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O PAPEL DA DISPERSÃO DE SEMENTES POR AVES NA MANUTENÇÃO DA DIVERSIDADE DE PLANTAS DE UMA FLORESTA TROPICAL

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Tese apresentada ao Instituto de Biociências da Universidade Estadual Paulista "Júlio de Mesquita Filho", campus Rio Claro, como requisito para obtenção do título de Doutor em Ecologia e Biodiversidade.

Orientador: Prof. Dr. Marco Aurélio Pizo Ferreira

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Resumo

A diversidade das florestas tropicais é fortemente moldada por interações mutualísticas envolvendo plantas e frugívoros que dispersam suas sementes. No entanto, ainda é pouco conhecido como frugívoros podem afetar os padrões de dispersão de sementes, a composição da comunidade de plantas e a coexistência de espécies em paisagens de floresta tropical. Outra lacuna no nosso conhecimento é entender como a variação das características de plantas e frugívoros ligadas a dispersão de sementes se combinam para estruturar as redes de interações. E ainda, como essa combinação de características de plantas e frugívoros podem ser aproveitadas na restauração florestal. Assim, ao longo de três capítulos, tentei elucidar cada uma dessas lacunas no nosso conhecimento através de um extensivo trabalho de campo em 12 paisagens fragmentadas na Mata Atlântica. Monitorei a produção de sementes dispersas por aves e a abundância de aves em fragmentos florestais, e amostrei a chuva de sementes e a atividade de aves atraídos para núcleos de árvores experimentais estabelecidos em pastagens adjacentes. No capítulo 1, mostro que a dispersão de sementes por aves pode ser manipulada em projetos de restauração com base na combinação de características entre plantas e aves, a fim acelerar a recuperação da floresta. No capítulo 2, mostro que os frutos proporcionalmente raros em fragmentos de Mata Atlântica têm uma probabilidade maior do que o esperado de dispersão de sementes devido ao efeito equalizador proporcionado por aves frugívoras, e que este efeito é aumentado com a diversidade de aves. Finalmente, no capítulo 3, mostro que uma maior diversidade funcional de aves e plantas permite uma maior correspondência de características e uma rede de interações mais conectada, o que proporciona uma maior riqueza funcional da chuva de sementes. Em conclusão, essa tese contribui para o nosso entendimento sobre o papel da dispersão de sementes por aves na manutenção da diversidade estrutural e funcional de plantas, bem como para a resiliência de uma floresta tropical.

Palavras-chave: dependência de densidade negativa, diversidade funcional, interação planta-ave, manutenção da diversidade, mutualismos, restauração florestal, sucessão florestal.

Abstract

The diversity of tropical forests is strongly shaped by mutualistic interactions involving plants and frugivores that disperse their seeds. However, little is known on how frugivores can affect seed dispersal patterns, plant community composition and species coexistence in tropical forest landscapes. Another gap in our knowledge is to understand how the trait diversity of plant and frugivores match to structure interaction networks, and how this plant-bird trait-matching can be used in forest restoration. Thus, over three chapters, I tried to clarify each of these knowledge gaps through extensive fieldwork in 12 fragmented landscapes in the Atlantic Forest. I monitored the production of bird-dispersed seeds and bird abundance in forest fragments and sampled the seed rain and the activity of birds attracted to experimental tree nuclei established in adjacent pastures. In chapter 1, I show that seed dispersal by birds can be manipulated in restoration projects through the plant-bird trait-matching to accelerate forest recovery. In chapter 2, I show that proportionally rare fruit resources in fragments of the Atlantic Forest have a greater than expected probability of seed dispersal due to the equalizing effect provided by frugivorous birds and that this effect is increased with bird diversity. Finally, in Chapter 3, I show that a greater functional diversity of birds and plants allows for a greater trait-matching and a more connected interaction network, which creates a greater functional richness in the seed rain. In conclusion, this thesis contributes to our understanding of the role of seed dispersal by birds in maintaining the structural and functional diversity of plants as well as the resilience of a tropical forest.

Keywords: forest restoration, forest succession, functional diversity, maintenance of diversity, mutualisms, negative density-dependence, plant-bird interaction

SUMÁRIO

1 Introdução Geral

1.1 Padrões de diversidade

Em florestas tropicais de alta diversidade, a maior parte da diversidade vegetal é composta por espécies consideradas raras (Hubbell 2001; Chave et al. 2002; Dinerstein et al. 2002; Tonhasca Jr. 2005; Hubbell 2013). Acredita-se que os trópicos abriguem entre 40.517 a 53.345 espécies de plantas arbóreas (Slik et al. 2015), das quais estima-se que pelo menos 50% são raras ou muito raras (Hubbell 2013). Na Amazônia, a porcentagem de espécies arbóreas raras se aproxima de 70% (ter Steege et al. 2013), chegando a 88% em algumas regiões (Pitman et al. 1999), enquanto que na Mata Atlântica a porcentagem de espécies arbóreas raras também é elevada, chegando a 59% (Caiafa e Martins 2010).

Durante anos, ecólogos têm procurado compreender os mecanismos que levam a esse padrão de espécies raras e de distribuição das espécies durante a montagem das comunidades (Flather e Sieg 2007). Todavia, é importante ressaltar que há diferença entre como esse padrão ocorre e como ele é mantido. Duas teorias contrastantes tentam explicar a estruturação das comunidades e os mecanismos condutores da distribuição e composição de espécies nestas comunidades: a Teoria do Nicho (MacArthur e Levins 1967) e a Teoria Neutra da Biodiversidade e Biogeografia (Hubbell 2001). A primeira teoria prediz que os recursos (ver Pocheville 2015 para um histórico sobre a definição do termo) são utilizados de forma diferente pelas espécies e que a especialização na obtenção de determinado recurso pode diminuir a eficiência na obtenção de outro (Tilman 2004). A teoria é centrada na competição entre as espécies (i.e., a distribuição de espécies é determinada por interações competitivas entre as espécies) e prevê que as habilidades competitivas das espécies mais aptas devem excluir as demais (Chesson 2000; Pocheville 2015). Desta forma, apenas espécies com nichos suficientemente diferenciados podem coexistir em uma mesma comunidade (Kneitel e Chase 2004) e as características ambientais podem determinar o padrão de composição das espécies.

Embora a Teoria do Nicho tenha suporte empírico em diversos trabalhos que investigaram a montagem das comunidades (e.g., Tilman 1981; Interlandi e Kilham 2001), Hubbell (2001) propôs a Teoria Neutra da Biodiversidade e Biogeografia segundo a qual todos os indivíduos da comunidade têm as mesmas chances de migrar, reproduzir-se, morrer e "especiar" (ver De Marco Jr. 2006 para explicação do termo), uma vez que todos são funcionalmente equivalentes. Neste sentido, ele afirma que a abundância de espécies é dependente do acaso e não da superioridade competitiva de uma espécie. A competição pode até ocorrer na comunidade, todavia, é altamente simétrica (Pocheville 2015). Relações tróficas e mutualismos assimétricos não são abordados no modelo (Bell 2001). Hubbell

(2001) prevê que os padrões de composição das espécies estão ligados às suas capacidades de dispersão (i.e., montagem da comunidade através de dispersão), sendo que as diferenças na composição e abundância das espécies derivam de processos probabilísticos na colonização e extinção dos indivíduos. Outra questão deste modelo é que, diferentemente da Teoria de Nicho, Hubbell (2001) propõe que a coexistência entre as espécies não é estável, principalmente devido à igualdade de aptidões entre elas. Coexistência instável é quando não há tendência para recuperação das densidades das espécies e, a longo prazo, elas não são mantidas no sistema. Por outro lado, a coexistência estável entre as espécies significa que as densidades das mesmas tendem a se recuperar em situações em que estejam baixas (Chesson 2000). Embora este ponto seja criticado pelo fato da maioria das comunidades apresentarem coexistência estável entre as espécies e ser difícil encontrar aptidões idênticas, ele pode ser verificado quando as diferenças de aptidão se equivalem às taxas de competição intraespecífica da espécie com maior aptidão (mecanismo de estabilização, ver abaixo) (Chesson 2000).

Em relação à manutenção da diversidade, há duas classes principais de mecanismos: efeitos de equalização que minimizam a aptidão e diferenças competitivas entre espécies e efeitos de estabilização que aumentam os efeitos negativamente dependentes da densidade quando as espécies se tornam mais abundantes (Chesson 2000; Muller-Landau 2008; Fig. 1). Este último mecanismo ocorre muitas vezes quando os efeitos de interações intraespecíficas (e.g., competição intraespecífica) são “mais negativos” do que os efeitos das interações interespecíficas (Chesson 2000). Neste sentido, os mecanismos de equalização e de estabilização, atuando juntos, podem aumentar as chances ou a durabilidade da coexistência (Chesson 2000; Adler et al. 2007). Por exemplo, demandas conflitantes (*trade-off*) interespecíficas que envolvem a capacidade de colonização e competição podem contribuir fortemente para a manutenção da diversidade de espécies de plantas devido aos efeitos equalizadores e/ou estabilizadores que essas demandas exercem nas comunidades (Chesson 2000; Muller-Landau 2008, Chesson 2018; Fig. 1).

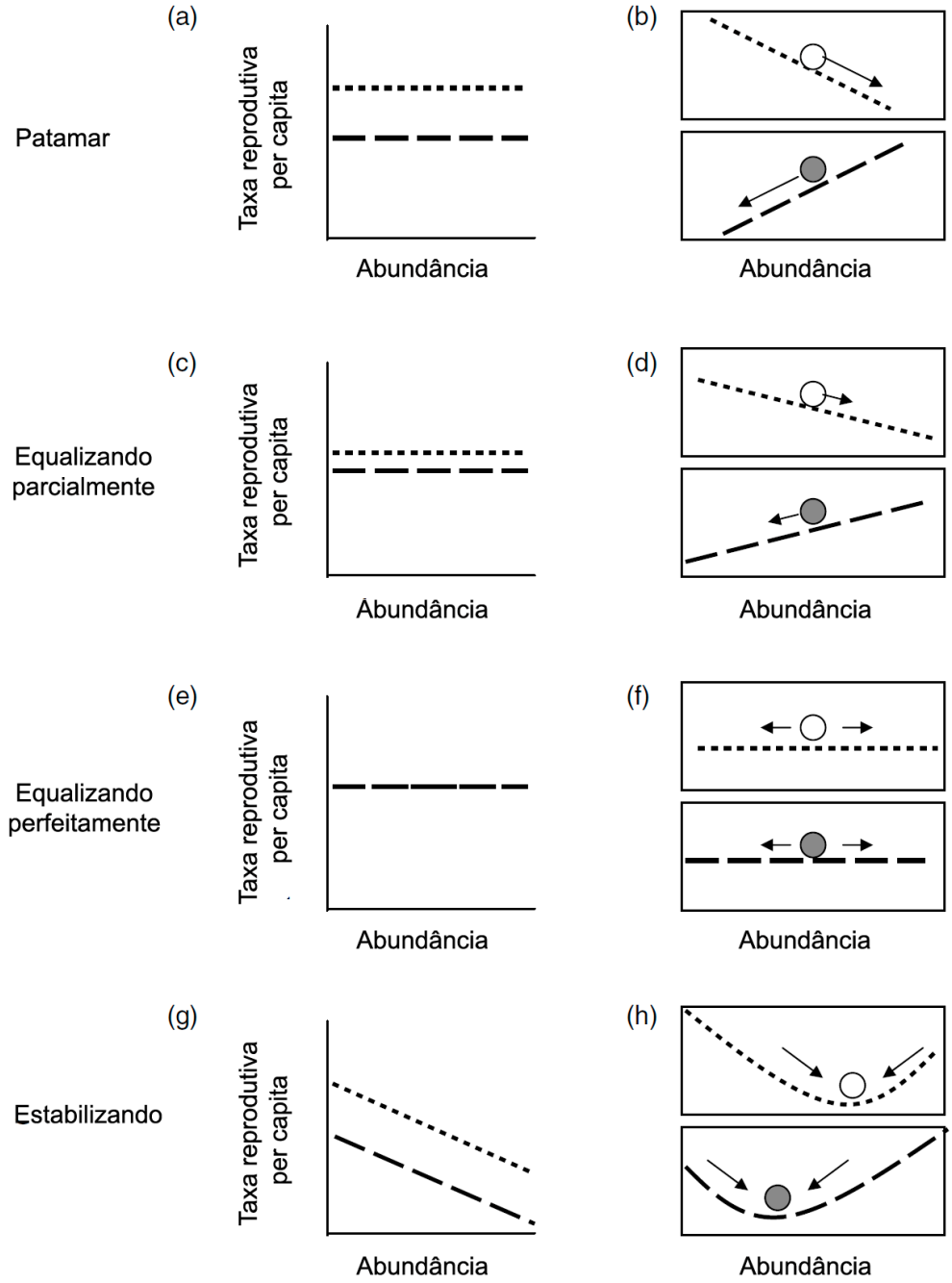

Fig. 1. Considere uma situação na qual existem diferenças competitivas fixas entre as espécies em suas taxas reprodutivas per capita (a) - diferenças que deterministicamente levariam à exclusão competitiva das espécies com a menor taxa reprodutiva (linha tracejada) pelas espécies com a maior taxa reprodutiva (linha pontilhada). Nesse caso, podemos pensar em cada espécie como uma bola precariamente localizada em uma encosta íngreme (b), pela qual ela inevitavelmente rolará, com as espécies mais fracas movendo-se para a abundância zero e a comum para a dominância. Se adicionarmos uma influência parcialmente equalizadora, as taxas reprodutivas das duas espécies tornam-se mais semelhantes (c), mas como uma ainda é superior, as espécies mais fracas ainda serão inevitavelmente perdidas, embora a uma taxa mais lenta (d). No caso extremo de influências perfeitamente equalizadoras, as taxas reprodutivas das duas espécies tornam-se idênticas (e). Este caso é análogo àquele em que ambas as espécies são bolas em uma mesa plana (f): não há nenhuma inclinação que os faça aumentar ou diminuir

em abundância, mas ambos estão sujeitos à deriva aleatória que pode resultar em sua abundância indo a zero ou ao domínio. Se, em vez disso, adicionarmos uma influência estabilizadora, então a taxa reprodutiva de cada espécie diminui à medida que se torna mais abundante e aumenta à medida que se torna mais rara (g); aqui, existem pares de abundâncias em que as espécies têm taxas reprodutivas iguais e podem coexistir de forma estável. Nesse caso, é como se cada espécie fosse uma bola dentro de uma tigela (h): qualquer perturbação de sua abundância para níveis superiores ou inferiores induzirá feedbacks negativos que a retornarão à sua posição de equilíbrio estável. Por exemplo, se sua abundância for reduzida, sua taxa reprodutiva aumentará e, assim, ele retornará ao seu equilíbrio de abundância. Adaptado integralmente de Muller-Landau (2008).

De certa forma, uma abordagem conjunta desses mecanismos (i.e., equalização e estabilização) tende a conciliar a Teoria do Nicho e a Teoria Neutra em uma estrutura unificada (Wennekes et al. 2012). Enquanto a igualdade de aptidões (ou diminuição das diferenças de aptidão) devido a mecanismos equalizadores é o centro da Teoria Neutra, mecanismos estabilizadores que permitem que uma espécie se limite (e.g., por competição intraespecífica) mais do que outras é uma ideia claramente pertencente à Teoria de Nicho (Wennekes et al. 2012; Pocheville 2015). De fato, vários trabalhos têm tentado conciliar abordagens das duas teorias para explicar a manutenção da diversidade e distribuição das espécies (e.g., Gravel et al. 2006; Adler et al. 2007; Chisholm e Pacala 2010). Da mesma forma, vários trabalhos têm levantado abordagens de ambas as teorias para explicar os padrões de raridade das espécies. Por exemplo, os padrões de raridade podem ser explicados por abordagens da teoria neutra como o mecanismo de limitação de dispersão (Volkov et al. 2003), ou por abordagens da teoria do nicho como características das espécies (Arellano et al. 2015) e efeitos dependentes da densidade de indivíduos coespecíficos (Comita et al. 2010).

1.2 Frugivoria e dispersão de sementes

É possível que animais que se alimentam de frutos (frugívoros) tenham grande importância nesse padrão de distribuição de plantas, uma vez que esses animais são responsáveis por dispersar a grande maioria das espécies de plantas lenhosas em florestas tropicais (Jordano 2000). Acredita-se que entre 70% a 90% das plantas lenhosas tropicais sejam dispersas por animais, sendo aves e mamíferos os principais agentes (Jordano 2000 e referências aí indicadas). Na Mata Atlântica, cerca de 75% das plantas lenhosas produzem frutos carnosos (Almeida-Neto et al. 2008). Desta forma, a prevalência de endozoocoria nestes sistemas indica a importância de frugívoros dispersores de sementes na manutenção de biodiversidade e torna o estudo da dispersão de plantas em grande parte uma questão de avaliar quais espécies de frugívoros são relevantes para o processo e compreender a probabilidade destes

frugívoros depositarem as sementes em locais apropriados (Schupp et al. 2010). Neste sentido, embora muitos outros grupos de animais como morcegos (e.g., Mello et al. 2011), primatas e ungulados (e.g., Bueno et al. 2013) sejam importantes dispersores, as aves são o grupo de frugívoros mais comum e diversificado nos trópicos e em outras regiões (Fleming e Kress 2011). Além disso, aves frugívoras são os principais dispersores de sementes em vários tipos de ambientes (Sekercioglu 2006).

Apesar disso, até recentemente, poucos estudos exploraram como frugívoros e plantas interagem para gerar padrões de diversidade nas comunidades vegetais, ou seja, quanto da estrutura das comunidades vegetais em termos de composição, abundância e coexistência de espécies é determinada pelos frugívoros. A maioria dos estudos destaca o papel importante dos efeitos dependentes de densidade negativa para a manutenção da diversidade vegetal nos trópicos, mas mostram esse padrão apenas em interações antagônicas, como competição, predação e herbivoria (Chesson 2000; Terborgh 2012). Nesse sentido, recentemente Carlo e Morales (2016) demonstraram que aves frugívoras tendem a apresentar um padrão antiapostático de seleção de frutos (i.e., padrão das aves que tendem a selecionar frutos raros), resultando em quantidades equalizadas de sementes dispersas em relação à disponibilidade de sementes no ambiente (Fig. 2). Assim, eles sugeriram que esse processo que beneficia espécies raras seria um mecanismo que permite o aumento da diversidade nas comunidades de plantas e a coexistência de espécies de plantas (Carlo e Morales 2016; Morán-López et al. 2018a).

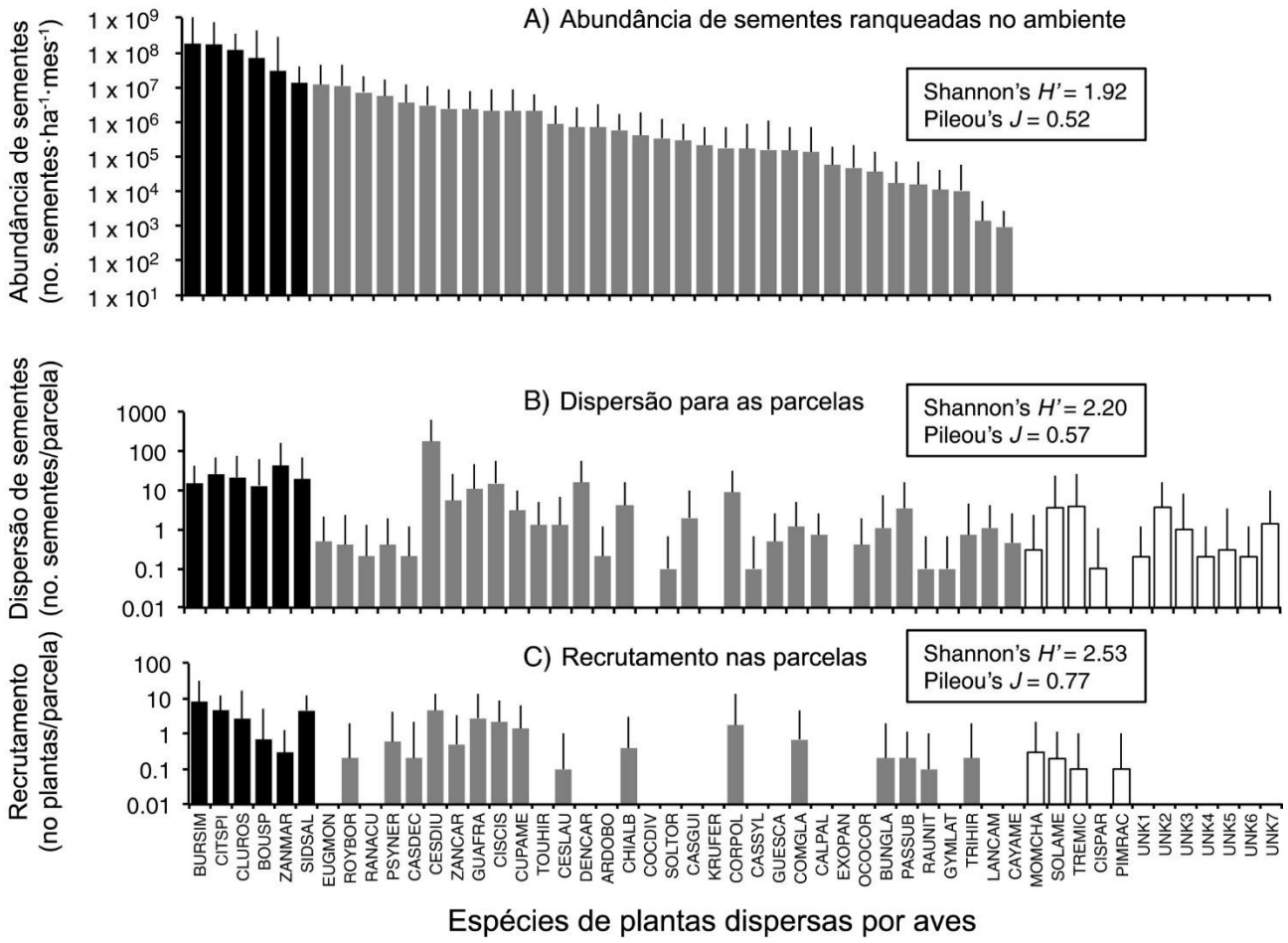

Fig. 2. Efeitos de equalização das aves sobre a dispersão e recrutamento em uma comunidade de 50 espécies de plantas ornitocóricas em Porto Rico registrados por Carlo e Morales (2016). As barras pretas mostram as 10 espécies mais abundantes (> 95% da produção de sementes) na comunidade. Nota-se que não há diferença entre as taxas de dispersão das plantas mais abundantes e raras (i.e., a dispersão foi amplamente equalizada). As taxas de recrutamento também foram altamente equalizadas mostrando como frugívoros podem contribuir para manter as espécies raras, e assim a maioria da diversidade, em comunidades.

Assim, os mecanismos compensatórios conferem vantagens às espécies de plantas raras, permitindo menores taxas de mortalidade per capita de patógenos, predadores de sementes e herbívoros, e reduzem a competição intraespecífica por recursos quando as plantas existem em baixas densidades populacionais (Janzen 1970; Comita et al. 2010; Johnson et al. 2012; Bagchi et al. 2014). Além disso, as espécies de plantas que produzem proporcionalmente poucos frutos podem fazer um maior investimento de energia por fruto e fornecer uma maior recompensa nutricional aos frugívoros (Howe 1993; Cazetta et al. 2008)

Fatores ambientais e a identidade das espécies que interagem podem afetar a força dos mecanismos compensatórios para espécies de plantas raras. Por exemplo, a magnitude dos efeitos de diversificação que ocorrem por meio da dispersão de sementes com viés para

espécies de plantas raras por frugívoros pode depender da heterogeneidade da paisagem e do comportamento de movimento das aves (Morán-López et al. 2018a). Isso ocorre porque o aumento da heterogeneidade da paisagem e a agregação espacial das plantas afetam os encontros entre plantas e animais e, portanto, as chances de plantas raras serem dispersas (Morán-Lopez et al. 2018a). Além disso, os modelos mostram que a tendência dos frugívoros consumirem os frutos de espécies raras surge do comportamento de forrageamento que maximiza a nutrição equilibrada quando os perfis nutricionais de diferentes espécies de frutos em uma comunidade são complementares entre si (Whelan et al. 1998; Morán-Lopéz et al. 2018b).

Os frugívoros variam em tamanho, comportamento alimentar, comportamento de movimento e fisiologia digestiva (Wheelwright 1985; Jordano 2000; Levy e Martínez del Rio 2001; Morales et al. 2013; González-Castro et al. 2015). Da mesma forma, os frutos variam em tamanho, exibição de cores, formato e recompensas nutricionais, características que influenciam a seleção de frutos e a dispersão de sementes pelos frugívoros. Nesse sentido, pode-se esperar que a diversidade de frugívoros também possa influenciar como tais mecanismos compensatórios afetam a dispersão de espécies raras. Por exemplo, as interações entre plantas e frugívoros são caracteristicamente aninhadas, na qual espécies abundantes generalistas são responsáveis pela maioria das interações em toda a comunidade. Em redes de frugivoria aninhadas, espécies raras e especializadas formam subconjuntos das interações das mais abundantes (Bascompte et al. 2003). Assim, com base na arquitetura comum de interações mutualísticas planta-frugívoro (Bascompte et al. 2003), o número de interações aumenta com o número de espécies interagindo em uma comunidade (por exemplo, García e Martínez 2012; Fricke et al. 2018).

Estudos recentes descobriram que diminuições na riqueza de frugívoros levam à perda de interações e co-extinção de espécies de plantas (Caughlin et al. 2015; Rumeu et al. 2017; Srbek-Araujo et al. 2017; Emer et al. 2019; Morán-López et al. 2020), ou mudanças na diversidade genética de populações de plantas (Carvalho et al. 2016; Pérez-Méndez et al. 2016). A regeneração e resiliência da floresta tropical também são afetadas pela atividade e diversidade de frugívoros (González-Castro et al. 2019; Gardner et al. 2019; Albert et al. 2020), o que pode impactar o estoque de carbono em remanescentes florestais (Bello et al. 2015) e plantações de restauração (Brancalion et al. 2018). Ainda assim, o papel da riqueza de frugívoros na manutenção da diversidade de plantas por meio de mecanismos comportamentais que afetam a dispersão de sementes, como a dispersão rara (antiapostática), permanece amplamente desconhecido.

1.3 Diversidade Funcional

Como os frugívoros variam em tamanho, comportamento alimentar, estrato de forrageamento e capacidade digestiva, bem como mobilidade e área de vida (Wheelwright 1985; Jordano 2000; Morales et al. 2013; González-Castro et al. 2015), características que podem moldar seus papéis funcionais como dispersores de sementes, é importante considerar também outras facetas da biodiversidade. Ou seja, a análise da diversidade de frugívoros apenas com riqueza e abundância de espécies nem sempre é capaz de prever a estrutura e funcionamento de suas comunidades e a qualidade dos serviços, principalmente da chuva de sementes gerada (Gagic et al. 2015). Isso porque essas medidas tradicionais não conseguem captar as particularidades de cada espécie envolvida e não consideram efeitos redundantes ou complementares que possam existir na comunidade (Cianciaruso et al. 2009; Mouchet et al. 2010).

A diversidade funcional surgiu como uma abordagem alternativa para descrever a variação de características das espécies dentro de uma comunidade e as funções ecológicas que desempenham (Mouchet et al. 2010; Flynn et al. 2011). De fato, a diversidade funcional mede a gama de características que capturam diferentes aspectos do uso de recursos e requisitos ecológicos das espécies (Villéger et al. 2008). Essas características podem prever potencialmente como as espécies influenciam os processos ecológicos, como a dispersão de sementes (de Bello et al. 2010). Neste sentido, a diversidade funcional pode integrar diferentes componentes e conceitos independentes, muitos dos quais se complementam (Mason et al. 2005; Villéger et al. 2008). Um deles é o espaço funcional, que é o espaço que todas as espécies ocupariam em uma determinada escala (por exemplo, local, regional, continental) se as representássemos em um espaço multidimensional, onde cada eixo representa uma ou mais características funcionais independentes. Dessa forma, podemos definir o nicho funcional de uma espécie como a posição em que ela ocupa no espaço funcional (Rosenfeld 2002). Baseado nas características funcionais das espécies (e.g. características morfológicas, bioquímicas, fisiológicas, estrutural, fenológica ou comportamental, Violle et al. 2007), é possível determinar as funções e o nicho funcional definido dentro do espaço funcional.

A partir do fato de que cada espécie ocupa uma posição dentro do espaço funcional, surge o conceito de riqueza funcional de uma comunidade (FRic). O FRic é expresso como o hipervolume que todas as espécies da comunidade ocupam no espaço funcional (Villéger et al. 2008), ou seja, o volume mínimo que as características funcionais dessas espécies ocupam (Fig. 3). Alta FRic indica que existem muitos traços dentro de uma comunidade (Laliberté et al., 2015) e maior complementaridade de funções. Da mesma forma, Mason et al. (2005) e

Villéger et al. (2008) apresentaram dois outros conceitos que fazem parte da diversidade funcional baseados no conceito de espaço funcional. Eles introduziram o conceito de equitabilidade funcional de uma comunidade (FEve) e a divergência funcional de uma comunidade (FDiv) (Fig. 3). FEve é definida como a regularidade da distribuição das abundâncias das espécies no espaço funcional da comunidade e leva em consideração a distribuição de frequência das espécies dentro do espaço funcional. Maior FEve significaria que os recursos disponíveis são utilizados de forma mais eficiente (Prescott et al., 2016). FDiv mede a distribuição da abundância de caracteres dentro deste volume, aumentando com valores extremos de caracteres (Mason et al., 2005; Villéger et al., 2008; Laliberté & Legendre, 2010). Assim, FDiv maior seria interpretado como uma grande diferenciação entre os nichos funcionais da comunidade e, portanto, menor competição.

Tomadas em conjunto, essas métricas podem indicar os processos de estruturação das comunidades por semelhança de limitação, filtragem de nicho, limitação de dispersão e processos neutros (Villéger et al. 2008; Mouchet et al. 2010). Ao mesmo tempo, podem revelar quais características funcionais específicas em uma comunidade influenciam as interações tróficas entre as espécies e os processos do ecossistema (Mokany et al. 2008; Gagic et al. 2015). Assim, particularmente em mutualismos de dispersão de sementes, o estudo da diversidade funcional de frugívoros e plantas pode nos fornecer uma compreensão mais profunda de como os papéis funcionais das espécies envolvidas atuam para estruturar o próprio processo e as comunidades florestais resultantes (Garnier et al. 2016; Lavabre et al. 2016; Pigot et al. 2016).

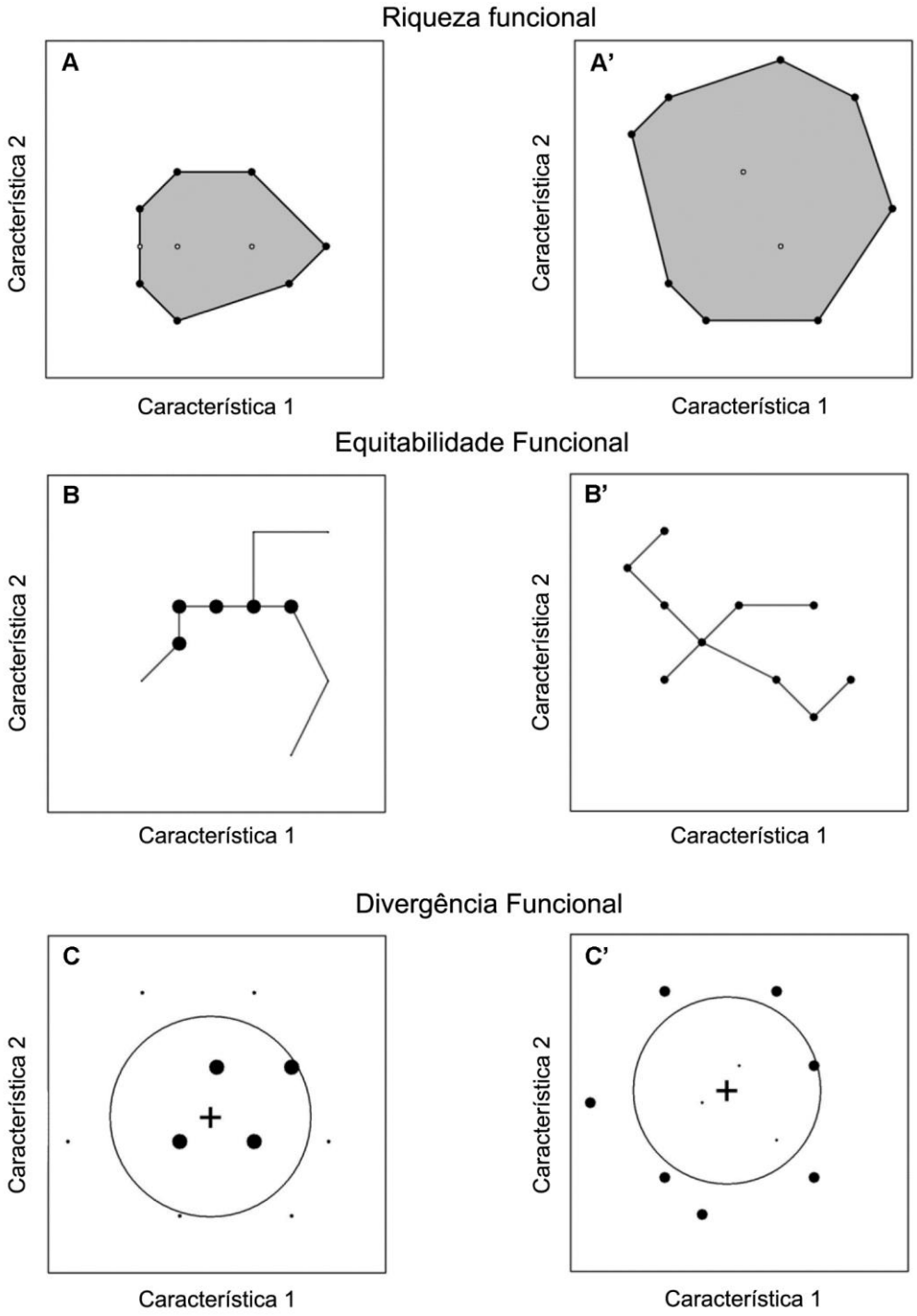

Fig. 3. Apresentação geométrica de índices de diversidade funcional. Duas características definem um espaço funcional bidimensional para uma comunidade local de dez espécies (pontos). As espécies são plotadas neste espaço de acordo com seus respectivos valores de características e com o tamanho do símbolo proporcional às suas abundâncias. A diversidade funcional de uma comunidade é, portanto, a distribuição das espécies e de suas abundâncias neste espaço funcional. Para cada componente da diversidade funcional, duas comunidades contrastantes são representadas, com valores de índice a, b, c baixos e a ′, b ′, c ′ altos. A riqueza funcional a e a ′ é o espaço funcional ocupado pela comunidade, a equitabilidade funcional b e b ′ é a regularidade na distribuição das abundâncias das espécies no espaço funcional, e a divergência funcional c e c ′ quantifica como as abundâncias das espécies divergem do centro do espaço funcional (Mouillot et al. 2011).

1.4 Papel dos frugívoros na regeneração florestal

Florestas tropicais em regeneração em terras previamente desmatadas oferecem uma excelente oportunidade para investigar e testar mecanismos de manutenção da diversidade que estão relacionados à montagem das comunidades através da dispersão, bem como testar o papel da diversidade funcional de aves e plantas na estruturação de redes de interação. Isso porque, mesmo com todos os impactos, essas florestas ainda abrigam boa parte da biodiversidade terrestre do mundo, suportam processos e fluxos de ecossistemas vitais e são cruciais para a estabilidade climática global (Raven 1988; Bradshaw et al. 2009; Morris 2010; Malhi 2012; Lawrence e Vandecar 2015). Além disso, uma vez que as florestas em regeneração estão entre os principais elementos de paisagens tropicais atuais (Letcher e Chazdon de 2009; Aide et al. 2013), é fundamental saber quão diversas e representativas estas áreas em recuperação podem ser e como mutualismos-chave moldam sua formação. De fato, em especial no Brasil, pouco se sabe efetivamente sobre os mecanismos associados à regeneração e o papel da interação planta-frugívoro neste processo (mas ver Silva et al. 2010; Rodrigues et al. 2011). Assim, compreender os processos que controlam as taxas de regeneração florestal e as regras de montagem que influenciam os padrões de biodiversidade de florestas sucessionais é fundamental para gerenciar com eficácia a biodiversidade remanescente (Chang e HilleRisLambers 2016; Boukili e Chazdon 2017).

Em áreas desmatadas, a dispersão de sementes pode ser severamente limitada, mesmo a alguns metros de distância dos fragmentos de floresta (Aide e Cavalier 1994; Cubiña e Aide 2001). Em parte, isso ocorre porque há relativamente poucas espécies de aves que dispersam sementes e forragem tanto em áreas abertas quanto florestadas (Pizo e dos Santos 2011; Carlo e Morales 2016). Portanto, o desenvolvimento de métodos para atrair dispersores de sementes importantes através de distâncias em paisagens tropicais desmatadas pode contribuir muito para reduzir a limitação de dispersão (Vieira et al. 1994; Slocum 2001; Kelm et al., 2008; Corbin & Holl, 2012; Peters et al. 2016). Estudos também mostraram que espécies de árvores que produzem frutos carnosos promovem mais dispersão do que espécies abioticamente dispersas (Vieira et al. 1994; Slocum 2001) e servem como focos de dispersão de longa distância em paisagens fragmentadas (Carlo et al. 2013). Árvores pioneiras dispersas por aves podem, em particular, desempenhar um papel importante na atração de dispersores de sementes para locais de restauração, dado seu rápido crescimento e produção abundante de frutos amplamente consumidos por muitas espécies de aves (Guevara e Laborde 1993; Guidetti et al. 2016). Uma lacuna de conhecimento crítica para manipular previsivelmente a dispersão de sementes em projetos de restauração é que não se sabe o quanto (ou seja, o

tamanho do efeito) características específicas das árvores pioneiras de frutos carnosos importam como atrativos para aves frugívoras. Esperamos que as características das espécies pioneiras - incluindo a variação no tipo de recompensa de nutrientes entre as espécies de frutos carnosos - afetem fortemente a quantidade, a riqueza e a composição da chuva de sementes produzida por aves frugívoras, uma vez que as redes mutualísticas de dispersão de sementes podem ser estruturadas pela correspondência de características entre as espécies que interagem entre si (Bascompte e Jordano 2007; Schleuning et al. 2015; Morán-López et al. 2020). É importante avaliar isso porque, se os efeitos forem grandes, os métodos de restauração que levam em conta características específicas podem promover a conectividade da paisagem, acelerar a regeneração da floresta e aumentar a recuperação da biodiversidade. Assim, os processos de correspondência de características inerentes às redes de frugivoria podem ter uma influência generalizada na montagem de comunidades florestais sucessionais (Schleuning et al. 2015; González-Castro et al. 2019), especialmente quando as características dos frutos de espécies pioneiras modificam subsequentemente padrões de dispersão de sementes. Esta é uma lacuna importante a ser preenchida para gerenciar a montagem de comunidades mutualísticas de plantas e animais em áreas desmatadas (Martínez e García 2017).

2 Objetivos e estrutura da tese

Nesta tese busco entender o papel da dispersão de sementes por aves na manutenção da diversidade de plantas e resiliência de uma floresta tropical. Especificamente, abordei os seguintes temas nos capítulos que compõem esta tese:

Capítulo 1. Investiguei os efeitos da combinação de características entre aves e plantas e distância de fragmentos de floresta sobre a chuva de sementes dispersas em pastagens em uma paisagem tropical fragmentada.

Capítulo 2. Examinei a hipótese de que aves frugívoras equalizam a representação e diversidade das espécies de plantas na chuva de sementes que ocorre em áreas desmatadas e leva ao aumento da riqueza vegetal. Também testei se o processo de equalização depende da riqueza e abundância das comunidades de aves frugívoras.

Capítulo 3. Estudei simultaneamente os efeitos da diversidade funcional de plantas e aves durante o processo de dispersão de sementes em paisagens desmatadas na Mata Atlântica. Especificamente, perguntei se uma maior diversidade funcional de aves e plantas aumenta a chance de correspondência de características entre eles e permite uma chuva de sementes mais diversificada funcionalmente.

