed in this study. Previous studies of Marantaceae species have suggested two main disperser groups, birds and ants (Horvitz 1991, Horvitz and Corff 1993). For three out of four studied species, we found that birds (for *G. altissima*) and ants (for *M. densiflorum* and *M. spicatum*) were indeed the most effective dispersers. Horvitz (1991) classified some *Ischnosiphon* as with an unknown dispersal syndrome, although their big dark seeds with an odor suggested bats as dispersers. However, after exhaustive monitoring by camera-trap, we still lack the information of the vertebrate seed dispersers for our *Ischnosiphon*.

The bigger seeds of *C. altissima* and *I. arouma* attracted more variety of invertebrate fauna than the seeds of the other two herbs assigned as ant-dispersed. Probably the higher seed/reward ratio is driving the interactions between invertebrates and the bigger Marantaceae species (Howe and Miriti 2004). Otherwise, according to (Hughes et al. 1994) the fat-acid elaiosomes chemical compositions of myrmecochoric seeds can be similar to components of insect haemolymph, suggesting a evolutive convergence of attractiveness for omnivorous and carnivorous ants. The lipid-rich arils of Marantaceae seeds and particularly, the odor exhalated by *I. arouma* seeds should be an indicative as well for the attractiveness of others omnivorous and carnivorous invertebrates. A important next step should be to understand which morpho-chemical factors are driving the interaction of invertebrates with those arilate seeds (Manzaneda et al. 2009).

We showed that the presence of multiple seed dispersers does not always increase the seed dispersal effectiveness for the plant (Rother et. al 2016). In complex seed disperser assemblages, it is likely that a few dispersal agents with low visitation rate but extremely high efficiency in diaspore handling contribute disproportionately to SDE (Jordano and Schupp 2000, Spiegel et al. 2007). We observed this for *G. altissima*, when the removal of birds from the seed dispersal system had a significant decrease on SDE and the removal of ants had the same effect for *M. densiflorum* and *M. spicatum.* The results from the simulations of group disperser removal also highlight the importance of other invertebrates, besides ants, to the seed dispersal system of some species, e.g. the surprising negative impact of cricket's removal on *I. arouma* SDE. Recent study pointed out that ants are the potential major invertebrate' seed dispersers in the event of disruption of zoochoric seed dispersal by vertebrates (Christianini et al. 2014). Previously, Santana et al. (2016) demonstrated that crickets tend to increase the number and the distance of seeds removed of Marantaceae species with bigger seeds compared to ants (i.e. *G. altissima* and *I. arouma*). The present study reinforces this finding. Showing that other invertebrates, such as crickets and cockroaches, can be equally or more (i.e crickets for *I. arouma*) effective on seed dispersal of some plant species.

In SDE framework there is a recognizable trade-off between seed dispersers efficacy in terms of quantity and quality components (Schupp et al. 2017). By comparing the SDE landscape one should note that almost none of seed dispersers presented both high values of QC and QL (Fig. 2). This trade-off between QC and QL in SDE could explain post-dispersal success of individual seeds as result of the spatial variation in deposition densities (Spiegel and Nathan 2012). Commonly, those dispersers responsible for higher consumer of diaspores may fail to drop the seeds in the best habitat for recruitment (Calviño-Cancela and Martín-Herrero 2009, Rother et al. 2016). In our system, invertebrates should be playing the role of ensuring local population persistence, through high dispersal effectiveness due to the quantity of seeds dispersed within habitat (Jordano and Schupp 2000, Camargo et al. 2016). Meanwhile, rare events of long-distance seed dispersal by vertebrates should spread the population across the landscape and drive population genetic diversity (Nathan 2006).

Our study shows that seed dispersal effectiveness can be assessed from different scales of complexity (i.e. differences between related plant species, multiple seed dispersers and across habitats), and should consider environmental heterogeneity as an intrinsic sub-component in dispersal effectiveness. The landscape heterogeneity should be considered in the SDE framework when the ultimate goal is to understand seed disperser's effect on plant population dynamics (Calvinõ-Cancela and Martín-Herrero 2009, Uriate et. al 2010, Rother et al. 2016). However, contrary to our expectation, the habitat heterogeneity has not always influenced the SDE. For the small diaspores species, ants were the disperser group consistently more important in most habitats, indicating in general a redundant role of the additional dispersers. However, for the bigger diaspore herb species, we also observed a turnover of seed disperser groups of invertebrates contributing for SDE across habitats, showing high local diversity and significant complementary roles in seed dispersal. For example, for *G. altissima*, seed removal events by ants and birds in the valleys was rare, where crickets increased the QC with a significant impact on SDE. For *I. arouma* the most effective seed dispersers were crickets, but not in the valleys, where cockroaches played the most effective role. The complementary role between dispersers groups was not observed for *M. densiflorum* and *M. spicatum* across-habitat types. Their main dispersers, ants, are themselves quite a diverse group in terms foraging habit (Dominguez-Haydar and Armbrecht 2011), and it probably leads to a complementarity role within ant group in a fine functional scale (Manzaneda and Rey 2009). On the other hand, for those species with big seeds, the changes in SDE should be explained by the effect of habitat type in seed disperser´s assemblages (Schupp et al. 2010). Our results suggest that the spatial distribution and population dynamics of herb species that produce seeds with more reward for seed dispersers (i.e. bigger aril) should be more affected by changes in the composition of the seed dispersers assemblage related to habitat type, than those herbs with small seeds and arils.

In the studied system, the highest dispersal effectiveness is not occurring at the most suitable habitat for seedling recruitment for most studied species, except *G. altissima*. Ideally, the SDE should incorporate the recruitment success after seed dispersal by each disperser species or group (Schupp 1993). However, the discordance between the seed rain generated by seed dispersers and seedling recruitment distribution is a common pattern in the seed dispersal cycle (Nathan and Muller-Landau 2000, Swamy et al. 2011). We could expect that seed dispersal effectiveness should match suitability for germination and recruitment across habitats in heterogeneous landscapes if: (1) the quality of seed dispersal effectiveness is high and dispersers are successfully dispersing seeds to favorable habitats (i.e. lack of seed dispersal limitation) (Spiegel and Nathan 2012); (2) all habitats are favorable for plant recruitment and higher SDE is directly related to higher plant abundance (lack of recruitment limitation) (Beckman and Rogers 2013). However, the second option is more unlike to occur in hyperdiverse environments such as Amazonia forest. Additionally, our results indicate that the valley may constitute a sink habitat for *G. altissima* (i.e. lack of reproductive individuals, lower germination and recruitment).

Habitat filters played the major role in determining germination and seedling recruitment irrespectively of the seed dispersal efficacy, for *I. arouma*, *M. densiflorum* and *M. spicatum*. For *I. arouma* SDE and germination rate were coupled, however, it had the lowest rates of seedling recruitment compared to the others. From all studied herbs, *I. aroma* seems to be the most limited by habitat filters in terms of dispersal and recruitment. We found an interesting trade-off between SDE and recruitment limitation for *M. densiflorum* and *M. spicatum*. The main dispersers of those herbs (i.e. ants), were less effective at the valleys which was the best habitat for germination and seedling recruitment, meanwhile, we found the highest values of SDE and the lowest germination and recruitment in the plateaus. Therefore, plants with seed limitation (e.g. mainly dispersed by invertebrates) may benefit of this trade-off by maintaining population under low SDE at suitable habitats for recruitment, while, at the less suitable habitat, combination of events of long seed dispersal and high local SDE ensures the persistence of those populations in even with strong habitat filters (Clark et al. 1999, Calviño-Cancela 2002, Beckman and Rogers 2013).

Many factors hinder a correct estimation of SDE, in many cases leading to the use proxies to estimate quantity and quality of seed dispersal. However, the very first step is to know the identity of all possible seed dispersers. Most of the unknown interactions reported here were observed during the night, reinforcing the importance of covering day and night periods in studies of diaspore-disperser interactions. The disproportional sampling effort to capture invertebrate (72 h) and vertebrate interactions (12,774 h) told us that at least for the system that we studied, interactions with vertebrates are extremely rare (i.e. approx. 0.15 interaction per 10 observation hours for *G. altissima*), to the point of probably existing but not being recorded in the case of *I. arouma*. The integrative sample effort used here, leads us to have a robust construction of the quantitative component of SDE. The quality is the most critical component of the SDE framework since it should incorporate prospects of plant recruitment into adult stage (Schupp et al. 2017). Normally, the requirements for seedling recruitment are beyond the seed limitation in each habitat and therefore this cannot be ignored regardless of the relative contribution of the quantitative component to the SDE. For instance, we could measure seed removal by seed dispersers and the potential success of seeds in a heterogeneous landscape by combining the data of seed sowing experiments and monitoring of first year recruitment within each habitat. We acknowledge that QL estimation is enhanced by integrating information of seed fate generated by each seed disperser, which we were unable to do here. To do so, it would be necessary track how spatially distributed is the seed rain generated by each seed disperser in the landscape (Cortês and Uriarte 2013). Once the multiple seed disperser´s identity is revealed, a natural follow up should be the incorporation of landscape heterogeneity and seed disperser´s movements into the SDE framework (Robledo-Arnuncio et al. 2014).

## Conclusions

The incorporation of all seed dispersal agents in the SDE framework is a big challenge specially when considering habitat heterogeneity, but allows a more realistic understanding of seed dispersal scenarios. Here we observed a large diversity of disperser fauna, mainly formed by invertebrates, affecting the SDE of animal-dispersed tropical herbs. Consequently, assumptions regardless the association between seed dispersal modes and recruitment patterns of herbs could have being misleading and further studies look carefully for dispersers assemblages. Our results indicate that the complementary roles of seed dispersers at local scale of herbs with big seeds combined with uncoupled pattern of SDE and suitable habitat for recruitment should help in drive the community structure of animal-dispersed understory herbs in tropical heterogeneous environments.

## Acknowledgements

The authors acknowledge Maria Águida and Nery Garcia for their assistance during seed removal observations. Sincere thanks to Mario Conh-Haft, Renato Cintra and Cassiano for birds identification and Lúciene Gimaque for cricket species identification. This study was supported by Brazil’s National Council for Scientific and Technological Development (CNPq), grant number 478908 / 2012-1. Flavia Santana received a PhD. scholarship from Brazil’s National Council for Scientific and Technological Development (CNPq).