3 Material e Métodos

3.1 Área de estudo

Os experimentos foram realizados em 12 locais no município de Paranapanema, São Paulo, sudeste do Brasil (23 ° 23 'S, 48 ° 43' W, Fig. 4). O município está localizado a 600 m de altitude, na região da bacia hidrográfica do Alto Paranapanema (Cielo-Filho et al. 2009). A precipitação média anual é de 1.407,9 mm e concentra-se na estação chuvosa de verão (dezembro a março), com temperatura média anual de 18° C (Cielo-Filho et al. 2009). As florestas cobrem apenas cerca de 6% da paisagem de Paranapanema (Fundação SOS Mata Atlântica 2013), que está localizada na segunda região biogeográfica mais ameaçada da Mata Atlântica, com apenas 7% de cobertura florestal remanescente (Ribeiro et al. 2009), um hotspot global para conservação da biodiversidade e restauração da floresta tropical (Laurance 2009, Brancalion et al. 2019). Os locais de estudo localizaram-se em terras particulares contendo pastagens para gado e fragmentos de Mata Atlântica semidecidual com mais 30 anos, variando de 12,2 a 98,8 hectares.

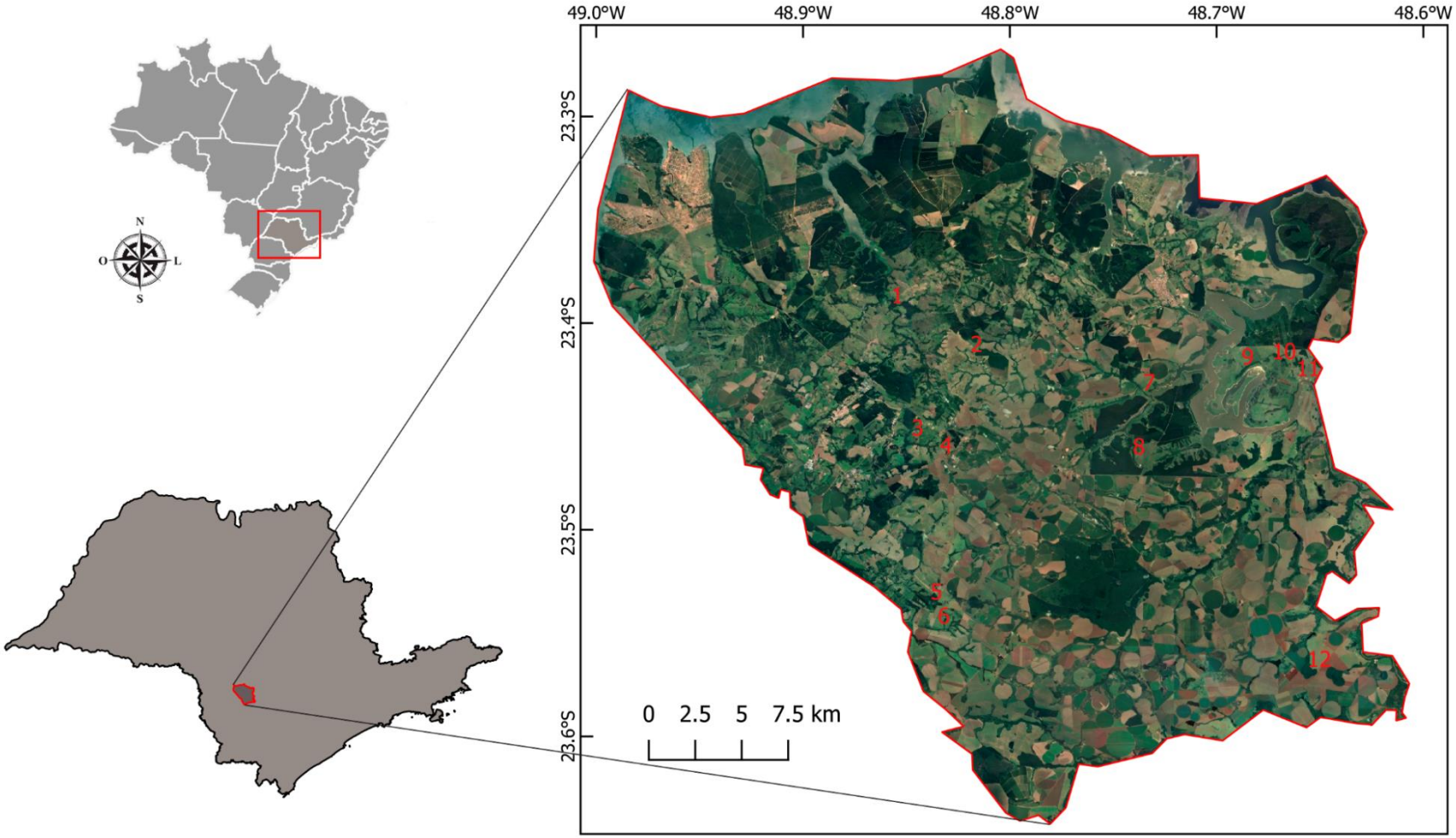

Fig. 4. O estudo foi realizado em 12 propriedades rurais privadas (marcadas com números vermelhos) localizadas no município de Paranapanema-SP, Brasil.

Capítulo 1

Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: implications for restoration

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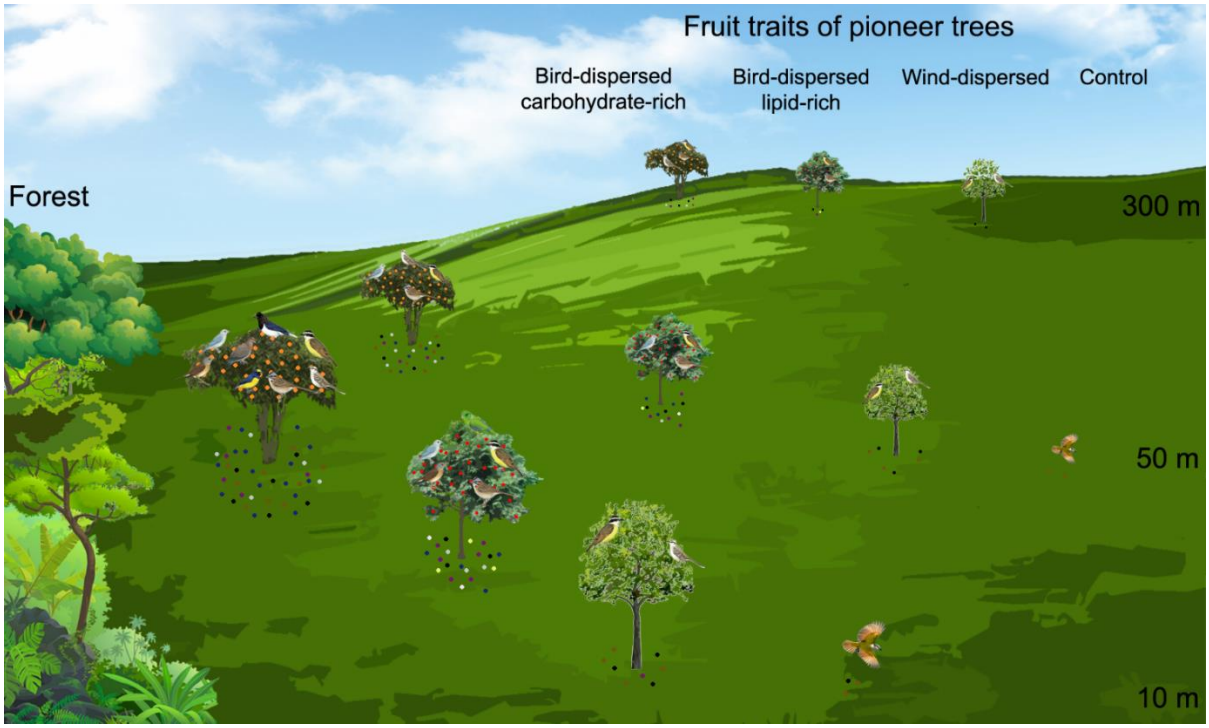

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Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: implications for restoration

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Abstract

1. Pioneer trees with fleshy fruits are typically planted in restoration projects to attract frugivores as a mean to increase dispersal and accelerate forest regeneration. Fruit traits of pioneer trees can potentially influence dispersal and their restoration outcomes.
2. We investigated the effects of bird and plant traits, and distance to forest fragments, on the seed rain using a tree-planting experiment replicated in 12 deforested sites in Brazil. Factors were fruit traits of pioneer trees (wind-dispersed, bird-dispersed with lipids or with carbohydrates, and controls) and distance (10, 50, 300 m) from forest fragments.
3. We found that density and richness of birds and seeds decreased exponentially with distance from fragments, yet these effects were minor compared to those of fruit traits on the structure of the seed rain.
4. The number of bird species and visits, as well as dispersed species and seeds, were greatest for plots with carbohydrate-rich plots, halved in lipid-rich fruit plots and declined by 84% in plots with wind-dispersed trees and by 98% in control plots when compared to responses in carbohydrate-rich plots. In addition to such quantitative differences, carbohydrate-and lipid-rich fruits were visited by birds with different morphologies, especially with different bill-gapes and flight capacities (wing-loading) that correlated with the observed structural differences in the seed rains among pioneers with different fruit traits.
5. *Synthesis and applications*. Understanding the effects of trait-matching on seed rains on deforested tropical landscapes across distance from forest fragments is critical for improving restoration efforts, especially in the context of applied nucleation. Avian seed dispersal can thus be manipulated in restoration projects in order to increase

connectivity and speed up forest recovery and the provision of the multiple ecosystem services that dovetail forest succession.

Keywords: applied nucleation; connectivity; forest restoration; frugivory; fruit chemical content; long-distance seed dispersal, natural regeneration; trait-matching.

Introduction

Tropical forest restoration is central to global strategies to face the most pressing environmental challenges of our time because its role in mitigating climate change, biodiversity loss, and the decline of essential ecosystem services for human wellbeing (Holl, 2017; Brancalion et al., 2019b; Lewis, Wheeler, Mitchard, & Koch, 2019). To date, over 170 million hectares – most of them in tropical countries − have been committed to the Bonn Challenge, a global forest landscape restoration program that aims to restore 350 million hectares of deforested and degraded landscapes by 2030 (Bonn Challenge, 2020). One critical barrier for achieving such ambitious commitments is the high-costs of tree planting (Shoo et al., 2017; Brancalion et al., 2019a). Although natural regeneration is a much more cost-effective restoration approach (Chazdon & Guariguata, 2016; Crouzeilles et al., 2017), it is still challenging to predict in which conditions regeneration processes will operate more effectively (Arroyo-Rodríguez et al., 2017; Borda-Niño, Meli, & Brancalion, 2020).

One potential strategy to foster natural regeneration is planting small tree patches across the targeted restoration area, which can attract seed dispersers and, through the ongoing regeneration of dispersed plants, promote the gradual expansion of forest nuclei up to their coalescence (Corbin & Holl, 2012). This approach, known as applied nucleation, has been employed worldwide to enhance human's capacity to upscale forest restoration and is one of the main promises to reduce restoration costs (Benayas, Bullock, & Newton, 2008; Zahawi, Holl, Cole, & Reid, 2013; Bechara et al., 2016; Corbin, Robinson, Hafkemeyer, & Handel, 2016). A key ecological process for applied nucleation success is the attraction of seed dispersers to restoration sites, which can be controlled by a myriad of factors as the distance to seed sources, the tree species planted, and the planting design (Reid, Harris, & Zahawi, 2012; Reid, Holl, & Zahawi, 2015; Viani et al., 2015). Thus, a better understanding of the

factors driving seed dispersal is critical to effectively manipulate this ecological process to favor restoration success (McAlpine et al., 2016).

Birds are one of the principal agents of seed dispersal for fleshy-fruited plant species on cleared lands because of their high abundance, mobility, and high diversity, (Wunderle Jr, 1997, Carlo & Morales 2016). In deforested areas seed dispersal can be severely limited even a few meters away from forest fragments (Aide & Cavalier, 1994; Cubiña & Aide, 2001). This is in part because there are relatively few bird species that disperse seeds and forage on both open and forested areas (Pizo & dos Santos, 2011; Carlo & Morales, 2016). Therefore, developing methods to attract key seed dispersers across distances on deforested tropical landscapes can greatly contribute to reduce dispersal limitation and costs to restoration projects (Viani et al., 2015; Peters et al., 2016).

Studies have also shown that tree species that bear fleshy fruits promote more dispersal than under abiotically-dispersed species (Vieira, Uhl, & Nepstad, 1994; Slocum, 2001), and serve as long-distance dispersal foci in fragmented landscapes (Carlo, García, Martínez, Gleditsch, & Morales, 2013). Bird-dispersed pioneer trees can, in particular, play an important role in attracting seed dispersers to restoration sites, given their fast growth and abundant production of fruits widely consumed by many bird species (Guevara & Laborde, 1993; Guidetti, Amico, Dardanelli, & Rodriguez-Cabal, 2016). One critical knowledge gap to predictably manipulate seed dispersal in restoration projects is that it is unknown how much (i.e., the effect-size) specific traits of among fleshy-fruited pioneer trees matter as attractants for birds and the seeds they disperse. It is also fundamental to understand how the attraction potential of traits is affected by distance from seed source, as distance to forest fragments have been one the major factors considered by restoration decision-making models to predict regeneration potential (Molin, Chazdon, Ferraz, & Brancalion, 2018; Crouzeilles et al., 2019).

We expect that traits of pioneer species – including variation in nutrient reward type among fleshy-fruited species – strongly affect the quantity, richness, and composition of the seed rain given that mutualistic networks of seed dispersal can be structured by the trait-matching (Bascompte & Jordano, 2007; Schleuning, Fründ, & García, 2015; Morán-López et al., 2020). This is important to assess because if the effects are large, then restoration methods that account for specific traits could promote landscape connectivity, accelerate forest regeneration, and increase biodiversity recovery. Alternatively, if the effects are inconsistent or small, then pioneer species can be used more interchangeably with respect to promoting seed rains with restoration project, giving way to managers to focus on other properties.

Trait-mediated seed dispersal by animals is fundamentally different from passive dispersal because morphological features like bill gape are positively correlated with bird body size and influence the sizes of seeds that participate in the initial stages of forest succession (Reid et al., 2015; González-Castro, Yang, & Carlo, 2019). Seed dispersal is also affected by the movement capacity of birds, which is affected by the ratio of body mass to wing size. However, not all trait-matching is morphological. Matching between physiological traits of frugivores and the nutritional chemistry of fruits and pulp further drives the fruit selection in frugivores (Levey & Martínez del Rio, 2001) and can structure frugivory networks by promoting specialized modules (González-Castro, Yang, Nogales, & Carlo, 2015).

Lipids and carbohydrates are important components in fleshy fruits that are negatively correlated in their abundance in fruit pulp of plant species (Herrera, 1987). Their distinct molecular structures require different metabolic pathways for absorption, which may filter distinct sets of frugivorous birds (Levey & Martínez del Rio, 2001). Thus, trait-matching processes inherent to frugivory networks could have a pervasive influence on the assembly of successional forest communities (Schleuning et al., 2015; González-Castro et al., 2019),

especially when the fruit traits of pioneer species modify subsequent seed dispersal patterns. This is a key gap to fill to manage the *de novo* assembly of mutualistic plant-animal communities on cleared lands (Martínez & García, 2017).

Here, we report on a large landscape-level experiment investigating the effects of bird-plant trait-matching and distance from forest fragments on the seed rain dispersed to pastures within a tropical fragmented landscape. We created a full-factorial experiment combining three types of fruit traits of native pioneer trees (wind-dispersed, bird-dispersed lipid-rich, bird-dispersed carbohydrate-rich, and control without tree planting) and three distances from fragments within a cattle ranching landscape of the Brazilian Atlantic Forest, a leading global hotspot for biodiversity conservation (Laurance, 2009) and tropical forest restoration (Brancalion et al., 2019b). We hypothesized that fruit traits would significantly affect the quantity, richness, and composition of both the bird communities active on pastures, and the seed rains they generate across distances from forest fragments.

Materials and methods

Study sites

We conducted the experiment in 12 sites of the Paranapanema municipality in São Paulo, southeastern Brazil (23°23'S, 48°43'W, Fig. 1). The municipality is located at ca. 600 m a.s.l. on the watershed region of the Alto Paranapanema river (Cielo-Filho et al., 2009). Average annual rainfall is 1.407,9 mm and concentrated in the wet summer season (December to March), with a mean annual temperature of 18 °C (Cielo-Filho et al., 2009). Forests cover only about 6% of the Paranapanema landscape (Fundação SOS Mata Atlântica, 2013), which is located within the second most threatened biogeographical region of the Atlantic Forest, with only 7% forest cover remaining (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Our study sites were located on private lands containing cattle pastures and fragments of

primary and secondary semideciduous Atlantic Forests >30 years old, ranging from 12.2 to 98.8 hectares.

Experiment set up

Between December 2016 and November 2018 we conducted a full-factorial experiment using two explanatory variables: *distance* to forest fragment (at three levels: 10, 50, 300 m), and *Fruit traits* of Pioneer trees at four levels: control without tree, *Heliocarpus popayanensis* Kunth with wind-dispersed fruits, *Acnistus arborescens* Schltdl., with bird-dispersed fruits composed of 48.3% of carbohydrates, 7.9% of proteins and 0.04% of lipids, and *Trema micrantha* (L.) Blume, with bird-dispersed fruits composed of 48.8% of lipid, 10.7% of proteins and 2.2% of carbohydrates. Our design yielded a total of 12 experimental plots from each *distance* and *fruit traits* combination, which across the 12 sites totaled 144 experimental plots on active pastures (Fig. 1). *Fruit traits* were assigned randomly within each of the three distance classes and spaced from each other at a distance equal to their respective distances from fragments. Plots measured 4.5 x 4.5 meters and were fenced with barbwire to keep cattle out (Fig. S1). Pioneer trees were grown in a forest nursery until they started to bear fruits, which happened when they were ~1.5 m height. The young trees were then planted at the center of plots, with a base fertilization of 300 g of 15-18-28 (NPK) fertilizer per plant, superficial application of 300 g the same fertilizer every six months, and permanent control of the African fodder grass *Urochloa decumbens* (Stapf) R.D.Webster by mowing.

Bird activity

We recorded bird visits in all experimental plots using a combination of video recording and direct focal observations equally distributed among experimental units. We took 135 hours of focal plot observations. We used 22 video cameras from four different brands (ten Bushnell

Trophy Cam, six Bushnell Trophy Cam HD, six Tigrinus, and six GoPro Hero 3). Camera traps operated 24 h/day for a total of 88,714.7 hours of filming, while the GoPro Hero 3 cameras filmed for about 2 hours before batteries were depleted, totaling 288 hours of filming. To prevent sampling bias associated with camera models, all units were constantly rotated to sample for the same amount of hours each experimental plot across the twelve study sites.

Seed rain

We sampled the seed rain of all plots using one 0.25-m² seed trap lined with a 0.2-mm nylon mesh and located at the center of the enclosure (Fig. S1). The sticky paste Formifuu® was applied to the support posts of traps to exclude ants. A wire screen (2.5 x 2.5 cm mesh) was used to cover traps and prevent vertebrate access. Seed trapped were collected in a monthly basis, counted and identified to the lowest taxonomic level in the laboratory with the aid of a dissecting scope and available reference books and collections for the local flora. Seeds from grasses or from the same experimental plants present in a plot were not included in the analyses.

Seed and bird traits

We classified birds and seeds found in plots by several traits. For birds we used wing-loading as a proxy for the species' movement capacity and the gape width as a proxy to their upper seed size dispersal potential, and the proportion of fruits in the species' diet. Wing-loading was calculated as:

$$WLo = BM/2 \times WL$$

where BM is the bird body mass and WL is wing length. Thus, high loadings are associated with less movement capacity, while low wing-loading mean that the bird can move over long

distances. Bird body data were obtained from Rodrigues et al. (2019) and diet data from Wilman et al. (2014). For plants we classified dispersed seeds based on their dispersal mode: dispersed by birds (bird-dispersed) and dispersed by the wind (wind-dispersed) or by the plant itself. In addition, we classified seeds by seed mass (averaged from our sample) and by the lipid score of their fruits given the importance of these traits for plant-disperser interactions. Values for lipid content of species were in a rank scale (1 - 0 to 10% lipids, 2 - 10 to 20%, 3 - 20 to 30% and 4 - above 30%) adapted from Bello et al. (2017).

Statistical Analyses

To assess the effects of *Fruit traits* and *distances* on the quantity and species richness of visiting birds and seeds we used Generalized Linear Mixed Models (GLMM) for count data (Poisson errors) where tree and distance were fixed effects, and study site was the random effect. The effects of treatments on species' traits (wing-loading, gape width, fruit diet, seed mass, dispersal mode, and lipid score) were analyzed using Generalized Linear Models (Gaussian errors or binomial errors depending on response type). Wing-loading, seed mass and lipid score values were Box-Cox transformed (fpp package; Hyndman, 2013) and the proportion of fruit in diet was re-scaled using scale function in R. We evaluated the significance of each variable by comparing models by likelihood ratio test and choosing the most parsimonious model (Quinn & Keough, 2002).

Non-Metric Multidimensional Scaling (vegan package; Oksanen et al., 2018) with Chao's distance was used to examine the effects of fruit traits and distances on the structure of bird communities and the seed rain. Compositional differences of the bird community and the seed rain as a function of treatments were tested with Permanova (999 randomizations). All analyses were performed in R version 3.5.1 (R Core Team, 2018).

Results

Bird activity and seed rain

Forty-one species of birds visited the experimental plots in a total of 635 visits (Table S1), while 953 seeds arrived in the traps (Table S2). Of these, 92.86% belonged to 115 species and at least 47 families of bird-dispersed plants and 7.14% belonged to 27 species and at least eight families of plants dispersed by wind or gravity. There was a strong correlation between the number of visits and the richness of bird species that visited the plots ($r^2 = 0.99$, n = 144, $p < 0.001$). Similarly, we also found a positive correlation between the amount and the species richness of dispersed seeds ($r^2 = 0.99$, n = 144, $p < 0.001$). We also found positive correlations between bird richness and the number of dispersed seeds ($r^2 = 0.719$, $p < 0.001$) and dispersed seed richness ($r^2 = 0.714$, $p < 0.001$).

Fruit traits and distance to forest affected bird activity and seed rain in experimental plots. The plots with bird-dispersed fruits (*Acnistus* and *Trema*) received higher quantity and richness of birds and seeds than plots with wind-dispersed fruits (*Heliocarpus*) and control plot (Fig. 2, Table S3). However, the bird-dispersed species also affected the amount and richness of the visiting bird and seed rain. Plots with carbohydrate-rich fruits (*Acnistus*) received on average 3.6 times more bird visits and 2.3 times more seeds than plots with lipid-rich fruits (*Trema*), regardless of distance. As expected, the amount and richness of bird visits and seeds in the experimental plots decreased with distance to forest, but remarkably the effects of trait-matching on bird activity and seed rain were stronger than the effects of distance to forest fragments (Fig. 2, Table S3). For instance, plots with carbohydrate-rich bird-dispersed fruits 300 m from forest received on average 2.7 times more visits and 2.7 times more richness of visiting than plots with wind-dispersed fruits (*Heliocarpus*) and control plot 10 m from the forest. Likewise, plots with *pioneer trees* (*Acnistus, Trema* and

Heliocarpus) 300 m to forest received a greater abundance and richness of seeds than traps located in control plots at 10 m to forest (Fig. 2).

Bird and seed communities

Examining the composition of visiting bird communities and seed species, we found markedly greater effects of trait-matching from fruit traits than effects of distance to forest fragments (Tables 1, S1-S2). The bests NMDS solutions were bidimensional with final stress of 0.13 for bird community (Fig. 3) and 0.11 for seed rain composition (Fig. S2). Bird communities were differentiated along axis one, with plots with lipid-rich *Trema* fruits (negative scores on Axis One, Fig. 3) being nearly completely separated from plots with carbohydrate-rich *Acnistus* fruits (positive scores on Axis One, Fig. 3). Treatments with wind-dispersed fruits and controls received sporadic visits and the composition of the visiting species seems to be less consistent. In the ordination graphic, it is clear the largest size of the 95% confidence ellipses of these two groups, compared to the groups with bird-dispersed trees (*Acnistus* and *Trema*) (Fig. 3). Predominantly frugivorous species (e.g. tanager species) were more associated with plots with *Trema* and more generalist or more insectivorous species (e.g. tyrant flycatchers) were more associated with plots with *Acnistus* (Fig. 3). Axis one of ordination was positively correlated with the proportion of invertebrates in visiting bird diets ($r^2 = 0.378$, $p = 0.018$), and negatively correlated with proportion of fruits ($r^2 = -0.347$, $p = 0.030$) and seeds ($r^2 = 0.320$, $p = 0.047$) in the diets of bird visitors.

The composition of the seed rain showed less differentiation along the NMDs ordination axes compared to the bird community (Table 1). Even so, trait-matching seems to influence seed arrival in association with the fruit traits. The composition of the species that arrived in the plots with bird-dispersed fruits was more consistent when compared to the other treatments. In the ordination graph (Fig. S2), we observed a smaller variation in relation to

plots with wind-dispersed and control. The axis two of ordination was positively correlated with the seed mass ($r^2 = 0.202$, $p = 0.038$), however, there was no difference in seed mass between treatments or between distances (Fig. 4, Table S4).

Effects on Traits

We found that fruit traits influenced the traits of visiting birds while distance to forest fragments had no effect (Tables S4-S5). Birds that visited plots with *Trema* were more morphologically distinct than birds that visited the other treatments. For instance, wing-loading did not differ among plots with *Heliocarpus*, *Acnistus* and Control plots, but was on average 1.2 times larger for birds visiting plots with *Trema* (Fig. 4, Table S5). Similarly, the proportion of fruits in diets of visiting birds did not differ among Control, *Heliocarpus*, and *Acnistus* plots, but was on average 1.3 times higher in plots with *Trema* (Fig. 4, Table S5). In addition, the proportion of fruits in the diet of visiting birds decreased with the distance from forest in all fruit traits treatments, making predominately insectivorous species clearly dominant as long-distance dispersers (Fig. 4). The bill gape of birds also decreased with distance from forest in Control, *Heliocarpus*, and *Acnistus* plots, but not in plots with *Trema*, which in turn increased with distance (Fig. 4, Table S5).

Fruit traits had an effect on traits of arriving seeds, especially those arriving at plots with bird-dispersed fruits. For instance, the proportion of bird-dispersed seeds did not differ between control and *Heliocarpus* plots, but was on average 1.3 and 1.4 times higher in plots with *Acnistus* and *Trema* (Fig. 4, Table S5). The average pulp-lipid score of plant species arriving to control plots was much lower than plant species arriving at plots with pioneer trees, being highest for plots with *Trema* (Fig. 4, Table S5). Plots with *Trema* (lipid-rich fruit) received a higher proportion of bird-dispersed our seeds than all other treatments (Fig. 4).

Most (90.45%) of the seeds dispersed by birds into our plots were small (< 1.0 g) and there was no effect of fruit traits or distance on seed sizes (Fig. 4, Table S5).

Discussion

The results of this large-scale experiment show that fruiting traits of pioneer trees can strongly affect the quantity, richness and composition of bird communities active on fragmented landscapes, and the seed rains they generate. As expected, the net distance to forest fragments negatively affected the quantity and richness of birds and seeds, but remarkably, the structuring effects of the treatments were little affected by distance. Responses to treatments remained differentiated across distances, with one of the tree treatments (*Acnistus*) more than doubling the seed rain responses when compared to the other treatments (Figs. 2-3). These findings have important implications for tropical forest restoration by suggesting that connectivity between restoration areas and forest fragments, and types of species assemblages, can be manipulated by the selective planting of pioneer tree species with certain traits. The factorial design, large-scale, and replication of this experiment provide a unique lens that revealed the consistency of trait-mediated effects of pioneer tree species, and possibly other plants, on dispersal agents they attract.

The structuring of the seed rain that resulted from the response of bird communities to pioneer tree traits can be useful to improve restoration practices based on nucleation principles (Corbin & Holl, 2012). Pioneers can be selected and strategically planted to reduce chronic limitations in seed dispersal, especially at long distances from forest fragments, and promote the passive regeneration and connectivity of fragmented tropical landscapes. We found an enormous difference between wind-dispersed and bird-dispersed pioneers in the species richness and density of bird activity and seed rain. Although previous authors and studies have documented such types of microhabitat-level differences in seed rain or

recruitment patterns (e.g., Slocum, 2001; Carlo et al., 2013), our study is the first to use a controlled experimental approach and thus provides new insights on the magnitude and consistency of such effects, including how effects decay with distance. For instance, plots with bird-dispersed pioneers (*Acnistus* and *Trema*) amounted to a staggering 92.9% of recorded bird visits, and 88.5% of dispersed seeds. Plots with the wind-dispersed *Heliocarpus* received more bird visits and eight times as many seeds than treeless control plots, which were, however, much lower than plots with fleshy-fruited pioneers. Results like this sum to the mounting evidence that seed dispersal patterns on landscapes are highly structured and directional towards resource-bearing fruiting trees (e.g., Carlo et al., 2013; Viani et al., 2015) that can be used as long-distance attractors for ecological restoration.

The large difference between the two bird-dispersed trees in their effects on the seed rain and bird activity was surprising as we expected these trees to have rather similar effects (Fig. 2). Overall the carbohydrate-rich fruits of *Acnistus* attracted more than twice the activity and seed rain than the lipid-rich fruits of *Trema*. Differences were large even over short distances from forest fragments, and *Acnistus* plots 50 m from fragments received more bird visits and seeds than *Trema* plots located just 10 m away from forest (Fig. 2). Still, when considering the traits of visiting birds and dispersed seeds, plots with *Trema* were the most distinct among all treatments (Figs. 2-4, S2). Thus, these results suggest that differences in fruiting plant traits have the potential to increase the fine-scale spatial heterogeneity of frugivore activity and the resulting spatial patterns of seed deposition (Schupp, Milleron, & Russo, 2002).

Our experiment illustrates how bird activity and seed dispersal decay with distance from forest fragments, but at far lower rates than reported by studies measuring seed arrival only on open microhabitats. For instance, in their classic work, Cubiña and Aide (2001) reported 97% of the captured seeds occurring at distances shorter than 4 m from the forest

edge, but they did not sample under perching structures that attract avian vectors. In contrast in our study, plots at 10 m received more than 60% of captured seeds while another 36% arrived at plots at 50 m. Only 3% of seeds (about 30 seeds in total) reached traps at 300 m from forest, but these seeds could have originated at even more distant sources. Moreover, plots with trees at 300 m received higher seed rain than control plots at 10 m distance from forest, especially plots with *Acnistus* (Fig. 2). The activity of birds also decreased with distance to forest (Fig. 2), and activity of common and heavily frugivorous species such as *Turdus*, *Tangara*, and *Euphonia* was basically restricted to the shortest distance classes (Fig. 3). Conversely, the primarily insectivorous tyrant flycatchers (Tyrannidae) were active throughout the entire range of distances and thus became proportionally more important at larger distances where more heavily frugivorous species were missing (Figs. 3, S2).

Curiously, tyrant flycatchers are often rated low in their frequency of fruit consumption and assumed to interact with few plant species as compared to more frugivorous species (Moermond & Denslow, 1985). Nonetheless, previous studies have shown the important role of some insectivorous bird species in seed dispersal on deforested Neotropical landscapes (Pizo & dos Santos, 2011; Carlo & Morales, 2016; González-Castro et al., 2019). In fact, our data shows that the most frequent visitors were the insectivorous generalists *Pitangus sulphuratus* and *Tyrannus melancholicus*, which together represented 42.7% of all bird visits to experimental plots. Species in these two iconic bird genera have been shown to be important seed dispersers in pastures and fragmented landscapes throughout the Neotropics (Pizo & dos Santos, 2011; Athiê & Dias, 2016; Carlo & Morales, 2016). We found tyrant flycatchers to be characteristically associated to plots with *Acnistus*, while plots with *Trema* were characterized by tanager (Thraupidae) visits (Fig. 3). The lack of tanager activity far from forest edge in this study helps explain the weaker role of *Trema* as an attractor of seeds at longer distances when compared to *Acnistus* (Figs. 2-3).

Pioneer tree traits significantly filtered the traits of visiting birds and the types of seeds they dispersed (Fig. 4, Table S5). On average, birds visiting plots with lipid-rich *Trema* had a higher wing-loading, more heavily frugivorous diets, and smaller bill gapes when compared to bird assemblages visiting the other treatments. Such differences can be expected to lead to differences in seed mobility (i.e., due to wing-load differences) and the sizes of seeds (i.e., due to bill-gape differences), which ultimately will generate different seed rains in association with each tree type. The predominance of small seeds in the seed rain can be in part a reflection of the lack of large frugivores in highly fragmented landscapes (Holl, 1999; Emer et al., 2018).

The identity of pioneer trees also affected other traits of plants dispersed into plots, such as the relative frequency of seed dispersal mode and the fruit lipid content (Fig. 4). Other studies have reported higher frequencies of bird-dispersed species under isolated trees as compared to open areas (Galindo-González, Guevara, & Sosa, 2000), between frugivore-dispersed and wind-dispersed trees in open areas (Slocum 2001) and in restoration plantations (Viani et al., 2015). However, no previous study has reported these types of differences between tree species of the same dispersal mode. Similarly, plots with *Trema* received seeds from plants that produce fruit pulp with a higher lipid content (Fig. 4). This pattern may be generated by the consistent fruit preferences of birds attracted to the lipid-rich *Trema* fruits.

In conclusion, our experiment shows that trait-matching shapes both frugivore and plant actors participating in the seed dispersal processes that take place on fragmented landscapes. The consistent qualitative and quantitative differences in the communities of birds and seeds that gravitated towards species of pioneer trees show the important and subtle role that mutualistic seed-dispersal interactions play in the early stages of tropical forest succession. From an ecological restoration perspective, our findings illustrate how the traits of pioneer trees can be used to reduce dispersal limitation and increase connectivity and diversity

transference from remnant forest fragments to the surrounding deforested areas across distances. The selective planting of long-distance attractors can be used to trigger the establishment of diverse and heterogeneous forest nuclei in short time periods (e.g., 1-2 years, Carlo & Morales, 2016; González-Castro et al., 2019). It remains to be investigated if, considering the characteristic properties that frugivory and seed dispersal processes can impart to successional communities, and the filtering effects of the trait-matching processes we found can lead to alternative successional pathways and community assembly processes in ways that models still do not fully account (Maggi, Bertocci, Vaselli, & Benedetti-Cecchi, 2011; Kraft et al., 2015).

Authors' contributions

PHSAC, MAP and TAC conceived the ideas; PHSAC, MAP, TAC and PHB designed the methods; MAP and PHB provided funding; PHSAC collected the data; PHSAC and TAC analyzed the data and wrote the first draft; all authors contributed to the writing and gave final approval for publication.

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Figure captions

Fig. 1. Study area located in the municipality of Paranapanema-SP, Brazil. In detail, the 12 study sites with experimental plots with pioneer tree species (*Acnitus arborescens*, *Heliocarpus popayanensis*, *Trema micrantha*) and control at three distances to forest fragments (10, 50 and 300 m).

Fig. 2. More birds visited experimental plots with bird-dispersed pioneer tree species located at three distances from forest fragments than plots with wind-dispersed pioneer trees (*Heliocarpus popayanensis*) and control plots with no trees (A-B). The seed rain (C-D) followed a similar pattern. Note that the carbohydrate-rich fruits of *Acnistus arborescens* attracted more than twice the activity and seed rain of the lipid-rich *Trema micrantha*, showing that plant species traits have a strong effect on seed dispersal patterns on deforested areas.

Fig. 3. Ordination (NMDS) for bird species by family (A), and frequency plots for bird families pooled across tree treatments (B) and distances (C). Dotted ellipses (A) are 95% C.I. for treatment centroids. Arrows represent mean family scores (Amplified 6X for visualization purpose).

Fig. 4. Traits of seeds (A-C) and visiting birds (D-F) in the experimental plots with pioneer tree treatments at three distances from forest fragments. Note that the traits of the seeds that arrived in the plots with bird-dispersed fruits pioneers (*Acnistus* and *Trema*) were differed from the traits of seeds that arrived in the other plots. In turn, the traits of birds that visited the

pioneer tree plots with lipid-rich bird-dispersed fruits (*Trema*) were differed from the traits of the birds that visited the other treatments.

Table 1. Permutational multivariate analysis of variance of composition of frugivorous birds and seeds in plots with pioneer tree treatments (*Acnistus, Trema, Heliocarpus*) and Control established at 10, 50, and 300 m from forest.

	SSQ	**Df**	**MS**	**F**	**R^2**	***P***
Frugivores						
Treatment	7.201	3	2.400	9.694	0.217	**0.001**
Distance	1.461	1	1.461	5.898	0.044	**0.001**
Treatment x distance	2.199	3	0.733	2.961	0.066	**0.001**
Residuals	22.286	90	0.248	0.672		
TSS	33.148	97				
Seeds						
Treatment	2.371	3	0.79034	1.98358	0.08072	**0.001**
Distance	0.799	1	0.7991	2.00556	0.0272	**0.002**
Treatment x distance	0.703	2	0.35166	0.88257	0.02394	0.745
Residuals	25.500	64	0.39844	0.86813		
TSS	29.374	70				

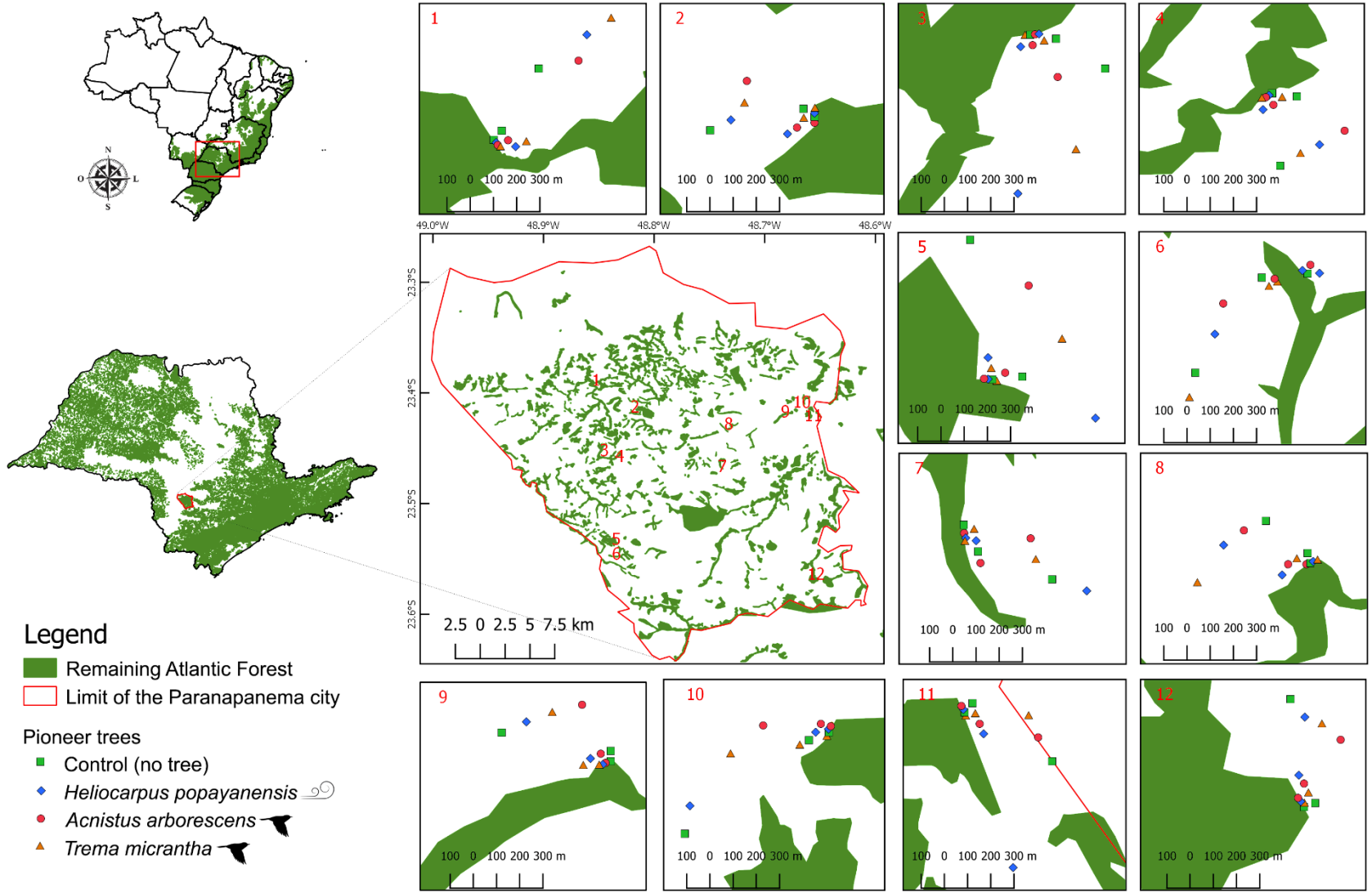

Legend
Remaining Atlantic Forest
Limit of the Paranapanema city
Pioneer trees
Control (no tree)
Heliocarpus popayanensis
Acnistus arborescens
Trema micrantha
2.5 0 2.5 5 7.5 km
49.0°W
48.9°W
48.8°W
48.7°W
48.6°W
23.3°S
23.4°S
23.5°S
23.6°S
100 0 100 200 300 m

Fig. 1

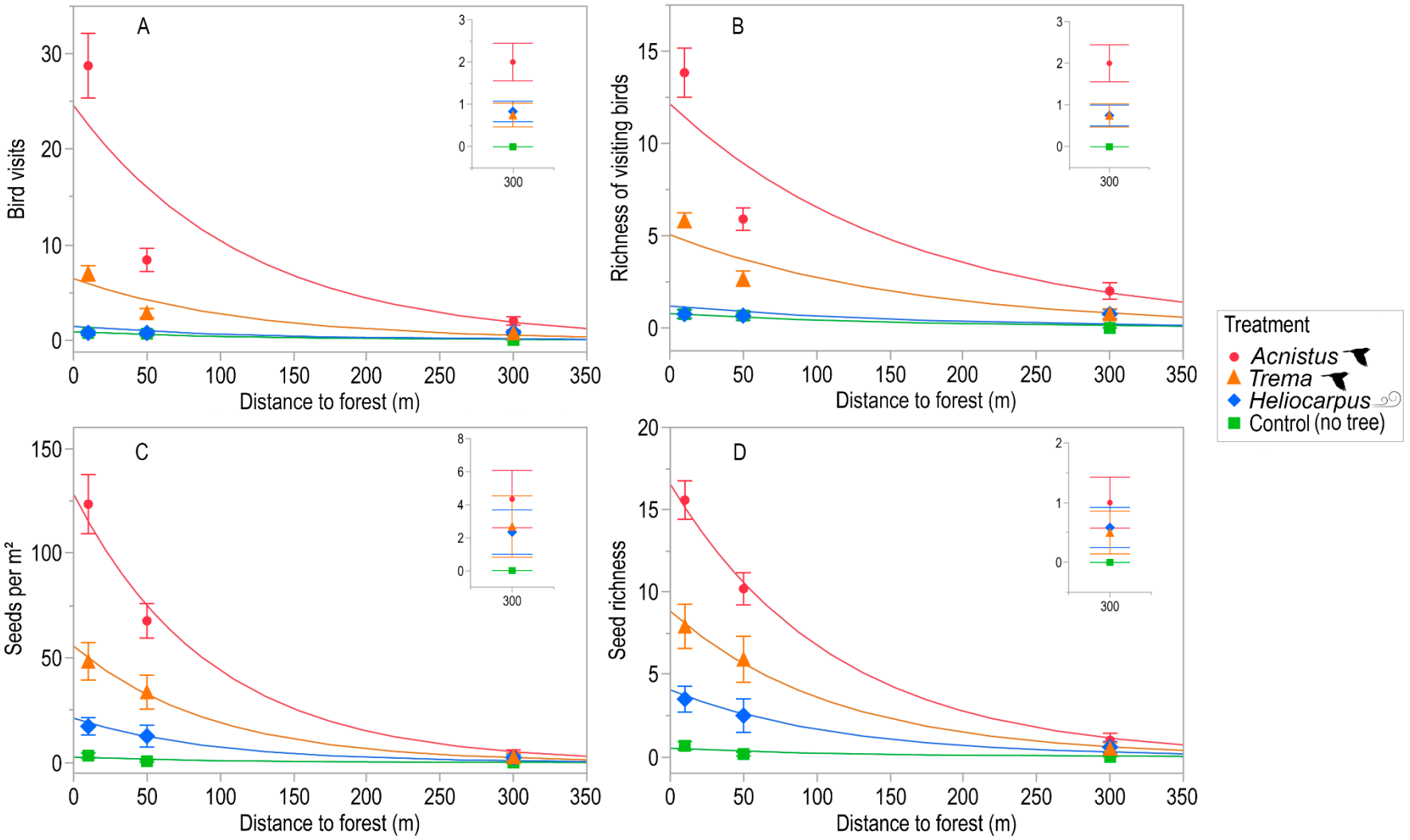

A
Bird visits
Distance to forest (m)
B
Richness of visiting birds
Distance to forest (m)
C
Seeds per m²
Distance to forest (m)
D
Seed richness
Distance to forest (m)
Treatment
Acnistus
Trema
Heliocarpus
Control (no tree)

Fig. 2

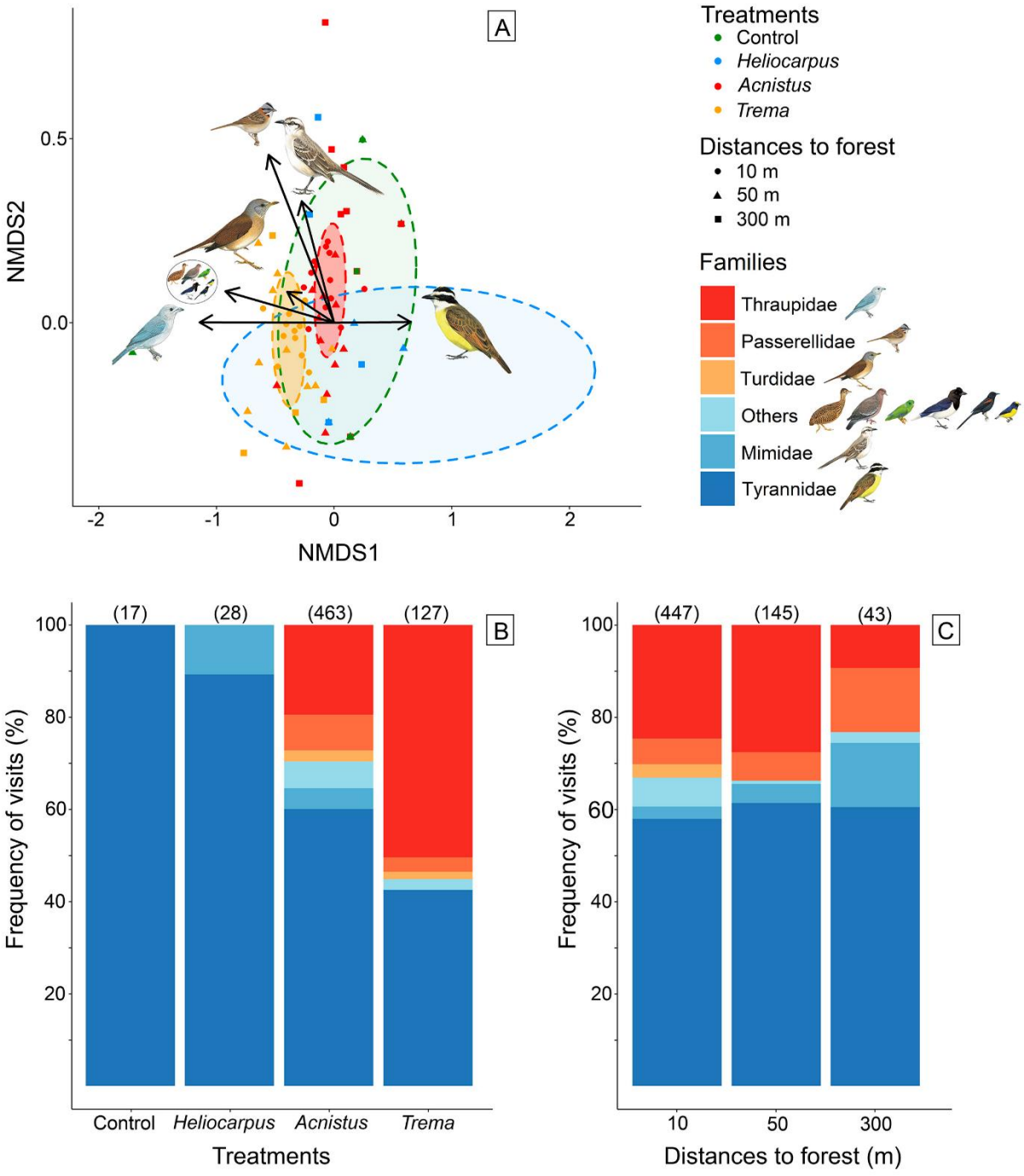

A
Treatments
Control
Heliocarpus
Acnistus
Trema
Distances to forest
10 m
50 m
300 m
Families
Thraupidae
Passerellidae
Turdidae
Others
Mimidae
Tyrannidae
NMDS2
NMDS1
0.5
0.0
-2
-1
0
1
2
B
(17)
(28)
(463)
(127)
Frequency of visits (%)
100
80
60
40
20
Control
Heliocarpus
Acnistus
Trema
Treatments
C
(447)
(145)
(43)
10
50
300
Distances to forest (m)

Fig. 3

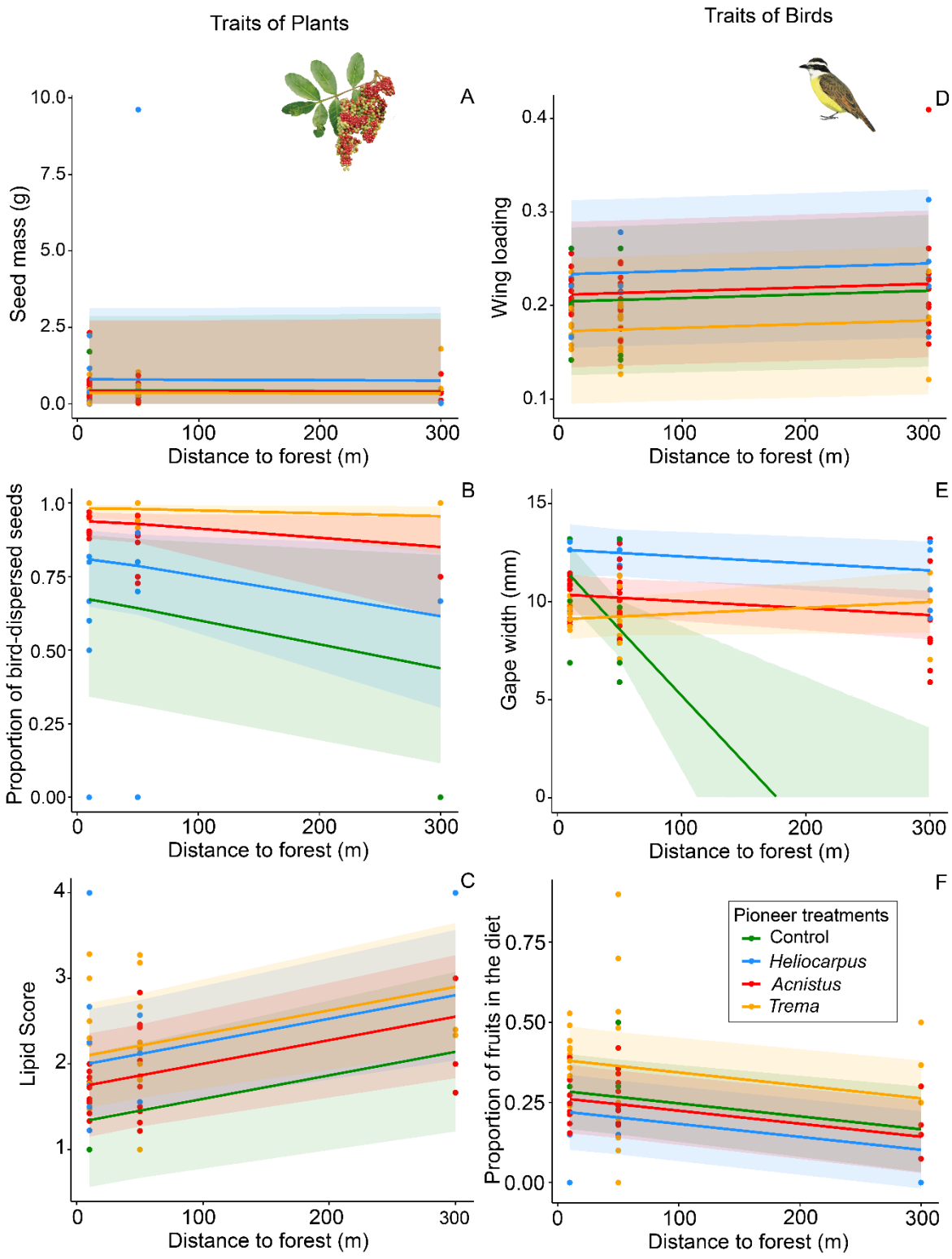

Traits of Plants
Traits of Birds
A
B
C
D
E
F
Seed mass (g)
Proportion of bird-dispersed seeds
Lipid Score
Wing loading
Gape width (mm)
Proportion of fruits in the diet
Distance to forest (m)
Pioneer treatments
Control
Heliocarpus
Acnistus
Trema

Fig. 4

Supplementary material

Table S1. Summary characteristics of the pioneer trees species experimentally planted in pastures within a tropical fragmented landscape in southeastern Brazil.

Characteristic	*Acnistus arborescens*	*Trema micrantha*	*Heliocarpus popayanensis*
Family	Solanaceae	Cannabaceae	Malvaceae
Growth form	shrub-tree	tree	tree
Initial crown radius (m)*	0.63 ± 0.17	0.52 ± 0.21	0.51 ± 0.21
Final crown radius (m)**	0.95 ± 0.21	0.82 ± 0.19	0.85 ± 0.19
Initial height (m)*	1.61 ± 0.37	1.56 ± 0.37	1.53 ± 0.46
Final height (m)**	2.42 ± 0.53	2.37 ± 0.51	2.52 ± 0.47
Fruit type	berry	drupe	indehiscent capsule
Fruit morphology	fleshy pulp	fleshy pulp	stiff hairs
Dispersal mode	bird-dispersed	bird-dispersed	wind-dispersed
Seeds per fruit	50	1	1
Fruit color (display)	orange	red	brown
Fruit length (cm)	0.9	0.3	2.5
Seed length (cm)	0.15	0.2	0.6
Fruit mass (g)	0.5	0.01	0.008
Seed mass (g)	0.0003	0.004	0.005
Main fruiting period	Sep-Jan	Jan-Jun	Aug-Nov
Fruit crop size†	4853 ± 5447	3460 ± 4685	-
Chemistry composition of the fleshy part of the diaspore (% dry mass)			
Lipids	0.04	48.8	-
Carbohydrates	48.3	2.2	-
Proteins	7.9	10.7	-

*Data collected up to the first six months from experiment setup, between December 2016 and May 2017 (n=36 for each plant species).
**Data collected in the last six months of the experiment, between June and November 2018 (n=36 for each plant species).
†Data collected only for a subset of plants after the end of the experiments, between December 2019 and January 2020 (n=12 for each plant species). Mann-Whitney' test: $U = 49$, $p = 0.1978$.

Table S2. Results from the factorial analysis of variance of the initial and final crown radius sizes and height of the pioneer trees species experimentally planted in pastures within a tropical fragmented landscape in southeastern Brazil. The analysis considered each site as a block. The independent variables were distance to forest (10, 50 and 300 m) and plant species (Acnistus, Trema and Heliocarpus). The data was log-transformed. The significant differences are in bold (P <0.05).

	SS	**MS**	**df**	**F**	**p**
Initial crown radius					
Site	0.854	0.854	1	6.981	**0.010**
Distance	0.709	0.355	2	2.900	0.060
Plant	1.369	0.684	2	5.595	**0.005**
Distance x Plant	0.201	0.050	4	0.410	0.801
Residuals	11.987	0.122	98		
Final crown radius					
Site	0.516	0.516	1	9.5707	**0.003**
Distance	0.166	0.083	2	1.540	0.220
Plant	0.458	0.229	2	4.247	**0.017**
Distance x Plant	0.126	0.032	4	0.586	0.674
Residuals	5.282	0.054	98		
Initial height					
Site	0.038	0.038	1	0.716	0.400
Distance	0.113	0.056	2	1.051	0.354
Plant	0.070	0.035	2	0.647	0.526
Distance x Plant	0.165	0.066	4	1.232	0.302
Residuals	5.268	0.054	98		
Final height					
Site	0.028	0.028	1	0.650	0.422
Distance	0.110	0.055	2	1.273	0.285
Plant	0.090	0.451	2	1.039	0.358
Distance x Plant	0.106	0.026	4	0.610	0.657

Residuals	4.255	0.043	98		

Table S3. Birds recorded in the experimental plots with pioneer tree treatments at three distances from forest fragments (separate file).

Table S4. Seeds recorded in the experimental plots with pioneer tree treatments at three distances from forest fragments (separate file).

*Podem ser obtidas na versão online do artigo:
Camargo, P.H.S.A, Pizo, M.A., Brancalion, P.H.S., Carlo, T.A. (2020) Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: implications for restoration. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.13697

Table S5. Summary of parameters of generalized linear mixed models fitting responses (bird visits, visit richness, seed per m², and seed richness) as a function of pioneer tree treatments (*Acnistus*, *Trema*, *Heliocarpus*) and Control established at 10 m, 50 m e 300 m from the forest.

	B	**SE**	**z**	**p**
Bird visits				
Treatment *Acnistus*	1.904	0.130	14.675	< **0.001**
Treatment Control	-3.515	0.638	-5.507	< **0.001**
Treatment *Heliocarpus*	-2.2038	0.211	-10.429	< **0.001**
Treatment *Trema*	-1.079	0.169	-6.366	< **0.001**
Treatment *Acnistus* x distance	-1.372	0.124	-11.108	< **0.001**
Treatment Control x distance	-0.303	0.833	-0.364	0.716
Treatment *Heliocarpus* x distance	1.421	0.224	6.360	< **0.001**
Treatment *Trema* x distance	0.333	0.216	1.538	0.124
Visit richness				
Treatment *Acnistus*	1.659	0.100	16.537	< **0.001**
Treatment Control	-3.236	0.638	-5.072	< **0.001**
Treatment *Heliocarpus*	-1.999	0.214	-9.321	< **0.001**
Treatment *Trema*	-0.870	0.164	-5.313	< **0.001**
Treatment *Acnistus* x distance	-0.870	0.109	-8.002	< **0.001**
Treatment Control x distance	-0.805	0.832	-0.968	0.333
Treatment *Heliocarpus* x distance	0.891	0.223	3.988	< **0.001**
Treatment *Trema* x distance	-0.061	0.205	-0.297	0.766
Seed per m²				
Treatment *Acnistus*	3.421	0.081	41.855	< **0.001**
Treatment Control	-6.671	1.010	-6.602	< **0.001**
Treatment *Heliocarpus*	-1.371	0.088	-15.706	< **0.001**
Treatment *Trema*	-0.646	0.077	-8.358	< **0.001**
Treatment *Acnistus* x distance	-1.555	0.064	-24.310	< **0.001**
Treatment Control x distance	-3.628	1.246	-2.911	**0.004**
Treatment *Heliocarpus* x distance	0.663	0.110	6.007	< **0.001**

Treatment *Trema* x distance	0.279	0.100	2.787	**0.005**
Seed richness				
Treatment *Acnistus*	1.677	0.110	15.243	**< 0.001**
Treatment Control	-5.908	2.031	-2.909	**0.004**
Treatment *Heliocarpus*	-1.149	0.181	-6.347	**< 0.001**
Treatment *Trema*	-0.616	0.171	-3.607	**< 0.001**
Treatment *Acnistus* x distance	-1.227	0.131	-9.363	**< 0.001**
Treatment Control x distance	-3.240	2.533	-1.279	0.201
Treatment *Heliocarpus* x distance	0.43179	0.226	1.911	0.056
Treatment *Trema* x distance	0.021	0.220	0.096	0.924

Table S6. Model selection by likelihood ratio test fitting responses of traits of birds and seeds (bird wing loading, bird gape width, proportion of fruits in diet, seed mass, proportion of bird-dispersed seeds, lipid score) as a function of pioneer tree treatments (*Acnistus*, *Trema*, *Heliocarpus*) and Control established at 10 m, 50 m e 300 m from the forest. The best model to explain each trait is underlined.

Variable under test	**χ^2**	**df**	**p**
Bird wing loading			
Treatment + distance + treatment x distance	35.913	7	< 0.001
Treatment + distance	5.201	1	0.158
Treatment	1.310	1	0.252
Distance	27.691	3	< 0.001
Bird gape width			
Treatment + distance + treatment x distance	38.723	7	< 0.001
Treatment + distance	12.25	3	0.007
Proportion of fruits in diet			
Treatment + distance + treatment x distance	31.042	7	< 0.001
Treatment + distance	0.646	3	0.886
Treatment	10.306	1	0.001
Distance	18.058	3	< 0.001
Seed mass			
Treatment + distance + treatment x distance	3.699	7	0.814
Proportion of bird-dispersed seeds			
Treatment + distance + treatment x distance	44.395	7	< 0.001
Treatment + distance	2.296	3	0.513
Treatment	2.218	1	0.136
Distance	39.624	3	< 0.001
Lipid Score in fruits			
Treatment + distance + treatment x distance	20.092	7	0.005
Treatment + distance	2.583	3	0.460
Treatment	9.753	1	0.002

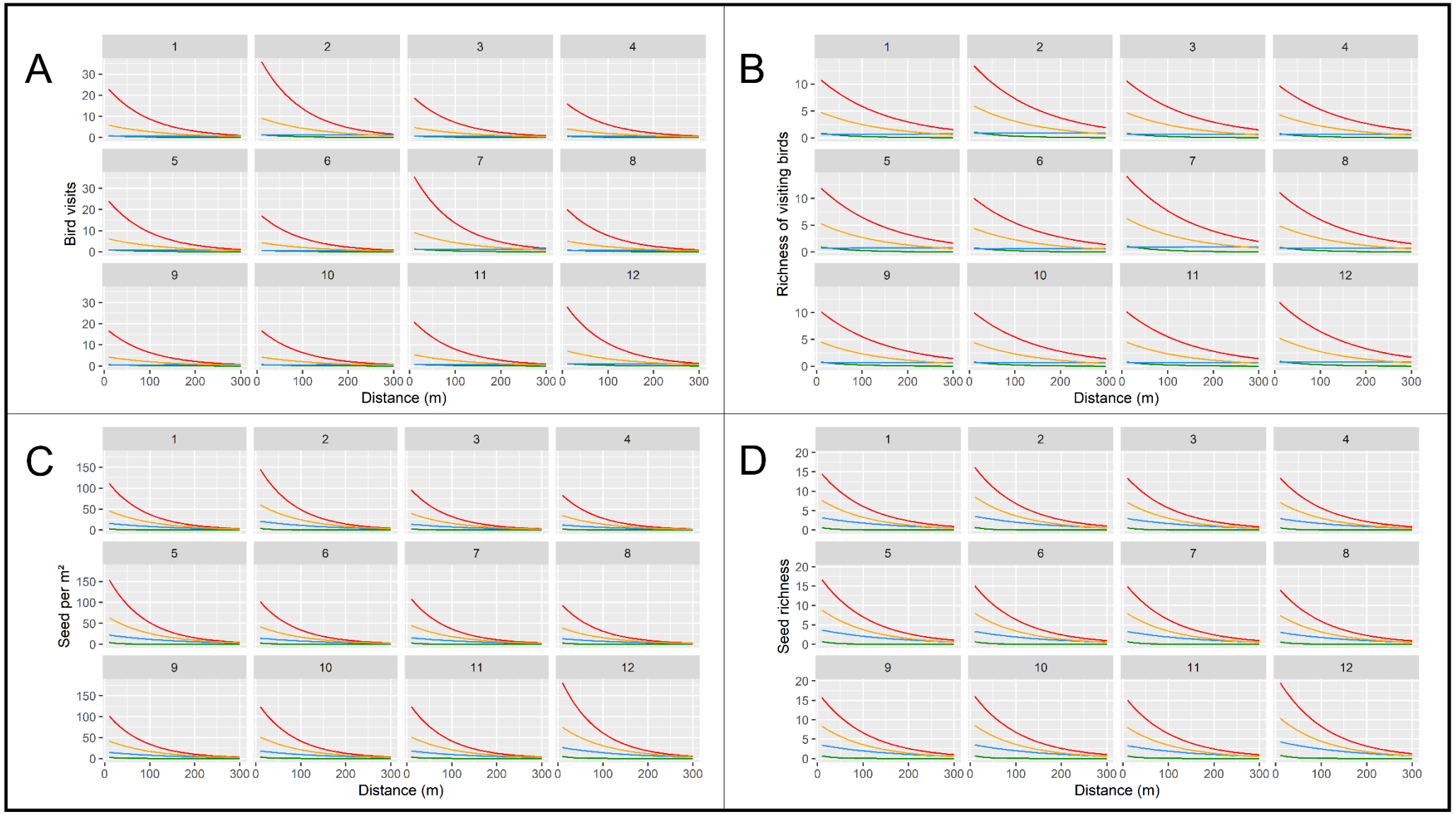
Distance	8.188	3	0.042

Table S7. Summary of parameters based on model selection of generalized linear models fitting responses of bird and seed traits (bird wing loading, bird gape width, proportion of fruits in diet, proportion of bird-dispersed seeds, lipid score) as a function of pioneer tree treatments (*Acnistus*, *Trema*, *Heliocarpus*) and Control established at 10 m, 50 m e 300 m from the forest. Control treatment was fixed as the intercept. *For the proportion of bird-dispersed seeds, as it has a binomial distribution, the coefficient is based on the z-statistic.

	β	**SE**	**t***	**P**
Bird wing loading				
Intercept	-1.615	0.047	-34.507	< **0.0001**
Treatment *Heliocarpus*	0.170	0.063	2.688	**0.0085**
Treatment *Acnistus*	0.067	0.056	1.203	0.2318
Treatment *Trema*	-0.135	0.057	-2.348	**0.0210**
Bird gape width				
Intercept	12.058	0.864	13.950	< **0.0001**
Treatment *Heliocarpus*	0.616	1.047	0.589	0.5574
Treatment *Acnistus*	-1.673	0.950	-1.762	0.0817
Treatment *Trema*	-2.959	0.951	-3.113	**0.0025**
Distance	-0.070	0.023	-2.989	**0.0036**
Treatment *Heliocarpus* x Distance	0.066	0.023	2.808	**0.0062**
Treatment *Acnistus* x Distance	0.066	0.023	2.822	**0.0059**
Treatment *Trema* x Distance	0.072	0.023	3.095	**0.0027**
Proportion of fruits in diet				
Intercept	0.288	0.038	7.570	**<0.0001**
Treatment *Heliocarpus*	-0.064	0.050	-1.293	0.1996
Treatment *Acnistus*	-0.023	0.043	-0.528	0.5988
Treatment *Trema*	0.096	0.044	2.205	**0.0302**
Distance	-0.001	0.000	2.257	**0.0016**
Proportion of bird-dispersed seeds				
Intercept	0.691	0.626	1.10	0.2692
Treatment *Heliocarpus*	0.623	0.672	0.93	0.3535

Treatment *Acnistus*	1.968	0.645	3.05	**0.0023**
Treatment *Trema*	3.245	0.771	4.21	< **0.0001**
Lipid score				
Intercept	1.316	0.293	4.485	< **0.0001**
Treatment *Heliocarpus*	0.663	0.324	2.044	**0.0453**
Treatment *Acnistus*	0.411	0.310	1.327	0.1895
Treatment *Trema*	0.759	0.313	2.426	**0.0183**
Distance	0.003	0.001	3.151	**0.0025**

Fig. S1. Setup of pioneer tree treatments in experimental plots (A) showing an bird-dispersed tree with carbohydrate-rich fruits, *Acnistus arborescens* (B); an bird-dispersed tree with lipid-rich fruits, *Trema micrantha* (C); an wind-dispersed tree, *Heliocarpus popayanensis* (D) and Control treatment without tree (E). In the center of each experimental plot, we place one 0.25 m² seed trap lined with a 0.2 mm nylon mesh (F). Formifuu® was applied to the support posts of traps exclude ant. A wire screen (2.5 x 2.5 cm mesh) was used to cover traps and prevent vertebrate access.


A
B
C
D
1
2
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6
7
8
9
10
11
12
Bird visits
Richness of visiting birds
Seed per m²
Seed richness
Distance (m)
0
100
200
300
Pioneer treatments
Control
Heliocarpus
Acnistus
Trema

Fig. S2. Effects of Pioneer treatment and distance on bird visits (A), richness of visiting birds (B), seed per m^2 (C) and seed richness (D), conditioned to each study site (random effects).

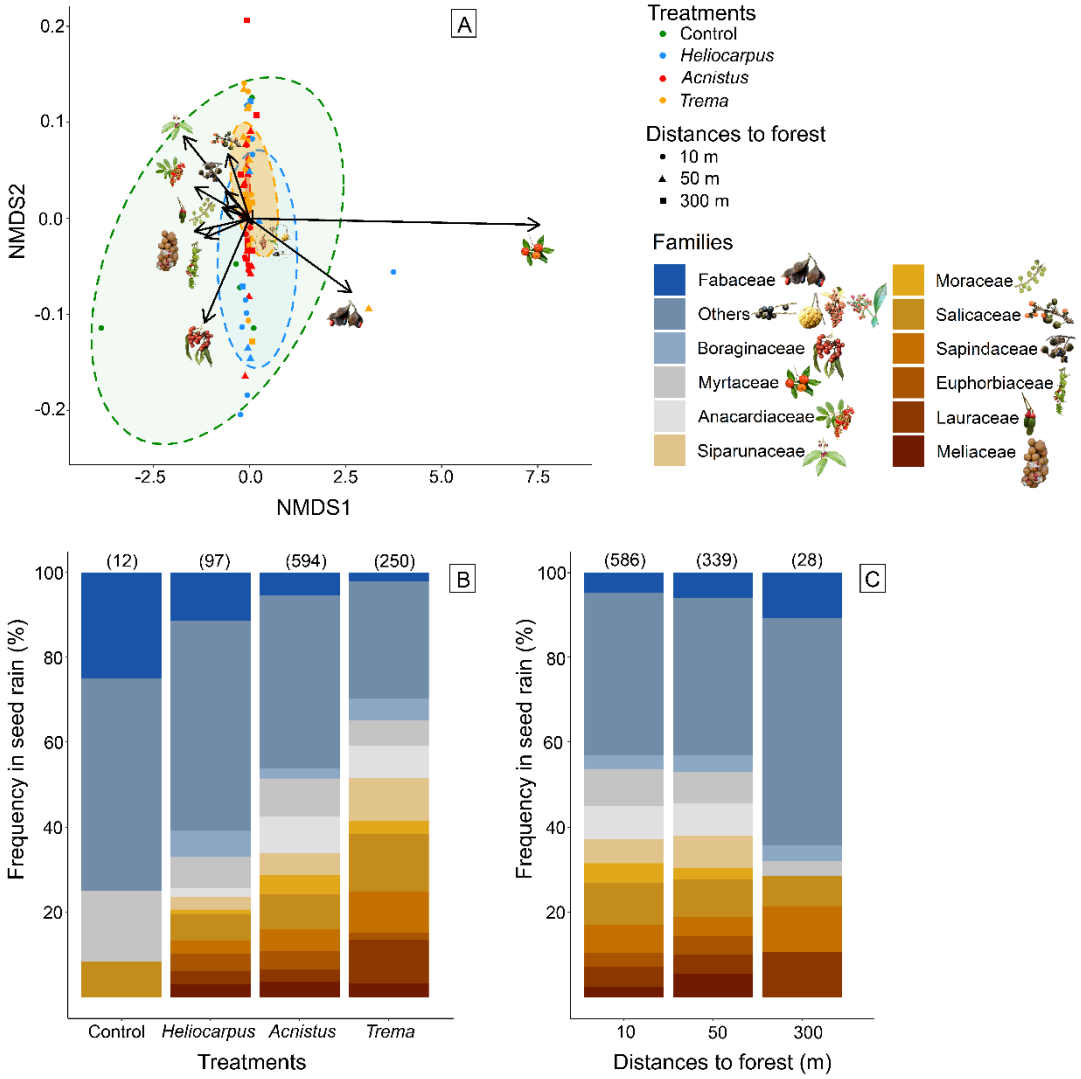
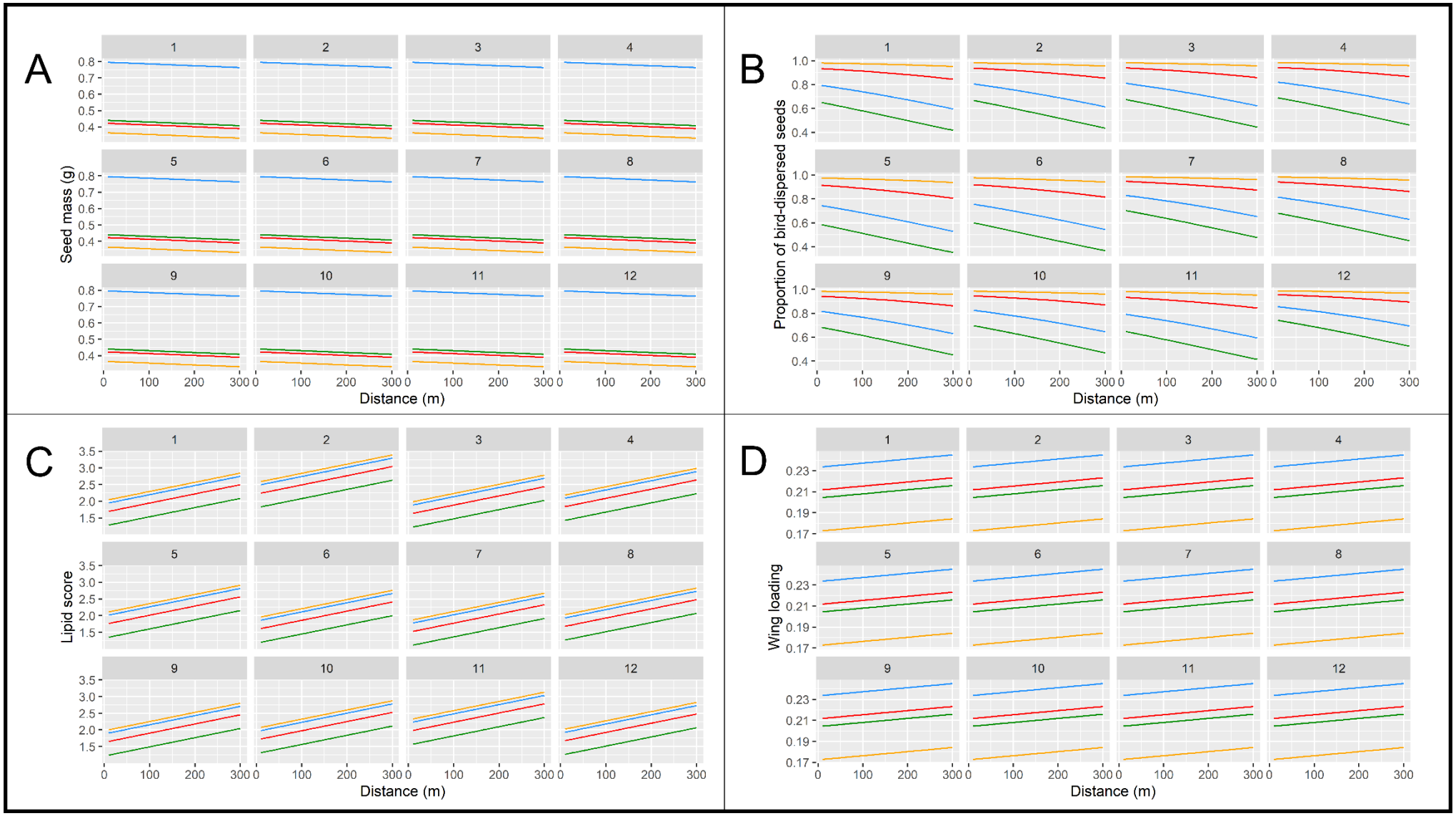


Fig. S3. Variation in the composition of seed rain as a function of the pioneer tree treatments (*Acnistus*, *Trema*, *Heliocarpus* and Control) and distances from forest showing an ordination graph (A) and the frequency of plant families in seed rain according to the pioneer tree treatments (B) and the distance from the forest (C). In NMDS ordination plot, the dotted ellipses denote the 95% confidence intervals for centroids of each treatment. To facilitate the visualization, plant species were grouped in the more common families. See Table S4 for information on all plant. Arrows represent the mean of scores for each family (amplified 20 times for graphical purposes).


A
B
C
D
1
2
3
4
5
6
7
8
9
10
11
12
Seed mass (g)
Proportion of bird-dispersed seeds
Lipid score
Wing loading
Distance (m)
0
100
200
300

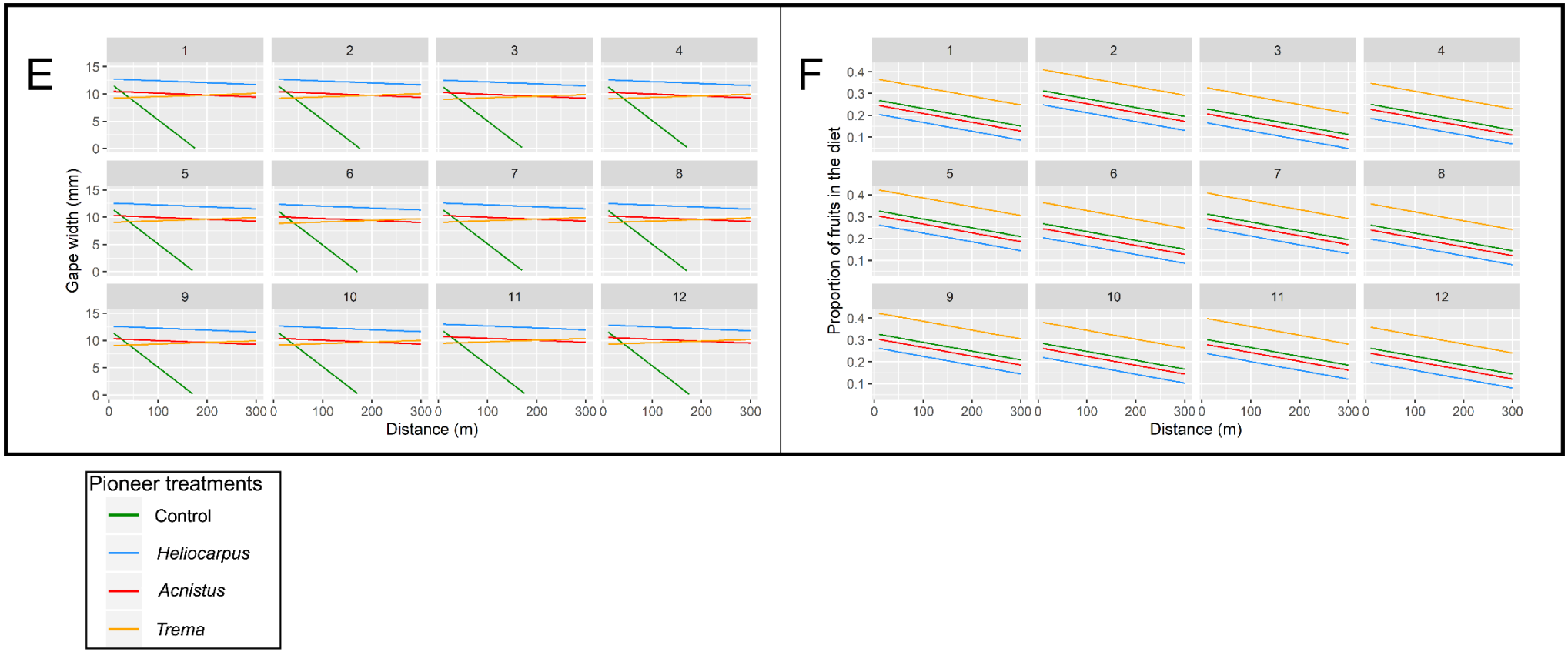


Fig. S4. Effects of Pioneer treatment and distance on traits of seeds (A-C) and visiting birds (D-F) conditioned to each study site (random effects).