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## List of Tables

**Table 1:** Results of GLM analyses evaluating the influence of seed disperser and habitat on the Seed Dispersal Effectiveness (SDE) of four species of Marantaceae. Analyses were conducted separately for each plant species and here it shows only the results when the p value was $\leq 0.05$. The GLM results for the species *M. densiflorum* and *M. spicatum* were not significant. See text for details on how SDE estimates were calculated.

| **Plant species** | **Predictor variables** | **estimate** | **std.error** | **F statistic** | **p.value** |
|---|---|---|---|---|---|
| *C. altissima* | | | | | |
| | Slope | 0.67 | 0.23 | 2.94 | 0.01 |
| | Valley | -0.72 | 0.29 | -2.44 | 0.02 |
| | Bird | 2.71 | 0.19 | 14.56 | < 0.01 |
| | Cricket | -0.65 | 0.16 | -3.95 | < 0.01 |
| | Valley:Cricket | 0.93 | 0.35 | 2.68 | 0.01 |
| *I. arouma* | | | | | |
| | Valley | 0.51 | 0.09 | 5.84 | < 0.01 |
| | Cockroach | 0.58 | 0.10 | 5.73 | < 0.01 |
| | Cricket | 1.02 | 0.08 | 12.78 | < 0.01 |
| | Grasshopper | 0.45 | 0.09 | 5.21 | < 0.01 |
| | Valley:Cricket | -0.45 | 0.10 | -4.37 | < 0.01 |

**Table 2:** Cumulative germination rate during 23 months, and 1st year recruitment of four species of Marantaceae along a topographic gradient in Central Amazonia. Highest values are green and lowest in red.

| | Cumulative germination | 1st year seedling recruitment |
|---|---|---|
| ***G. altissima*** | | |
| Plateau | 0.6038 | 0.283 |
| Slope | 0.6226 | 0.340 |
| Valley | 0.2453 | 0.132 |
| ***I. arouma*** | | |
| Plateau | 0.2857 | 0.000 |
| Slope | 0.1429 | 0.00036 |
| Valley | 0.0357 | 0.000 |
| ***M. densiflorum*** | | |
| Plateau | 0.1111 | 0.000 |
| Slope | 0.1098 | 0.037 |
| Valley | 0.1548 | 0.095 |
| ***M. spicatum*** | | |
| Plateau | 0.1688 | 0.000 |
| Slope | 0.1231 | 0.015 |
| Valley | 0.1757 | 0.095 |

## Figure Legends

**Figure 1:** Characteristics of the four species of Marantaceae at Reserva Ducke, in Central Amazonia. Predicted seed disperser information from Horvitz (1991).

**Figure 2:** Seed dispersal effectiveness (SDE) landscapes of the four species of Marantaceae studied: *G. altissima*, *I. arouma*, *M. densiflorum* and *M. spicatum*. The Quantity component (QC) and Quality component (QL) are showed, respectively, on the X- and Y-axes. Seed dispersers were clustered as functional groups and distinguished by the labels. Different colors represent three types of habitats along a topographical gradient. Note scale differences on axes of different plant species.

**Figure 3:** Simulated loss of individuals from different groups of seed dispersers of four species of Marantaceae, and its consequences for Seed Dispersal Effectiveness (SDE). Each dot represents the net change in the SDE value after complete removal of a given group. The black line represents the decline of SDE after random removal of individuals, with 95% CI (in gray). SDE values were log-transformed for presentation.

**Figure 4:** Boxplots showing the relative contribution of each seed disperser group to Seed Dispersal Effectiveness (SDE) of four species of Marantaceae, along a topographical gradient, in Central Amazonia. Graphics showing the median, the 25th and 75th percentiles.

**Figure 1**

| Plant Species | Diaspore characteristic | Actual disperser | Weight (g) mean (SD) | Length (cm) mean (SD) | Width (cm) mean (SD) | Seed size | Diaspores | Abundance (mean/SD) per habitat | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Plateau | Slope | Valley |
| *Monotagma densiflorum* (Körn.) K.Schum. | Dark seed with white aril | ant | 0.055 (0.008) | 1.341 (0.138) | 0.300 (0.061) | small |  | 19.5 (23.9) | 11 (9.6) | 23.3 (30) |
| *Monotagma spicatum* (Aubl.) J. F. Macbr. | Dark seed with white aril | ant | 0.067 (0.014) | 0.950 (0.050) | 0.264 (0.048) | small |  | 4.9 (4.9) | 6.1 (8) | 148.1 (110.1) |
| *Goeppertia altissima* (Poepp. & Endl.) Borchs. & S. Suárez | Blue seed with white aril in an orange capsule | bird | 0.347 (0.052) | 1.090 (0.142) | 0.853 (0.109) | large |  | 5.38 (2.8) | 4.4 (4.7) | 2.6 (2.88) |
| *Ischnosiphon arouma* (Aubl.) Körn. | Dark seed with white aril and strong smell | small mammal or bat | 0.348 (0.053) | 2.253 (0.153) | 0.570 (0.094) | large |  | 7 (9.8) | 4.8 (3.1) | 12.7 (13.1) |

**Figure 2**

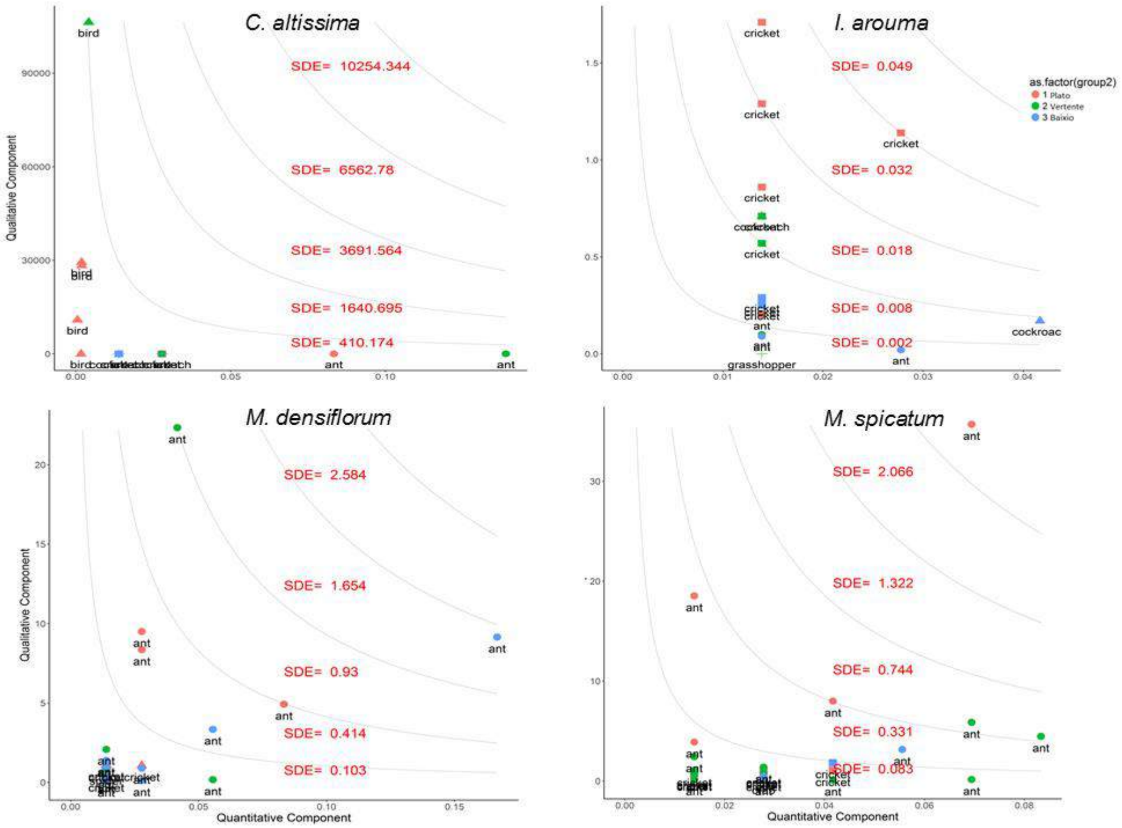
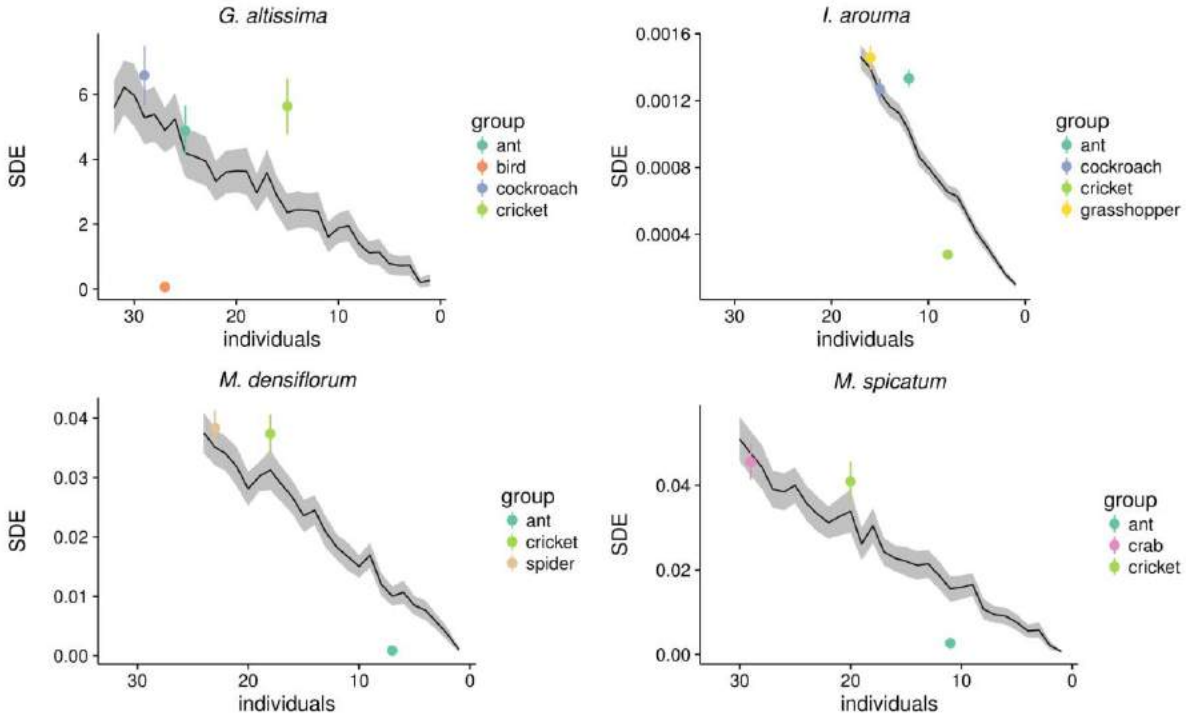