Capítulo 2

Frugivore diversity promotes plant diversity by magnifying equalizing effects on the seed rain on deforested tropical landscapes

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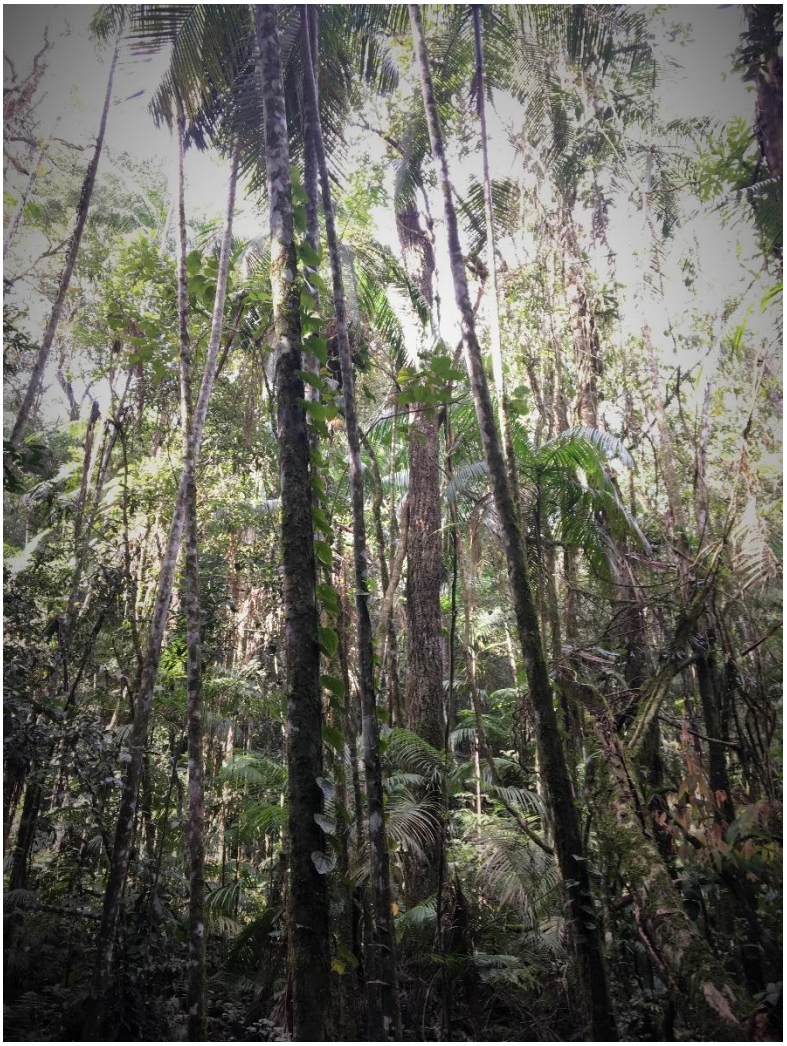

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Frugivore diversity promotes plant diversity by magnifying equalizing effects on the seed rain on deforested tropical landscapes

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Abstract

The diversity of tropical forests is strongly shaped by mutualistic interactions involving plants and frugivores that disperse their seeds. However, it is little known how decreases in the diversity of frugivores can affect seed dispersal patterns, plant community composition and species' coexistence in tropical forest landscapes. Here, we investigated the effects of bird frugivore diversity on rare-biased seed dispersal patterns and on the magnitude of equalizing effects on the seed rain in open areas within 12 fragmented landscapes in the Brazilian Atlantic Forest. We monitored the production of bird-dispersed seeds and bird abundance in forest fragments, and sampled the seed rain and the activity of birds attracted to experimental tree nuclei established in neighboring pastures. The activity of frugivores in tree nuclei was positively correlated with the diversity of birds recorded in nearby forest fragments, and the seed rain diversity increased with frugivore activity. The proportion of seeds dispersed more frequently than expected by chance in tree nuclei increased linearly with the species' richness of birds. The richness and abundance of active frugivores in deforested areas promoted a seed rain with evenness and diversity up to five times greater than the seed pool available in forest fragments due to the proportional increase in the dispersal of rare plant species and a concomitant proportional decrease in the dispersal of dominant fruiting plants. In addition, the increase in each bird species increased by 10% the equalizing effect the dispersed seeds’ relative abundance. Our results show that the aggregated behavior of avian frugivore communities on deforested areas results in higher species richness in the seed rain of plant communities and underscore the urgency to reduce bird specie's loss and the simplification of their communities in tropical landscapes.

Keywords: animal diversity; diversity maintenance; mutualisms; forest restoration; forest succession; negative density dependence; plant-bird interactions; plant–frugivore assemblages

Introduction

Studies on plant-frugivore mutualistic interactions are often focused on determining the role of frugivores in the reproductive success of plants, regeneration of plant communities, and understanding how these interactions help to structure spatially and act on the gene flow between plant populations (Carlo et al. 2013, de la Peña-Domene et al. 2014, González-Varo et al. 2017, Timóteo et al. 2018, Camargo et al. 2019). However, until recently, few studies have explored how frugivorous birds and bird-dispersed plant species interact to generate patterns of diversity in plant communities, that is, how much of the structure of plant communities in terms of composition, abundance, and species coexistence is determined by frugivore activity. In this sense, recently Carlo and Morales (2016) demonstrated that frugivorous birds tend to exhibit an antiapostatic fruit selection pattern, resulting in equalized amounts of dispersed seeds compared to the availability of seeds in the environment. Thus, they suggested that this process can be a mechanism that increases diversity in plant communities and promotes species' coexistence (Carlo and Morales 2016, Morán-López et al. 2018a, Camargo et al., in prep.).

Mechanisms of species coexistence, which have been broadly grouped into stabilizing and equalizing components (Chesson 2000), have recently received much attention in theoretical and empirical studies (Muller-Landau 2008, Chesson 2018). Such studies demonstrate that compensatory negative density-dependent processes are essential for maintaining diversity in plant communities, especially in the tropics, where most plant diversity is composed of rare species (Terborgh 2012, Hubbell 2013). In fact, compensatory mechanisms confer advantages to rare plant species by allowing lower *per capita* mortality rates from pathogens, seed predators, and herbivores, and reduce intraspecific competition for resources when plants exist at low population densities (Janzen 1970, Comita et al. 2010, Johnson et al. 2012, Bagchi et al. 2014). In addition, plant species that proportionally produce few fruits can make a greater energy

investment in a per-fruit basis and provide a greater nutritional reward to frugivores (Howe 1993, Cazetta et al. 2008) – which is an important reproductive strategy as most tropical trees are dispersed by animals (Jordano 2000).

Environmental factors and the identity of interacting species can affect the strength of compensatory mechanisms for rare plant species. For example, the magnitude of the diversification effects that take place through rare-biased seed dispersal of plant species by frugivores may depend on landscape heterogeneity and on the movement behavior of birds (Morán-López et al. 2018a). This is because increased landscape heterogeneity and plant spatial aggregation affect plant-animal encounters and thus the chances of rare plants being dispersed (Morán-Lopez et al. 2018a). In addition, models show that frugivore bias towards rare fruiting plant species arise from foraging behaviors that maximize balanced nutrition when the nutritional profiles of different fruiting species in a community are complementary to each other (Whelan et al. 1998, Morán-Lopéz et al. 2018b).

Frugivores vary in size, feeding behavior, movement behavior, and digestive physiology (Wheelwright 1985, Jordano 2000, Levy and Martínez del Rio 2001, Morales et al. 2013, González-Castro et al. 2015). Similarly, fruits vary in size, color displays, shape, and nutritional rewards, all of which influence fruit selection and seed dispersal by frugivores. In this sense, it can be expected that the diversity of frugivores can also influence how such compensatory mechanisms affect rare-biased dispersal. For instance, interactions between plants and frugivores are characteristically nested, where abundant generalist species are responsible for most community-wide interactions. In nested frugivory networks, rare and specialized species form subsets of the interactions of the most abundant ones (Bascompte et al. 2003). Thus, based on the common architecture of mutualistic plant-frugivore interactions (Bascompte et al. 2003), the

number of interactions increases with the number of interacting species in a community (e.g. García and Martínez 2012; Fricke et al. 2018).

Recent studies have found that decreases in frugivore richness lead to the loss of interactions and co-extinction of plant species (Caughlin et al. 2015, Srbek-Araujo et al. 2017, Emer et al. 2019, Morán-López et al. 2020), or changes in the genetic diversity of plant populations (Carvalho et al. 2016, Pérez-Méndez et al. 2016). Tropical forest regeneration and resilience are also affected by frugivore activity and diversity (González-Castro et al. 2019, Gardner et al. 2019, Albert et al. 2020), which ultimately can impact carbon stocking by forest remnants (Bello et al. 2015) and restoration plantations (Brancalion et al. 2018). Still, the role of frugivore richness on the maintenance of plant diversity via behavioral mechanisms that affect seed dispersal, such as rare-biased (antiapostatic) dispersal, remains largely unknown.

Here we conducted a study replicated at the landscape scale and presenting a gradient of frugivore diversity to examine the hypothesis that avian frugivores equalize plant species' representation and diversity on the seed rain occurring on deforested areas and leading to increased plant richness. We also tested whether the equalizing process depends on the richness and abundance of avian frugivore communities. Due to the effects of dietary complementarity (Morán-Lopéz et al. 2018b), we expect that a greater richness and abundance of frugivores will increase the dispersal of rare plant species relative to common ones. We also predicted that the richness of frugivore species will be positively correlated with stronger equalizing effects on the seed rain species' diversity. Alternatively, the correlation between frugivore richness and equalizing effect sizes could be negative if the dominance of common plant species increase due to increases in the nestedness of plant-frugivorous networks (Bascompte et al. 2003).

Materials and methods

Study sites

The study was conducted in 12 landscapes of the Paranapanema municipality in São Paulo, southeastern Brazil (23°23' S, 48°43' W, Fig. 1). The sites were located in private farms with cattle pastures and > 30-year-old fragments of secondary semideciduous forests ranged from 12.2 to 98.8 ha. The study area is located within the second most threatened biogeographical zone (<7% forest cover remaining) of the Atlantic Forest (Ribeiro et al. 2009), a global hotspot for biodiversity conservation and tropical rainforest restoration (Laurance 2009, Brancalion et al. 2019). The local climate is Köppen type Cfa, humid subtropical, with hot summer winter (Alvares et al. 2013). Average annual rainfall, concentrated in the wet summer season (December to March), is 1.407,9 mm, while mean annual temperature is 18 °C (Cielo-Filho et al. 2009).

Tree nuclei in pastures

In December 2016 we established at each site eight 4.5 x 4.5 m plots in cattle pastures to sample bird visits and the seed rain. Plots were established at 10 and 50 m from the nearest forest fragment (Fig. 1). We used plots at these distances because there was not much difference in the parameters of the seed rain between plots at 10 or 50 m from the forest fragments (see Camargo et al. 2020). At each distance class, we established four plots: three with a tree planted and one Control with no tree. Plots were fenced with barbwire to keep cattle off, grasses inside plots were mowed and mechanically controlled throughout the experiment. At the center of each plot, we planted one pioneer tree of reproductive age at least 1.5 m in height to form small tree nuclei on pastures. We planted pioneer trees with different functional characteristics of fruits to maximize interactions with the bird community: *Heliocarpus popayanensis* Kunth with wind-dispersed seeds, *Acnistus arborescens* Schltdl. with fleshy fruits composed of 48.3% of carbohydrates,

7.9% of proteins and 0.04% of lipids, and *Trema micrantha* (L.) Blume with fleshy fruits composed of 48.8% of lipid, 10.7% of proteins and 2.2% of carbohydrates.

Fruit abundance in forest fragments

To quantify the abundances of bird-dispersed fruits in forest fragments, we systematically established 10 5 x 5 m vegetation inventory plots at each forest fragment, totaling 250 m^2 sampled in each study site (Fig. 1). Overall, we marked a total of 1827 plants including trees, shrubs, vines, herbs, mistletoes; mean ± SD of 152.25 ± 21.09 individuals per site and 7.30 ± 15.96 individuals per species), of which 72.5% (n = 1324) corresponded to 187 bird-dispersed species (38.3 ± 10.2 species per site). From October 2017 to November 2018, we counted monthly the number of ripe fruits of all bird-dispersed species monitored within forest plots. Whenever possible, we directly counted all fruits without extrapolation, but for large trees with a lot of fruits, we counted fruits in some branches or portions of the canopy and extrapolated to the rest of the canopy area bearing fruit. For each species, we average the fruit per individual and calculated the fruit density per plot. Then, we extrapolated the average density across plots to obtain the density of fruits in the whole fragment (fruits/hectare). We obtained the abundance of seeds available in the fragment by multiplying the density of fruits by the average number of seeds per fruit of each species.

Bird abundance in forest fragments

To estimate the abundance of birds, we conducted 10-min point counts at the five vegetation sampling plots per forest fragment (Fig. 1). Bird surveys were conducted once a month between October 2017 and November 2018 from 6:00 to 7:30 when all birds visually and acoustically detected within a 50 m radius were recorded. Abundances were calculated by dividing the

number of records of each species by the number of sampled point counts and averaged across months.

Bird activity in tree nuclei

From October 2017 to November 2018 we recorded bird activity in the experimental plots of tree nuclei in the pastures using direct focal observations and video recording. Each plot was observed once a month by one observer (PHSAC Camargo) using a pair of binoculars from a distance of 50 m for 20 min, during morning hours (07:30–10:30), totalizing 13.3 h of focal observations per site. We complemented these focal observations with 22 camera-traps. Each camera-trap operated 24 h/day for a total of 59,152.9 h. In addition, we also used six GoPro Hero 3 cameras that filmed for about 2 h before batteries were depleted, totaling 193.5 h of filming. All the cameras were rotated, and the sampling efforts of focal observations and filming were equally distributed among the plots and sites to prevent sampling bias. For more details see Camargo et al. (2020).

Seed rain

To sample seed rain we used one 0.25 m^2 seed trap lined with a 0.2 mm nylon mesh placed at the center of each tree nuclei plot. We applied Formifuu® to the legs of the traps to prevent ant access and covered the traps with a wire screen (2.5 x 2.5 cm mesh) to exclude vertebrate seed predators. Seeds were collected monthly from the traps and counted and identified to the lowest taxonomic level possible in the laboratory with the aid of a dissecting scope, available reference books and reference seed collections for the local flora. We did not include in the analysis the number of grass seeds or those from the pioneer tree species planted in a particular plot (as they may have originated *in situ*).

Statistical Analyses

Structure of bird and plant communities. We used Non-Metric Multidimensional Scaling (Vegan package, Oksanen et al. 2018) with Chao distance to examine the structure of bird and plant communities in the forest fragments and in tree nuclei in pastures. The patterns of variation in the composition of birds and plants recorded in the forest and tree nuclei in pastures were analyzed by Procrustes analysis (Vegan package). In this analysis, we ordered the communities found in the forest and tree nuclei in pasture separately by two Principal Coordinates Analysis with Jaccard distance. Then, the two ordinations were superimposed by Procrustes analysis and the significance of correlation was calculated with a Protest analysis. Separate analyses were done for bird and plant communities.

Relationship between seed availability, bird activity and seed dispersal. We used linear regressions to examine the relationship between the relative monthly abundance of seeds (i.e., the proportional representation of each plant species) in forest fragments with the proportion of seeds dispersed to tree nuclei at the site level. Then, we used the correlation coefficients transformed into z-score (effect size) and correlated them to the number of visits and richness of visiting birds at each site. We calculated diversity (Shannon's *H'*) and evenness (Pielou's *J*) for the seeds that were available to be dispersed, and the seeds that were dispersed to seed traps using the average values across plots for each plant species at each site. For each site, we calculated the ratio between the evenness of the seed rain in the tree nuclei and the evenness of the plant communities sampled in forest fragments, which was used as a proxy for the equalizing effects. We then regressed the size of the equalizing effect on the number of bird visits and richness of bird species visiting the experimental plots.

Bird-generated seed rain patterns. We used an approach similar to that of Carlo and Morales (2016) and examined if the bird-generated seed rain of each plant species at each site was higher than expected, lower than expected, or proportional to its seed availability in the forest. To estimate the proportion of each species that would be expected at random in the seed rain, we calculated the monthly average abundance of available seeds for each species recorded in the vegetation plots in forest fragments. From the averages, we calculated the 95% confidence intervals and the proportion that each value represented in relation to the total. Thus, plant species with proportional representation in the seed rain falled within the values of its 95% C.I. If the proportion value in the seed rain was higher than the 95% C.I., the species had more dispersal than expected by chance, and if the value was lower the 95% C.I., the species had a lower dispersal than expected by chance.

Antiapostatic dispersal. We used a Bayesian approach to assess whether the availability of each species influenced the proportionality of its seed dispersal patterns (random, higher or lower than random) by fitting multinomial mixed-effect models with softmax link functions using Hamiltonian Monte Carlo estimation (HMC, Monnahan et al. 2017) in Rstan package (Carpenter et al. 2017, Stan Development Team 2020). For that, we used as fixed predictor variables the monthly proportion of available seeds (abundance) for the 20 species of plants with the greatest abundance in each site and the species order in a ranking of abundance per site. As random effect variables, we used site and the month. We adapted the models and scripts of Koster and McElreath (2017) and presented six models, which vary in structure and complexity. The simplest models include only random effects for the site, while the complete models also add random effects for month. Then, for each of these random effect structures, we ran models without a fixed effect, with abundance as a fixed effect, or with both fixed effects (abundance and

species). For each model, we ran three chains of 2000 iterations, half of which are dedicated to the warm-up. We did the model selection using the Widely Applicable Information Criterion (WAIC, Watanabe 2010). For more details on model fitting, please see appendixes 1-2 in the supplementary material.

To assess if the seed dispersal patterns (random, higher or lower than random) were correlated to the number of visits and or to the frugivore richness, we conducted a multinomial logistic regression. We also regressed the proportion of seed dispersal events higher than expected by chance as a function of the number of visits and the richness of frugivores. All analyses were performed in R version 3.5.1 (R Core Team 2018).

Results

Birds in forests and tree nuclei

We recorded a total of 176 bird species in forest fragments (avg. = 110 ± 23.3 SD) and 39 species (avg. = 16 ± 4.2 SD) on tree nuclei (Tables S1-S2). We found a positive correlation between the richness of bird species in the forest and in the adjacent tree nuclei in pastures ($r_s = 0.624$, $p = 0.029$). However, the composition of bird communities in forest fragments and pastures was markedly different (Fig. S1a). The best NMDS solution was bidimensional with final stress of 0.04 showing that bird communities differentiated along the first axis, where forest plots had negative scores and were clearly separated from tree nuclei in pasture that scored positively on the first axis (Fig. S1a). Large-bodied and specialized frugivores such as *Penelope superciliaris, Trogon surrucura, Ramphastos toco, Procnias nudicollis, Pyroderus scutatus* and *Psarocolius decumanus* were recorded only in forest fragments (Table S1), while some granivorous and predominantly insectivorous species such as *Ammodramus humeralis* and *Xolmis velatus* were abundant on pastures (Table S2). Despite this, there was an agreement in the variation in species

composition found in bird communities in forest fragments and tree nuclei in pastures across sites (Procrustes analysis: r = 0.59, p = 0.029, Fig. S1b). For both locations, the Procrustes rotation graph separated the sites into two groups along axis 1 (Fig. S1b), most likely driven by the environmental specificity of each site.

Seed availability and seed dispersal

The richness and composition of plant species in forest fragments varied among sites (Table S3). Only ten plant species (5%) of the 187 recorded was common for at least half of the sites. Four species (2.1%) were common to at least 75% of the sites and only *Casearia sylvestris* (0.5% of species) was common to all sites. As consequence, seed availability also varied markedly among sites (Fig. 2). The availability of seeds of bird-dispersed species was dominated by five species that represented more than 90% of the seed production (90.97 ± 6.64%, mean ± SD). Overall, 33 species were among the top five species with the highest seed production in any given study location (Fig. 2, Table S3), but six species should be highlighted because they are among the dominant ones regarding the availability of seeds in several sites: *Casearia sylvestris* (in 9 sites), *Maclura tinctoria* and *Schinus terebinthifolia* (in 5 sites), *Campomanesia xanthocarpa, Croton floribundus* and *Guazuma ulmifolia* (in 4 sites).

In 13 months we collected 925 seeds in the seed traps within tree nuclei, 92.86% of which belonged to 115 species of bird-dispersed plants and in 47 plant families (Table S4). Ninety-one percent of the seeds of bird-dispersed species were dispersed under the planted trees with fleshy-fruits, 8.3% fell under the pioneer species with wind-dispersed seeds, and less than 1% fell in the control plots without trees (see Camargo et al. 2020 for more details). The most abundant species in the seed rain were *Casearia sylvestris* (10.0 ± 5.1%, n = 12), *Schinus terebinthifolia* (7.4 ± 4.9%), *Siparuna guianensis* (7.3 ± 2.8%) and *Cupania vernalis* (4.6 ± 2.1%). There was also 3.8

± 2.9% of the seed rain belonging to 20 unknown morphospecies (Table S4). In general, 60.6 ± 9.6% of the bird-dispersed species with fruits available in the forest were represented in the seed rain (Fig. 2).

There was a positive correlation between the richness of bird-dispersed species in the forest and the richness of bird-dispersed species represented in traps ($r_s = 0.739$, $p = 0.006$). For every additional bird-dispersed species detected in a location, the seed rain increased by 43%. In addition, we found no clear differences between the species composition of plant communities in forest fragments and the species composition of the seed rain (Fig. S2a). The best NMDS solution with final stress of 0.13 shows much overlap between the two compositions (Fig. S2a). On the other hand, we didn't find congruence between the patterns of variation in the composition of plants in the forest and in the seed rain in tree nuclei across sites showed in their ordinations (Procrustes analysis: $r = 0.24$, $p = 0.797$, Fig. S2b).

Bird species richness and antiapostatic selection

Seed dispersal by birds was positively correlated with the availability of seeds across sites (Fig. S3a). On the other hand, the effect size of this relationship does not appear to be correlated with the richness of birds or number of bird visits to tree nuclei in pasture (Fig. S3b-c). In addition, although there was a positive correlation between fruit availability and number of dispersed seeds, the magnitude of the differences between the abundances of species in the seed rain and the availability of such seeds in the forest decreased by 10^6 (Fig. 2). As consequence, the five most common bird-dispersed species in each site, which altogether produced 91.0 ± 6.6% of all seeds available in the forest (black bars, Fig. 2), were responsible for an only quarter (26.69 ± 9.51%, mean ± SD across sites) of the seed rain. Other seeds in the seed rain (73.3 ± 9.5%) belonged to less abundant plant species. The diversity (Shannon's *H'*) and evenness (Pielou's *J*)

of the seed communities that reached the tree nuclei were, respectively, on average 2.4 ± 1.0 and 2.1 ± 1.4 times greater than the plant communities available in the forest fragments (Fig. 2), meaning that frugivory by birds equalized plant species representation in the seed rain. Furthermore, the greater the activity and richness of bird species visiting plots, the greater the equalizing effect was on the dispersed seeds' relative abundance (Fig. 3).

When examining the monthly availability of each plant species in the forest fragments and the seed rain, we see that rare-biased (antiapostatic) dispersal was very common (Fig. S4). This means that in most of the sites, the most abundant plant species were dispersed either proportionally or at lower rates than expected by their abundance in the community (Fig. S4). In contrast, we observed disproportionally high dispersal in months when plant seeds were proportionally rare (Fig. S4). Of the six multinomial models that we tested, the model that included the site and month as random effects and the availability of seeds and species ranking as fixed effects received the strongest support from the WAIC comparison used to explain the seed dispersal patterns (random, higher than random and lower than random, Table S5).

Seed dispersal was characterized by negative frequency-dependence, although with great variation among sites and months (Table 1). The probability of a species having dispersal higher than random was greater when its seeds were proportionally rare in the environment, and this probability decreased as the proportion of its seed availability increased in the community. The chances of a species having lower than expected dispersal, on the other hand, increased with the proportional availability of its seeds (Fig. S5). Likewise, while the probability of higher than expected dispersal increased in the lower positions of a species' abundance ranking, the probability of equal to or lower than random dispersal increased in the top positions of that ranking (Fig. S6).

The seed dispersal patterns were also related to the role of birds. More than 40% of the variability in the proportion of seed rain higher than random can be explained by the richness of visiting birds in each site ($r^2 = 0.41$, $p = 0.02$, $n = 12$, Fig. 4). Our multinomial logistic model also showed that bird richness is an important predictor to classify the dispersal probabilities (higher than expected, random or lower than expected) for the 10 most abundant species at each site (Table S6, Fig. S7). In contrast to bird species richness, the total number of bird visits did not explain cases of disproportionally high seed dispersal rates of plant species ($r^2 = 0.31$, $p = 0.06$, $n = 12$).

Discussion

Our extensive field study shows that proportionally rare fruit resources in fragments of Atlantic Forest have higher-than-expected probabilities of seed dispersal to isolated tree nuclei across pasturelands due to the equalizing effect of avian frugivores (Fig. 2). As demonstrated by recent field experiments, rare-biased (antiapostatic) seed dispersal by avian frugivores promotes the quick establishment of diverse nuclei of successional tropical forests (Carlo and Morales 2016, González-Castro et al. 2019). Our findings also imply that the equalization of the seed-rain of diverse tropical forests is indeed an important and general Negative Density-Dependent (NDD) mechanism promoting coexistence and resilience of tropical plant communities (Carlo and Morales 2016, Morán-López et al. 2018a and 2018b). Furthermore, by studying twelve independent communities representing a gradient of frugivore diversity, we were able to show there is a positive effect of frugivore richness on the size of the resulting antiapostatic effect on seed dispersal. The increase in the effect size of rare-biased seed dispersal with frugivore species richness demonstrates a novel mechanism by which interaction diversity promotes resilience and stability to tropical forests.

Rare-biased seed dispersal and plant community diversity

Fruit abundance has been shown to be the main driver for the attraction of mutualistic frugivores in plant populations across scales (Levey 1988, García and Ortiz-Pulido 2004, Blendinger and Villegas 2011). In general, fruit resource abundance predicts that the quantity and/or proportion of dispersed seeds increases positively with fruit abundance at the individual, neighborhood, or population levels (Howe and Estabrook 1977, Sallabanks 1993, Saracco et al. 2005, Ortiz-Pulido et al. 2007, Christianini and Oliveira 2009). Although there is much evidence for this general relationship (see Palacio and Ordano 2018 for a meta-analysis), the size and sign of this effect can vary according to factors such as co-variation of plant species, spatial aggregation patterns and bird abundance (Carlo and Morales 2008) and ecoregion (e.g. temperate vs. tropical, Palacio and Ordano 2018). In our study sites, increasing seed availability of a given species also increased the quantity in the seed rain, but this relationship was weak (Fig. S3a) due to the widespread interaction of frugivores with fruits of low abundance (Fig. 2).

Theoretical and empirical evidence show that frugivores play an important role in the maintenance of plant diversity in tropical forests through fruit selection patterns that favor rare fruiting plant species (Carlo and Morales 2016, Morán-Lopéz et al. 2018a, 2018b, González-Castro et al. 2019). Our results are in line with such evidences as they show that seed dispersal by frugivorous birds equalized the representation of species that differed by up to six orders of magnitude (logarithmic scale) in seed availability, making the relative representation of plant species in the seed rain much more even (Fig. 2). Although many plant species were not detected in the seed rain (38.0 ± 9.2%), the increased evenness in the communities formed by the dispersed seeds has not only maintained, but also increased the resulting diversity.

More equal seed rains were due to higher per capita seed dispersal of plant species with low fruit availability, while species with high seed abundance most commonly showed lower capita seed dispersal (Fig. 2 and S4-S6). Our results thus provide strong empirical evidence for the notion that dispersal as mediated by frugivores is negative frequency-dependent (Carlo and Morales 2016, Morán-Lopez et al. 2018a). For example, in site 4, *Maclura tinctoria*, which produced 55% of the available seeds, had the same amount of dispersed seeds as *Mollinedia widgrenii*, which produced only 0.01%. Similarly, *Casearia sylvestris*, the which produced 23% of the seeds in site 3 was equally represented in the seed rain by *Cupania vernalis*, which produced only 0.08% of the total seeds. This pattern was similar for almost all common species in all sites (Fig. 2). In addition, the seed rain had species that were not recorded in our vegetation surveys (Fig. 2), likely brought from other fragments (immigrant seeds, Jordano et al. 2007) or belonging to rare species that escaped representation in our vegetation plots, but that clearly were tracked by frugivores.

Similar patterns were observed intra-specifically as the fruiting phenology changed the relative fruit abundance of plant species. During periods of peak fruit abundance, seeds of several plant species were dispersed at rates equal or lower than expected by availabilities, but when such species became proportionally rare (i.e., phenologically off-peak), dispersal was higher than expected by chance. For example, *Casearia sylvestris*, *Croton floribundus*, *Schinus terebinthifolia*, *Guarea kunthiana*, *Maclura tinctoria*, highly abundant in several sites, were overrepresented in the seed rain when its fruits were rare, but underrepresented when abundant (Fig S4). The same occurred with some locally rare species, such as *Cupania vernalis*, *Euterpe edulis*, *Tabernaemontana hystrix*, and *Allophylus edulis*, which were dispersed at the expected rates when abundant, but at higher than expected rates when relatively rare (Fig. S4), showing that antiapostatic selection can occur in both common and rare species depending on their fruiting

phenology patterns. This highlights the role of density-compensatory dependent mechanisms also on mutualistic interactions such as seed dispersal, a mechanism documented almost exclusively in antagonistic interactions, such as competition, predation, and herbivory (Chesson 2000, Terborgh 2012).

The antiapostatic foraging behavior of frugivores makes seed dispersal of plants to be less affected by temporal fluctuations and large differences in relative abundance that characterize plant communities, specially those of high diversity. Thus, antiapostatic dynamics in fruit choices can allow for more flexibility in the energy-investment strategies and tradeoffs inherent to plant reproduction and growth (Obeso 2002). Energy saved from dispersal at low levels of fruit availability may allow a greater investment in fruit pulp (Howe 1993), providing a greater nutritional reward for frugivores and increasing the chances of dispersal (Cazetta et al. 2008). Morán-López et al. (2018b) provided an important theoretical approach to the basis of antiapostatic seed dispersal by theoretically demonstrating that selection patterns emerge from frugivores that seek limiting nutrients from different fruits to complement their diets. Thus, we expect a strong antiapostatic dispersal pattern when rare species provide limiting or more nutritious and energy-rich resources. The effects of nutrient complementarity also imply that dispersal is not all an individual attribute of a plant species, but one implicating co-dispersal of multiple species (Whelan et al. 1998).

Generalist birds that feed on both fruits and insects are some of the most abundant types of birds in fragmented landscapes (Pizo and dos Santos 2011, Carlo and Morales 2016). Such birds prefer lipid-rich fruits that provide a greater energy reward (Moermond and Denslow 1985, Stiles 1993). However, as in other tropical or temperate biomes, most plants in the Brazilian Atlantic Forest are lipid-poor (Jordano 2000, Galetti et al. 2011, Bello et al. 2017). Thus, it is possible that some species that have lipid-rich fruits and, therefore, can provide a richer and/or

complementary diet to other fruits, present a high proportion of dispersal. In fact, 75% of the species that generally had low fruit abundance in the forest but had porportionally high seed dispersal rates produce lipid-rich fruits (e.g., *Trichilia casaretti*, *T. catigua*, *T. pallida*, *Tabernaemontana hystrix*, *Cupania vernalis*, *Randia calycina*, *Mollinedia widgrenii* and *Siparuna guianensis*, Fig. 2 and S4) (Bello et al 2017). This supports the hypothesis that the search for energy-rich fruits, or those with complementary nutrients, can favor rare plant species (Morán-López et al. 2018b)

Although the pattern of diversity detected in the seed rain may not translate directly into patterns of plant recruitment and community regeneration (Reid and Holl 2013, *but see* Carlo and Morales 2016, González-Castro et al. 2019) our findings were remarkably consistent across sites. This suggests that antiapostatic seed dispersal is a common pattern influencing the seed rain of tropical communties. Because the seed rain sets the templates for subsequent plant recruitment, antiapostatic dispersal may an yet another driver of the prevalence of rare plant species in tropical forests (Pitman et al. 1999, Caiafa and Martins 2010, Hubbell 2013, ter Steege et al. 2013).

Frugivore richenss and rare-biased seed dispersal

The diversity of seed dispersal agents can improve the dispersal function and influences the diversity of the seed rain and community regeneration patterns (Wandrag et al. 2017, García et al. 2018, Camargo et al. 2020). But little was known about how antiapostatic selection at the community level is affected by the diversity of frugivore agents in the environment since previous field studies took place on a species-poor island community (i.e., Carlo and Morales 2016). Our study is the first to test this question and demonstrate that the diversity of frugivores can increase the magnitude (effect size) of antiapostatic seed dispersal. Our results show that while both richness and abundance of birds had positive effects on equalizing the representations

of plant species in the seed rain, only bird richness positively affected the proportion of plant species receiving higher than expected dispersal (Fig. 3-4).

The effects of frugivore abundance on the dispersal of relatively rare plant species have a quantitative effect on the seed rain, but the effects of frugivore richness are of a qualitative nature (Carlo 2005, García and Martínez 2012, González-Castro et al. 2015). A higher diversity of frugivores increases the chances of interactions with plants based on behavioral intra and interspecific facilitation mechanisms that take place among foraging frugivores (Saracco et al. 2004, Schleuning et al. 2015). The increased abundance of frugivorous birds that track each other during foraging allows greater efficiency and safety in locating resources (Valburg 1992, García and Martínez 2012). Based on the need of frugivores to balance their nutrition (Whelan et al. 1998 Morán-López et al. 2018b), the presence of frugivore-frugivore facilitation mechanisms in foraging could contribute to increase the dispersal of rare plant species (García and Martínez 2012, Gleditsch et al. 2017). Frugivore diversity and activity levels are thus candidate factors affecting the strength of the effect size of the equalizing effect of frugivores on the plant composition of the seed rain (Fig. 3).

Frugivore richness increased the magnitude of the equalizing effect and the antiapostatic dispersal probably through complementary effects among frugivore species (Schleuning et al. 2015) since the identity of the frugivore has an important role in determining patterns of fruit choice and the dispersal of rare seeds (González-Castro et al. 2015; Morán-López et al. 2020). Frugivore diveristy affects the structure of seed dispersal networks and can increase the functional complementarity of species in a community (Petchey and Gaston 2002, Bastolla et al. 2009, Sebastián-González et al. 2015, Peña et al. 2020) even in low-specialized networks with high redundancy and low complexity as in plant-frugivore networks in tropical fragmented

landscapes such as our study sites (Menke et al. 2012, Schleuning et al. 2012, Emer et al. 2018, 2020).

A high richness of frugivores also increase the chances of plant-bird matching of traits involving morphological (fruit size and body/gape size, Wheelwright 1985), chemical (e.g. physiological traits of frugivores and the nutritional chemistry of fruits, Levey and Martínez del Rio 2001), behavioral, and spatio-temporal traits (phenology, Plein et al. 2013). All of which often prevent rare plants from being dispersed. For example, large fruits with larger seeds often occur in low densities in tropical forests (e.g. Galetti et al. 2011). In our study, fruits from plant species that had low fruit abundance have seeds slightly larger (by a factor of 1.4) than the five most abundant species in each site (Fig. S8). Larger fruits with larger seeds rely more heavily on large-bodied birds for dispersal, which are associated with species-rich sites (Galetti et al. 2013). In fact, we found a positive correlation between the richness of visiting birds in each site and the average gape size of birds ($r_s = 0.58$, $p = 0.04$, unpublished data). Thus, the increase in the frugivore richness can decrease constraints that limit interactions in the community, which can favor rare species (Leibold and McPeek 2006) and contribute to amplify the positive antiapostatic effect on the species diversity of the seed rain (Fig. 3B).

Our findings imply that the widespread reduction or extirpation of frugivore populations worldwide (Dirzo et al. 2014, Emer et al. 2018) can result in a decrease of the compensatory effects of antiapostatic dispersal on plant community diversity. Decreasing this species coexistence mechanism can lead to the competitive exclusion of less abundant species and generate increasingly less diverse plant communities with increasingly greater dominance of common species (Chesson 2000, Muller-Landau 2008). Although we recorded a narrow gradient of richness of birds visiting tree nuclei in pastures (11 to 25 species), this richness is equivalent to or greater than several other bird communities in open landscapes in temperate and tropical areas

including islands (e.g. Athiê and Dias 2016, Carlo and Morales 2016, García et al. 2018). In addition, the richness of visiting birds in tree nuclei in pastures is strongly correlated with the richness of bird communities in the adjacent forests with a much wider range of species richness (66 to 129). Our findings thus highlight the need to refrain defaunation to prevent the elimination of compensatory effects promoted by antiapostatic dispersal and the consequent decrease of plant diversity in tropical forests.

Authors' contributions

PHSAC, MAP and TAC conceived the ideas; PHSAC, MAP, TAC and PHSB designed the methods; MAP and PHSB provided funding; PHSAC collected and analyzed the data, and wrote the first draft; all authors contributed to the writing and gave final approval for publication.

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Figure captions

Fig. 1. Study area located in the municipality of Paranapanema, São Paulo, Brazil. In each of 12 study sites (in detail), we established 10 5x5m-vegetation plots in forest fragments (red) and set experimental plots in open pastures (yellow) planted with pioneer tree species (*Acnitus arborescens*, *Heliocarpus popayanensis*, *Trema micrantha*) and control (no species planted) at two distances from forest fragments (10 and 50 m).

Fig. 2. Bird-dispersed plant species ranked by the average abundance of seeds available at each of 12 study sites. The abundance of seeds available in the forest (per hectare; top graph), and the number of dispersed seeds (per m^2; bottom graph) are shown for each site. Black points represent the five species with the highest seed production (90.97 ± 6.64% of total production), while maroon bars are rare bird-dispersed species that were not detected in forest fragments during vegetation surveys but were present in the seed rain. Note that overall, through seed dispersal frugivores increased the diversity and evenness of the seeds of the plant community in the seed rain.

Fig. 3. Equalizing effect size upon seed representation in the seed rain increases with number of bird visits (A) ($r^2 = 0.61, p = 0.002$) and with richness of visiting birds (B) ($r^2 = 0.69$, $p < 0.001$) to experimental plots. Equalizing effect size is calculated as the ratio between the evenness (Pielou's *J*) for seed communities that sampled in seed traps place in pastures and estimated values for the seed communities available in adjacent forests.

Fig. 4. The proportion of seed dispersal higher than random increased with the richness of visiting birds, suggesting that antiapostatic selection increases with frugivore diversity (r^2 = 0.411, p = 0.025, n = 12).

Table 1. Summary of the mixed-effects multinomial logistic model based in Bayesian approach that included site and month as random effects, and the abundance of seeds and abundance rank of plant species as fixed effects used to explain the seed dispersal patterns - random, higher than random, and lower than random

Predictor variable	**Parameter symbol**	**mean**	**sd**	**95% Confiance interval**	**n_eff**	**Rhat4**
Intecept [higher]	α_1	-1.686	0.478	-2.655 to -0.679	992.731	1.00
Intercept [lower]	α_2	-2.533	0.562	-3.719 to -1.432	3083.798	1.00
Abundance [higher]	β_{A1}	-2.016	0.331	-2.703 to -1.367	3218.438	1.00
Abundance [lower]	β_{A2}	0.426	0.548	-0.727 to 1.567	2585.426	1.00
Abundance squared [higher]	β_{A1}^2	0.221	0.261	-0.381 to 0.683	2932.101	1.00
Abundance squared [lower]	β_{A2}^2	0.365	0.196	-0.019 to 0.791	2481.303	1.00
Species ranking [higher]	β_{S1}^2	0.025	0.020	-0.015 to 0.064	3941.895	1.00
Species ranking [lower]	β_{S2}^2	-0.524	0.138	-0.836 to -0.264	3023.998	1.00
(Site random effect variation) [higher]	σ_site_1	0.189	0.127	0.008 to 0.495	1381.185	1.00
(Site random effect variation) [higher]	σ_site_2	0.542	0.431	0.012 to 1.723	1110.627	1.00
(Month random effect variation) [higher]	σ_month_1	1.547	0.399	0.929 to 2.552	1017.460	1.00
(Month random effect variation) [lower]	σ_month_2	0.295	0.254131	0.008 to 1.018	1744.803	1.00

Parameter symbols are those used in the model's equations (see Appendix 1). Random effect variation is presented as standard deviation. All predictor variables were standardized prior to model fitting.