Figure 3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cricket
I. arouma
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0.0012
0.0008
0.0004
group
ant
cockroach
cricket
grasshopper
M. densiflorum
0.04
0.03
0.02
0.01
0.00
group
ant
cricket
spider
M. spicatum
0.04
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0.00
group
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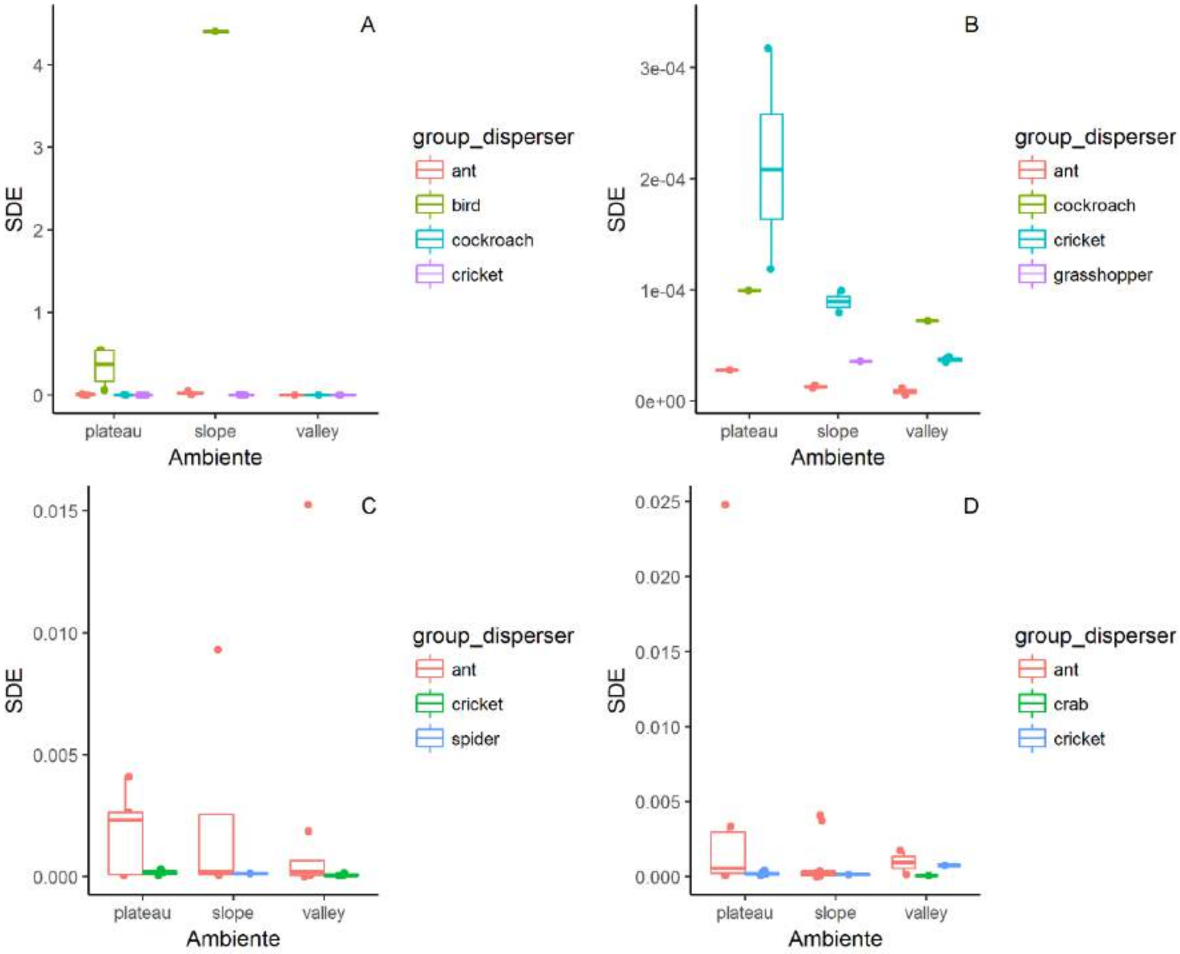
crab
cricket

**Figure 4**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## APPENDICES

## APPENDIX S1

**Table S1:** Camera-trap monitoring effort for recording fruit-frugivore interactions of four species of Marantaceae at Reserva Ducke, Central Amazonia. *calculation was made considering 12 hours of monitoring duration per day given that just birds were recorded (see Results for details).

| Plan species | year | habitat | number of individuals monitored | number of independent visits | number of monitoring days | total monitoring hours | n_days/ individual | n_visits/ hour* |
|---|---|---|---|---|---|---|---|---|
| *G. altissima* | 2015 | plateau | 1 | 2 | 86 | 1032 | 86.00 | 0.002 |
| *G. altissima* | 2016 | plateau | 1 | 7 | 24 | 288 | 24.00 | 0.024 |
| *G. altissima* | 2016 | slope | 5 | 6 | 212 | 504 | 42.00 | 0.002 |
| Total *G. altissima* | | | 7 | 15 | 322 | 1824 | 152.00 | 0.029 |
| *I. arouma* | 2015 | valley | 2 | 0 | 109 | 2616 | 54.50 | 0.000 |
| *I. arouma* | 2016 | valley | 4 | 0 | 238 | 5712 | 59.50 | 0.000 |
| *I. arouma* | 2017 | plateau | 3 | 0 | 147 | 3528 | 49.00 | 0.000 |
| *I. arouma* | 2017 | valley | 2 | 0 | 84 | 2016 | 42.00 | 0.000 |
| Total *I. arouma* | | | 11 | 0 | 578 | 13872 | 205 | 0 |
| *M. densiflorum* | 2016 | plateau | 1 | 0 | 55 | 1320 | 55.00 | 0.000 |
| *M. densiflorum* | 2017 | slope | 3 | 0 | 254 | 6096 | 84.67 | 0.000 |
| *M. densiflorum* | 2017 | slope | 2 | 0 | 89 | 2136 | 44.50 | 0.000 |
| Total *M. densiflorum* | | | 6 | 0 | 398 | 9552 | 184.17 | 0 |
| *M. spicatum* | 2015 | valley | 1 | 0 | 163 | 3912 | 163.00 | 0.000 |
| *M. spicatum* | 2016 | valley | 6 | 0 | 359 | 8616 | 59.83 | 0.000 |
| *M. spicatum* | 2017 | valley | 5 | 0 | 309 | 7416 | 61.80 | 0.000 |
| *Total M. spicatum* | | | 12 | 0 | 831 | 19944 | 284.63 | 0 |

## APPENDIX S2

**Table S2:** Identity of the bird seed dispersers registered in camera-traps during monitoring of *G. altissima* infrutescence in Reserva Ducke, Central Amazonia. The body weight (W) data was extracted from literature. The foraging area was calculated based on a modified allometric equation, dispersal distance used for SDE calculation were the converted value of foraging area from square kilometers to meters.

| Order | Family | Animal_sp | Code | Body weight (kg) | foraging area (km$^2$) | dist (m) | literature source |
|---|---|---|---|---|---|---|---|
| Passeriformes | Dendrocolaptidae | *Hylexetastes perrotti* | Hyl_per | 0.13 | 0.241 | 521.22 | del Hoyo et al. 2003 |
| Coraciiformes | Momotidae | *Momotus momota* | Mom_mom | 0.15 | 0.292 | 540.80 | Dunning Jr 2008 |
| Passeriformes | Tityridae | *Schiffornis turdina* | Sch_tur | 0.03 | 0.040 | 200.47 | Dunning Jr 2008 |
| Passeriformes | Tyrannidae | *Tinamus major* | Tin_maj | 1.10 | 4.075 | 2018.63 | Erard et al. 2007 |
| Gruiformes | Psophiidae | *Psophia crepitans* | Pso_cre | 1.00 | 3.600 | 1897.37 | Erard et al. 2007 |

### Equation S2

$$FA\ (km^2) = AW^{x_3}$$

Modified equation from Schoener (1968), where FA is the foraging area, A is the total utilized sector of a large area which is assumed constant, A=3.6 km$^2$, W is the and $x_3$ is the regression coefficient from the relationship of territory size and body weight. According to the author, omnivores and herbivories birds had similar regression values, therefore, based on the values presented by the author, we used a mean coefficient value for all our birds, $x_3 = 0.70$.

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# APPENDIX S3

**Table S3:** List of all seed dispersers morphospecies of the four Marantaceae herbs. Seed dispersers were recorded during camera-trap monitoring (birds) and seed removal experiments on ground (invertebrates) at Reserva Ducke, Central Amazonian. Data shows the summary of total number of seed removal events of each morphospecies. For data proposes morphospecies were clustered into dispersers groups.

| Disperser group | Animal species | Code name | #Code | Plant species | Habitat | Events |
|---|---|---|---|---|---|---|
| bird | *Hylexetastes perrotti* | Hyl_per | 71 | *G. altissima* | plateau | 7.4 |
| bird | *Momotus momota* | Mom_mom | 72 | *G. altissima* | plateau | 7.1 |
| bird | *Schiffornis turdina* | Sch_tur | 73 | *G. altissima* | plateau | 2 |
| ant | *Ectatomma lugens* | Ect_lug | 3 | *G. altissima* | plateau | 4 |
| ant | *Atta sexdens* | Att_sex | 1 | *G. altissima* | plateau | 2 |
| cockroach | coc_sp.1 | coc_sp.1 | 5 | *G. altissima* | plateau | 2 |
| cockroach | coc_sp.2 | coc_sp.2 | 6 | *G. altissima* | plateau | 1 |
| cricket | cri_sp.18 | cri_sp.18 | 10 | *G. altissima* | plateau | 1 |
| cricket | cri_p.17 | cri_p.17 | 7 | *G. altissima* | plateau | 1 |
| ant | *Neoponera apicalis* | Neo_api | 4 | *G. altissima* | plateau | 1 |
| ant | *Ectatomma edentatum* | Ect_ede | 2 | *G. altissima* | plateau | 1 |
| cricket | cri_sp.22 | cri_sp.22 | 12 | *G. altissima* | plateau | 1 |
| cricket | cri_sp.11 | cri_sp.11 | 8 | *G. altissima* | plateau | 1 |
| cricket | *Luzarida lata* | Luz_lat | 13 | *G. altissima* | plateau | 1 |
| cricket | cri_sp.15 | cri_sp.15 | 9 | *G. altissima* | plateau | 1 |
| cricket | cri_sp.20 | cri_sp.20 | 11 | *G. altissima* | plateau | 1 |
| bird | *Tinamus major* | Tin_maj | 74 | *G. altissima* | plateau | 6.3 |
| bird | *Psophia crepitans* | Pso_cre | 75 | *G. altissima* | slope | 16 |
| ant | *Pachycondila crassinoda* | Pac_cra | 14 | *G. altissima* | slope | 5 |
| cricket | cri_sp.18 | cri_sp.18 | 10 | *G. altissima* | slope | 2 |
| cricket | cri_sp.10 | cri_sp.10 | 15 | *G. altissima* | slope | 1 |
| ant | *Neoponera apicalis* | Neo_api | 4 | *G. altissima* | slope | 2 |
| cricket | *Phalangpsis sp.* | Pha_sp. | 20 | *G. altissima* | slope | 2 |
| cricket | cri_sp.12 | cri_sp.12 | 16 | *G. altissima* | slope | 1 |
| cricket | cri_sp18 | cri_sp18 | 19 | *G. altissima* | slope | 1 |
| cricket | cri_sp.9 | cri_sp.9 | 18 | *G. altissima* | slope | 1 |
| cricket | cri_sp.16 | cri_sp.16 | 17 | *G. altissima* | slope | 1 |
| cricket | cri_sp.13 | cri_sp.13 | 23 | *G. altissima* | valley | 2 |
| cricket | cri_sp.23 | cri_sp.23 | 25 | *G. altissima* | valley | 1 |
| ant | *Pheidole sp.5* | Phe_sp5 | 21 | *G. altissima* | valley | 1 |
| cockroach | coc_sp.3 | coc_sp.3 | 22 | *G. altissima* | valley | 1 |
| cricket | cri_sp.21 | cri_sp.21 | 24 | *G. altissima* | valley | 1 |
| cricket | cri_sp.28 | cri_sp.28 | 27 | *I. arouma* | plateau | 2 |
| cricket | cri_sp.7 | cri_sp.7 | 30 | *I. arouma* | plateau | 1 |
| cricket | cri_sp.30 | cri_sp.30 | 29 | *I. arouma* | plateau | 1 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| cricket | cri_sp.29 | cri_sp.29 | 28 | *I. arouma* | plateau | 1 |
| cockroach | coc_sp.4 | coc_sp.4 | 26 | *I. arouma* | plateau | 1 |
| ant | *Atta sexdens* | Att_sex | 1 | *I. arouma* | plateau | 1 |
| cricket | cri_sp.26 | cri_sp.26 | 33 | *I. arouma* | slope | 1 |
| *(continue)* |  |  |  |  |  |  |
| cricket | coc_sp.5 | coc_sp.5 | 32 | *I. arouma* | slope | 1 |
| ant | *Pheidole sp.12* | Phe_sp12 | 31 | *I. arouma* | slope | 1 |
| ant | *Pheidole sp. 5* | Phe_sp5 | 21 | *I. arouma* | slope | 1 |
| grasshopper | gra_sp.1 | gra_sp.1 | 34 | *I. arouma* | slope | 1 |
| cockroach | coc_sp.6 | coc_sp.6 | 37 | *I. arouma* | valley | 3 |
| cricket | cri_sp.32 | cri_sp.32 | 39 | *I. arouma* | valley | 1 |
| cricket | cri_sp.31 | cri_sp.31 | 38 | *I. arouma* | valley | 1 |
| cricket | cri_sp.8 | cri_sp.8 | 40 | *I. arouma* | valley | 1 |
| ant | ant_sp.5 | ant_sp.5 | 35 | *I. arouma* | valley | 1 |
| ant | *Pheidole biconstricta* | Phe_bic | 36 | *I. arouma* | valley | 2 |
| ant | *Odontomachus caelatos* | Odo_cae | 43 | *M. densiflorum* | plateau | 6 |
| ant | *Neoponera apicalis* | Neo_api | 4 | *M. densiflorum* | plateau | 2 |
| ant | *Ectatomma lugens* | Ect_lug | 3 | *M. densiflorum* | plateau | 2 |
| cricket | *Luzarida lata* | Luz_lat | 13 | *M. densiflorum* | plateau | 2 |
| cricket | cri_sp.15 | cri_sp.15 | 9 | *M. densiflorum* | plateau | 1 |
| ant | *Mayaponera constricta* | May_con | 42 | *M. densiflorum* | plateau | 1 |
| cricket | cri_sp.14 | cri_sp.14 | 44 | *M. densiflorum* | plateau | 1 |
| ant | *Crematogaster tenuicula* | Cre_ten | 41 | *M. densiflorum* | plateau | 1 |
| ant | *Ectatomma lugens* | Ect_lug | 3 | *M. densiflorum* | slope | 3 |
| ant | *Mayaponera constricta* | May_con | 42 | *M. densiflorum* | slope | 1 |
| spider | *Spider* | spi_sp.1 | 46 | *M. densiflorum* | slope | 1 |
| ant | *Pheidole prox. Meinerti* | Phe_mei | 45 | *M. densiflorum* | slope | 4 |
| ant | ant_sp.5 | ant_sp.5 | 35 | *M. densiflorum* | slope | 1 |
| ant | *Odontomachus caelatos* | Odo_cae | 43 | *M. densiflorum* | valley | 6 |
| ant | *Mayaponera constricta* | May_con | 42 | *M. densiflorum* | valley | 4 |
| ant | *Pheidole sp. 5* | Phei_sp5 | 51 | *M. densiflorum* | valley | 2 |
| ant | *Gmptogenys acumita* | G_acu | 49 | *M. densiflorum* | valley | 1 |
| ant | *Campootus femoratus* | Cam_fem | 48 | *M. densiflorum* | valley | 1 |
| cricket | cri_sp.27 | cri_sp.27 | 54 | *M. densiflorum* | valley | 1 |
| cricket | *Luzarida lata* | Luz_lat | 13 | *M. densiflorum* | valley | 1 |
| cricket | cri_sp.24 | cri_sp.24 | 53 | *M. densiflorum* | valley | 1 |
| ant | *Pheidole embolopyx* | Phe_emb | 50 | *M. densiflorum* | valley | 1 |
| ant | *Trachymyrmex cornetzi cf.* | Tra_cor | 52 | *M. densiflorum* | valley | 2 |
| ant | Phe_sp.1 | Phe_sp.1 | 47 | *M. densiflorum* | valley | 1 |
| ant | *Pachycondyla crassinoda* | Pac_cra | 14 | *M. spicatum* | plateau | 5 |
| ant | *Ectatomma edentatum* | Ect_ede | 2 | *M. spicatum* | plateau | 3 |
| ant | *Ectatomma lugens* | Ect_lug | 3 | *M. spicatum* | plateau | 1 |
| ant | ant_sp.4 | ant_sp.4 | 56 | *M. spicatum* | plateau | 1 |

| | | | | | | |
|---|---|---|---|---|---|---|
| cricket | *Luzarida lata* | Luz_lat | 13 | *M. spicatum* | plateau | 3 |
| ant | *Pheidole biconstricta* | Phe_bic | 36 | *M. spicatum* | plateau | 2 |
| cricket | cri_sp.5 | cri_sp.5 | 62 | *M. spicatum* | plateau | 2 |
| cricket | cri_sp.2 | cri_sp.2 | 59 | *M. spicatum* | plateau | 2 |
| cricket | cri_sp.19 | cri_sp.19 | 58 | *M. spicatum* | plateau | 2 |
| cricket | cri_sp.6 | cri_sp.6 | 63 | *M. spicatum* | plateau | 2 |
| cricket | cri_sp.4 | cri_sp.4 | 61 | *M. spicatum* | plateau | 1 |
| *(continue)* | | | | | | |
| ant | *Pheidole sp. 5* | Phe_sp5 | 21 | *M. spicatum* | plateau | 1 |
| cricket | cri_sp.3 | cri_sp.3 | 60 | *M. spicatum* | plateau | 1 |
| cricket | cri_sp.1 | cri_sp.1 | 57 | *M. spicatum* | plateau | 1 |
| ant | ant_sp.1 | ant_sp.1 | 55 | *M. spicatum* | plateau | 1 |
| ant | *Pachycondila crassinoda* | Pac_cra | 14 | *M. spicatum* | slope | 5 |
| ant | *Ectatomma edentatum* | Ect_ede | 2 | *M. spicatum* | slope | 3 |
| ant | ant_sp.2 | ant_sp.2 | 64 | *M. spicatum* | slope | 2 |
| ant | ant_sp.3 | ant_sp.3 | 65 | *M. spicatum* | slope | 1 |
| ant | *Pheidole sp. 25* | Phe_sp25 | 66 | *M. spicatum* | slope | 2 |
| cricket | cri_sp.26 | cri_sp.26 | 33 | *M. spicatum* | slope | 1 |
| ant | *Pheidole sp.5* | Phe_sp5 | 21 | *M. spicatum* | slope | 5 |
| ant | *Pachycondyla crassinoda* | Pac_cra | 14 | *M. spicatum* | slope | 1 |
| ant | *Pheidole sp. 25* | Phe_sp25 | 66 | *M. spicatum* | slope | 3 |
| ant | *Pheidole sp. 24* | Phe_sp24 | 67 | *M. spicatum* | slope | 2 |
| ant | *Pheidole biconstricta* | Phe_bic | 36 | *M. spicatum* | slope | 1 |
| ant | *Pachycondyla harpax* | Pac_har | 68 | *M. spicatum* | valley | 4 |
| cricket | cri_sp.25 | cri_sp.25 | 70 | *M. spicatum* | valley | 3 |
| ant | *Pheidole embolopyx* | Phe_emb | 50 | *M. spicatum* | valley | 2 |
| crab | *Fredius denticulatus cf.* | cra_sp.1 | 69 | *M. spicatum* | valley | 2 |

# CAPÍTULO 3

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Santana, F. D. Fortin, M-J, Costa. Population structures patterns of understory herbs across heterogeneous landscape are mediated by diaspores size at Central Amazonia. *Manuscrito em preparação para a Ecology*

## Abstract

Herbs represent at least 25% of plant species richness in tropical forests. However, we still poorly know how dispersal influences herb species distribution in tropical environments. Spatial patterns of plant distribution could either be explained by dispersal or establishment limitation. Within environmental factors, light is one of the most important in changes of population structure of understory herbs. A metapopulation dynamic model suggests that light regime interacts with dispersal syndromes, affecting population structure across the landscape. Therefore, ornitochoric herbs are gap-associated while myrmecochoric herbs are shade-tolerant. Here we aimed to integrate diaspore size and multiple environmental controls to access dispersal and establishment limitation on four Marantaceae species with multiple seed dispersers. We evaluated whether population abundance was related to life stages, habitat types or with the interaction between them and we also we used spatially explicit analyses to access the aggregation pattern of herb species at local (within habitats) and landscape scale. We observed here patterns of distribution that are indicative of limited seed dispersal for species with small seeds but not for species with large seeds. The two large-seeded species were widely spread in the landscape while small seeds had a large very local (within habitats) aggregation of abundances. Environmental filtering, leading to recruitment limitation, was strong for all species but the vertical distance to the water table was the most important predictor of abundances of most species life-stages. Light conditions did not affect population structure of our species consistently. This filtering is not associated to seed size or dispersal mode, but to vegetative traits of these species. Herbs with small seeds are associated with low leaf mass area, which should explain the association of a fast-growth strategy. In a landscape with strong contrasts in water supply up, this vegetative strategy ends up breaking the expected link between reproductive strategies and light environments. In conclusion, the abundance patterns are partially associated with the dispersal mode and to the interaction of growth strategies and the landscape patterns of water and light distribution in the heterogeneous landscape. Landscape spatial pattern of herbs species emerges from the combination of dispersal and establishment limitation acting in different spatial scales.

**Key words**: abundance patterns, Marantaceae, environmental filters, seed dispersal

## Introduction

In tropical systems, the seed dispersal of sexually reproductive plants usually relies on multiple seed dispersers (Vander Wall and Longland 2004) and the abundance and spatial patterns of individuals partially reflect seed dispersal process and subsequent filters (Muller-Landau et al. 2002). Comparative abundance patterns of animal-dispersed plants in heterogeneous landscapes in temperate and tropical forests, shows that populations may be structured upon the trade-off between dispersal vs. recruitment limitation (Eriksson and Erlhén 1992, Münzbergová and Herben 2005, Seidler and Plotkin 2006). At a small and landscape scale, widespread species showed to have population structure changing between habitats because of site limitation, while habitat-restricted species should be limited by dispersal. Therefore, plant species less limited by seed dispersal should be more efficient in tracking more suitable habitats for recruitment, while those with limited seed dispersal should be more tolerant to less suitable habitats (Horvitz 1991, Maron and Gardner 2000). The consequences of dispersal and site limitation on the patterns of distribution across species with different dispersal strategies have been mostly studied on trees (Seidler and Plotkin 2006, Swamy et al. 2011). Very few studies have addressed how dispersal influence the distribution of understory herbs at local and regional scales (Uriarte et al. 2010, Uriarte et al. 2011, Horvitz & Le Corff 1993). Yet, understory herb species can represents between 25% - 40% of the plant diversity in tropical rainforests (Gentry and Emmons 1987), many of which are important food resources for animal seed dispersers (Uriarte et al. 2011, García-Robledo and Kuprewicz 2009).

The study of changes in spatial structure of plant populations across scales can provide valuable information about the requirements for establishment of new individuals in heterogeneous landscapes (Nathan & Muller-Landau 2000).  The abundance of each plant life stage is expected to vary across habitats, due to limiting factors at the local habitat scale, such as seed dispersal limitation, behavior and movement patterns of seed dispersers and establishment limitations (Schupp 1993, Clark et al. 1998, Cortês and Uriarte 2013). However, studies that integrate empirical information of seed dispersers to the patterns of dispersal and site limitation across scales are rare (but see Calviño-Cancela 2002, Uriarte et al. 2010). Most of the studies concerning the spatial pattern of seed dispersal focus on earlier stages of seedling establishment and do not evaluate how the suitability of sites for recruitment change from one stage to another, i.e. do not integrate dispersal and site limitation at the landscape scale (Schupp and Fuentes 1995). Seedling establishment can be the most important bottleneck for plant recruitment and is the strongest determinant of seedling limitation (Clark et al. 2007, Comita et al. 2009, Uriarte et al. 2010). However, to achieve full comprehension of seed dispersal role on plant distribution patterns it is necessary to go beyond the analysis of requirements for initial seedling establishment and in fact understand how habitat suitability changes across life-stages (Jones et al. 2017). Therefore, differences in demography across an heterogeneous landscape could help to understand the most critical life stages transitions among plant species with different dispersal strategies (Bruna and Kress 2002, Uriarte et al. 2010).