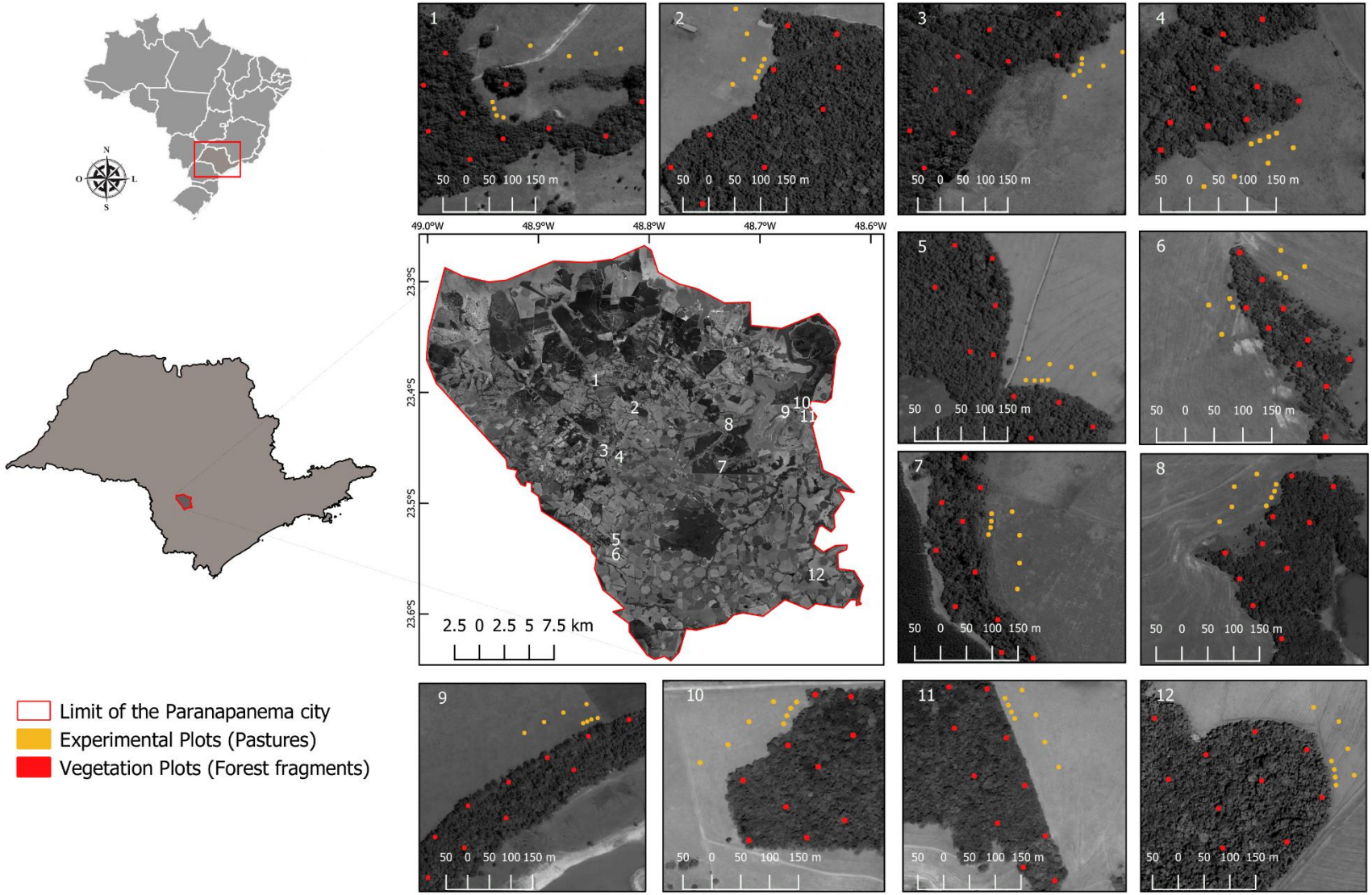

Limit of the Paranapanema city
Experimental Plots (Pastures)
Vegetation Plots (Forest fragments)
49.0°W
48.9°W
48.8°W
48.7°W
48.6°W
23.3°S
23.4°S
23.5°S
23.6°S
2.5 0 2.5 5 7.5 km
50 0 50 100 150 m

Fig. 1

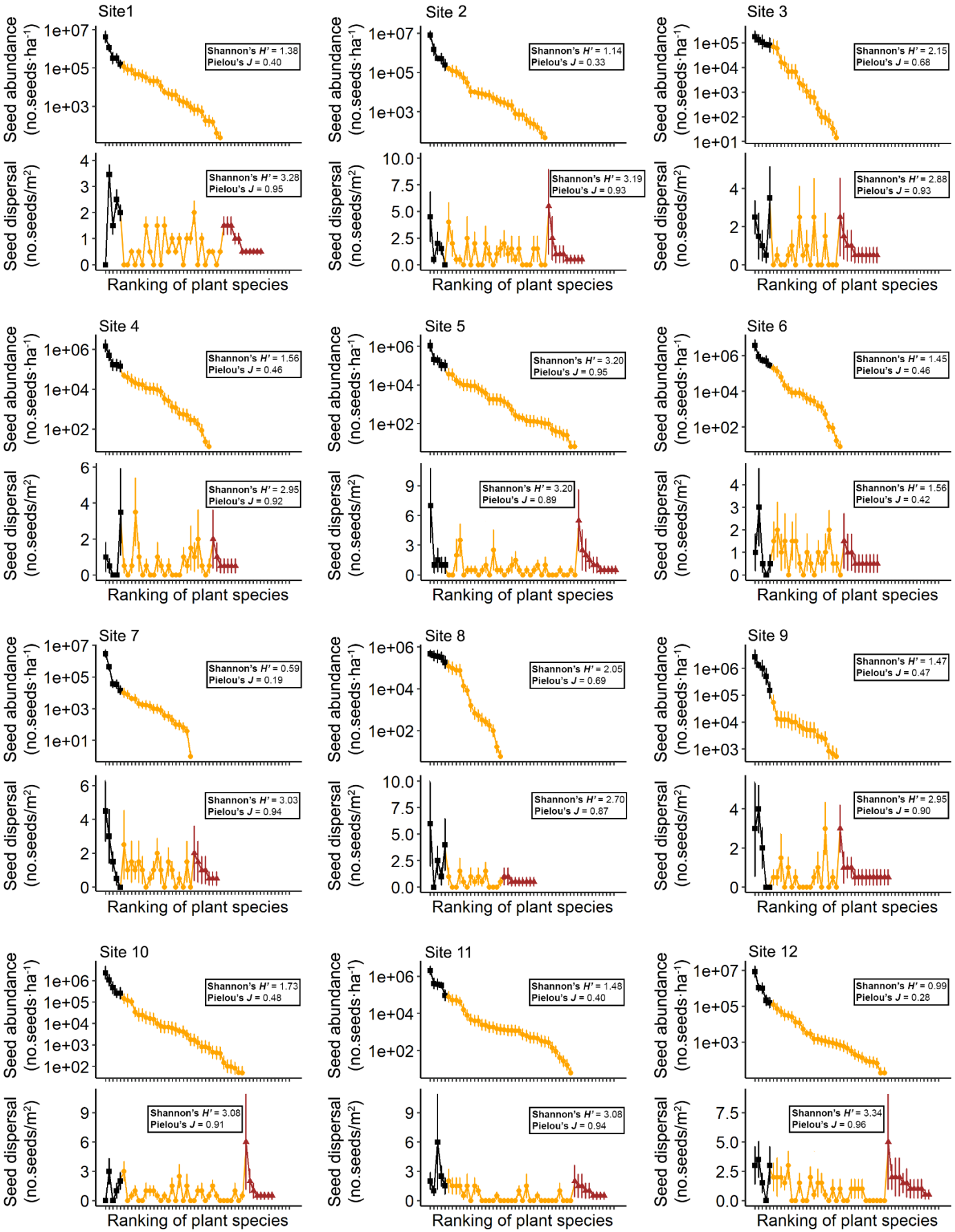

Site1
Seed abundance (no.seeds·ha⁻¹)
1e+07
1e+05
1e+03
Shannon's H' = 1.38
Pielou's J = 0.40
Seed dispersal (no.seeds/m²)
4
3
2
1
0
Shannon's H' = 3.28
Pielou's J = 0.95
Ranking of plant species
Site 2
Seed abundance (no.seeds·ha⁻¹)
1e+07
1e+05
1e+03
Shannon's H' = 1.14
Pielou's J = 0.33
Seed dispersal (no.seeds/m²)
10.0
7.5
5.0
2.5
0.0
Shannon's H' = 3.19
Pielou's J = 0.93
Ranking of plant species
Site 3
Seed abundance (no.seeds·ha⁻¹)
1e+05
1e+04
1e+03
1e+02
1e+01
Shannon's H' = 2.15
Pielou's J = 0.68
Seed dispersal (no.seeds/m²)
4
2
0
Shannon's H' = 2.88
Pielou's J = 0.93
Ranking of plant species
Site 4
Seed abundance (no.seeds·ha⁻¹)
1e+06
1e+04
1e+02
Shannon's H' = 1.56
Pielou's J = 0.46
Seed dispersal (no.seeds/m²)
6
4
2
0
Shannon's H' = 2.95
Pielou's J = 0.92
Ranking of plant species
Site 5
Seed abundance (no.seeds·ha⁻¹)
1e+06
1e+04
1e+02
Shannon's H' = 3.20
Pielou's J = 0.95
Seed dispersal (no.seeds/m²)
9
6
3
0
Shannon's H' = 3.20
Pielou's J = 0.89
Ranking of plant species
Site 6
Seed abundance (no.seeds·ha⁻¹)
1e+06
1e+04
1e+02
Shannon's H' = 1.45
Pielou's J = 0.46
Seed dispersal (no.seeds/m²)
4
3
2
1
0
Shannon's H' = 1.56
Pielou's J = 0.42
Ranking of plant species
Site 7
Seed abundance (no.seeds·ha⁻¹)
1e+07
1e+05
1e+03
1e+01
Shannon's H' = 0.59
Pielou's J = 0.19
Seed dispersal (no.seeds/m²)
6
4
2
0
Shannon's H' = 3.03
Pielou's J = 0.94
Ranking of plant species
Site 8
Seed abundance (no.seeds·ha⁻¹)
1e+06
1e+04
1e+02
Shannon's H' = 2.05
Pielou's J = 0.69
Seed dispersal (no.seeds/m²)
10.0
7.5
5.0
2.5
0.0
Shannon's H' = 2.70
Pielou's J = 0.87
Ranking of plant species
Site 9
Seed abundance (no.seeds·ha⁻¹)
1e+06
1e+05
1e+04
1e+03
Shannon's H' = 1.47
Pielou's J = 0.47
Seed dispersal (no.seeds/m²)
4
2
0
Shannon's H' = 2.95
Pielou's J = 0.90
Ranking of plant species
Site 10
Seed abundance (no.seeds·ha⁻¹)
1e+06
1e+05
1e+04
1e+03
1e+02
Shannon's H' = 1.73
Pielou's J = 0.48
Seed dispersal (no.seeds/m²)
9
6
3
0
Shannon's H' = 3.08
Pielou's J = 0.91
Ranking of plant species
Site 11
Seed abundance (no.seeds·ha⁻¹)
1e+06
1e+04
1e+02
Shannon's H' = 1.48
Pielou's J = 0.40
Seed dispersal (no.seeds/m²)
9
6
3
0
Shannon's H' = 3.08
Pielou's J = 0.94
Ranking of plant species
Site 12
Seed abundance (no.seeds·ha⁻¹)
1e+07
1e+05
1e+03
Shannon's H' = 0.99
Pielou's J = 0.28
Seed dispersal (no.seeds/m²)
7.5
5.0
2.5
0.0
Shannon's H' = 3.34
Pielou's J = 0.96
Ranking of plant species

Fig. 2

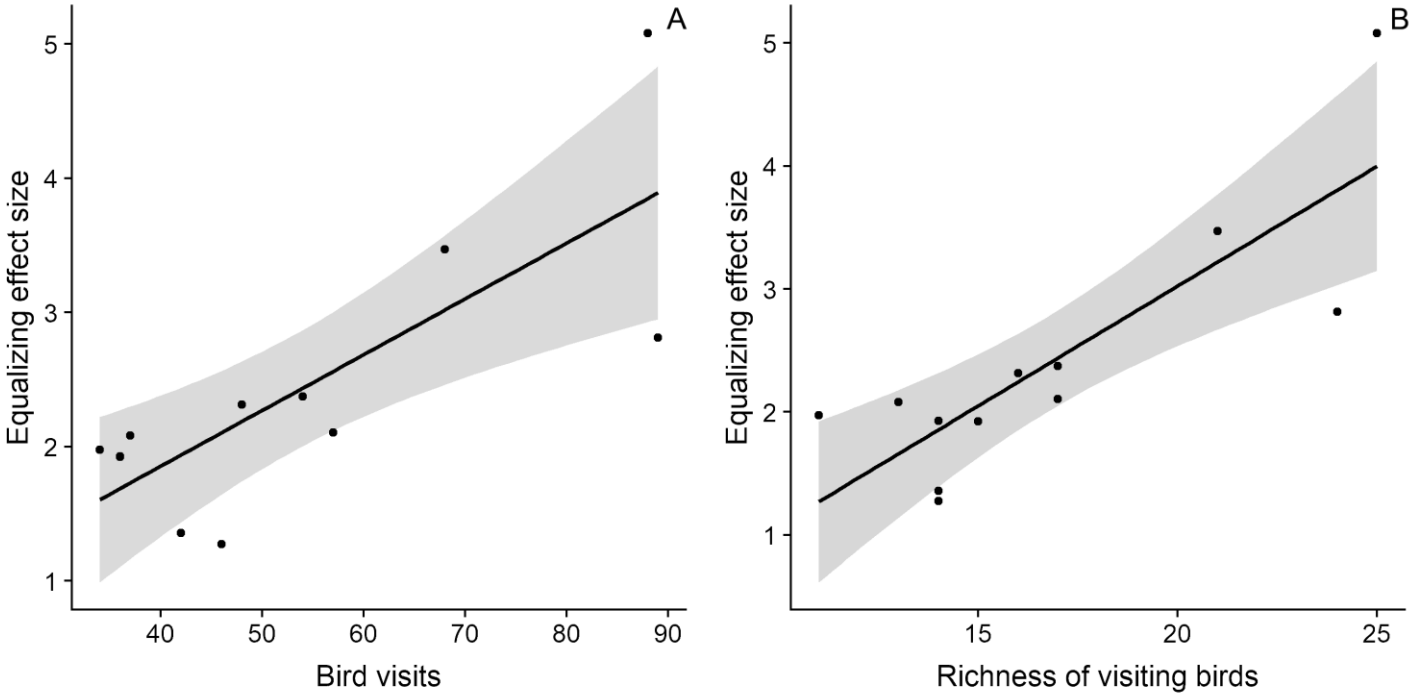

A
B
Equalizing effect size
Bird visits
Richness of visiting birds
1
2
3
4
5
40
50
60
70
80
90
15
20
25

Fig. 3

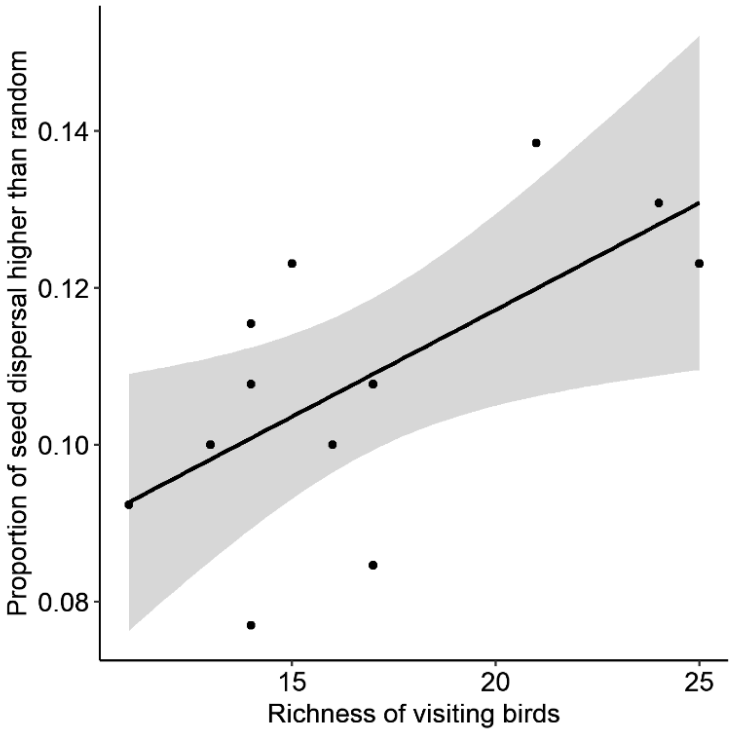

Proportion of seed dispersal higher than random
0.14
0.12
0.10
0.08
15
20
25
Richness of visiting birds

Fig. 4

Supplementary material

Table S1. Bird species recorded at point counts in forest fragments of the 12 study sites.

	Sites											
Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Amazona aestiva	5	10	0	0	18	0	7	0	10	19	18	14
Amazilia lactea	1	1	1	0	4	7	1	3	2	0	2	4
Amazilia versicolor	3	1	0	0	1	0	1	0	2	3	1	1
Ammodramus humeralis	0	0	4	2	0	0	4	2	0	6	3	2
Anthus lutescens	1	0	2	5	0	0	1	0	2	0	0	0
Anthracothorax nigricollis	0	0	0	0	0	0	1	0	2	0	2	3
Aramides saracura	3	3	6	0	0	2	0	0	1	0	0	0
Attila rufus	2	1	0	0	0	0	0	0	0	0	0	5
Automolus leucophthalmus	15	6	0	0	10	0	10	0	9	6	0	15
Baryphthengus ruficapillus	0	3	0	0	11	13	6	0	0	9	10	10
Basileuterus culicivorus	31	50	21	30	49	41	25	36	43	40	25	63
Brotogeris chiriri	0	3	0	0	8	0	1	0	0	11	7	4
Bubulcus ibis	10	0	0	0	0	0	0	0	0	0	0	0
Buteo brachyurus	0	0	0	0	0	1	2	0	0	0	0	0
Camptostoma obsoletum	35	29	29	31	40	32	26	20	34	18	30	26
Campephilus robustus	4	5	11	0	0	0	0	0	0	2	1	1
Cariama cristata	2	2	4	2	0	3	1	0	0	0	2	1
Caracara plancus	2	4	2	1	3	9	5	3	1	0	0	5
Cathartes aura	0	0	0	0	0	0	0	0	1	0	0	0
Celeus flavescens	1	1	0	0	4	0	0	0	1	4	1	2
Certhiaxis cinnamomeus	6	0	11	0	0	11	0	0	27	0	0	0
Chiroxiphia caudata	4	35	0	2	31	0	0	22	21	24	23	27

	Sites											
Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Chloroceryle amazona	2	0	1	0	0	0	0	0	0	0	0	0
Chloroceryle americana	1	0	1	0	0	0	0	0	0	0	0	0
Chlorostilbon lucidus	1	4	7	2	6	8	7	4	4	6	4	8
Chrysomus ruficapillus	11	0	9	0	0	0	0	0	0	0	0	0
Coereba flaveola	41	34	23	22	30	26	34	25	31	27	28	28
Colaptes campestris	3	3	2	0	3	0	1	4	4	0	3	1
Colonia colonus	0	11	0	0	0	0	0	7	0	0	0	0
Colaptes melanochloros	1	1	0	0	11	14	3	0	8	9	3	8
Columbina squammata	12	4	11	0	19	10	4	0	29	14	14	15
Columbina talpacoti	50	14	28	24	32	32	23	28	45	34	19	29
Conopophaga lineata	2	13	0	0	17	0	12	0	9	12	18	13
Conirostrum speciosum	5	3	0	0	16	26	9	0	6	9	17	16
Coragyps atratus	1	9	0	0	0	0	0	2	1	0	4	0
Coryphospingus cucullatus	2	1	2	10	20	18	10	9	11	8	9	4
Corythopis delalandi	0	3	0	0	10	0	3	0	5	10	15	7
Cranioleuca pallida	2	0	3	0	0	0	4	0	4	3	5	5
Crotophaga ani	20	10	24	17	4	12	0	3	9	14	16	18
Crypturellus parvirostris	0	0	0	0	0	0	0	0	0	0	1	3
Cyanocorax chrysops	13	21	27	15	13	27	36	0	31	16	34	39
Cyanocorax cristatellus	35	24	26	38	53	36	25	32	38	10	29	26
Cyclarhis gujanensis	24	33	22	32	32	42	28	25	33	33	41	35
Dacnis cayana	11	8	21	15	20	22	19	23	9	12	22	35
Dryocopus lineatus	3	3	0	6	6	0	1	9	1	8	16	4
Dysithamnus mentalis	0	8	0	0	14	0	7	0	9	9	17	11

	Sites											
Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Elaenia flavogaster	6	10	10	19	19	9	13	23	19	15	18	9
Elanus leucurus	0	0	2	0	0	0	1	0	1	0	0	1
Elaenia sp.	0	0	0	0	0	0	1	0	0	0	0	0
Emberizoides herbicola	0	1	0	0	0	0	0	0	0	0	0	0
Empidonomus varius	2	0	0	0	23	14	7	25	1	5	8	8
Estrilda astrild	0	0	0	0	0	0	1	0	1	0	0	0
Eupsittula aurea	7	0	0	0	0	0	0	0	0	0	0	0
Euphonia chlorotica	24	24	23	27	34	24	26	16	31	21	20	33
Euphonia cyanocephala	8	10	0	0	20	32	13	0	10	10	7	16
Eupetomena macroura	2	2	1	2	7	6	6	5	1	6	4	4
Euphonia violacea	0	5	0	0	15	0	10	0	9	7	11	13
Falco sparverius	0	0	0	0	0	0	1	0	0	0	0	1
Florisuga fusca	0	2	0	0	1	0	1	0	0	2	0	0
Forpus xanthopterygius	8	18	0	0	24	28	12	0	12	64	36	15
Furnarius rufus	8	22	13	19	24	19	11	26	14	24	14	20
Geothlypis aequinoctialis	0	0	2	2	0	0	5	0	0	0	0	0
Geranoaetus albicaudatus	1	0	0	0	0	7	0	0	0	0	1	0
Gnorimopsar chopi	2	0	1	2	7	5	2	14	3	0	0	8
Guira guira	2	18	14	15	1	11	7	3	12	27	9	14
Habia rubica	0	14	0	0	37	0	20	0	22	16	25	27
Herpetotheres cachinnans	1	0	0	0	0	0	1	0	0	1	1	0
Heterospizias meridionalis	0	0	0	0	0	0	1	2	0	1	0	0
Hirundinea ferruginea	0	0	7	0	1	0	0	0	0	0	0	0
Hirundo rustica	0	0	0	0	0	0	1	0	0	0	0	0

	Sites											
Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Ictinia plumbea	0	0	0	0	0	0	0	3	0	0	0	0
Icterus pyrrhopterus	0	6	0	0	14	0	8	43	12	13	15	7
Knipolegus cyanirostris	0	0	0	0	0	0	2	0	0	0	0	0
Lathrotriccus euleri	0	5	0	0	7	0	4	0	8	8	10	18
Legatus leucophaius	0	11	11	1	7	0	7	3	6	11	8	0
Leptopogon amaurocephalus	2	0	4	0	0	0	0	0	0	0	0	0
Lepidocolaptes angustirostris	4	22	1	14	23	11	3	12	15	16	12	16
Leptotila rufaxilla	0	7	0	0	9	9	9	0	6	11	16	7
Leptotila verreauxi	28	24	35	22	21	26	42	34	26	21	33	30
Lochmias nematura	2	0	5	0	0	8	0	0	7	0	0	0
Machetornis rixosa	1	2	14	0	14	7	1	2	3	11	2	17
Malacoptila striata	2	4	0	0	5	8	4	0	5	5	33	11
Megarynchus pitangua	7	15	20	13	15	10	6	15	14	11	8	10
Melanerpes candidus	2	1	3	2	4	4	2	3	5	0	1	0
Micrastur semitorquatus	1	1	0	0	0	0	0	0	0	1	0	1
Milvago chimachima	1	2	2	2	2	8	1	2	0	2	1	2
Mimus saturninus	14	19	12	6	24	13	54	7	15	20	19	25
Mionectes rufiventris	7	10	0	0	15	17	7	0	5	9	11	8
Molothrus bonariensis	2	2	2	0	5	0	0	38	0	0	0	0
Myiarchus ferox	3	5	10	0	38	5	9	5	9	12	14	16
Myiothlypis flaveola	0	3	0	0	0	0	9	0	8	15	6	13
Myiothlypis leucoblephara	0	9	8	0	28	16	11	0	25	24	13	21
Myiodynastes maculatus	21	29	41	20	13	42	15	15	17	11	16	26
Myiozetetes similis	0	3	0	0	3	10	3	0	4	7	7	8

	Sites											
Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Myiarchus swainsoni	9	10	37	1	32	10	18	5	10	16	12	11
Myiarchus tyrannulus	7	4	0	0	10	11	6	0	3	7	5	0
Nemosia pileata	5	4	0	0	11	6	9	0	7	10	10	13
Nothura maculosa	1	3	0	0	0	2	0	0	0	0	0	0
Nyctidromus albicollis	2	6	0	0	0	0	0	0	0	0	0	0
Pachyramphus polychopterus	0	0	0	0	0	0	0	0	0	5	0	0
Pachyramphus validus	0	5	0	0	8	0	3	0	7	16	15	11
Patagioenas cayennensis	0	4	0	0	9	0	0	0	8	8	6	7
Patagioenas picazuro	49	80	45	29	51	20	80	67	42	44	61	72
Penelope superciliaris	6	4	0	0	10	0	3	0	4	5	7	12
Phaethornis pretrei	0	2	2	0	1	9	3	0	6	3	2	4
Phyllomyias fasciatus	2	1	0	0	7	0	1	0	0	11	0	4
Phylloscartes ventralis	0	13	0	0	11	11	5	0	10	12	36	7
Piaya cayana	10	11	7	6	14	25	5	8	19	12	10	6
Picumnus temminckii	39	24	48	40	26	24	20	10	22	17	22	21
Pionus maximiliani	0	7	0	0	25	0	0	0	0	9	29	19
Pipraeidea melanonota	8	9	11	0	14	0	11	0	9	14	14	12
Pitangus sulphuratus	36	54	35	24	50	35	54	36	55	46	49	43
Platyrinchus mystaceus	0	6	0	0	10	0	0	13	19	8	10	14
Podager nacunda	0	0	0	0	0	0	0	0	1	0	0	0
Poecilotriccus plumbeiceps	2	13	0	0	10	12	7	0	13	11	12	20
Progne chalybea	0	0	0	0	6	0	0	0	0	0	0	0
Procnias nudicollis	2	4	0	0	8	0	0	0	9	9	16	6
Progne tapera	0	0	0	1	0	0	0	0	0	0	0	0

	Sites											
Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Psarocolius decumanus	2	30	0	0	11	0	0	0	33	25	31	0
Pseudoleistes guirahuro	1	0	1	0	0	0	0	0	0	0	0	0
Psittacara leucophthalmus	56	69	24	35	46	41	32	20	27	35	33	46
Pygochelidon cyanoleuca	0	4	1	0	3	0	0	0	0	3	0	1
Pyriglena leucoptera	3	3	0	0	7	0	0	0	8	5	7	13
Pyrocephalus rubinus	0	0	0	0	0	0	1	0	0	1	0	0
Pyroderus scutatus	0	2	0	0	0	0	0	0	0	8	10	7
Ramphocelus carbo	0	4	0	0	16	0	8	0	4	12	4	8
Ramphastos toco	6	18	29	9	20	32	12	16	22	21	20	37
Rupornis magnirostris	2	4	2	1	0	3	1	4	2	4	1	2
Saltator similis	0	3	0	0	14	0	5	0	0	8	13	17
Serpophaga subcristata	8	23	32	20	30	27	17	19	19	15	17	16
Setophaga pitiayumi	13	11	6	19	23	9	4	8	12	10	6	9
Sicalis flaveola	1	0	1	0	12	4	3	0	0	5	3	0
Sicalis luteola	0	0	0	0	2	0	3	0	0	10	0	0
Sittasomus griseicapillus	0	6	0	0	9	0	0	0	5	7	10	9
Spinus magellanicus	6	0	0	0	0	0	1	0	0	0	0	0
Sporophila caerulescens	0	3	2	13	26	21	14	14	7	25	18	18
Sporophila lineola	2	3	0	9	10	3	12	6	14	8	6	11
Sturnella superciliaris	3	0	0	0	0	0	0	0	0	0	0	0
Synallaxis frontalis	34	36	29	17	30	13	28	14	23	18	20	13
Synallaxis ruficapilla	0	8	0	0	12	0	5	11	9	16	9	13
Synallaxis spixi	4	2	20	11	14	11	15	13	18	18	11	19
Syrigma sibilatrix	4	0	0	0	0	0	0	0	0	0	0	0

	Sites											
Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Tachyphonus coronatus	20	15	9	16	35	20	16	15	15	20	12	30
Tangara cayana	36	20	15	28	29	15	25	30	26	11	25	28
Tangara palmarum	22	9	16	17	12	18	21	13	18	9	21	13
Tangara sayaca	35	63	30	36	57	48	35	79	47	47	46	34
Tapera naevia	8	16	0	3	2	0	0	3	7	7	4	3
Tersina viridis	0	2	0	0	16	10	5	0	7	11	10	0
Thamnophilus caerulescens	17	25	23	26	25	26	23	19	16	21	27	21
Thamnophilus doliatus	12	7	11	8	10	18	8	8	11	18	11	15
Thalurania glaucopis	0	0	0	0	0	0	0	0	0	0	0	1
Thamnophilus ruficapillus	2	0	0	0	8	0	3	0	5	4	9	7
Theristicus caudatus	1	0	0	0	0	0	1	0	2	0	1	0
Thlypopsis sordida	6	0	0	0	0	0	5	4	0	12	3	0
Todirostrum cinereum	31	44	36	24	25	29	28	31	33	17	21	28
Todirostrum poliocephalum	12	7	13	6	23	15	12	34	10	12	14	24
Tolmomyias sulphurescens	7	12	31	18	27	8	13	22	12	16	13	22
Trichothraupis melanops	2	15	11	0	18	10	9	0	19	7	7	7
Troglodytes musculus	18	19	27	22	23	50	27	25	32	15	26	21
Trogon surrucura	0	9	0	0	7	0	0	0	5	6	10	25
Turdus albicollis	2	0	0	0	11	26	8	0	8	10	11	13
Turdus amaurochalinus	7	15	17	15	27	32	14	31	19	20	33	25
Turdus leucomelas	29	47	31	36	48	41	38	41	46	42	45	47
Turdus rufiventris	4	4	0	0	22	24	6	0	12	11	26	13
Turdus subalaris	2	1	0	0	11	0	0	0	0	6	8	0
Tyrannus melancholicus	34	37	31	25	57	51	47	33	49	39	36	45

	Sites											
Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Tyrannus savana	6	2	9	0	4	12	3	3	12	3	3	3
Vanellus chilensis	13	3	3	2	1	2	14	2	0	0	1	4
Veniliornis spilogaster	0	0	0	0	3	0	2	0	3	4	9	4
Vireo chivi	6	4	6	9	9	0	5	0	5	6	10	22
Volatinia jacarina	3	0	21	2	0	0	2	1	0	0	0	1
Xenops rutilans	0	0	0	0	0	0	1	0	0	0	0	0
Xolmis cinereus	4	0	3	0	5	20	5	1	0	3	0	4
Xolmis velatus	5	0	0	0	6	5	0	4	2	4	2	3
Zenaida auriculata	31	45	26	20	56	30	43	45	32	41	27	41
Zonotrichia capensis	1	4	7	1	4	2	9	2	3	9	4	7

Table S2. Birds species recorded in the experimental plots on open pastures in the 12 study sites.

Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Ammodramus humeralis	2	1	4	4	0	1	3	4	0	0	0	0
Coereba flaveola	1	2	0	0	1	0	2	1	0	1	0	0
Columbina talpacoti	0	0	0	0	0	0	0	0	0	0	0	1
Coryphospingus cucullatus	2	2	0	0	0	1	6	0	1	2	0	0
Cyanocorax chrysops	1	1	0	0	0	0	1	0	1	0	1	1
Cyanocorax cristatellus	0	1	0	0	0	0	0	0	0	0	2	0
Dacnis cayana	1	0	0	0	2	2	3	0	1	0	0	0
Elaenia flavogaster	0	0	1	0	0	1	0	0	0	0	1	2
Elaenia sp.	1	3	0	1	2	1	2	2	1	0	0	1
Empidonomus varius	1	2	1	1	1	0	0	0	0	2	2	1
Euphonia chlorotica	0	2	0	0	1	0	1	0	0	0	0	1
Euphonia cyanocephala	0	1	0	0	0	0	1	0	0	1	1	1
Euphonia violacea	0	1	0	0	0	0	0	0	0	0	0	1
Forpus xanthopterygius	0	0	0	0	0	0	0	0	0	0	1	0
Icterus pyrrhopterus	0	0	0	0	0	0	0	0	1	1	1	0
Leptotila sp.	0	1	0	0	0	0	0	0	0	0	0	0
Machetornis rixosa	0	0	0	0	0	0	2	0	0	0	0	1
Megarynchus pitangua	0	2	0	0	2	0	0	0	0	1	2	1
Mimus saturninus	3	4	3	1	0	2	3	2	0	0	0	0
Myiarchus ferox	0	0	0	0	0	0	1	0	0	0	1	0
Myiodynastes maculatus	1	0	0	0	1	0	0	0	0	0	0	2
Myiarchus sp.	0	0	1	0	0	0	2	1	0	0	0	0
Nemosia pileata	0	0	0	0	0	0	0	0	0	1	1	0

Bird species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Nothura maculosa	0	0	0	0	0	0	1	0	0	0	0	0
Patagioenas picazuro	0	0	1	0	0	1	0	0	0	0	1	2
Pipraeidea melanonota	0	0	0	0	0	0	0	0	0	0	0	2
Pitangus sulphuratus	13	24	8	11	18	9	18	8	9	11	14	23
Tachyphonus coronatus	0	2	1	0	0	0	2	1	1	0	0	2
Tangara cayana	2	5	0	0	4	0	6	2	3	1	2	3
Tangara palmarum	0	2	0	0	1	0	1	0	0	2	1	1
Tangara sayaca	6	8	3	3	4	4	8	1	2	3	9	6
Turdus amaurochalinus	0	0	0	0	1	0	0	0	0	0	0	2
Turdus leucomelas	1	2	1	0	2	0	1	0	0	0	0	0
Turdus rufiventris	0	1	0	0	0	0	2	0	0	0	0	0
Tyrannus melancholicus	7	13	6	5	8	7	5	7	6	7	7	10
Tyrannus savana	0	1	2	3	3	3	2	4	2	1	0	1
Volatinia jacarina	4	1	1	1	0	1	1	2	1	0	0	0
Xolmis velatus	2	0	3	2	0	3	7	4	0	0	0	0
Zonotrichia capensis	3	0	2	2	0	0	4	2	2	0	0	0

Table S3. Bird-dispersed plant species in forest fragments of the 12 study sites showing species density (mature individuals per hectare), growth form and average seeds availability (seeds per hectare).

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Site 1				
Allophylus edulis	Sapindaceae	4	small tree	176.7
Campomanesia guaviroba	Myrtaceae	4	tree	120000
Campomanesia xanthocarpa	Myrtaceae	32	tree	333333.3
Casearia sylvestris	Salicaceae	68	small tree	1180000
Celtis iguanaea	Cannabaceae	28	shrub	153.3
Cissus erosa	Vitaceae	4	liana	40
Citharexylum myrianthum	Verbanaceae	4	tree	946.7
Cordia superba	Boraginaceae	4	tree	39500
Cupania vernalis	Sapindaceae	20	tree	5655
Eugenia hiemalis	Myrtaceae	4	tree	180
Eugenia sp.	Myrtaceae	4	tree	0
Eugenia uniflora	Myrtaceae	28	tree	21820
Ficus trigona	Moraceae	4	tree	4201666.7
Guarea guidonia	Meliaceae	4	tree	0
Guarea macrophylla	Meliaceae	4	tree	0
Guazuma ulmifolia	Malvaceae	8	tree	334166.7
Lithraea molleoides	Anacardiaceae	12	tree	48333.3
Maytenus evonymoides	Celastraceae	12	tree	20666.7
Myrcia sp.	Myrtaceae	8	tree	0
Myrcia tomentosa	Myrtaceae	4	tree	4666.7
Nectandra megapotamica	Lauraceae	20	tree	20666.7
Ocotea silvestris	Lauraceae	8	tree	48333.3
Ormosia arborea	Fabaceae	12	tree	2000
Phoradendron crassifolium	Santalaceae	4	aerial hemiparasite	31833.3
Piper gaudichaudianum	Piperaceae	4	shrub	11500
Psidium guajava	Myrtaceae	4	tree	0
Randia calycina	Rubiaceae	4	shrub	656
Schinus terebinthifolia	Anacardiaceae	20	tree	155366.7

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Siparuna guianensis	Siparunaceae	4	tree	666.7
Syagrus romanzoffiana	Arecaceae	4	palm	533.3
Trema micrantha	Cannabaceae	4	tree	83333.3
Trichilia casaretti	Meliaceae	12	small tree	23.3
Trichilia elegans	Meliaceae	36	small tree	1488.3
Vitex megapotamica	Lamiaceae	8	tree	3923.3
Xylosma pseudosalzmanii	Salicaceae	12	tree	1733.3
Zanthoxylum acuminatum	Rutaceae	4	tree	4000
Zanthoxylum rhoifolium	Rutaceae	4	tree	80133.3
Site 2				
Abuta selloana	Menispermaceae	4	liana	233.3
Aegiphila integrifolia	Lamiaceae	4	tree	2133.3
Calyptranthes concinna	Myrtaceae	4	small tree	48.3
Casearia decandra	Salicaceae	4	small tree	8700
Casearia gossypiosperma	Salicaceae	4	tree	400
Casearia sylvestris	Salicaceae	88	small tree	8126446.7
Chrysophyllum gonocarpum	Sapotaceae	8	tree	4000
Chrysophyllum marginatum	Sapotaceae	4	tree	0
Cordia sellowiana	Boraginaceae	16	tree	121203.3
Croton floribundus	Euphobiaceae	36	tree	527505
Cupania vernalis	Sapindaceae	60	tree	10170
Endlicheria paniculata	Lauraceae	4	tree	810
Eugenia uniflora	Myrtaceae	4	tree	700
Guarea guidonia	Meliaceae	4	tree	85
Guarea kunthiana	Meliaceae	16	tree	502837
Inga striata	Fabaceae	4	tree	700
Lacistema hasslerianum	Lacistemataceae	36	shrub	7188.3
Maclura tinctoria	Moraceae	8	tree	1466666.7
Nectandra lanceolata	Lauraceae	16	tree	81320
Nectandra oppositifolia	Lauraceae	8	tree	5000
Nectandra sp.	Lauraceae	8	tree	0
Ocotea silvestris	Lauraceae	4	tree	54033.3

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Pera glabrata	Euphobiaceae	4	tree	29900
			aerial	
Phoradendron crassifolium	Santalaceae	12	hemiparasite	109833.3
Prockia crucis	Salicaceae	4	tree	10666.7
Randia calycina	Rubiaceae	4	shrub	266.7
Schefflera morototoni	Araliaceae	4	tree	240133.3
Siparuna guianensis	Siparunaceae	116	tree	157246.7
Sorocea bonplandii	Moraceae	36	small tree	2281.7
Syagrus romanzoffiana	Arecaceae	8	palm	3166.7
Tabernaemontana hystrix	Apocynaceae	8	tree	3008
Trichilia catigua	Meliaceae	8	small tree	163.3
Xylosma pseudosalzmanii	Salicaceae	4	tree	8333.3
Zanthoxylum rhoifolium	Rutaceae	8	tree	7000
Site 3				
Alchornea glandulosa	Euphobiaceae	12	tree	0
Allophylus edulis	Sapindaceae	4	small tree	14.3
Campomanesia xanthocarpa	Myrtaceae	20	tree	108000
Casearia sylvestris	Salicaceae	24	small tree	178666.7
Citharexylum myrianthum	Verbenaceae	20	tree	6973.3
Cupania vernalis	Sapindaceae	8	tree	600
Enterolobium contortisiliquum	Fabaceae	4	tree	0
Erythroxylum pelleterianum	Erythoxylaceae	4	shrub	0
Eugenia hiemalis	Myrtaceae	4	tree	100
Faramea montevidensis	Rubiaceae	12	small tree	70.7
Guazuma ulmifolia	Malvaceae	8	tree	133333.3
Lacistema hasslerianum	Lacistemataceae	4	shrub	0
Maclura tinctoria	Moraceae	4	tree	6666.7
Margaritopsis cephalantha	Rubiaceae	4	tree	33.3
Maytenus gonoclada	Celastraceae	4	tree	213.3
Nectandra megapotamica	Lauraceae	92	tree	85527.3
Ocotea velutina	Lauraceae	12	tree	69666.7

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
			aerial	
Phoradendron crassifolium	Santalaceae	4	hemiparasite	16666.7
Piper gaudichaudianum	Piperaceae	16	shrub	14000
Prockia crucis	Salicaceae	4	tree	6833.3
Randia calycina	Rubiaceae	8	shrub	1866.7
Rhamnidium elaeocarpum	Rhamnaceae	4	tree	1083.3
Schinus terebinthifolia	Anacardiaceae	4	tree	80366.7
Siparuna guianensis	Siparunaceae	4	tree	2333.3
Syagrus romanzoffiana	Arecaceae	4	palm	0
Trema micrantha	Cannabaceae	4	tree	666.7
Trichilia pallida	Meliaceae	4	tree	92.7
Vitex megapotamica	Lamiaceae	16	tree	60000
Zanthoxylum monogynum	Rutaceae	4	tree	0
Site 4				
Actinostemon concepcionis	Euphobiaceae	4	shrub	1310
Aegiphila integrifolia	Lamiaceae	4	tree	550
Allophylus edulis	Sapindaceae	4	small tree	176.7
Annona sylvatica	Annonaceae	4	tree	9450
Casearia sylvestris	Salicaceae	56	small tree	142000
Celtis iguanaea	Cannabaceae	4	shrub	13.3
Citrus limon	Rutaceae	8	small tree	23.3
Cordia superba	Boraginaceae	28	tree	28333.3
Cupania vernalis	Sapindaceae	28	tree	11570
Endlicheria paniculata	Lauraceae	24	tree	7516.7
Eugenia uniflora	Myrtaceae	4	tree	0
Guapira hirsuta	Nyctaginaceae	4	tree	1166.7
Guazuma ulmifolia	Malvaceae	8	tree	166666.7
Jacaratia spinosa	Caricaceae	4	tree	2586.7
Maclura tinctoria	Moraceae	16	tree	1480000
Maprounea guianensis	Euphobiaceae	8	tree	508000
Matayba elaeagnoides	Sapindaceae	4	tree	0
Mollinedia widgrenii	Monimiaceae	8	tree	276.3