Light is considered one of the most important limiting factors for seed germination and seedling recruitment of understory herbs (Uriarte et al. 2005, Westerband and Horvitz 2015). A theoretical model of metapopulation dynamics (Horvitz and Schemske 1986) proposes that the understory light regimes are correlated with dispersal syndromes, affecting population structure across the landscape. Therefore, the spatial pattern of understory herb species should be influenced by the trade-off between dispersal modes and shade tolerance strategies. According to Horvitz (1991) herbs with ornitochoric seeds are more associated with forest gaps because are frequently transported far from mother plants, given flight distances and behavior of birds, having a higher probability of arriving at this type of environment. Herbs with myrmecochoric seeds are disperse close to the mother plant, and are less dependent on forest gaps for recruitment. Consequently, the spatial scale of plant distribution was related with dispersal mode and showed to be larger for ornitochoric than for myrmecochoric herb species.

When proposed, the theoretical model of metapopulation dynamics assumed that each species has a single main disperser (Horvitz 1991) and the effect of other environmental factors beyond light on germination or recruitment was not considered, although both are unlikely assumptions. Indeed, light is not the only limiting factor for understory species, the habitat variations due to topography and soil moisture gradients are major determinants of herb distribution patterns in Central Amazonia (Costa 2006), and are expected to interact with patterns set by seed dispersers.

Here we aimed to integrate diaspore size, as proxy for type of seed disperser, and multiple environmental controls to access dispersal and site limitation on Marantaceae species with multiple seed dispersers. At our study site Marantaceae species with large diaspores are widespread (Costa 2006), while those with small diaspores are limited to a few habitats. For those species with small diaspores, we hypothesized that dispersal limitation is the main factor influencing the spatial pattern at landscape scale and across habitats, therefore, those herbs should be more restricted in the landscape, while at habitat scale it should be more aggregated and adult’s abundance will be positively related to the other life stages. Uncoupled distribution patterns among different life stages across habitats (i.e. no adults observed in the neighborhood of saplings and or juveniles), can indicate long-seed dispersal events. Moreover, we considered that variation in both soil and light are important environmental factors affecting herbs distribution pattern (Horvitz et al. 2002, Jones et al. 2006) and may play important roles in site limitation. Therefore, we focused in understanding the relationship between herb species distribution and diaspore size across life history stages in a heterogeneous landscape and we addressed the following questions: 1) Do species with similar diaspore size have similar population structure across habitats? 2) Is light or hydrology the main determinant of population structure at the local scale? 3) Do species with similar diaspore size present similar aggregation patterns at local and landscape scale?

## Methods

### *Study site and plant species*

The study was conducted at Reserva Ducke (02º 55’-03º 01’ S, 59º53’-59º59’ W), a 10,000 ha (10 x10 km) protected forest in the State of Amazonas - Brazil (Fig. 1). The site is covered by upland “*terra firme”* tropical moist forest with a 30 - 37 m closed canopy and high abundance of understory sessile palms (Ribeiro et al. 1999). Mean annual temperature is around 26◦C and mean annual rainfall ca. 2400 mm (Marques-Filho et al. 1982). Reserva Ducke has a rugged terrain crossed by a dense drainage network, creating topographic and soil gradients that originate a heterogeneous landscape even in the scale of a few hundred meters, with plateaus and valleys, separated by 40 - 120 meters. Soil follows topography, forming a gradient from high clay (yellow latosol) in the upland areas, transitioning to less clayey red-yellow soils on slopes until sandy podzols in the valleys. Valley soils are wetter and close to the water-table, while plateaus are vertically far from the water-table and may become dry during the dry season (Tomasella et al. 2008). This topo-hydrologic gradient structure plant (Costa 2006, Schietti et al. 2014) and animal dispersers assemblages, such as birds (Menger et al. 2017) and ants (Oliveira et al. 2009).

Marantaceae is the most conspicuous family within the understory herb community at Reserva Ducke, represented by 22 species which contribute to 36.5 percent of the total herb cover (Costa 2006). Four species within this family were chosen by their diaspore size that suggest their main seed dispersers (Horvitz 1981, 1991): *Goeppertia altissima* and *Ischnosiphon arouma,* with large diaspores (> 0.3 g), and *Monotagma densiflorum* and *Monotagma spicatum,* with small diaspores (< 0.07 g). The studied species have sexual reproduction and the presence of clones is low and easy to detect in the field.

### *Sampling design*

Reserva Ducke is crossed by a grid system with north-south and east-west trails covering 64 $km^2$, allowing access to 72 permanent plots evenly distributed at each 1 km that have been monitored along the past 17 years as part of the Brazilian Long Term Ecological Project (Costa et al. 2005, Pezzini et al. 2012). For this study surveys were conducted across the grid in 29 blocks of 3 plots each, each block separated from the next by a minimum distance of 1 km (Fig.1). Within the block, plots were placed in different habitats (plateau, slope or valley). In total, we sampled 87 plots evenly distributed among habitats. Due to variations in topography, distance between plots within a block ranged from 20 to 100 meters, maximum distance between plateaus and valleys within a block never larger than 250 m. Plots were 100 m long and 5 m wide, following the altitudinal contour, which minimize the internal variation of topography, soil and distance to the water-table. At each plot, we mapped all individuals of the studied species in a X, Y coordinate system and sampled their height and reproductive status (i.e. not reproductive, with inflorescence or infrutescence). We determined the population structure of the studied species by the proportion of seedlings, juveniles and adults across the habitat types. The individuals were assigned to life stage based on their height and the presence of reproductive structures, within each species (Figure 2). The size limits for life stages were defined according to literature and personal field observations.

Plot environment was described by two environmental variables: light and vertical distance from drainage. As a proxy for light we measured canopy openness using a rapid assessment method called canopy scope, an acrylic square with an array of 25 dots which is pointed toward the largest canopy gap and the number of dots in the gap are counted (Brown et al. 2011). We took measurements of canopy openness each 10 meter along the plots, totaling ten points. For data analyses, we used the mean of canopy openness percentage per plot, which ranged from 2.6 - 25 % (mean = 5.4 %). The hydrologic variable used was the vertical distance from drainage, obtained from a digital elevation model (HAND-DEM) (Rennó et al. 2008). The HAND grid of Reserva Ducke was calculated using the SRTM-DEM data at a 1 arc-second resolution (~ 30 meters) (Moulatlet *in prep.*). Using a geographical information system (GIS), we extracted (with bilinear interpolation) HAND values for 10 points along each plot. We used the mean values of HAND per plot, which ranged from 0.50 - 48 m (mean = 18 m).

### *Data analyses*

To understand how plant abundances were related to developmental stage, habitat and the interaction between them, we performed a two-way ANOVA, followed by Tukey's HSD on significant results for each study species. We examined how the environmental factors (light and vertical distance from drainage) influenced herb population structure by performing generalized linear mixed models (GLMM). Within each species, we evaluated whether the life stage abundance was influenced by light, the distance from drainage and their interaction. Block was considered the random factor. Each GLMM was fitted with a different distribution error family, and we chose the best one based on AIC criteria.

We used spatially explicit analyses to access the aggregation pattern of herb species at local (within habitats) and landscape scale. At local scale, we analyzed whether there was a spatial autocorrelation of individual abundance within each life stage per habitat. Each plot was divided into 2.5 x 2.5 meters grid cells where the number of individuals per each life stage was counted. The presence of significant spatial autocorrelation between cells with similar number of individuals within each life stage was given by the Moran's I index within a standardized lag of 2.5 m. We considered as significant spatial autocorrelation whenever the Moran's I index values were > 0.1 associated with a $p < 0.05$.

The spatial aggregation at the landscape scale was accessed using Local Indication of Spatial Association (LISA). The LISA compared the abundance of individuals of each life stage within the plots at the same block, and between blocks (N=29). LISA was performed considering different indexes of spatial association and we selected the local G* index that indicates whether the value of a plot was higher or smallest than the mean values in the neighborhood, using the Z score statistical significance ($p < 0.05$) threshold values (Anselin 1995). The plots with values above the mean indicate hotspots for higher abundance of a given life stage. LISA analyses were performed in the software Passage (Rosenberg and Anderson 2011). Out of LISA, the analyses were performed using R statistical programing language (R Core Team 2016) and using the packages vegan, agricolae, gamlss and ncf.

## Results

### *Changes in population structure across habitats*

A total of 5,557 individuals were sampled in all 87 plots, where *M. spicatum* was the most abundant species (n = 4140) followed by *I. arouma* (n = 640), *M. densiflorum* (n = 507) and *G. altissima* (n = 270). All the studied species were recorded in the three habitat types, although in different frequencies of occurrence and abundance (Fig. 3). *I. arouma* was the most frequent species, occurring in 79 out of 87 plots but with higher abundance in the valleys, while *G. altissima* was present in 59 out of 87 plots with higher abundance in the plateaus. Within the herbs with small diaspores, *M. spicatum* occurred in 52 out of 87 plots but mainly in the valleys, and *M. densiflorum* was the less frequent species at the study site occurring in 32 out of 87 plots, mostly at plateaus and slopes.

Generally, across habitats, the largest difference in abundance occurred between valleys and plateaus, and this was not related to diaspore size/dispersal mode. On average, *G. altissima* and *M. densiflorum* were more abundant in the plateaus and less abundant in the valley, while *I. arouma* and *M. spicatum* had the opposite abundance pattern.

Population structure of the two species with large diaspores differed across habitats (Fig. 3 and Table 1). For *I. arouma*, both seedlings and adults were more abundant in valleys and plateaus, while for *G. altissima*, each life stage was more abundant in a different habitat (e.g. seedlings in plateaus; juveniles in slopes) (Fig. 3). Otherwise, *G. altissima* had lowest population abundance in valleys compared to slopes and plateaus (Fig. 3 and Table 1). Population structure of the two species with small diaspores did not differ across habitats, although total population abundance of *M. spicatum* was significantly higher in valleys (Table 1).

### *Environmental factors as determinants of population structure*

Associations of species to the distance from drainage and light were not related to their diaspore size/dispersal agent, and distance from drainage was a stronger predictor of abundances than light. The higher abundances of the overall population of *I. arouma* and *M. spicatum*, with large and small diaspores, respectively, were associated to small distances to the drainage. Only adults of *I. arouma* were not associated to the drainage, but instead increased in abundance in response to light. On the other hand, the abundance of early stages of *G. altissima* and the abundance of saplings and adults of *M. densiflorum* increased far from drainage (Fig.4).

Light had a secondary importance as a determinant of population structure of the studied herbs. However, patterns were mostly the opposite as expected from Horvitz' model. Small seeded, ant dispersed species, expected to be associated to shaded environments were more associated to light than the large seeded, vertebrate dispersed species. For instance, all life-stages of *M. spicatum* were associated to lighter environments and also the juveniles of *M. densiflorum* (Fig. 4). We did not find any association of population structure of *G. altissima*, our most typical bird-dispersed species, and light. Adults of *I. arouma*, a large seeded and potentially vertebrate dispersed species, were more associated with lighter habitats.