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Nectandra cuspidata	Lauraceae	12	tree	10666.7
Nectandra megapotamica	Lauraceae	96	tree	48866.7
Ocotea nutans	Lauraceae	8	tree	173333.3
Ocotea silvestris	Lauraceae	24	tree	39966.7
			aerial	
Phoradendron crassifolium	Santalaceae	4	hemiparasite	16666.7
Piper amalago	Piperaceae	4	shrub	10666.7
Piper arboreum	Piperaceae	8	shrub	3333.3
Psidium guajava	Myrtaceae	4	tree	17400
Psychotria carthagenensis	Rubiaceae	4	shrub	586.7
Sebastiania brasiliensis	Euphobiaceae	4	tree	500
Siparuna guianensis	Siparunaceae	4	tree	21066.7
Sorocea bonplandii	Moraceae	8	small tree	86.7
Styrax pohlii	Styracaceae	8	tree	0
Tabernaemontana hystrix	Apocynaceae	4	tree	288
Site 5				
Actinostemon concepcionis	Euphobiaceae	36	shrub	6451
Allophylus edulis	Sapindaceae	8	small tree	123.3
Amaioua intermedia	Rubiaceae	8	tree	116.7
Casearia sylvestris	Salicaceae	32	small tree	1062933.3
Celtis iguanaea	Cannabaceae	4	shrub	0
Chionanthus filiformis	Oleaceae	4	tree	0
Colubrina glandulosa	Rhamnaceae	4	tree	35000
Cordia ecalyculata	Boraginaceae	16	tree	105666.7
Cordia sellowiana	Boraginaceae	24	tree	1000
Croton floribundus	Euphobiaceae	32	tree	196300
Cupania vernalis	Sapindaceae	40	tree	12465
Diospyros inconstans	Ebenaceae	8	tree	0
Eriobotrya japonica	Rosaceae	4	tree	0
Erythroxylum deciduum	Erythoxylaceae	4	tree	0
Eugenia blastantha	Myrtaceae	8	small tree	97
Eugenia florida	Myrtaceae	4	tree	0

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Eugenia hiemalis	Myrtaceae	8	tree	1866.7
Eugenia subterminalis	Myrtaceae	4	tree	6.7
Eugenia uniflora	Myrtaceae	12	tree	101900
Ficus luschnathiana	Moraceae	4	tree	36000
Geissanthus ambiguus	Primulaceae	4	shrub	136.7
Ilex dumosa	Aquifoliaceae	48	tree	1766.7
Inga vera	Fabaceae	4	tree	0
Ixora venulosa	Rubiaceae	4	shrub/small tree	146.7
Mabea fistulifera	Euphobiaceae	4	tree	0
Maclura tinctoria	Moraceae	4	tree	213333.3
Maprounea guianensis	Euphobiaceae	4	tree	5000
Maytenus evonymoides	Celastraceae	16	tree	10064.7
Miconia ligustroides	Melastomataceae	4	shrub	1840
Micrandra elata	Euphobiaceae	4	tree	0
Mollinedia widgrenii	Monimiaceae	8	tree	100
Myrcianthes pungens	Myrtaceae	4	tree	26.7
Myrsine umbellata	Primulaceae	4	tree	6.7
Nectandra cuspidata	Lauraceae	8	tree	0
Ocotea silvestris	Lauraceae	4	tree	0
Phoradendron crassifolium	Santalaceae	4	aerial hemiparasite	133.3
Pilocarpus pauciflorus	Rutaceae	8	tree	0
Piper amalago	Piperaceae	12	shrub	17066.7
Piper gaudichaudianum	Piperaceae	4	shrub	0
Prockia crucis	Salicaceae	8	tree	1333.3
Protium heptaphyllum	Burseraceae	8	tree	3800
Prunus myrtifolia	Rosaceae	8	tree	266.7
Psychotria carthagenensis	Rubiaceae	4	shrub	50
Psychotria leiocarpa	Rubiaceae	4	shrub	40
Randia calycina	Rubiaceae	4	shrub	37.3
Rhamnidium elaeocarpum	Rhamnaceae	4	tree	0
Sebastiania brasiliensis	Euphobiaceae	4	tree	8872
Siparuna guianensis	Siparunaceae	8	tree	0

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Solanum argenteum	Solanaceae	4	small tree	10000
Strychnos brasiliensis	Loganiaceae	4	tree	25
Tapirira guianensis	Anacardiaceae	4	tree	9000
Trichilia casaretti	Meliaceae	28	small tree	197.7
Trichilia catigua	Meliaceae	36	small tree	218
Trichilia elegans	Meliaceae	52	small tree	522.7
Xylopia brasiliensis	Annonaceae	4	tree	0
Zanthoxylum rhoifolium	Rutaceae	8	tree	1700
Site 6				
Allophylus edulis	Sapindaceae	4	small tree	17.3
Calyptranthes clusiifolia	Myrtaceae	8	tree	3333.3
Campomanesia guazumifolia	Myrtaceae	48	tree	560000
Campomanesia xanthocarpa	Myrtaceae	64	tree	292666.7
Casearia sylvestris	Salicaceae	88	small tree	200266.7
Cecropia pachystachya	Urticaceae	4	tree	63000
Cordia sellowiana	Boraginaceae	4	tree	0
Croton floribundus	Euphobiaceae	8	tree	132000
Cupania vernalis	Sapindaceae	4	tree	500
Diospyros inconstans	Ebenaceae	4	tree	14000
Endlicheria paniculata	Lauraceae	4	tree	0
Enterolobium contortisiliquum	Fabaceae	8	tree	490000
Eriobotrya japonica	Rosaceae	4	tree	0
Eugenia uniflora	Myrtaceae	4	tree	8
Guazuma ulmifolia	Malvaceae	8	tree	3750000
Hybanthus bigibbosus	Violaceae	8	herb	2800
Lacistema hasslerianum	Lacistemataceae	4	shrub	0
Lithraea molleoides	Anacardiaceae	4	tree	4166.7
Matayba elaeagnoides	Sapindaceae	4	tree	0
Nectandra cuspidata	Lauraceae	4	tree	21433.3
Nectandra megapotamica	Lauraceae	4	tree	0
Pera glabrata	Euphobiaceae	8	tree	8500
Prockia crucis	Salicaceae	4	tree	6666.7

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Psidium guajava	Myrtaceae	4	tree	0
Sapium glandulosum	Euphobiaceae	4	tree	0
Schinus terebinthifolia	Anacardiaceae	24	tree	902033.3
Sebastiania brasiliensis	Euphobiaceae	4	tree	0
Siparuna guianensis	Siparunaceae	4	tree	106.7
Syagrus romanzoffiana	Arecaceae	4	palm	1533.3
Tabernaemontana hystrix	Apocynaceae	4	tree	1320
Trichilia casaretti	Meliaceae	12	small tree	85
Vitex megapotamica	Lamiaceae	4	tree	0
Zanthoxylum fagara	Rutaceae	12	tree	8000
Zanthoxylum petiolare	Rutaceae	4	tree	0
Zanthoxylum rhoifolium	Rutaceae	4	tree	8000
Site 7				
Aegiphila integrifolia	Lamiaceae	4	tree	783.3
Allophylus edulis	Sapindaceae	16	small tree	1763.3
Amaioua intermedia	Rubiaceae	4	tree	0
Casearia sylvestris	Salicaceae	96	small tree	433546.7
Celtis iguanaea	Cannabaceae	8	shrub	1466.7
Citrus limon	Rutaceae	4	small tree	366.7
Cordia ecalyculata	Boraginaceae	4	tree	38.7
Cordia sellowiana	Boraginaceae	4	tree	0
Cupania vernalis	Sapindaceae	24	tree	0
Endlicheria paniculata	Lauraceae	4	tree	0
Erythroxylum cuneifolium	Erythoxylaceae	4	shrub	0
Eugenia uniflora	Myrtaceae	4	tree	0
Guazuma ulmifolia	Malvaceae	4	tree	0
Hybanthus bigibbosus	Violaceae	16	herb	14273.3
Ilex dumosa	Aquifoliaceae	4	tree	0
Inga edulis	Fabaceae	8	tree	1666.7
Lithraea molleoides	Anacardiaceae	4	tree	933.3
Maclura tinctoria	Moraceae	4	tree	33333.3
Maytenus evonymoides	Celastraceae	8	tree	0

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Maytenus gonoclada	Celastraceae	8	tree	4133.3
Paullinia meliifolia	Sapindaceae	4	liana	66.7
			aerial	
Phoradendron crassifolium	Santalaceae	8	hemiparasite	340
Piper amalago	Piperaceae	4	shrub	0
Protium heptaphyllum	Burseraceae	4	tree	0
Prunus myrtifolia	Rosaceae	4	tree	1000
Psidium guajava	Myrtaceae	16	tree	36900
Psychotria carthagenensis	Rubiaceae	12	shrub	97.3
Rubus bogotensis var. brasiliensis	Rosaceae	4	shrub	2030
Schinus terebinthifolia	Anacardiaceae	32	tree	2945366.7
Siparuna guianensis	Siparunaceae	24	tree	4300
Solanum pseudoquina	Solanaceae	4	small tree	10000
Strychnos brasiliensis	Loganiaceae	8	tree	1
Syagrus romanzoffiana	Arecaceae	4	palm	200
Symplocos sp.	Symplocaceae	4	tree	0
Tabernaemontana hystrix	Apocynaceae	4	tree	0
Trichilia casaretti	Meliaceae	4	small tree	100
Trichilia elegans	Meliaceae	4	small tree	0
Zanthoxylum fagara	Rutaceae	12	tree	7666.7
Site 8				
Aparisthmium cordatum	Euphobiaceae	8	tree	8133.3
Campomanesia guazumifolia	Myrtaceae	4	tree	0
Campomanesia xanthocarpa	Myrtaceae	8	tree	74666.7
Casearia sylvestris	Salicaceae	88	small tree	470666.7
Chomelia pohliana	Rubiaceae	4	small tree	0
Citrus limon	Rutaceae	8	small tree	183.3
Croton floribundus	Euphobiaceae	16	tree	315400
Cupania vernalis	Sapindaceae	8	tree	0
Enterolobium contortisiliquum	Fabaceae	4	tree	0
Ficus luschnathiana	Moraceae	8	tree	76500
Hyeronima alchorneoides	Phyllanthaceae	8	tree	0

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Maclura tinctoria	Moraceae	4	tree	356666.7
Nectandra megapotamica	Lauraceae	20	tree	13400.7
Ocotea silvestris	Lauraceae	4	tree	100
Prunus myrtifolia	Rosaceae	4	tree	666.7
Psidium guajava	Myrtaceae	4	tree	0
Schinus terebinthifolia	Anacardiaceae	8	tree	181333.3
Siparuna guianensis	Siparunaceae	16	tree	260
Solanum sp.	Solanaceae	16	shrub	119666.7
Strychnos brasiliensis	Loganiaceae	4	tree	16.7
Syagrus romanzoffiana	Arecaceae	4	palm	516.7
Tabernaemontana hystrix	Apocynaceae	8	tree	1600
Trema micrantha	Cannabaceae	20	tree	382833.3
Trichilia elegans	Meliaceae	8	small tree	6
Xylosma pseudosalzmanii	Salicaceae	12	tree	97166.7
Zanthoxylum fagara	Rutaceae	4	tree	333.3
Site 9				
Actinostemon concepcionis	Euphobiaceae	28	shrub	2680
Annona sylvatica	Annonaceae	4	tree	4900
Campomanesia xanthocarpa	Myrtaceae	36	tree	1008000
Casearia decandra	Salicaceae	4	small tree	12000
Casearia sylvestris	Salicaceae	112	small tree	1305533.3
Chrysophyllum marginatum	Sapotaceae	4	tree	833.3
Cissus serroniana	Vitaceae	4	liana	533.3
Copaifera langsdorffii	Fabaceae	8	tree	0
Cupania vernalis	Sapindaceae	8	tree	12500
Eugenia involucrata	Myrtaceae	4	tree	666.7
Ficus citrifolia	Moraceae	20	tree	2655433.3
Ficus enormis	Moraceae	4	tree	500000
Maclura tinctoria	Moraceae	8	tree	13333.3
Nectandra lanceolata	Lauraceae	4	tree	10000
Nectandra megapotamica	Lauraceae	28	tree	12333.3
Persea willdenovii	Lauraceae	4	tree	151666.7

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Piper amalago	Piperaceae	4	shrub	5866.7
Piper gaudichaudianum	Piperaceae	4	shrub	5000
Psidium guajava	Myrtaceae	4	tree	9840
Randia calycina	Rubiaceae	12	shrub	5200
Siparuna guianensis	Siparunaceae	4	tree	0
Syagrus romanzoffiana	Arecaceae	8	palm	3030
Tabernaemontana hystrix	Apocynaceae	16	tree	2344
Xylosma pseudosalzmanii	Salicaceae	4	tree	7166.7
Zanthoxylum caribaeum	Rutaceae	4	tree	53333.3
Site 10				
Actinostemon concepcionis	Euphobiaceae	4	shrub	100
Actinostemon concolor	Euphobiaceae	4	shrub	0
Allophylus edulis	Sapindaceae	4	small tree	1266.7
Amaioua intermedia	Rubiaceae	4	tree	1733.3
Calyptranthes sp.	Myrtaceae	4	small tree	6666.7
Campomanesia guazumifolia	Myrtaceae	8	tree	0
Casearia decandra	Salicaceae	20	small tree	102585
Casearia sylvestris	Salicaceae	36	small tree	256000
Citronella paniculata	Cardiopteridaceae	4	tree	0
Colubrina glandulosa	Rhamnaceae	4	tree	25200
Copaifera langsdorffii	Fabaceae	8	tree	0
Cordia sellowiana	Boraginaceae	12	tree	34503.3
Cordia superba	Boraginaceae	4	tree	0
Cupania vernalis	Sapindaceae	48	tree	4420
Endlicheria paniculata	Lauraceae	12	tree	805
Erythroxylum pelleterianum	Erythoxylaceae	24	shrub	19086.7
Eugenia myrcianthes	Myrtaceae	8	tree	800
Eugenia uniflora	Myrtaceae	4	tree	433.3
Ficus trigona	Moraceae	12	tree	2294750
Guapira hirsuta	Nyctaginaceae	16	tree	3006.7
Guapira opposita	Nyctaginaceae	8	tree	1673.3
Guarea macrophylla	Meliaceae	4	tree	7500

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Guazuma ulmifolia	Malvaceae	4	tree	0
Hyeronima alchorneoides	Phyllanthaceae	8	tree	24500
Lithraea molleoides	Anacardiaceae	8	tree	15833.3
Matayba elaeagnoides	Sapindaceae	16	tree	467320
Mollinedia widgrenii	Monimiaceae	4	tree	0
Myrceugenia sp.	Myrtaceae	8	small tree	0
Myrcianthes pungens	Myrtaceae	4	tree	0
Myrciaria floribunda	Myrtaceae	4	tree	150
Myrsine lancifolia	Primulaceae	4	tree	98.3
Nectandra lanceolata	Lauraceae	8	tree	118000
Nectandra megapotamica	Lauraceae	16	tree	10000
Pera glabrata	Euphobiaceae	16	tree	1060200
Phoradendron crassifolium	Santalaceae	20	aerial hemiparasite	256600
Plinia rivularis	Myrtaceae	4	tree	4066.666667
Prunus myrtifolia	Rosaceae	4	tree	16666.7
Psidium guajava	Myrtaceae	4	tree	0
Psychotria carthagenensis	Rubiaceae	8	shrub	690
Rauvolfia sellowii	Apocynaceae	8	tree	400
Rudgea jasminoides	Rubiaceae	4	tree	50.7
Schinus terebinthifolia	Anacardiaceae	8	tree	0
Siparuna guianensis	Siparunaceae	84	tree	146883.3
Syagrus romanzoffiana	Arecaceae	4	palm	466.7
Tabernaemontana hystrix	Apocynaceae	4	tree	80
Tapirira guianensis	Anacardiaceae	8	tree	6666.7
Trichilia casaretti	Meliaceae	4	small tree	0
Trichilia elegans	Meliaceae	4	small tree	50
Urera baccifera	Urticaceae	8	shrub	0
Zanthoxylum fagara	Rutaceae	4	tree	6100
Zanthoxylum monogynum	Rutaceae	12	tree	5333.3
Site 11				
Aegiphila integrifolia	Lamiaceae	4	tree	4000

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Alibertia concolor	Rubiaceae	4	shrub	2363.3
Amaioua intermedia	Rubiaceae	4	tree	1833.3
Aparisthmium cordatum	Euphobiaceae	4	tree	333.3
Byrsonima laxiflora	Malpighiaceae	4	tree	1205
Cabralea canjerana	Meliaceae	4	tree	52866.7
Calyptranthes concinna	Myrtaceae	4	small tree	6.3
Casearia gossypiosperma	Salicaceae	4	tree	0
Casearia sylvestris	Salicaceae	16	small tree	41733.3
Citharexylum myrianthum	Verbenaceae	4	tree	0
Citronella paniculata	Cardiopteridaceae	4	tree	0
Cordia ecalyculata	Boraginaceae	4	tree	4000
Cordia sellowiana	Boraginaceae	8	tree	1183.3
Croton floribundus	Euphobiaceae	20	tree	0
Cupania vernalis	Sapindaceae	8	tree	7800
Diospyros inconstans	Ebenaceae	8	tree	300
Erythroxylum deciduum	Erythoxylaceae	4	tree	91666.7
Eugenia blastantha	Myrtaceae	4	small tree	88.3
Eugenia involucrata	Myrtaceae	8	tree	4733.3
Eugenia uniflora	Myrtaceae	4	tree	0
Ficus pulchella	Moraceae	4	tree	366666.7
Guapira opposita	Nyctaginaceae	4	tree	450
Guatteria nigrescens	Annonaceae	4	tree	16.7
Holocalyx balansae	Fabaceae	4	tree	2400
Hyeronima alchorneoides	Phyllanthaceae	8	tree	500
Ixora venulosa	Rubiaceae	8	shrub/small tree	733.3
Maprounea guianensis	Euphobiaceae	80	tree	2061550
Matayba elaeagnoides	Sapindaceae	4	tree	0
Maytenus gonoclada	Celastraceae	4	tree	640
Miconia albicans	Melastomataceae	4	shrub	1386.7
Myrcia rostrata	Myrtaceae	4	tree	141.3
Myrcia tomentosa	Myrtaceae	8	tree	1300
Myrsine umbellata	Primulaceae	4	tree	26.7
Nectandra lanceolata	Lauraceae	8	tree	0

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Ocotea corymbosa	Lauraceae	12	tree	400666.7
Ouratea spectabilis	Ochnaceae	4	tree	1833.3
Pera glabrata	Euphobiaceae	12	tree	77000
			aerial	
Phoradendron crassifolium	Santalaceae	4	hemiparasite	15666.7
Protium heptaphyllum	Burseraceae	8	tree	52000
Psychotria leiocarpa	Rubiaceae	4	shrub	41.3
Rauvolfia sellowii	Apocynaceae	12	tree	268.3
Schefflera vinosa	Araliaceae	4	tree	500
Schinus terebinthifolia	Anacardiaceae	8	tree	0
Sebastiania brasiliensis	Euphobiaceae	12	tree	1200
Siparuna guianensis	Siparunaceae	152	tree	323286.7
Sloanea hirsuta	Elaeocarpaceae	4	tree	0
Syagrus romanzoffiana	Arecaceae	8	palm	1150
Terminalia triflora	Combretaceae	4	tree	0
Zanthoxylum monogynum	Rutaceae	4	tree	1466.7
Site 12				
Actinostemon concepcionis	Euphobiaceae	36	shrub	3086
Actinostemon concolor	Euphobiaceae	24	shrub	470
Allophylus edulis	Sapindaceae	8	small tree	207
Campomanesia xanthocarpa	Myrtaceae	4	tree	0
Casearia sylvestris	Salicaceae	24	small tree	30666.7
Cecropia pachystachya	Urticaceae	4	tree	75000
Chrysophyllum marginatum	Sapotaceae	4	tree	0
Cordia sellowiana	Boraginaceae	24	tree	1113186.7
Croton floribundus	Euphobiaceae	20	tree	158500
Cupania vernalis	Sapindaceae	36	tree	120600
Dendropanax cuneatus	Araliaceae	4	tree	1541.7
Eugenia ramboi	Myrtaceae	4	tree	0
Eugenia sp2	Myrtaceae	4	tree	0
Eugenia sp3	Myrtaceae	4	tree	216666.7
Eugenia uniflora	Myrtaceae	4	tree	0

Plant species	Family	Mature ind. ha^{-1}	Growth Form	Avg. seeds ha^{-1}
Euterpe edulis	Arecaceae	28	palm	11833
Guapira hirsuta	Nyctaginaceae	4	tree	611.7
Guazuma ulmifolia	Malvaceae	12	tree	33333.3
Ilex dumosa	Aquifoliaceae	4	tree	0
Lacistema hasslerianum	Lacistemataceae	8	shrub	1200
Maclura tinctoria	Moraceae	4	tree	13333.3
Maytenus floribunda	Celastraceae	4	tree	0
Maytenus ilicifolia	Celastraceae	4	tree	0
Mollinedia widgrenii	Monimiaceae	4	tree	673.3
Myrciaria floribunda	Myrtaceae	8	tree	78
Myrtaceae sp3	Myrtaceae	4	tree	0
Nectandra megapotamica	Lauraceae	4	tree	0
Ocotea silvestris	Lauraceae	4	tree	8392953.3
Ocotea velutina	Lauraceae	8	tree	1021666.7
Pera glabrata	Euphobiaceae	4	tree	50000
Persea willdenovii	Lauraceae	4	tree	0
Psychotria leiocarpa	Rubiaceae	4	shrub	20
Randia calycina	Rubiaceae	4	shrub	906.7
Rauvolfia sellowii	Apocynaceae	8	tree	66.7
Rhamnidium elaeocarpum	Rhamnaceae	4	tree	793.3
Schoepfia brasiliensis	Schoepfiaceae	8	tree	83.3
Siparuna guianensis	Siparunaceae	4	tree	1500
Sorocea bonplandii	Moraceae	32	small tree	1275.7
Strychnos brasiliensis	Loganiaceae	8	tree	20
Styrax acuminatus	Styracaceae	20	tree	1000
Syagrus romanzoffiana	Arecaceae	12	palm	2976.7
Tabernaemontana hystrix	Apocynaceae	4	tree	316
Trichilia catigua	Meliaceae	28	small tree	94.7
Trichilia elegans	Meliaceae	20	small tree	137.3
Trichilia pallida	Meliaceae	12	tree	166.7
Xylosma pseudosalzmanii	Salicaceae	4	tree	25666.7
Zanthoxylum monogynum	Rutaceae	4	tree	5333.3

Table S4. Bird-dispersed plant species (per m²) recorded in seed traps in experimental plots on open pastures in the 12 study sites.

	Sites											
Plant species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Abuta selloana	0	1.5	0	0	0	0	0	0	0	0	0	0
Aegiphila integrifolia	0	1.5	0	1	0	0.5	1	0	0	0	1	0
Alchornea glandulosa	0	1	0	0	0	0	0	0.5	0	0.5	0	0
Allophylus edulis	0.5	0	0	2	1	0.5	1	0	0	1	0	1
Annona sylvatica	0	0	0	1	0	0	0	0	0.5	0	0	0
Cabralea canjerana	0	0	0	0	0	0	0	0	0	0	1.5	0
Calyptranthes sp	0	0	0	0	0	0.5	0	0	0	0	0	0
Campomanesia guaviroba	0	0	0	0	0	0.5	0	0	0	0.5	0	0
Campomanesia xanthocarpa	2.5	0	1	0.5	0	0.5	0	1.5	2	0	0	1.5
Casearia decandra	0	0	0	0	0	0	0	0	1	0.5	0	0
Casearia sylvestris	3.5	4.5	2	3.5	7	1.5	3	6	4	2	1.5	3
Cecropia pachystachya	0	0	0	0	0	1	0	0	0	0	0	2
Celtis iguanaea	0.5	0	0	0.5	0	0	0.5	0	0.5	0	0	0
Chrysophyllum gonocarpum	0	1	0	0	0	0	0	0	0	0	0	0

	Sites											
Plant species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Chrysophyllum marginatum	0	0	0	0	0	0	0	0	0	0	0.5	0
Citharexylum myrianthum	1	0	0.5	0	0	0	0	0	0	0	1	0
Copaifera langsdorffii	0	0	0	0	0	0	0	0	1	0	0	0
Cordia ecalyculata	1.5	0	1	0	1	0	1.5	0	0	0	1.5	0
Cordia sellowiana	0	2	0	0	0.5	0.5	0	0	0.5	1	0	3.5
Cordia superba	0	0	0	0.5	0	0	0	0	0	0	0	0
Croton floribundus	0	2	0	0	1.5	2	0	1	0.5	0	1	3
Cupania vernalis	1.5	2	2.5	0.5	3.5	1	0.5	1	1.5	2.5	1.5	2
Dendropanax cuneatus	0	0	0	0	0	0	0	0	0	0	0	0.5
Endlicheria paniculata	0	0.5	0	0.5	0	0	1	0.5	0	1	0.5	0
Erythroxylum deciduum	0	0	0	0	0.5	0	0	0	0	0	1.5	0
Erythroxylum pelleterianum	0	0	0.5	0	0	0	0	0	0	1	0	0
Eugenia involucrata	0	0	0	0	0	0	0	0	0.5	0	0	0
Eugenia uniflora	0.5	1.5	0	0.5	1	0	1.5	0	0.5	0.5	0	2
Euterpe edulis	0	0.5	0.5	0	0	0	0	0	0	0	0	1.5

	Sites											
Plant species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Ficus sp	0	0	0	0	0	0	0	0	3	0	6	0
Guapira sp	0	0	0	0	0	0.5	0	0	0	1.5	0	0
Guarea kunthiana	1.5	1.5	0	0	0	0	0	0	0	0	0	0
Guatteria nigrescens	0	0	0	0	0	0	0	0	0	0	0.5	0
Guazuma ulmifolia	1.5	0	1.5	0	0	1	0	0	0	0.5	0	1.5
Hyeronima alchorneoides	0	0	0	0	0	0	0	0.5	0	0	0	0
Ilex sp	0	0	0	0	0.5	0.5	0	0.5	0	0	0	1
Ixora venulosa	0	0	0	0	0.5	0	0	0	0	0	0	0
Jacaratia spinosa	0	0	0	0.5	0	0	0	0	0	0	0	0
Lacistema hasslerianum	0	2	0	0	0	0	0	0	0	0	0	0.5
Lauraceae 1	0	0	0	0.5	0	1.5	0	1	0.5	0	0	0
Lauraceae 2	0	0	0	0	1.5	0	0	0	0.5	0	0	0
Lauraceae 3	0	0	0	0	0	0.5	0	0	0	0	0	3
Lauraceae 4	0	0	0	0	0	0	0	0	1	0	0	0
Lauraceae 5	0	0	0	0	0	0	0	0	0	0	1	0

	Sites											
Plant species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Lauraceae 6	0	0	0	0	0	0	0	0	0	0	0	1.5
Lithraea molleoides	0.5	0.5	0	0	0	1	2	0	0	1	0	0
Maclura tinctoria	0	0.5	0	1	1	0	0.5	2.5	0.5	0	0	0
Magnolia Ovata	0	0	0	0	0	0	0	0	0	0	1.5	0
Maprounea guianensis	0	0	0	0.5	0.5	0	0	0	0	0	2	0
Maytenus gonoclada	0	0	0	0.5	0	0	1	0	0	0	1.5	0
Melastomataceae 1	0	0	2.5	0	2.5	0	0	0	0	0	0	0
Melastomataceae 2	0	0	0	0	0	0	0	0	0	0	0	1.5
Melastomataceae 3	0	0	0	0	0	0	0	0	0	6	0	0
Mollinedia widgrenii	0	0	0	1	1	0	0	0	0.5	0.5	0	1
Myrceugenia sp	0.5	0	0	0	0	0	0	0	0	0	0	0
Myrsine sp	0	0	0	0	0.5	0	0	0	0	0	0	0
Mytaceae 1	0.5	0	0	0	0.5	0	0.5	0	0	0	0	0
Mytaceae 2	0	1	0	0	0	0	0	0	0	0	1.5	0
Mytaceae 3	0	0	0	0	0	0	0	0.5	0	0	0	0.5

	Sites											
Plant species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Mytaceae 4	0	0	0	0	0	0	0	0.5	0	0	0	2
Mytaceae 5	0	0	0	0	0	0	0	0	0	0	0	0.5
Nectandra lanceolata	0	0.5	0	0	0	0	0	0	0	0	0	0
Nectandra megapotamica	1.5	0	0.5	0.5	0	0	0	0.5	0	0.5	0	1
Ormosia arborea	1	0	0	0	0	0	0	0	0	0	0	0
Pera glabrata	0.5	2.5	1.5	0	1	1.5	0	0	0	3	2	2
Phoradendron crassifolium	1.5	0.5	0	0	0.5	0	1.5	0	0	1	0.5	0
Piper sp	0	0	0	2	2	0	2	0	0.5	0	0	2
Prockia crucis	0	0	1	0	0	0	0	0	0	0	0	0
Protium heptaphyllum	0	0	0	0	1	0	0.5	0	0	0	1.5	0
Prunus myrtifolia	0	0	0	0	1.5	1	1	0.5	0	1	0	0
Psidium guajava	1	5.5	0	1	0	0	1.5	0	0.5	0.5	0	0
Psychotria sp	0.5	0	0.5	0	2	0	0.5	0	0	0.5	1	0
Randia calycina	0	0	0	0	0.5	0	0	0	0	0	0	1
Rhamnidium elaeocarpum	0	0	1	0	0.5	0	0	0	0	0	0	0

	Sites											
Plant species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Rubus bogotensis var. brasiliensis	0	0	0	0	0	0	1.5	0	0	0	0	0
Schinus terebinthifolia	2	2.5	3.5	0	5.5	3	4.5	4	1	2	2	0
Sebastiania brasiliensis	0	0	0	0.5	0.5	0	0	0	0	0	0	0
Siparuna guianensis	2	4	2.5	3.5	2.5	2	1.5	1.5	3	3	2.5	1.5
Smilax sp	0	1	0	0	0	0	0	0	0	0	0	0
Solanum sp	1.5	0	0	0	0	0	2.5	1	0	0	0	0
Solanum sp2	0	0	0	0	0.5	0	0	0	0	0	0	5
Sorocea bonplandii	0	1	0	0.5	0	0	0	0	0	0	0	1.5
Syagrus romanzoffiana	1	1.5	0	0	0	1	1	1	1	1.5	1	2
Tabernaemontana hystrix	0	2	0	1.5	0	0.5	1	1	3	1	0	1
Tapirira guianensis	0	0	0	0	0.5	0	0	0	0	0.5	0	0
Trichilia casaretti	0.5	0	0	0	0	0	0	0	0	0	0	0
Trichilia catigua	0	1.5	0	0	0.5	0	0	0	0	0	0	0
Trichilia elegans	1	0	0	1	1	0.5	0	0	0	0	0	0
Trichilia pallida	0	0	1.5	0	0	0	0	0	0	0	0	1

	Sites											
Plant species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Trichilia sp	0	0	0	0	0	0.5	0	0.5	0.5	0.5	0.5	1
Unknown 01	0.5	0	0	0	0	0	0	0	0	0	0	0
Unknown 02	0.5	0	0	0	0	0	0	0	0	0	0.5	1
Unknown 03	1	0	0	0	0	0	0	0	0	0	0	0
Unknown 04	0.5	0	0	0	0	0	0	0	0	0	0	0
Unknown 05	0	0.5	0	0	0	0	0	0	0	0	0	0
Unknown 06	0	0.5	0	0	0	0	0	0	0	0	0	0
Unknown 07	0	0.5	0	0	0	0	0	0	0	0	0	0
Unknown 08	0	0	0.5	0	0	0	0	0	0	0	0	0
Unknown 09	0	0	1	0	0	0	0	0	0	0	0	0
Unknown 10	0	0	0.5	0	0	0	0	0	0	0	0	0
Unknown 11	0	0	0.5	0	0	0	0	0	0	0	0	0
Unknown 12	0	0	0	0.5	0	0	0	0	0	0	0	0
Unknown 14	0	0	0	0	1	0	0	0	0	0	0	0
Unknown 16	0	0	0	0	0.5	0	0	0	0	0	0	0

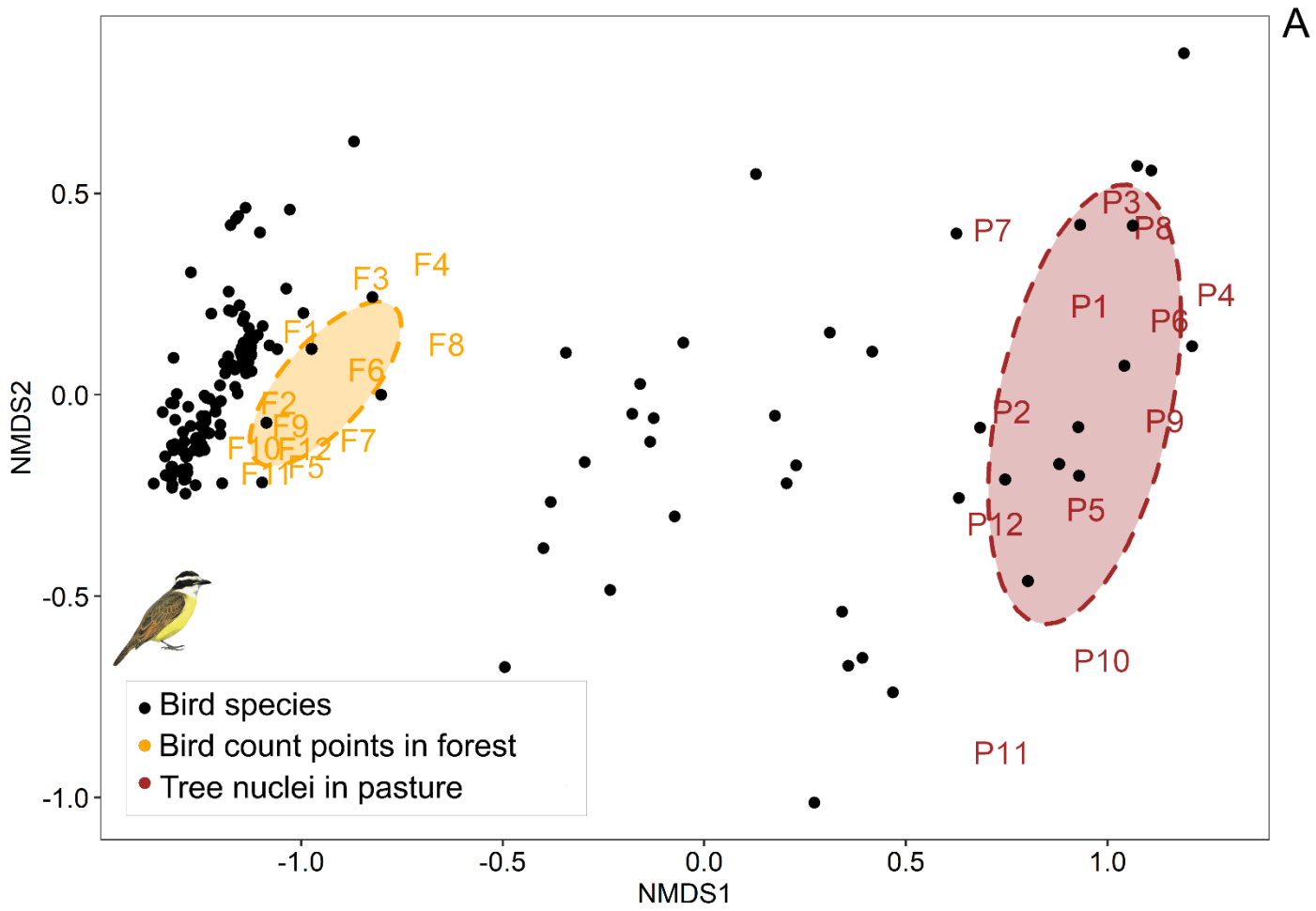
	Sites											
Plant species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Unknown 17	0	0	0	0	0.5	0	0	0	0	0	0	0
Unknown 18	0	0	0	0	0	1.5	0	0	0	0	0	0
Unknown 19	0	0	0	0	0	1	0	0	0	0	0	0
Unknown 22	0	0	0	0	0	0	0	0	0.5	0	0	0
Unknown 23	0	0	0	0	0	0	0	0.5	0	0	0	1
Unknown 27	0	0	0	0	0	0	0	0	0	1	0	0
Vitex megapotamica	0.5	0	0.5	0	0	0.5	0	0	0	0	0	0
Zanthoxylum rhoifolium	0.5	1	0	0	0.5	0.5	0	0	0	0	0	0
Zanthoxylum sp	1	0	0	0	0	1.5	1	0.5	0.5	1.5	0.5	0

Table S5. Model comparison using Weighted Akaike Information Criterion (WAIC).

Model	**WAIC (SE)**	**Effective parameters**	**ΔWAIC (SE)**	**Weight**
Seed availability + plant species ranking (fixed effects) + Site + month (random effects)	854.1 (30.40)	24.0		0.97
Seed availability (fixed effect) + Site + month (random effects)	861.1 (28.88)	21.9	7.0 (8.14)	0.03
Seed availability + plant species ranking (fixed effects) + site (random effect)	967.1 (25.79)	14.8	112.9 (17.80)	0.00
Seed availability (fixed effect) + site (random effect)	982.1 (23.31)	12.8	128.0 (19.63)	0.00
Site + month (random effects)	1118.6 (35.30)	20.5	264.5 (31.26)	0.00
Site (random effect)	1254.6 (31.28)	9.3	400.5 (35.60)	0.00

Table S6. Summary of multinomial logistic model used to investigate the influence of richness of bird visiting on the seed dispersal patterns - random, higher than random, and lower than random.

Variables	**Estimate**	**SE**	**z**	**p**
Intercept [Higher]	-2.589	0.031	-82.68	< 0.001
Intercept [Lower]	-5.510	0.078	-70.29	< 0.001
Richness [Higher]	0.029	0.002	16.47	< 0.001
Richness [Lower]	0.085	0.005	20.46	< 0.001


A
NMDS2
NMDS1
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
F1
F2
F3
F4
F5
F6
F7
F8
F9
F10
F11
F12
P1
P2
P3
P4
P5
P6
P7
P8
P9
P10
P11
P12
Bird species
Bird count points in forest
Tree nuclei in pasture

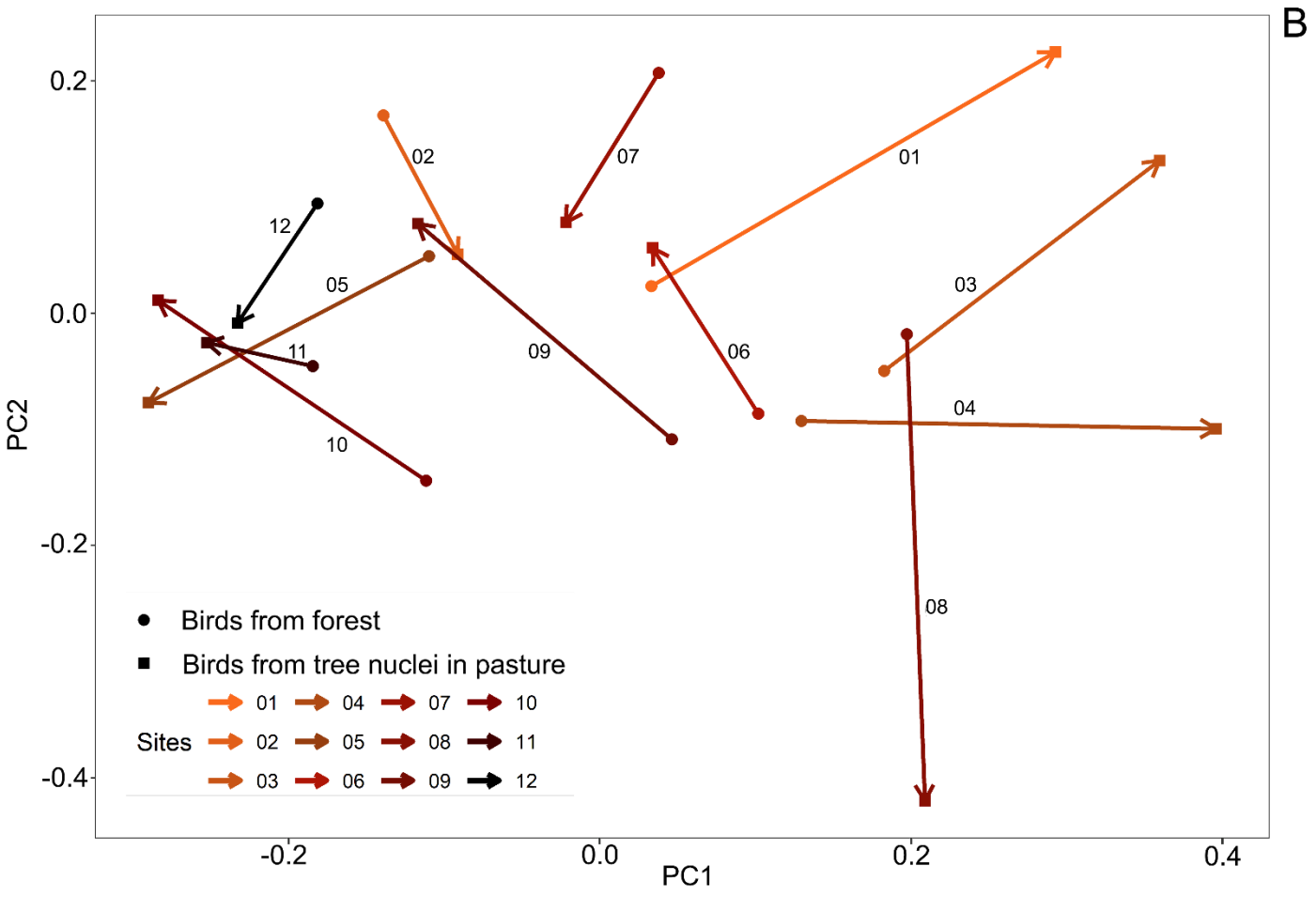
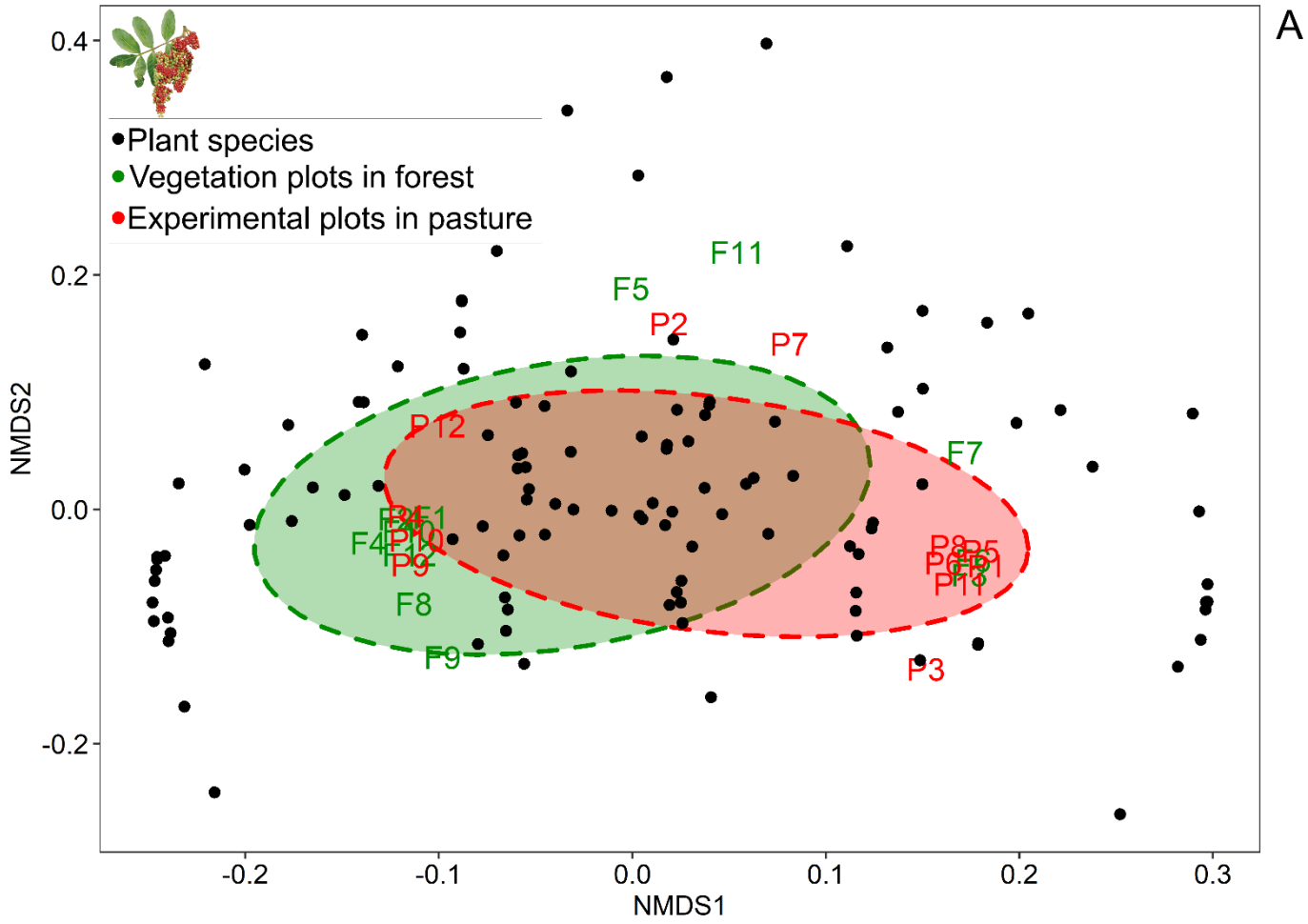

B
PC2
PC1
0.2
0.0
-0.2
-0.4
-0.2
0.0
0.2
0.4
01
02
03
04
05
06
07
08
09
10
11
12
Birds from forest
Birds from tree nuclei in pasture
Sites
01 04 07 10
02 05 08 11
03 06 09 12

Fig. S1. NMDS ordination plot of bird abundance averages in five point-count stations inside forest fragment (F) and eight visitation tree nuclei established in the pasture (P) in each of the twelve study sites (final stress = 0.04) (A). Note that the dotted ellipses that indicate the 95% confidence intervals for the centroid of each local (forest and pasture) show a quite different species composition. Despite this, there was an agreement in the variation in species composition found in bird communities in forest fragments and tree nuclei in pastures across sites (B) (Procrustes analysis: $r = 0.59$, $p = 0.029$).


A
Plant species
Vegetation plots in forest
Experimental plots in pasture
F11
F5
P2
P7
P12
F7
F8
F9
P3
NMDS1
NMDS2
0.4
0.2
0.0
-0.2
-0.2
-0.1
0.0
0.1
0.2
0.3

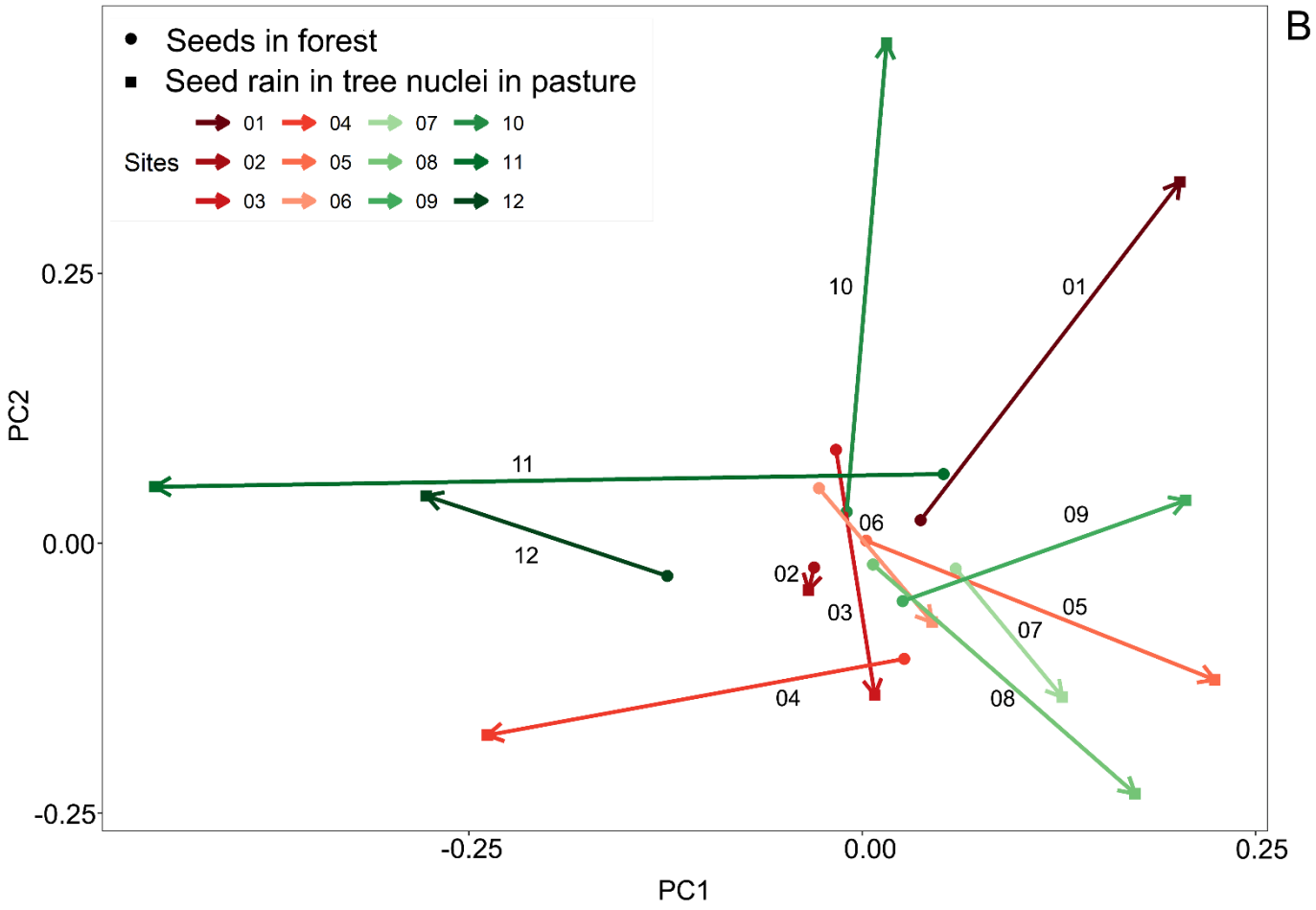

B
Seeds in forest
Seed rain in tree nuclei in pasture
Sites
01
02
03
04
05
06
07
08
09
10
11
12
PC1
PC2
0.25
0.00
-0.25
-0.25
0.00
0.25

Fig. S2. NMDS ordination plot of seed detection averages in ten vegetation sampling plots in forest fragments (F) and eight seed traps in experimental tree nuclei in pastures (P) in each of the 12 study sites (final stress = 0.13) (A). The overlapping between the dotted ellipses that indicate the 95% confidence intervals for the centroid of each local (forest and pasture) denotes a similar species composition. Despite this, we didn't find congruence between the patterns of variation in the composition of plants in the forest and in the seed rain in tree nuclei across sites showed in their ordinations (B) (Procrustes analysis: $r = 0.24$, $p = 0.797$).

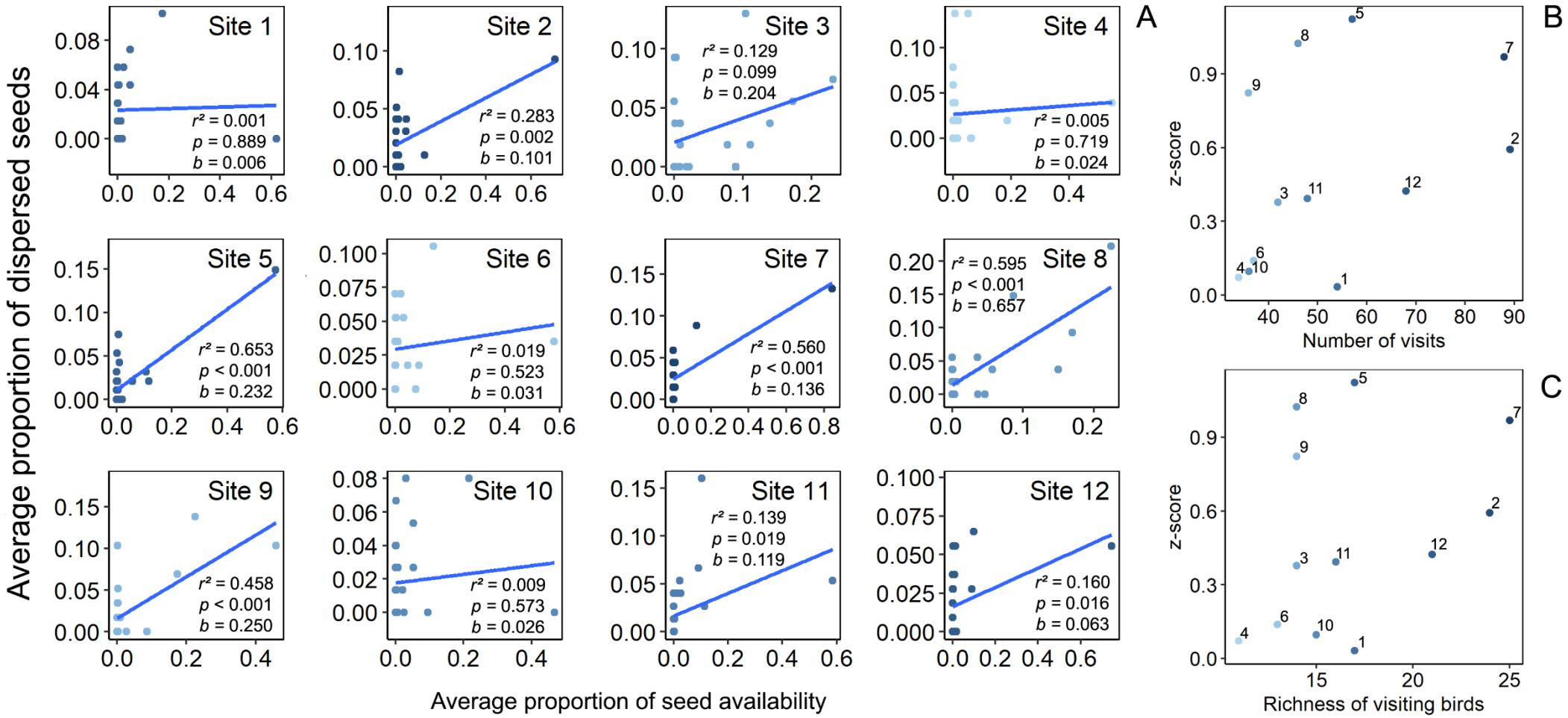
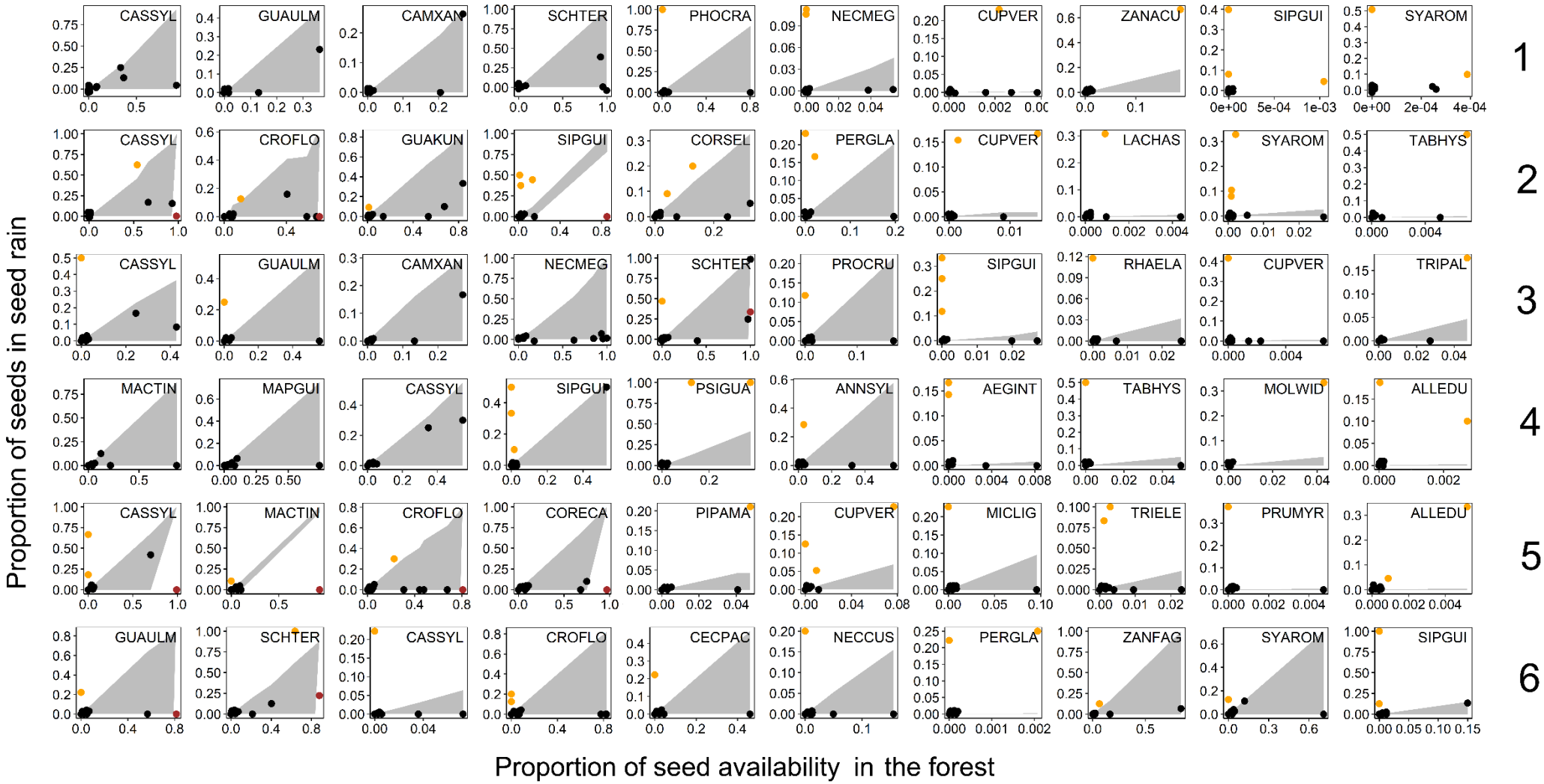


Fig. S3. Linear regressions relating seed dispersal (as denoted by the average of seeds dispersed to seed traps) to average seed availability in forest fragments at each of the 12 study sites (A). The coefficients of determination (r^2), *p*-value, and slopes of regressions (*b*) are shown. Each point represents the average proportion of seed availability and dispersal for each plant species in the community. Points are represented by a gradient of blue tones indicating the variation in the

abundance and richness of birds among the sites, from the least diverse (lightest) to the most diverse (darkest). The effect size (r) of each relationship (standardized on z-score) is not correlated with the number of bird visits ($r = 0.40$, $p = 0.19$) (B) or the richness of birds ($r = 0.36$, $p = 0.25$) (C).


Proportion of seeds in seed rain
Proportion of seed availability in the forest
1
2
3
4
5
6
CASSYL
GUAULM
CAMXAN
SCHTER
PHOCRA
NECMEG
CUPVER
ZANACU
SIPGUI
SYAROM
CASSYL
CROFLO
GUAKUN
SIPGUI
CORSEL
PERGLA
CUPVER
LACHAS
SYAROM
TABHYS
CASSYL
GUAULM
CAMXAN
NECMEG
SCHTER
PROCRU
SIPGUI
RHAELA
CUPVER
TRIPAL
MACTIN
MAPGUI
CASSYL
SIPGUI
PSIGUA
ANNSYL
AEGINT
TABHYS
MOLWID
ALLEDU
CASSYL
MACTIN
CROFLO
CORECA
PIPAMA
CUPVER
MICLIG
TRIELE
PRUMYR
ALLEDU
GUAULM
SCHTER
CASSYL
CROFLO
CECPAC
NECCUS
PERGLA
ZANFAG
SYAROM
SIPGUI

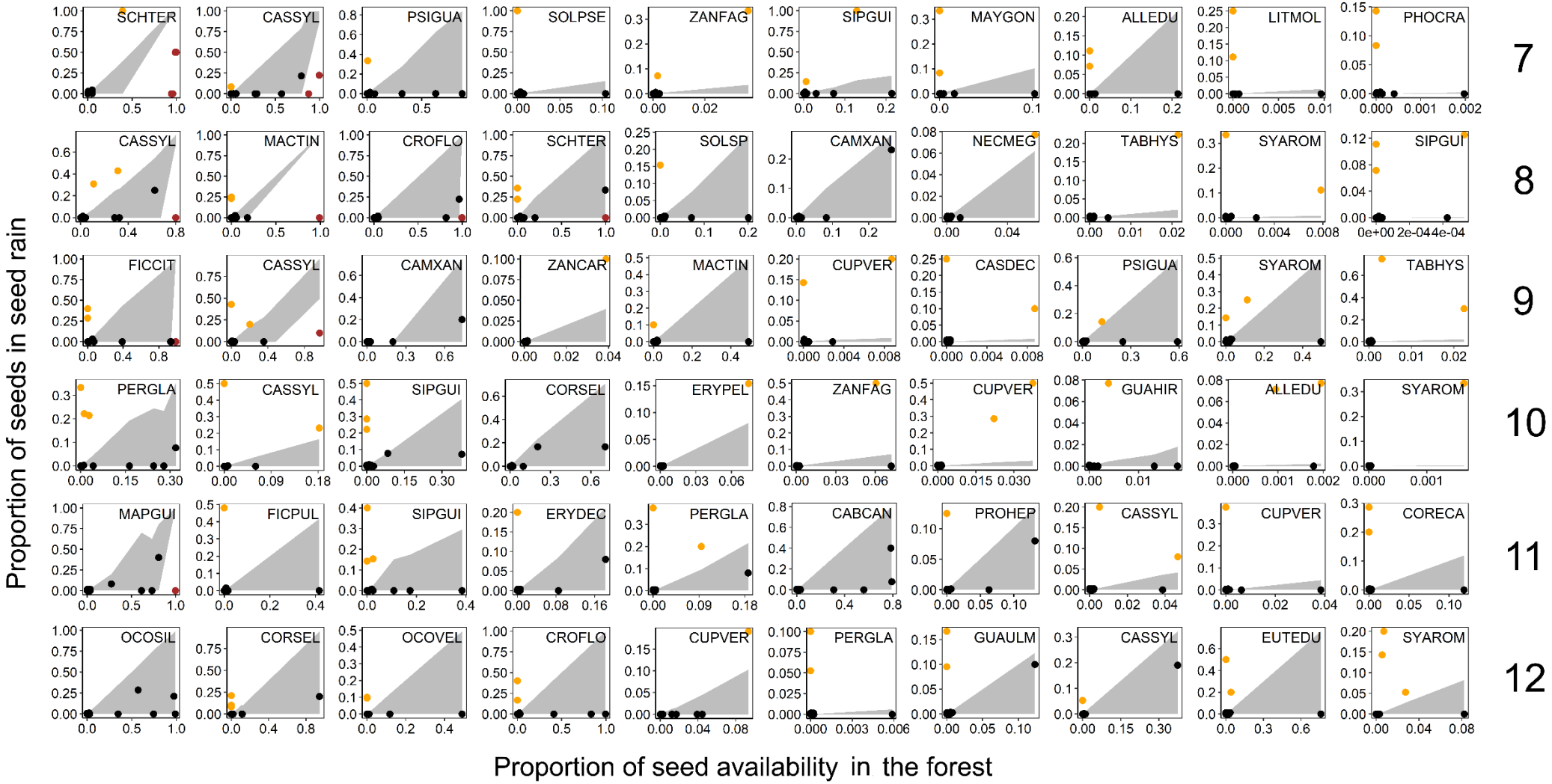


Fig. S4. Scatterplots showing the proportion of monthly seed abundance of the 10 bird-dispersed plant species with the highest seed production in forest fragments (x-axis) with the proportion of seeds dispersed to experimental plots in pastures (y-axis) at each study site. For each site (each row), plant species are ordered from the most abundant (from left to right), being represented only species with records in at least three months in the seed rain. The probability of dispersal by birds

was significantly higher than random (orange points) for species when points lie above shaded areas and significantly lower than random below the shaded areas (maroon points). Points within the shaded areas (black points) represent species that were dispersed in proportion to their availability in the forest. Shaded areas are 95% confidence intervals of the average proportion of seed availability per month in the forest.

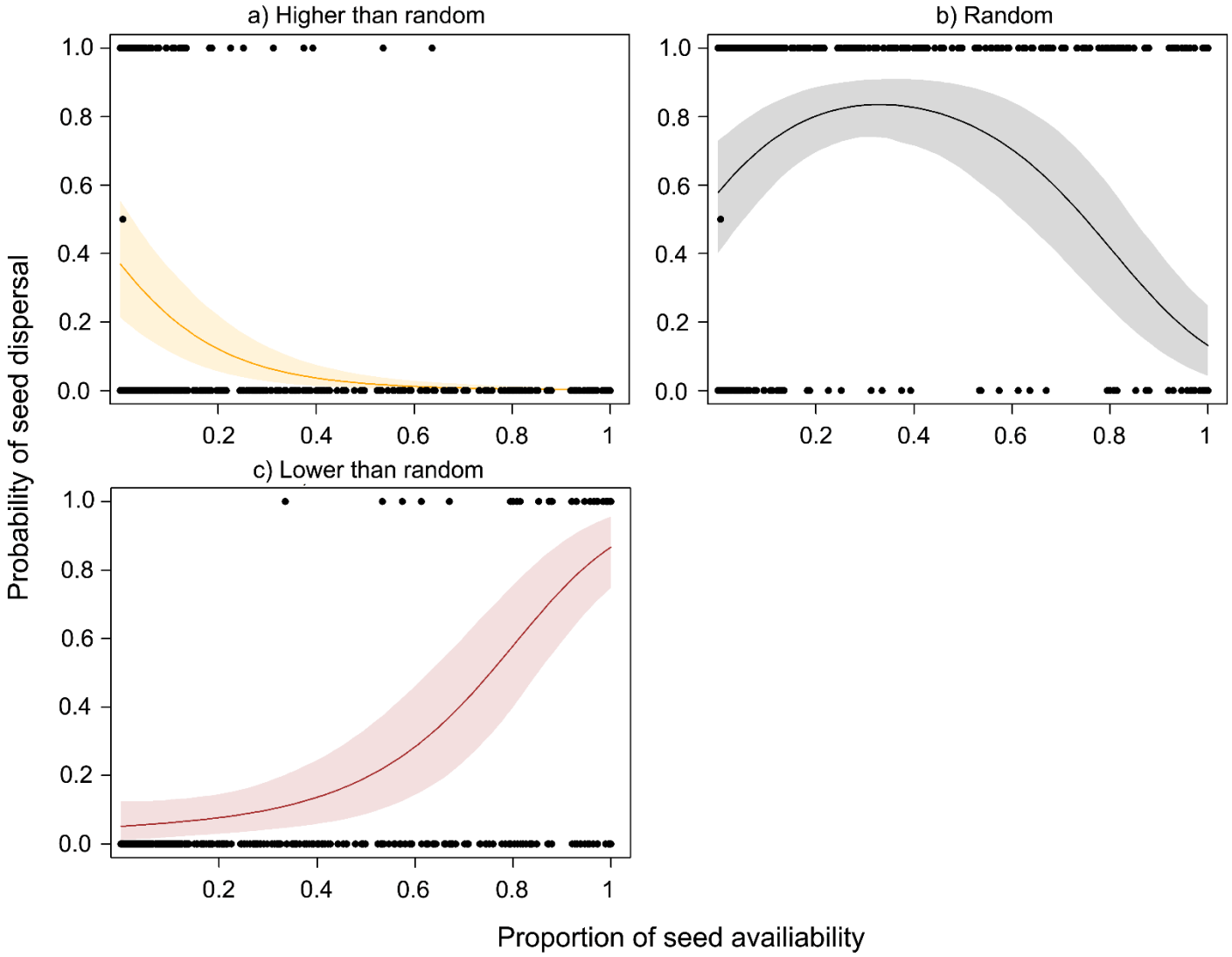


Fig. S5. The mixed-effects multinomial logistic shows that the probability of a species having a higher than random dispersal to pastures decreased with the proportional representation of its seeds in the forest (A). The random dispersal showed a dome pattern in which higher probabilities were obtained with intermediate proportions of seed availability but with a sharp decrease with high proportional availability of seeds (B). The probability of a species having a lower than random dispersal increased with the proportional availability of seeds (C). See also Table 1 for the coefficients.

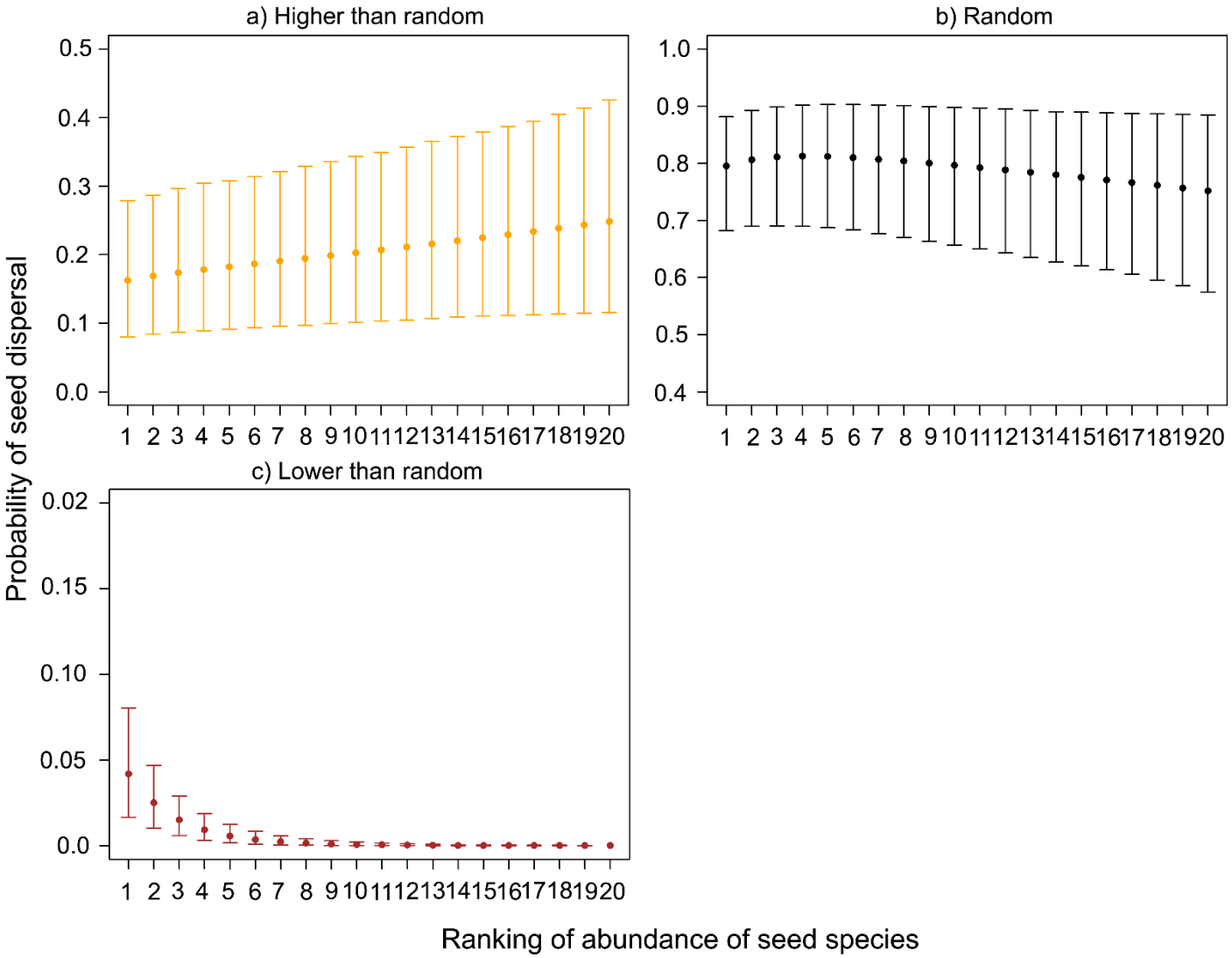


Fig. S6. The mixed-effects multinomial logistic shows that the probability of a species having a higher than random dispersal increased over the plant species ranking according to its seed abundance (A), while the probability of random dispersal decreased over the species ranking (B). The probability of a species having a lower than random dispersal had a sharp decrease over the species ranking (C). See also Table 1 for the coefficients.

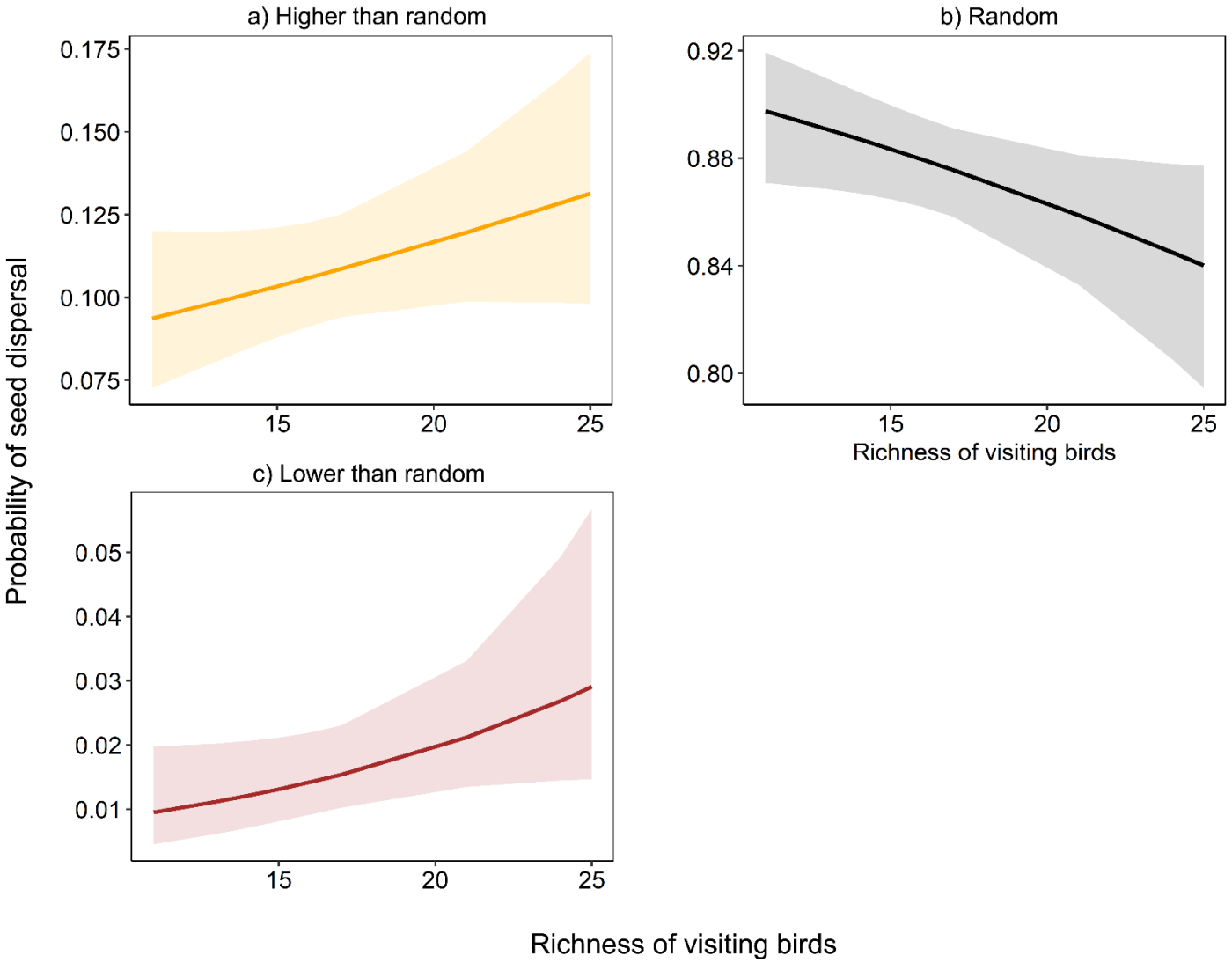
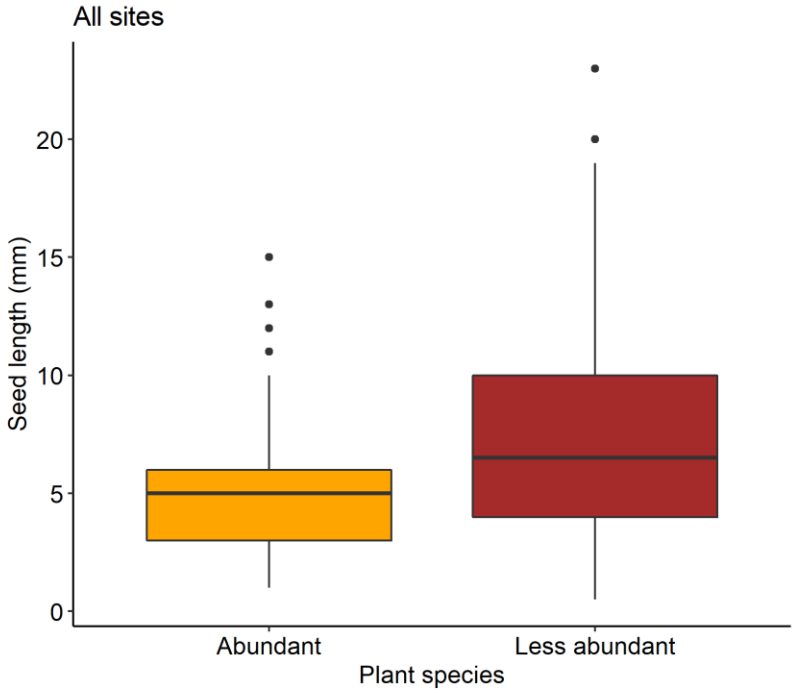


Fig. S7. The multinomial logistic shows that the probability of a species having a higher than random dispersal increased with the richness of visiting birds to experimental plots (A), while the probability of a species having a random dispersal decreased with the richness of visiting birds (B). The richness of visiting birds also increased the probability of a plant species having lower than random dispersal (C).


All sites
Seed length (mm)
0
5
10
15
20
Abundant
Less abundant
Plant species

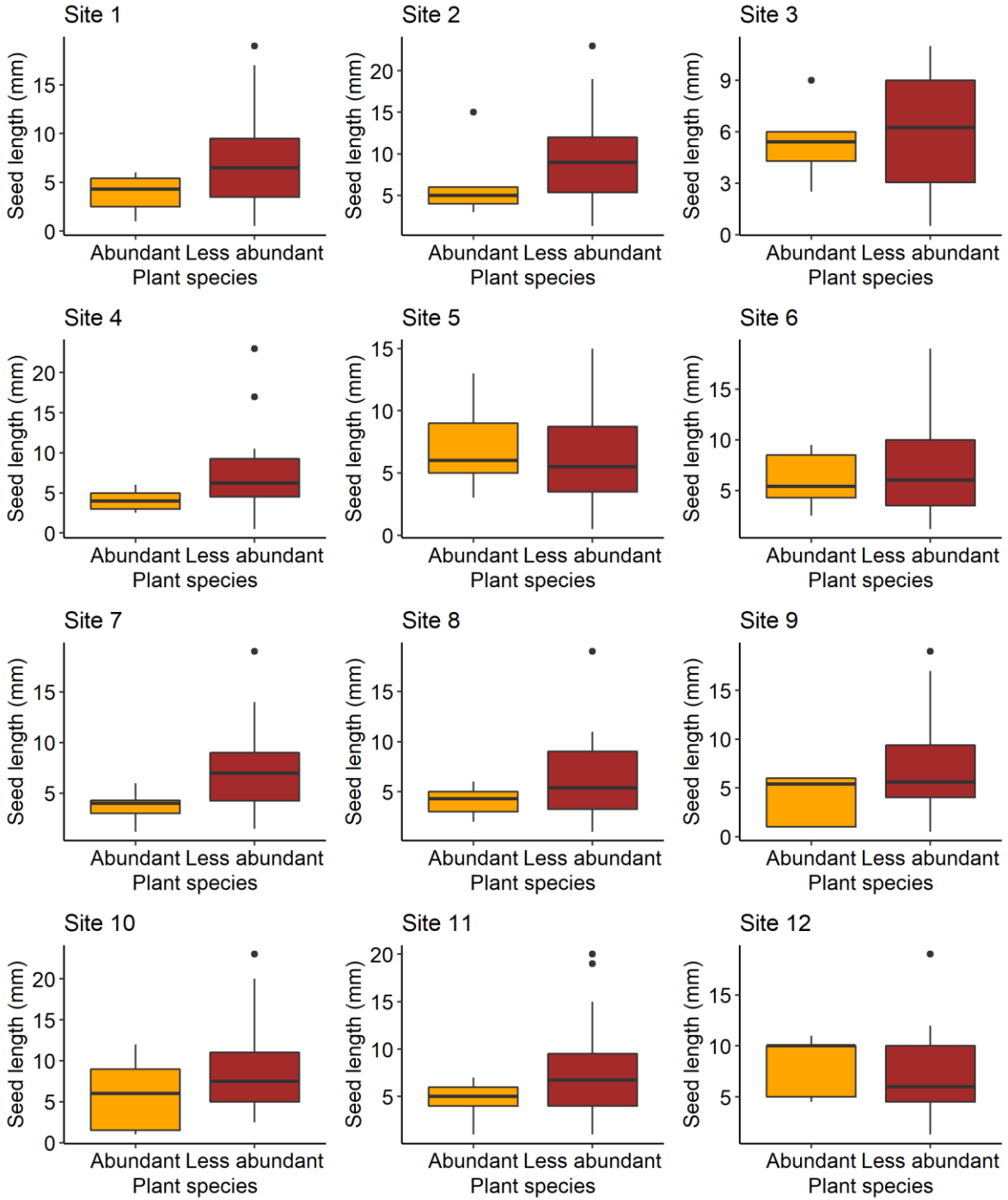

Site 1
Site 2
Site 3
Site 4
Site 5
Site 6
Site 7
Site 8
Site 9
Site 10
Site 11
Site 12
Seed length (mm)
Abundant
Less abundant
Plant species

Fig. S8. Comparative seed length for the five most abundant plant species and for the rest of less abundant species in each site. Note that on most sites, species with less seed abundance had longer seeds than the top five abundant species. When we grouped all the sites, the less abundant plants had a seed length 1.4 times longer than the abundant plants ($t = 3.36$, $df = 358$, $p < 0.001$).