### *Spatial aggregation patterns of herbs abundance at local and landscape scale*

The spatial explicit analyses at local and regional scales revealed that in most cases, the individuals were not more aggregated than expected by chance. At the local scale, there was significant spatial aggregation of adult (3 out of 26 plots) and juvenile (1 out of 27 plots) stages for *M. spicatum* at the valleys; of juvenile at the plateau (1 out of 22) and at the valleys (1 out of 22) for *I. arouma* and of adults (1 out of 29) of *M. densiflorum* at the plateau (Tab. 4).

At the regional scale, we did not detect significant G* index for most analyses, but regardless of that, we examine here the values as they indicate patterns that are worth exploring. Hot spots of abundance of the large diaspore species were more aggregated across the blocks. Species with small diaspores presented higher G* values meaning more intensity of spatial aggregation within habitat type, and also there was less plots with high abundance within the same block, as observed for large diaspore herbs (Fig. 5 C and 4D).

For *G. altissima*, spatial association in plateaus and slopes was similar across blocks reinforcing the importance of these environments for recruitment (Fig. 5A). *I. arouma* had higher spatial association mainly in valleys and in plateaus within the block, due to the number of hot spots for seedlings and adults respectively, suggesting a decoupling pattern in habitat preferences for those life stages. The herb *M. densiflorum* was absent in almost half of the sampled areas.

The number of hot spots for high abundance of seedlings and juveniles was higher in plateaus, followed by slopes. Few areas in the valleys presented spatial association of seedlings, what can indicate that population structure in valleys is drive by recruitment limitation (Fig. 5C). In almost all habitats in the valleys there was hot spots of high abundance for least one life stages of *M. spicatum*. There was less observation of hot spots out of the valleys and when happened, were mostly in the plateaus. For *M. spicatum,* like what was observed for *I. arouma* hot spots pattern, the slopes seem to represent a relevant habitat for population limitation.

## Discussion

We observed here patterns of distribution that are indicative of limited seed dispersal for species with small seeds but not for species with large seeds. The two large-seeded species were widely spread in the landscape, occurring in most blocks and most plots within blocks, i.e. wide occurrence in both local and landscape scales. Small-seeded species were absent in more blocks and plots within blocks, although with large very local (within plots) aggregation of abundances. In understory herbs, large seeds tend to be associated to dispersal by larger animals, and therefore have potential larger maximum distance of dispersal. We have previously observed (Santana et al. in prep.) that the events of long distance dispersal are very rare for our species, but given the observed spatial patterns, these must be enough to overcome the barriers set by environmental filtering and maintain at least marginal occupation of less suitable environments, such as valleys for *G. altissima* and slopes for *I. arouma*.

Environmental filtering, leading to recruitment limitation, was strong for all species and more accentuated for *M. spicatum*, with small seeds. Vertical distance to the water table (HAND), a proxy for soil availability, was the most important predictor of abundances of most species life-stages. This filtering is not associated to seed size or dispersal mode, but to vegetative traits of these species. Leaf mass per area (LMA), an indicator of the leaf economic spectrum (Wright et al. 2004), is lower for species more associated to wet valleys and increase towards species more associated to dry plateaus, i.e. species with potential faster growth are associated to a larger and constant water supply (Table 3) (Cosme et al. 2017).

Population structure of our species did not follow the predictions of the model proposed by Horvitz (1991). According to this model, species with large seeds and vertebrate dispersal modes should be more associated to lighter environments (Matlaga and Horvitz 2009), given the chance that long distance movements of these animals would have a greater chance of finding forest gaps. Light conditions did not affect population structure of our species consistently, except for *M. spicatum*, although adults/juveniles of some species were associated to more light. *M. spicatum* has small seeds and is predominantly dispersed by ants and other small invertebrates (Santana et al. 2016), therefore would not be expected to be the most light associated according to that model. At the same time, *G. altissima* has big seeds and was observed to be dispersed by birds, but was not associated to light.

To understand the mismatch between our observations and Horvitz model, we need to incorporate the landscape perspective and vegetative traits (Stahl et al. 2014, Herben et al. 2016). The primary filter of herb species distribution in our landscape was water availability, which filtered species according to their LMA (Table 3). Seed size tends to be inversely related to LMA (Westoby and Wright 2006), and this was the case here. Low LMA is associated to faster growth and larger demand for light, but larger photosynthetic rates also demand more water (Reich et al. 1999). This association of a fast-growth strategy with small seeds, in a landscape with strong contrasts in water supply up, ends up breaking the expected link between reproductive strategies and light environments. The environment studied by Horvitz (1991) is probably more homogeneous in water supply both in space and time, allowing herbs to differentiate more in reproductive than vegetative traits.

In conclusion, we have shown that the landscape spatial pattern of our herb species emerges as consequence of both dispersal limitation (Ehrlen and Eriksson 2000), given by seed size and main dispersal mode, and seedling recruitment (Schleuning et al. 2009, Uriarte et al. 2010), given by the interaction of growth strategies and the landscape patterns of water and light distribution in occurrence or abundance patterns of understory herbs in heterogeneous landscapes. To our knowledge, no other study had empirically compared herbaceous species with different functional strategies in relation to an environmental gradient to accesses limitations of dispersion and recruitment.

## Acknowledgements

The authors acknowledge Nery Garcia, João Araújo, Célio Correia, Cassiano Gatto, Arthur, Maria Águida, Mariana Tolentino, Thuane for their assistance during field work. This study was supported by Brazil’s National Council for Scientific and Technological Development

(CNPq), grant number 478908 / 2012-1. F.D.S received a PhD. Scholarship from Brazil's National Council for Scientific and Technological Development (CNPq). M-J.F and F.D.S received scholarships program for "Special Visiting Researcher" funding from program Science Without Borders, Brazil.

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## Tables

**Table 1.** Summary of the Two-Way Anova analyses and the Tuckey test. We asked whether abundance was structured by the type of habitat and the interaction. Tests were performed separately for each herb species.

| | TWO-WAY ANOVA | | | | | TUKEY Test | | | |
|---|---|---|---|---|---|---|---|---|---|
| *G. altissima* | Sum Sq | Mean Sq | F value | Pr(>F) | | Habitat Type | | Life Stage | |
| Life Stage | 77.4 | 38.7 | 17 | <0.0001 | *** | valley | **b** | seedling | **b** |
| Habitat type | 53.6 | 26.79 | 12 | <0.0001 | *** | slope | **a** | juvenile | **a** |
| Stage: Habitat | 17.8 | 4.46 | 2 | 0.094 | . | plateau | **a** | adult | **c** |
| Residuals | 559.9 | 2.22 | | | | | | | |
| *I. arouma* | | | | | | Habitat Type | | Life Stage | |
| Life Stage | 809 | 404.7 | 24 | <0.0001 | *** | valley | **a** | seedling | **b** |
| Habitat type | 374 | 187.2 | 11 | <0.0001 | *** | slope | **b** | juvenile | **a** |
| Stage: Habitat | 277 | 69.3 | 4 | 0.003 | ** | plateau | **b** | adult | **b** |
| Residuals | 4263 | 16.9 | | | | | | | |
| *M. densiflorum* | | | | | | Habitat Type | | Life Stage | |
| Life Stage | 107 | 53.7 | 2 | 0.19 | | - | | - | |
| Habitat type | 122 | 61.11 | 2 | 0.15 | | - | | - | |
| Stage: Habitat | 59 | 14.82 | 0.45 | 0.77 | | - | | - | |
| Residuals | 8011 | 31.79 | | | | | | | |
| *M. spicatum* | | | | | | Habitat Type | | Life Stage | |
| Life Stage | 2042 | 1021 | 1.72 | 0.18 | | valley | **a** | - | |
| Habitat type | 118272 | 59136 | 100.03 | <0.0001 | *** | slope | **b** | - | |
| Stage: Habitat | 3966 | 992 | 1.68 | 0.16 | | plateau | **b** | - | |
| Residuals | 148983 | 591 | | | | | | | |

**Table 2:** Summary of the number of plots (from a total 87) per life stage, where spatial autocorrelation was detected at the local scale, within the plots (Moran's I index) and at the landscape scale (Z scores of G* statics), for four Marantaceae species. The third column shows the total number of plots which the herb species occurred according to life stage.

| Plant Species |  | *G. altissima* |  |  | *I. arouma* |  |  | *M. densiflorum* |  |  | *M. spicatum* |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Life Stages |  | Adu | Juv | Seedl | Adu | Juv | Seedl | Adu | Juv | Seedl | Adu | Juv | Seedl |
|  | Habitat |  |  |  |  |  |  |  |  |  |  |  |  |
| Number of plots with presence (Plots/habitat = 29) | Plateau | 12 | 21 | 19 | 14 | 22 | 11 | 12 | 13 | 9 | 7 | 8 | 4 |
|  | Slope | 9 | 20 | 15 | 11 | 21 | 13 | 10 | 12 | 9 | 11 | 11 | 7 |
|  | Valley | 2 | 10 | 5 | 22 | 27 | 16 | 4 | 5 | 5 | 26 | 27 | 26 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Number of plots with spatial autocorrelation at local scale (**Moran's I > 0.1**) | Plateau | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
|  | Slope | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Valley | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 1 | 0 |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Number of plots with spatial autocorrelation at regional scale (**G* above the average**) | Plateau | 12 | 16 | 13 | 13 | 13 | 11 | 8 | 8 | 6 | 4 | 6 | 4 |
|  | Slope | 8 | 12 | 11 | 5 | 5 | 3 | 4 | 4 | 4 | 4 | 5 | 2 |
|  | Valley | 2 | 3 | 5 | 11 | 11 | 12 | 3 | 2 | 2 | 18 | 17 | 15 |

**Table 3.** Summary of how reproductive and vegetative traits of the studied Marantaceae species and their association with recruitment and dispersal limitations. LMA values were extracted from Figueiredo et al. (2017).

| Plant Species | Seed size (g) | Potencial disperser | Restricted on landscape? | Associated to light? | Associated to water? | LMA $g.m^{-2}$ |
|---|---|---|---|---|---|---|
| *M. spicatum* | 0.067 | Ant | Yes | Yes | Yes | 46.24 |
| *M. densiflorum* | 0.055 | Ant | Yes | Juveniles | Yes | 55.37 |
| *I.arouma* | 0.348 | Small mammal/Bat | No | Adults | Juveniles | 58.24 |
| *G. altissima* | 0.347 | Bird | No | No | No | 65.53 |

## Figure Legends

**Figure 1.** Map of the study site in Reserva Florestal Adolpho Ducke (RFAD) and sample design. Surveys of herbs individuals of the four Marantaceae species took place in the 87 plots of 5 m x 100 m represented by colored rectangles which were placed in the main habitat types of the study area: plateau (red); slope (yellow); valley (blue).

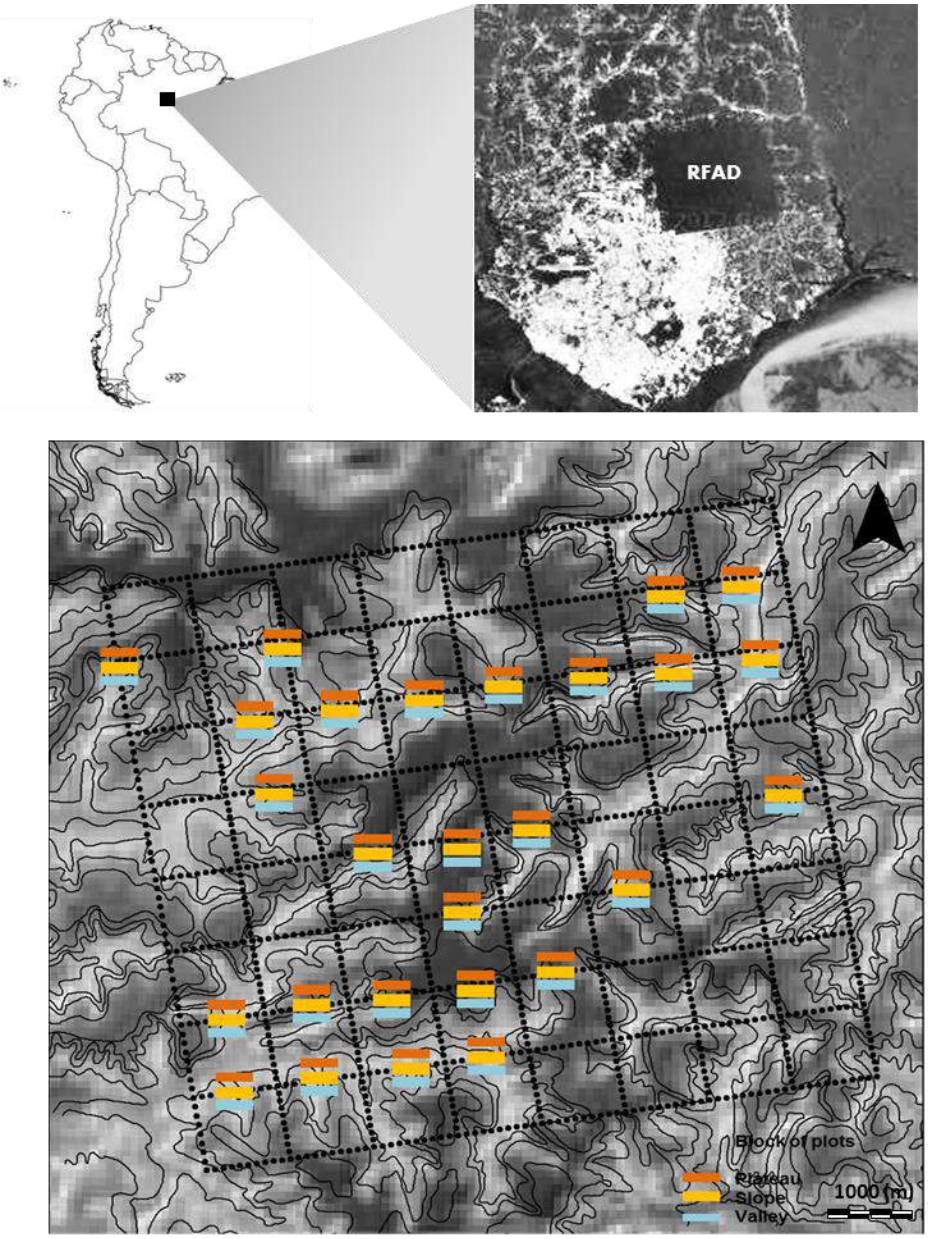
**Figure 2.** Characteristics of the four species of Marantaceae at Reserva Ducke, in Central Amazonia. Predicted seed disperser information from Horvitz (1991).

**Figure 3.** Abundance of four herb species across life history stages in the main different microhabitat of study. Life history stages were separated based on individual heights. The line near the middle of the boxplot represents the median, and the bottom and top of the box represents the 25th and 75th percentile, respectively. Extreme data are represented by black points. Plant species are ordered by diaspore size: Large diaspores on above graphs (*Goeppertia altissima* and *Ishchnosiphon arouma*) and; Small diaspores on under graphs (*Monotagma densiflorum* and *Monotagma spicatum*).

**Figure 4.** Influence of environmental factors in the abundance of four herb species across life history stages. HAND is a proxy for "distance from drainage", Light were measured with canopy scope. Estimates values are from GLMM models and variable's values were standardized to permit comparisons. Life history stages were separated based on individual heights. Species are divided according to diaspore size: Large diaspores *Goeppertia altissima* and *Ischnosiphon arouma* and; Small diaspores *Monotagma densiflorum* and *Monotagma spicatum*.

**Figure 5:** Maps showing the spatial associations of life stages within blocks contain the three main habitats at study site (i.e. plateau, slope and valley) distinguished by colors. Symbols type represent the life stages adults, juveniles and seedlings. The symbols size is in accordance with the G* score value, bigger symbols strongest is the spatial association. The colored crosses represent the plots where the species were presented but with the G* score below the average.

**Figure 1**



## Figure 2

| Plant Species | Abundance (mean/SD) per habitat | | | Life Stages by height ranges (m) | | | Diaspore size | Weight (g) mean (SD) | Assigned disperser | Diaspores |
|---|---|---|---|---|---|---|---|---|---|---|
| | Plateau | Slope | Valley | Seedling | Juveniles | Adults | | | | |
| Monotagma spicatum (Aubl.) J. F. Macbr. | 4.9 (4.9) | 6.1 (8) | 148.1 (110.1) | ≤ 0.20 | 0.21 - 0.59 | ≥ 0.60 | Small | 0.055 (0.008) | ant |  |
| Monotagma densiflorum (Körn.) K.Schum. | 19.5 (23.9) | 11 (9.6) | 20.3 (30) | ≤ 0.20 | 0.21-0.39 | ≥ 0.40 | Small | 0.067 (0.014) | ant |  |
| Goeppertia altissima (Poepp. & Endl.) Borchs. & S. Suárez | 5.375 (2.8) | 4.4 (4.7) | 3.6 (2.8) | ≤ 0.20 | 0.21 - 0.69 | ≥ 0.70 | Large | 0.347 (0.052) | bird |  |
| Ischnosiphon arouma (Aubl.) Körn. | 7 (9.8) | 4.8 (3.1) | 12.7 (13.1) | ≤ 0.30 | 0.31 - 1.49 | ≥ 1.50 | Large | 0.348 (0.053) | small mammal or bat |  |

**Figure 3**

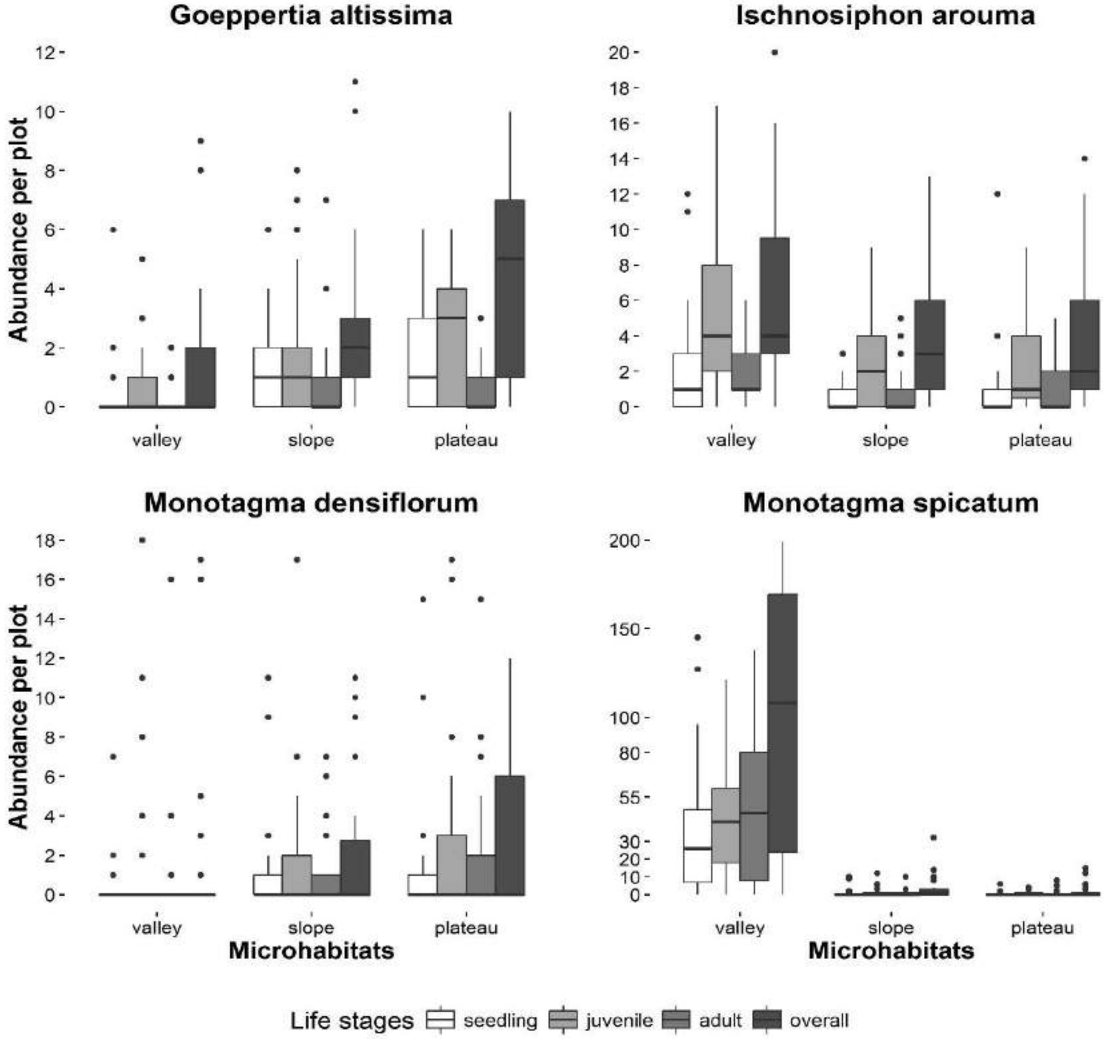

Goeppertia altissima
Ischnosiphon arouma
Monotagma densiflorum
Monotagma spicatum
Abundance per plot
Abundance per plot
0
2
4
6
8
10
12
0
2
4
6
8
10
12
14
16
18
20
0
2
4
6
8
10
12
14
16
18
0
10
20
30
55
80
100
150
200
valley
slope
plateau
valley
slope
plateau
valley
slope
plateau
valley
slope
plateau
Microhabitats
Microhabitats
Life stages
seedling
juvenile
adult
overall

**Figure 4**

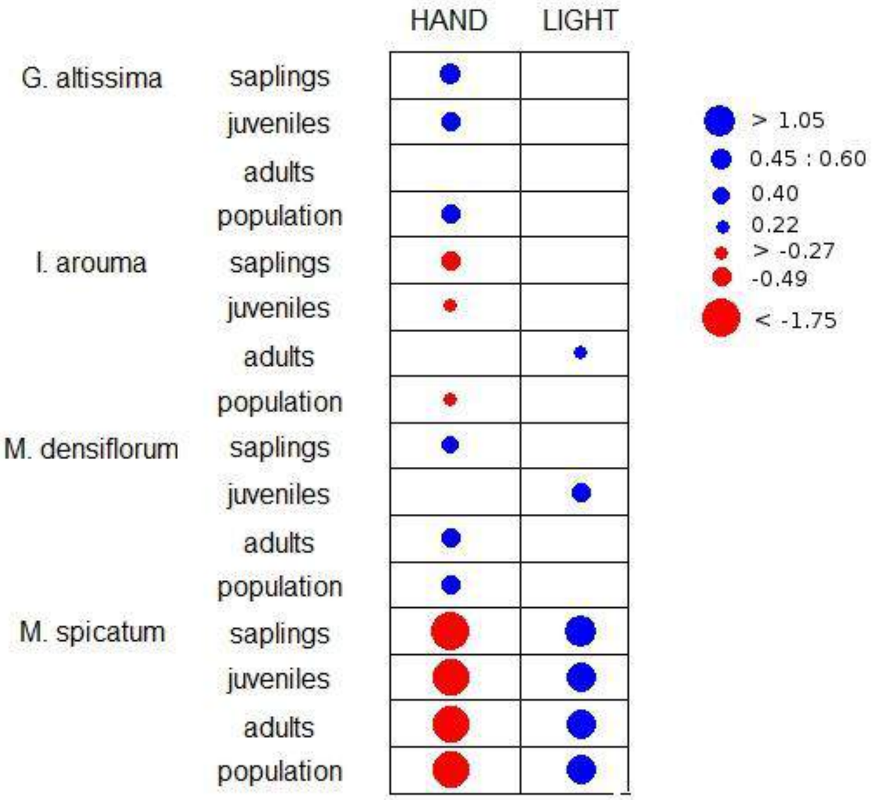
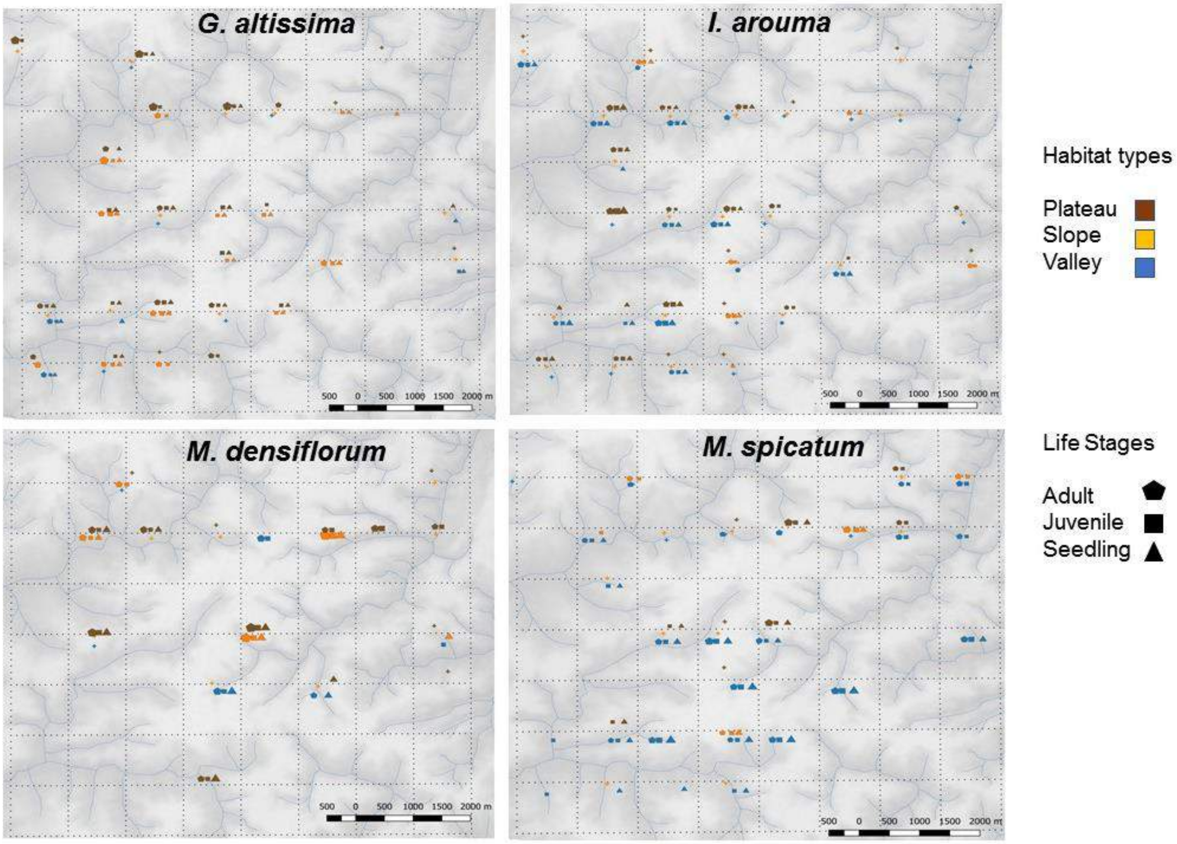

HAND
LIGHT
G. altissima
saplings
juveniles
adults
population
I. arouma
saplings
juveniles
adults
population
M. densiflorum
saplings
juveniles
adults
population
M. spicatum
saplings
juveniles
adults
population
> 1.05
0.45 : 0.60
0.40
0.22
> -0.27
-0.49
< -1.75

**Figure 5**


G. altissima
I. arouma
M. densiflorum
M. spicatum
500 0 500 1000 1500 2000 m
Habitat types
Plateau
Slope
Valley
Life Stages
Adult
Juvenile
Seedling

## SÍNTESE

Nessa tese demonstramos que o processo de dispersão de sementes de espécies herbáceas é mais complexo do que sugerido anteriormente, e envolve uma variedade de grupos dispersores. Os invertebrados são os dispersores mais frequentes, mesmo para as espécies que possuem diásporos grandes. A heterogeneidade do ambiente teve um papel crucial na efetividade de dispersão e nas limitações de dispersão e recrutamento, porém influenciou diferentemente cada espécie herbácea estudada.

Até o presente estudo, as espécies de Marantaceae eram classificadas quanto ao modo de dispersão baseado nas características morfológicas das suas infrutescências/sementes e os estudos de dispersão de sementes focavam quase exclusivamente em entender a importância dos nomeados dispersores primários. Porém como mostramos no capítulo 2, mesmo que classificados em grupos, os dispersores de sementes das espécies de Marantaceae diferiram bastante na efetividade de dispersão tanto no componente quantitativo quanto no componente qualitativo (fig. 1, capítulo 2). No geral, os grupos dispersores previamente nomeados como primários desempenharam o papel de dispersor mais efetivo. Esse padrão foi mais consistente para as espécies que possuem sementes pequenas que são dispersas principalmente por formigas. Das espécies de sementes grandes, as características morfológicas e a designada síndrome de dispersão coincidiu apenas em *G. altíssima* para a qual o grupo de aves foi o que mais contribuiu para a efetividade. Esperava-se que *I. arouma,* que possui semente grande e um odor característico pudesse atrair algum tipo de mamífero, porém os dispersores mais efetivos de *I. arouma* foram os grilos. Como demonstrado no capítulo 1, em termos quantitativos os grilos não diferem das formigas, reconhecidas até então como o principal dispersor invertebrado nos sistemas neotropicais. Embora não tenha sido objetivo direto dessa tese, pela primeira vez, realizou-se estudos comparativos sobre a importância relativa de diferentes dispersores invertebrados. No capítulo 1 mostramos que potencialmente os grilos removem sementes maiores mais longe do que formigas. E no capítulo 2, vimos que grilos e baratas foram mais efetivos do que formigas como dispersores de pelo menos 1 espécie com diásporos grandes.

Para todas as espécies estudadas, a heterogeneidade do ambiente foi importante para a substituição de grupos dispersores entre os ambientes como demonstrado no capítulo 2. Porém nem sempre essa substituição significa mudança na efetividade de dispersão da espécie vegetal.

A heterogeneidade ambiental influenciou mudanças na efetividade de dispersão das espécies com diásporos grandes, que também atraíram mais grupos de dispersores. Nós relacionamos este achado com o fato dos diásporos grandes possuírem mais recursos e por isso são atrativos para uma diversidade maior de dispersores. Desta forma, sugere-se que a atratividade do diásporo e o tipo de ambiente devem covariar na relação com a efetividade de dispersão de espécies herbáceas. As espécies com diásporos pequenos possuem menos recursos, com menos atrativos para determinados grupos dispersores e a heterogeneidade não influenciou a efetividade de dispersão. Esses resultados vão ao encontro dos padrões de distribuição explorados no capítulo 3 que mostram que a distribuição espacial dessas espécies com diásporos pequenos é influenciado principalmente pela limitação de dispersão.

O padrão de distribuição na escala da paisagem que encontramos para as espécies de ervas corroborou com o esperado com relação ao tamanho do diásporo e a capacidade de dispersão. As espécies com diásporos maiores tendem a ser associadas à dispersores maiores, o que sugere maior potencial de dispersar os diásporos mais longe. De fato, no capítulo 3 nós mostramos que as espécies com diásporos grandes são mais distribuídas na paisagem e as espécies com sementes pequenas são mais restritas a determinados tipos de ambiente da paisagem. Para três das quatro espécies é possível relacionar os grupos dispersores mais efetivos (capítulo 2) com a ausência/presença de limitação de dispersão na escala da paisagem (capítulo 3). Por exemplo, a espécie *G. altíssima,* cujo dispersor mais efetivo são as aves, os resultados não mostraram limitação de dispersão, por outro lado, para as espécies *M. densiflorum* e *M. spicatum* que têm as formigas como dispersoras mais efetivas, os padrões encontrados sugerem limitação de dispersão na escala da paisagem. No o caso do *I. arouma,* na ausência da detecção de dispersores vertebrados, os invertebrados foram os mais efetivos, o que diverge do padrão de distribuição detectado para essa espécie. Embora não se possa descartar a dispersão de sementes por vertebrados para *I. arouma,* seguramente são eventos extremamente raros, mas que ainda assim devem ser importantes para manter a espécie bem distribuída na escala da paisagem como foi observado no capítulo 3.

As espécies estudadas sofrem com limitações de recrutamento ao longo de vários estágios de vida na escala do ambiente em diferentes graus de intensidade. A relação entre o ambiente com maior efetividade e o mais favorável para a germinação não foi observada para todas as espécies e também não foi relacionada com o tamanho do diásporo. Da mesma forma, o ambiente mais favorável para a germinação e para o recrutamento de plântulas até onze meses de vida (capítulo 2), nem sempre representam os ambientes onde foram observadas maiores abundâncias nos estágios de plântula, jovens e adultos (capítulo 3).

Esses resultados integrados mostram que existe um gradiente entre espécies principalmente limitadas por estabelecimento e espécies principalmente limitadas por dispersão. Dentre as herbáceas estudadas, os resultados sugerem que as espécies *G. altissima* e *M. spicatum* são representantes dos dois extremos deste gradiente. A erva *G. altissima*, apresentou maior efetividade, maior taxa de germinação, maior recrutamento inicial e maiores abundâncias em todos os estágios de vida no mesmo tipo de ambiente, no platô. Ou seja, a forte limitação de ambiente nas áreas de baixio é governada pela alta eficiência de dispersão e recrutamento no ambiente mais favorável. No outro extremo do gradiente está a *M. spicatum,* espécie de diásporos pequenos, que apresentou maior efetividade no ambiente de platô, enquanto que, a germinação de sementes, o recrutamento inicial e as maiores abundâncias dos estágios de vida acontecem nos ambientes de baixio. Isso significa que a alta limitação de dispersão favorece o recrutamento desproporcional nas áreas de baixio, muito embora, a efetividade mais alta no ambiente de platô deve compensar a alta limitação de dispersão com manutenção de indivíduos em baixa abundância nos platôs.

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