Appendix 1 – Bayesian model details

For our mixed-effect multinomial models for seed dispersal, we adapted the models and explanations used by Koster and McElreath (2017). We considered that seed dispersal can present patterns higher than random, lower than random and random (K = 3) according to the proportion of dispersed seeds, in relation to the quantity of seeds available (see methods). Here, we use positive integers (1,2 and 3) to index these categories. According to the categorical distribution (generalized Bernoulli), the probability of observing each category k is defined as π_k. One of these categories will be the reference category from which the other categories will be compared. That is, the model is composed of K - 1 equations that contrast the odds of presenting the k pattern instead of the reference pattern.

In the context of our multinomial models, the use of mixed-effects modeling allows the probabilities of presenting the k pattern to vary between sites, for example. For each of the sub-equations, a random effect is added that allows sites to have a greater or lesser odds of presenting the k pattern instead of the reference pattern. Thus, we can estimate the correlations of these random effects across the K - 1 response categories, providing insights into the co-occurrence of different patterns on each site. By providing more information, correlations can also help to reduce overfitting and improve parameter estimates in the model.

Thus, considering the three possible patterns (higher than random, lower than random and random) and that the last category (random dispersal, k = 3) serves as the reference category. Assuming discrete observations at time t, the log-odds on site i to present the remaining patterns instead of the reference category are notated as:

$$\log\left(\frac{\pi_{1it}}{\pi_{3it}}\right) = \beta_{1it} + v_{1i}$$
$$\log\left(\frac{\pi_{2it}}{\pi_{3it}}\right) = \beta_{2it} + v_{2i}$$
$$\begin{bmatrix} v_{1i} \\ v_{2i} \end{bmatrix} \sim \text{Normal}(0,\Omega_v): \Omega_v = \begin{bmatrix} \sigma_{v1}^2 & \\ \sigma_{v1,2} & \sigma_{v2}^2 \end{bmatrix}$$
$$\pi_1 + \pi_2 + \pi_3 = 1$$

where β_{1it} and β_{2it} are the intercepts that contrast the first and second dispersal patterns against the reference category, and v_{1i} and v_{2i} are the site-level random effects, which are assumed to be multivariate

normally distributed with zero means and a homogeneous 2 × 2 variance-covariance matrix. For brevity, we present equations with only intercepts, but additional covariables (i.e., fixed effects) can be included to model (see scripts in Appendix 2) the extent to which sites present relatively more or less the *k* pattern instead of the reference.

When an individual-level varying intercept is positive ($v_{ki} > 0$), it indicates that site *i* has an above-average chance of presenting the *k* pattern instead of the reference pattern. The inverse is true of varying intercepts that are negative. The above parameterization models the correlation of these random effects across the *K* - 1 response categories. In the example above, the correlation is derived per usual: $\rho_{1,2} = \sigma_{v1,2} / (\sigma_{v1}\, \sigma_{v2})$ The correlation is standardized to be between -1 and 1. When the correlation is positive, it indicates that the sites that present more of the first pattern also present more of the second (in relation to the reference category in both cases). A negative correlation implies that sites that have relatively more of the first pattern have relatively less of the second pattern.

Our models include yet another random effect, which was the months when we measured available abundance and seed rain. Thus, a simplified notation corresponding to models in this paper is:

$$\log\left(\frac{\pi_{1it}}{\pi_{3it}}\right) = \beta_{1it} + v_{1i} + v\_month_{1i}$$
$$\log\left(\frac{\pi_{2it}}{\pi_{3it}}\right) = \beta_{2it} + v_{2i} + v\_month_{2i}$$
$$\begin{bmatrix} v_{1i} \\ v_{2i} \end{bmatrix} \sim \text{Normal}(0, \Omega_v) : \Omega_v = \begin{bmatrix} \sigma^2_{v1} & \\ \sigma_{v1,2} & \sigma^2_{v2} \end{bmatrix}$$
$$\begin{bmatrix} v\_month_{1i} \\ v\_month_{2i} \end{bmatrix} \sim \text{Normal}(0, \Omega_v) : \Omega_v = \begin{bmatrix} \sigma^2_{v\_month1} & \\ \sigma_{v\_month1,2} & \sigma^2_{v\_month2} \end{bmatrix}$$
$$\pi_1 + \pi_2 + \pi_3 = 1$$

Appendix 2 – Bayesian model scripts

```
# For our mixed-effect multinomial models for seed dispersal,
# we adapted the scripts and explanations used by Koster and McElreath (2017)
## This script uses functions from three R packages and their dependencies:
## 1) rstan -- see quickstart instructions here: http://mc-stan.org/interfaces/rstan
## 2) rethinking -- see installation instructions: http://xcelab.net/rm/software/
## 3) chron -- available on CRAN
library(rstan)
library(rethinking)
library(chron)

## This code reads in the data frame.
d <- read.table (file = "data.txt", h=T) ## Change this path as needed.
str(d)
head(d)

## What follows is the preparation of data needed in the STAN model. In general,
## STAN requires categorical variables (including for higher-level random effects)
## to be formatted as sequential integers. From the rethinking package,
## the coerce_index function is designed to convert vectors into the integer format
## required by STAN.
## We employ z-score transformation of our continuous variable. This
## is primarily to make the sampling more efficient. Note that standardization
## is based on sample means and standard deviations, where the sample is all
## observations in the dataset.
## Transformed data that correspond to the observational data are appended to
## the "d' data frame. We also create index variables (N, K, N_id, N_month)
## that will be necessary for the STAN model code. These latter variables index
## the number of observations, the number of response categories, and the number
## of units in the higher-level classifications (for the random effects).
N <- nrow(d) ## Number of observations
d$y <- coerce_index (d$response) ## Renaming response variable
K <- max(d$y) ## Number of response categories
d$id <- coerce_index (d$Site_id) ## Index of site (random)
```

```
N_id <- max(d$id) ## Number of site
d$Sp_id <- coerce_index (d$Sp) ## Index of species
N_Sp_id <- max(d$Sp_id) ## Number of species (Sp)
d$Ab_z <- (d$Ab-mean(d$Ab))/sd(d$Ab) ## Standardized of available seed abundance
d$Ab_zq <-d$Ab_z^2 ## Quadratic transformation of standardized abundance
d$month_id <- coerce_index(d$Month) ## Index of month (random)
N_month_id <- max(d$month_id ) ## Number of months
################################################################################################
################
## Data lists
## In the call to STAN, there is a "data' argument, which calls for a list of data to be used.
## We find it helpful to prepare lists in advance of the call to STAN, and what follows is
## data lists for each of the models that we implement in this script.
## Note that we use suffixes to distinguish our models:
## (i) is the suffix for models with only site random effects
## (im) is the suffix for models with random effects for site (i) and month (m)
## (iF) has site random effect and the all fixed effects
## (iA) has site random effect and only abundance as fixed effect
## (imF) has the two aforementioned random effects and all fixed effects
## (imA) has the two aforementioned random effects and only abundance as fixed effect
################################################################################################
################

dat_list_i <- list(
  K = K,
  N = N,
  N_id = N_id,
  y = d$y,
  id = d$id
)

dat_list_im <- list(
  K = K,
  N = N,
  N_id = N_id,
```

```
  N_month_id  = N_month_id ,
  y = d$y,
  id = d$id,
  month_id  = d$month_id
)

dat_list_iF <- list(
  K = K,
  N = N,
  N_id = N_id,
  N_Sp_id = N_Sp_id,
  y = d$y,
  id = d$id,
  Sp_id = d$Sp_id,
  Ab_z = d$Ab_z,
  Ab_zq = d$Ab_zq
)
#dat_list_iF <- edit(dat_list_iF)

dat_list_imF <- list(
  K = K,
  N = N,
  N_id = N_id,
  N_month_id  = N_month_id ,
  N_Sp_id = N_Sp_id,
  y = d$y,
  id = d$id,
  month_id  = d$month_id ,
  Sp_id = d$Sp_id,
  Ab_z = d$Ab_z,
  Ab_zq = d$Ab_zq
)

dat_list_iA <- list(
  K = K,
```

```
  N = N,
  N_id = N_id,
  y = d$y,
  id = d$id,
  Ab_z = d$Ab_z,
  Ab_zq = d$Ab_zq
)


#dat_list_iA <- edit(dat_list_iF)

dat_list_imA <- list(
  K = K,
  N = N,
  N_id = N_id,
  N_month_id  = N_month_id ,
  y = d$y,
  id = d$id,
  month_id  = d$month_id ,
  Ab_z = d$Ab_z,
  Ab_zq = d$Ab_zq
)
################################################################################################
################
## The call to STAN also requires model code. Using the same suffixes as above, we generate the model
## code for the all models. We begin by stating the data, distinguishing between integers and "real"
## continuous variables. Those variables originating in the "d" data frame are appended with [N] in
## brackets to denote that there is a data point corresponding to each observation in our dataset. In the
#"generated quantities" block, all matrices must be defined prior to the generation of the correlations (i.e., the
#rhos for the random effects).
################################################################################################
################

model_code_i <- "
data{
```

```
int N;
int N_id;
int y[N];
int id[N];
int K;
}
parameters{
real a[K-1];                                    // intercepts for each category, minus reference category
matrix[K-1,N_id] z_id;                  // matrix of standardized random effects
vector<lower=0>[K-1] sigma_id;      // stddev of random effects
cholesky_factor_corr[K-1] L_Rho_id; // correlation matrix of random effects, Choleskey decomposition
}
transformed parameters{
matrix[N_id,K-1] v_id;                                  // matrix of scaled random effects
v_id = (diag_pre_multiply(sigma_id,L_Rho_id) * z_id)';   // note transpose in this transformation
}
model{

// priors for fixed effects, mean followed by standard deviation
a ~ normal(0,1);

// hyper-priors
to_vector(z_id) ~ normal(0,1);
sigma_id ~ exponential(1);
L_Rho_id ~ lkj_corr_cholesky(2);

// Likelihood function
// This code sets up a function for each of the K-1 responses.
// For each function (k), an intercept (a) is paramaterized along with
// a site varying intercept (v_id). We use STAN's built-in categorical_logit
// function for multinomial logistic regression.
for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] = a[k] +
```

```
v_id[id[i],k];
p[K] = 0;
y[i] ~ categorical_logit( p );
}
}

// In this block, we generate the variance-covariance matrix of site-level
// random effects for the K-1 responses. We then calculate the correlation between
// these effects, Rho_id, via a recomposition from the Cholesky matrix.
// We also define a vector of length N for the log likelihood values, subsequently calling
// STAN's categorical_logit_lpmf to generate the likelihood of each observation, conditional
// on the model. Note that this step requires a repetition of the likelihood function, as above.
generated quantities{
matrix[K-1,K-1] Rho_id;
vector[N] log_lik;
Rho_id = L_Rho_id * L_Rho_id';

for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] = a[k] +
v_id[id[i],k];
p[K] = 0;
log_lik[i] = categorical_logit_lpmf( y[i] | p );
}
}
"

## The following models are a straigthforward extension of the model code, adapted to include
## one additional random effect, month.

model_code_im <- "
data{
int N;
int N_id;
```

```
int N_month_id ;
int y[N];
int id[N];
int month_id [N];
int K;
}
parameters{
real a[K-1];                // intercepts for each category
matrix[K-1,N_id] z_id;                  // matrix of site-level standardized random effects
vector<lower=0>[K-1] sigma_id;      // stddev of site-level random effects
cholesky_factor_corr[K-1] L_Rho_id;  // correlation matrix of site-level random effects
matrix[K-1,N_month_id ] z_month_id ;                  // matrix of month -level standardized random effects
vector<lower=0>[K-1] sigma_month_id ;   // stddev of month -level random effects
cholesky_factor_corr[K-1] L_Rho_month_id ;        // correlation matrix of month -level random effects
}
transformed parameters{
matrix[N_id,K-1] v_id;
matrix[N_month_id ,K-1] v_month_id ;
v_id = (diag_pre_multiply(sigma_id,L_Rho_id) * z_id)';
v_month_id  = (diag_pre_multiply(sigma_month_id ,L_Rho_month_id ) * z_month_id )';
}
model{
// priors
a ~ normal(0,1);

// hyper-priors
to_vector(z_id) ~ normal(0,1);
sigma_id ~ exponential(1);
L_Rho_id ~ lkj_corr_cholesky(2);
to_vector(z_month_id ) ~ normal(0,1);
sigma_month_id  ~ exponential(1);
L_Rho_month_id  ~ lkj_corr_cholesky(2);



// likelihood
```

```
for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] <- a[k] + v_id[id[i],k] + v_month_id [month_id [i],k];
p[K] = 0;
y[i] ~ categorical_logit( p );
}
}
generated quantities{
matrix[K-1,K-1] Rho_id;
matrix[K-1,K-1] Rho_month_id ;
vector[N] log_lik;
Rho_id = L_Rho_id * L_Rho_id';
Rho_month_id  = L_Rho_month_id  * L_Rho_month_id ';
for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] <- a[k] + v_id[id[i],k] + v_month_id [month_id [i],k];
p[K] = 0;
log_lik[i] = categorical_logit_lpmf( y[i] | p );
}
}
"

## The following model adds fixed effects. The inclusion of additional parameters requires
## the naming of the beta parameters. We follow a convention of denoting the beta parameters
## by appending a lower-case "b" prefix to an upper-case letter that denotes the predictor.

model_code_iF <- "
data{
int N;
int N_id;
int N_Sp_id;
int y[N];
int id[N];
```

```
int Sp_id[N];
real Ab_z[N];
real Ab_zq[N];
int K;
}
parameters{
real a[K-1];              // intercepts for each behavior
real bD[K-1];                        // fixed effect for Abundance
real bQ[K-1];                        // fixed effect for Abundance squared
real bS[K-1];                        // fixed effect for Species

matrix[K-1,N_id] z_id;      // matrix of standardized random effects
vector<lower=0>[K-1] sigma_id;   // stddev of random effects
cholesky_factor_corr[K-1] L_Rho_id;         // correlation matrix of random effects
}
transformed parameters{
matrix[N_id,K-1] v_id;      // matrix of scaled random effects
v_id = (diag_pre_multiply(sigma_id,L_Rho_id) * z_id)';
}
model{

// priors
a ~ normal(0,1);
bD ~ normal(0,1);
bQ ~ normal(0,1);
bS ~ normal(0,1);

// hyper-prior
to_vector(z_id) ~ normal(0,1);
sigma_id ~ exponential(1);
L_Rho_id ~ lkj_corr_cholesky(2);

// likelihood
for ( i in 1:N ) {
vector[K] p;
```

```
for ( k in 1:(K-1) )
p[k] = a[k] + bD[k] * Ab_z[i] + bQ[k] * Ab_zq[i] + bS[k] * Sp_id[i]  +
v_id[id[i],k];
p[K] = 0;
y[i] ~ categorical_logit( p );
}
}
generated quantities{
matrix[K-1,K-1] Rho_id;
vector[N] log_lik;
Rho_id = L_Rho_id * L_Rho_id';

for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] = a[k] + bD[k] * Ab_z[i] + bQ[k] * Ab_zq[i] + bS[k] * Sp_id[i] +
v_id[id[i],k];
p[K] = 0;
log_lik[i] = categorical_logit_lpmf( y[i] | p );
}
}
"

model_code_imF <- "
data{
int N;
int N_id;
int N_month_id ;
int N_Sp_id;
int y[N];
int id[N];
int month_id [N];
int Sp_id[N];
real Ab_z[N];
real Ab_zq[N];
```

```
int K; // number of categories
}
parameters{
real a[K-1];                // intercepts for each category
real bD[K-1];                          // fixed effect for Abuncance (Ab)
real bQ[K-1];                         // fixed effect for Abundance squared
real bS[K-1];                         // fixed effect for Species (Sp)
matrix[K-1,N_id] z_id;                // matrix of site-level standardized random effects
vector<lower=0>[K-1] sigma_id;      // stddev of site-level random effects
cholesky_factor_corr[K-1] L_Rho_id;  // correlation matrix of site-level random effects
matrix[K-1,N_month_id ] z_month_id ;                // matrix of month-level standardized random effects
vector<lower=0>[K-1] sigma_month_id ;   // stddev of month -level random effects
cholesky_factor_corr[K-1] L_Rho_month_id ;        // correlation matrix of month -level random effects
}
transformed parameters{
matrix[N_id,K-1] v_id;      // matrix of scaled random effects
matrix[N_month_id ,K-1] v_month_id ;
v_id = (diag_pre_multiply(sigma_id,L_Rho_id) * z_id)';
v_month_id  = (diag_pre_multiply(sigma_month_id ,L_Rho_month_id ) * z_month_id )';
}
model{
// priors
a ~ normal(0,1);
bD ~ normal(0,1);
bQ ~ normal(0,1);
bS ~ normal(0,1);


// hyper-prior
to_vector(z_id) ~ normal(0,1);
sigma_id ~ exponential(1);
L_Rho_id ~ lkj_corr_cholesky(2);
to_vector(z_month_id ) ~ normal(0,1);
sigma_month_id  ~ exponential(1);
L_Rho_month_id  ~ lkj_corr_cholesky(2);
```

```
// likelihood
for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] <- a[k] + bD[k] * Ab_z[i] + bQ[k] * Ab_zq[i] + bS[k] * Sp_id[i] + v_id[id[i],k] + v_month_id
[month_id [i],k];
p[K] = 0;
y[i] ~ categorical_logit( p );
}
}
generated quantities{
matrix[K-1,K-1] Rho_id;
matrix[K-1,K-1] Rho_month_id ;
vector[N] log_lik;
Rho_id = L_Rho_id * L_Rho_id';
Rho_month_id  = L_Rho_month_id  * L_Rho_month_id ';

for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] <- a[k] + bD[k] * Ab_z[i] + bQ[k] * Ab_zq[i] + bS[k] * Sp_id[i] + v_id[id[i],k] + v_month_id
[month_id [i],k];
p[K] = 0;
log_lik[i] = categorical_logit_lpmf( y[i] | p );
}
}
"

## by appending a lower-case "b" prefix to an upper-case letter that denotes the predictor.

############ The following models have only Abundance as a fixed effect

model_code_iA <- "
```

```
data{
int N;
int N_id;
int y[N];
int id[N];
real Ab_z[N];
real Ab_zq[N];
int K;
}
parameters{
real a[K-1];              // intercepts for each behavior
real bD[K-1];                          // fixed effect for Abundance
real bQ[K-1];                          // fixed effect for Abundance squared


matrix[K-1,N_id] z_id;      // matrix of standardized random effects
vector<lower=0>[K-1] sigma_id;   // stddev of random effects
cholesky_factor_corr[K-1] L_Rho_id;        // correlation matrix of random effects
}
transformed parameters{
matrix[N_id,K-1] v_id;      // matrix of scaled random effects
v_id = (diag_pre_multiply(sigma_id,L_Rho_id) * z_id)';
}
model{

// priors
a ~ normal(0,1);
bD ~ normal(0,1);
bQ ~ normal(0,1);


// hyper-prior
to_vector(z_id) ~ normal(0,1);
sigma_id ~ exponential(1);
L_Rho_id ~ lkj_corr_cholesky(2);
```

```
// likelihood
for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] = a[k] + bD[k] * Ab_z[i] + bQ[k] * Ab_zq[i] +
v_id[id[i],k];
p[K] = 0;
y[i] ~ categorical_logit( p );
}
}
generated quantities{
matrix[K-1,K-1] Rho_id;
vector[N] log_lik;
Rho_id = L_Rho_id * L_Rho_id';

for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] = a[k] + bD[k] * Ab_z[i] + bQ[k] * Ab_zq[i] +
v_id[id[i],k];
p[K] = 0;
log_lik[i] = categorical_logit_lpmf( y[i] | p );
}
}
"

model_code_imA <- "
data{
int N;
int N_id;
int N_month_id ;
int y[N];
int id[N];
int month_id [N];
```

```
real Ab_z[N];
real Ab_zq[N];
int K; // number of categories
}
parameters{
real a[K-1];                // intercepts for each category
real bD[K-1];                 // fixed effect for Abundance
real bQ[K-1];                // fixed effect for Abundance squared
matrix[K-1,N_id] z_id;              // matrix of site-level standardized random effects
vector<lower=0>[K-1] sigma_id;      // stddev of site-level random effects
cholesky_factor_corr[K-1] L_Rho_id;  // correlation matrix of site-level random effects
matrix[K-1,N_month_id ] z_month_id ;              // matrix of month -level standardized random effects
vector<lower=0>[K-1] sigma_month_id ;   // stddev of month -level random effects
cholesky_factor_corr[K-1] L_Rho_month_id ;        // correlation matrix of month -level random effects
}
transformed parameters{
matrix[N_id,K-1] v_id;      // matrix of scaled random effects
matrix[N_month_id ,K-1] v_month_id ;
v_id = (diag_pre_multiply(sigma_id,L_Rho_id) * z_id)';
v_month_id  = (diag_pre_multiply(sigma_month_id ,L_Rho_month_id ) * z_month_id )';
}
model{
// priors
a ~ normal(0,1);
bD ~ normal(0,1);
bQ ~ normal(0,1);


// hyper-prior
to_vector(z_id) ~ normal(0,1);
sigma_id ~ exponential(1);
L_Rho_id ~ lkj_corr_cholesky(2);
to_vector(z_month_id ) ~ normal(0,1);
sigma_month_id  ~ exponential(1);
L_Rho_month_id  ~ lkj_corr_cholesky(2);
```

```
// likelihood
for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] <- a[k] + bD[k] * Ab_z[i] + bQ[k] * Ab_zq[i] + v_id[id[i],k] + v_month_id [month_id [i],k];
p[K] = 0;
y[i] ~ categorical_logit( p );
}
}
generated quantities{
matrix[K-1,K-1] Rho_id;
matrix[K-1,K-1] Rho_month_id ;
vector[N] log_lik;
Rho_id = L_Rho_id * L_Rho_id';
Rho_month_id  = L_Rho_month_id  * L_Rho_month_id ';

for ( i in 1:N ) {
vector[K] p;
for ( k in 1:(K-1) )
p[k] <- a[k] + bD[k] * Ab_z[i] + bQ[k] * Ab_zq[i] + v_id[id[i],k] + v_month_id [month_id [i],k];
p[K] = 0;
log_lik[i] = categorical_logit_lpmf( y[i] | p );
}
}
"

#############################################################################################
################
## What follows is the call to STAN for each of the models. Prior to the call, we define
## (1) starting values for the fixed effects, (2) the variance of the random effects for each of the
## K-1 responses, (3) the variance-covariance matrix of the random effects for the K-1 responses, and
## (4) the unit-by-unit matrix of standardized random effects.
## In each case, we opt for uninformative starting values, which are then indexed by the init object
```

```
## that is supplied to the model call.
## We also supply values for the number of chains
#################################################################################################
################

################################################
## Model i

start_i <- list (
  a = rep(0,K-1),
  sigma_id = rep(1,K-1),
  L_Rho_id = diag(K-1),
  z_id = matrix(0,nrow=K-1,ncol=N_id)
)

n_chains_i <- 3
init_i <- list()
for ( i in 1:n_chains_i ) init_i[[i]] <- start_i

## We define a model fit object (mfit_i in this case), as is common with other model fitting functions
## in R.
mfit_i <- stan ( model_code=model_code_i , data=dat_list_i , chains=n_chains_i , cores= n_chains_i ,
warmup=1000, iter=2000, init=init_i , control = list(adapt_delta = 0.95))

## The precis function is from the rethinking package, and it provides summary information about
## the posterior samples. We specify 96% credibility intervals as an acknowledgement of the
## historical circumstance that led 0.05 to become the accepted threshold for statistical
## significance.
#precis(mfit_i, depth = 2, prob = .96)


## Model results can be exported by creating an object from the precis output, then
## exporting the object, which we accomplish via the write.csv function. We include a file
## path as a possible example of the destination folder.
#mfit_i_out <- precis(mfit_i, depth = 3, prob = .96)
```

```
#str(mfit_i_out)
#write.csv(mfit_i_out, file = "mfit.i.csv")


################################################
## Model im

start_im <- list (
  a = rep(0,K-1),
  sigma_id = rep(1,K-1),
  L_Rho_id = diag(K-1),
  z_id = matrix(0,nrow=K-1,ncol=N_id),
  sigma_month_id  = rep(1,K-1),
  L_Rho_month_id  = diag(K-1),
  z_month_id  = matrix(0,nrow=K-1,ncol=N_month_id )
)

n_chains_im <- 3
init_im <- list()
for ( i in 1:n_chains_im ) init_im[[i]] <- start_im

mfit_im <- stan ( model_code=model_code_im , data=dat_list_im , chains=n_chains_im , cores=
n_chains_im , warmup=1000, iter=2000, init=init_im , control = list(adapt_delta = 0.95))

#precis(mfit_im, depth = 2, prob = .96)

#mfit_im_out <- precis(mfit_im, depth = 2, prob = .96)
#write.csv(mfit_im_out, file = "mfit.im.csv")

################################################
## Model iF

start_iF <- list(
  a = rep(0,K-1),
  bD = rep(0,K-1),
```

```
  bQ = rep(0,K-1),
  bS = rep(0,K-1),
  sigma_id = rep(1,K-1),
  L_Rho_id = diag(K-1),
  z_id = matrix(0,nrow=K-1,ncol=N_id)
)

n_chains_iF <- 3
init_iF <- list()
for ( i in 1:n_chains_iF ) init_iF[[i]] <- start_iF

mfit_iF <- stan( model_code=model_code_iF , data=dat_list_iF , chains=n_chains_iF , cores= n_chains_iF ,
warmup=1000, iter=2000, init=init_iF , control = list(adapt_delta = 0.95))

#precis(mfit_iF, depth = 2, prob = .96)

#mfit_iF_out <- precis(mfit_iF, depth = 2, prob = .96)
#write.csv(mfit_iF_out, file = "mfit.iF.csv")

################################################
## Model imF

start_imF <- list(
  a = rep(0,K-1),
  bD = rep(0,K-1),
  bQ = rep(0,K-1),
  bS = rep(0,K-1),
  sigma_id = rep(1,K-1),
  L_Rho_id = diag(K-1),
  z_id = matrix(0,nrow=K-1,ncol=N_id),
  sigma_month_id  = rep(1,K-1),
  L_Rho_month_id  = diag(K-1),
  z_month_id  = matrix(0,nrow=K-1,ncol=N_month_id )
)
```

```
n_chains_imF <- 3
init_imF <- list()
for ( i in 1:n_chains_imF ) init_imF[[i]] <- start_imF

mfit_imF <- stan( model_code=model_code_imF , data=dat_list_imF , chains=n_chains_imF , cores=
n_chains_imF , warmup=1000, iter=2000, init=init_imF , control = list(adapt_delta = 0.95))

precis(mfit_imF, depth = 2, prob = .96)

mfit_imF_out <- precis(mfit_imF, depth = 2, prob = .96)
write.csv(mfit_imF_out, file = "mfit.imF.csv")



################################################
## Model iA

start_iA <- list(
  a = rep(0,K-1),
  bD = rep(0,K-1),
  bQ = rep(0,K-1),
  sigma_id = rep(1,K-1),
  L_Rho_id = diag(K-1),
  z_id = matrix(0,nrow=K-1,ncol=N_id)
)

n_chains_iA <- 3
init_iA <- list()
for ( i in 1:n_chains_iA ) init_iA[[i]] <- start_iA

mfit_iA <- stan( model_code=model_code_iA , data=dat_list_iA , chains=n_chains_iA , cores= n_chains_iA
, warmup=1000, iter=2000, init=init_iA , control = list(adapt_delta = 0.95))

precis(mfit_iA, depth = 2, prob = .96)

mfit_iA_out <- precis(mfit_iA, depth = 2, prob = .96)
```

```
#write.csv(mfit_iA_out, file = "mfit.iA.csv")


################################################
## Model imA

start_imA <- list(
  a = rep(0,K-1),
  bD = rep(0,K-1),
  bQ = rep(0,K-1),
  sigma_id = rep(1,K-1),
  L_Rho_id = diag(K-1),
  z_id = matrix(0,nrow=K-1,ncol=N_id),
  sigma_month_id  = rep(1,K-1),
  L_Rho_month_id  = diag(K-1),
  z_month_id  = matrix(0,nrow=K-1,ncol=N_month_id )
)

n_chains_imA <- 3
init_imA <- list()
for ( i in 1:n_chains_imA ) init_imA[[i]] <- start_imA

mfit_imA <- stan( model_code=model_code_imA , data=dat_list_imA , chains=n_chains_imA , cores=
n_chains_imA , warmup=1000, iter=2000, init=init_imA , control = list(adapt_delta = 0.95))

precis(mfit_imA, depth = 2, prob = .96)

mfit_imA_out <- precis(mfit_imA, depth = 2, prob = .96)
write.csv(mfit_imA_out, file = "mfit.imA.csv")

################################################################################################
################
## Model comparison using WAIC
## Employing the compare function from the rethinking package, we compare the fit of our models
## using the Watanabe-Akaike information criterion.
```

```
##############################################################################################
################
models <- compare (mfit_i, mfit_im, mfit_imF, mfit_iF, mfit_iA, mfit_imA)
plot(models)

##############################################################################################
################
## The first step toward plotting predicted probabilities of our fixed effects is to extract the
## posterior samples using the extract.samples function in the STAN package.
##############################################################################################
################
## We can visually inspect the site random effects by creating a new objects, "v_est…"
## Subsequently, the dens function allows us to see the posterior distribution of the correlation
## between those categories.

post_imF <- extract.samples(mfit_imF)
v_est_imF <- apply(post_imF$v_id,2:3,median)
pairs(v_est_imF)
v_est_month_id _imF <- apply(post_imF$v_month_id ,2:3,median)
pairs(v_est_month_id _imF)
dens(post_imF$Rho_id[,1,2])


## Multinomial version of link function for model imF
## Much like the link function in the rethinking package, the following function can be used to
## generate predictions for a customized data frame.
## The script begins by defining a sequence length that should correspond to the dimensions of
## data frame that is created to generate the predictions. We use 100 in this case, but other
## values are possible.
## We define additional quantities at the beginning of the function, and the function derives
## the values from the posterior. For example, K is the number of response categories (3), as before.
## The quantity, ns, is the number of samples.
## The function relies on an intermediate step, the creation of ptemp, which is tied to the likelihood
## function. Essentially, the function works by taking the supplied values for each of the i rows
## in the newly created data frame, then multipying those values by the value of the parameter in each
```

```
## sample from the posterior. In other words, for each of the samples from the posterior, the
## parameters vary, which are used to generate predicted probabilities for each of the supplied
## combinations of values in the new data frame that we will create. We can subsequently
## use the distribution of predicted values to understand the effets of the values we supply.
## It is common for researchers to average over the random effects. In other words, predicted
## probabilies are based only on the fixed effects, not accounting for the random effects.
## To accomplish that, our function requires users to supply a 0 for the random effects. By contrast,
## one can include random effects by supplying the integer that corresponds to the unit of interest
## in the higher-level classification. The varying intercept for that unit will then be incorporated
## as part of the predicted probability.
###########################################################################################
################

seq.length <- 100

link.mn.imF <- function( data ) {
  K <- dim(post_imF$v_id)[3] + 1
  ns <- dim(post_imF$v_id)[1]
  if ( missing(data) ) stop( "BOOM: Need data argument" )
  n <- seq.length

  softmax2 <- function(x) {
    x <- max(x) - x
    exp(-x)/sum(exp(-x))
  }

  p_imF <- list()

  for ( i in 1:n ) {
    p_imF[[i]] <- sapply( 1:K , function(k) {
      if ( k < K ) {
        ptemp_imF <- post_imF$a[,k] +
          post_imF$bD[,k] * data$Disp_z[i] +
          post_imF$bQ[,k] * data$Disp_zq[i]+
          post_imF$bS[,k] * data$Sp_id[i]
```

```
      if ( data$id[i]>0 ) ptemp_imF <- ptemp_imF + post_imF$v_id[,data$id[i],k]
      if ( data$mes_id[i]>0 ) ptemp_imF <- ptemp_imF + post_imF$v_mes_id[,data$mes_id[i],k]
    } else {
      ptemp_imF <- rep(0,ns)
    }
    return(ptemp_imF)
  })

  for ( s in 1:ns ) p_imF[[i]][s,] <- softmax2( p_imF[[i]][s,] )
 }#i

 return(p_imF)
}

#############################################################################################
################
## Generating predictions across the range of proportion of abundances in the sample

## In addition to the posterior predictions, we develop scatterplots that include the empirical data.
## That is, we present the aggregated proportions for each site.
## To facilitate that calculation of those proportions, we use the response vector in our
## data frame, d. The for loop creates an additional vector in the data frame for each of the
## categories in our response variable. Then for each observation in the data set, a 1 is added to
## the vector if the if the dispersal pattern is the same as that predicted. Otherwise, a zero is added.
## We include a prefix, "r_", for these new vectors as a reminder to ourselves that these are
## based on the response variable. The prefix is not necessary. An examination of the vectors
## created by this for loop should make it clear what is being accomplished.
for(t in unique(d$response)) {d[paste("r_",t,sep="")] <- ifelse(d$response==t,1,0)}

## To create the aggregated proportions, we use the aggregate functions from the R base package.
agg <- aggregate ( cbind (r_HRandom, r_ZRandom, r_LRandom) ~ id + month_id + Ab_z, data = d, FUN =
mean)

## The following generates a vector of abundances which we use to generate predicted probabilities.
## We use the seq function to generate a sequence across the range of abundances in the empirical data.
```

```
## Note that the length of this vector is seq.length, as defined above.

Abun_seq <- seq (from= min(d$Ab_z), to= max(d$Ab_z), length.out = seq.length)

## We create a data frame from Abun_seq and its second order polynomial, holding the predictor
## at its sample mean.
## Also, as we noted earlier in the notes about the multinomial link function, we set "id" and “month_id” to
## zero in order to average over the random effects.

pred_dat_d_imF <- data.frame(
  id = 0,
  month_id  = 0,
  Ab_z = Abun_seq,
  Ab_zq = Abun_seq^2,
  Sp_id = 0
)
## The following an object with 100 predicted probabilities (as in seq.length) corresponding
## to the different values of standardized abundances that were supplied in the pred_dat_d_imF data frame,
## as repeated for each of the K response categories.

p_imF <- link.mn.imF(pred_dat_d_imF)

## The following calculates the mean of the predicted samples.
p_mean_imF <- sapply( 1:length(p_imF) , function(i) apply(p_imF[[i]],2,mean) )

## Note that the PI function embedded in the plot calls below is what generates
## the prediction intervals around the means. The PI function is from the rethinking package.

## We intend to place tick marks on the x-axis at 0.2 intervals across our abundance (proportion),
## so we define those abundances and then calculate their values on the scale of standardized abundances.
preferred.Ab <- c(0.2,0.4,0.6,0.8,1)
labels.at <- (preferred.Ab - mean(d$Ab))/sd(d$Ab)

## The quartz device on Mac operating systems can be supplied with preferred heights
## and widths for the plotting region. This code would need to be modified for other plot devices.
```

```
quartz(height = 6 , width = 10)
par(mfrow=c(1,3), mar=c(1,1.5,1,1.5) + 0.1, oma=c(1,2.5,1,0.5))

## The following plots on the multi-panel quartz device display the means and prediction intervals
## for each of the K response categories. The intervals are displayed with the shade function
## from the rethinking package. Other arguments are from the graphics functionality in the base R
## package.

plot( NULL , xlim=c(-0.5, 3.0) , ylim=c(0,1) , xaxt = "n", main = "1) Higher than random", ylab =
"Probability", xlab = "", cex.main = .9)
for ( k in 1:1 ) {
  lines( Abun_seq , p_mean_imF[k,])
  p_PI_imF <- sapply( 1:length(p_imF) , function(i) PI(p_imF[[i]][,k]) )
  shade( p_PI_imF , Abun_seq)
}
points(agg$Ab_z, agg$r_HRandom)
axis( side = 1, at =labels.at, labels =preferred.Ab)

plot( NULL , xlim=c(-0.5, 3.0) , ylim = c(0,1) , xaxt = "n", main = "3) Lower than Random", ylab = "", xlab
= "", cex.main = .9)
for ( k in 2:2 ) {
  lines( Abun_seq , p_mean_imF[k,])
  p_PI_imF <- sapply( 1:length(p_imF) , function(i) PI(p_imF[[i]][,k]) )
  shade( p_PI_imF , Abun_seq)
}
points(agg$Ab_z, agg$r_LRandom)
axis( side = 1, at = labels.at, labels = preferred.Ab)

plot( NULL , xlim=c(-0.5, 3.0) , ylim=c(0,1) , xaxt = "n", main = "2) Random", ylab = "", xlab = "",
cex.main = .9)
for ( k in 3:3 ) {
  lines( Abun_seq , p_mean_imF[k,])
  p_PI_imF <- sapply( 1:length(p_imF) , function(i) PI(p_imF[[i]][,k]) )
  shade( p_PI_imF , Abun_seq)
```

```
}
points(agg$Ab_z, agg$r_ZRandom)
axis( side = 1, at = labels.at, labels =preferred.Ab)

mtext(text="Probability",side=2,line=1,outer=TRUE)

dev.off()

## Because the script uses the same link.mn_imF function to plot predictions by species ranking,
## as a precautionary measure, we remove the objects that we will create using a different
## data frame of supplied values.
rm(p_imF)
rm(p_mean_imF)
rm(p_PI_imF)
rm(labels.at)

##############################################################################################
#################
## Generating predictions by species ranking
pred_dat_sp <- data.frame(
  id = 0 ,
  mes_id = 0,
  Disp_z = Disp_seq,
  Disp_zq = Disp_seq^2,
  Sp_id = unique(d$Sp_id)
)

seq.length <- 20 ## We need to alter the value for seq.length to match the size of the new data frame

p_imF <- link.mn_imF (pred_dat_sp)

p_mean_imF <- sapply( 1:length(p_imF) , function(i) apply(p_imF[[i]],2,mean) )

labels.at <- unique(d$Sp_id)
Sp_seq <- unique(d$Sp_id)
```

```
quartz(height = 6 , width = 10)

par(mfrow=c(1,3), mar=c(1,1.5,1,1.5) + 0.1, oma=c(1,2.5,1,0.5))

plot( NULL , xlim=c(1, 20) , ylim=c(0,1) , xaxt = "n", main = "1) Higher than random", ylab = "Probability",
xlab = "", cex.main = .9)
for ( k in 1:1 ) {
  points( Sp_seq , p_mean_imF[k,])
  p_PI_imF <- sapply( 1:length(p_imF) , function(i) PI(p_imF[[i]][,k]) )
  arrows(Sp_seq, p_PI_imF[1,], Sp_seq, p_PI_imF[2,], length=0.05, angle=90, code=3)
  }

axis( side = 1, at = labels.at, labels =F)


plot( NULL , xlim=c(1, 20) , ylim = c(0,1) , xaxt = "n", main = "3) Lower than random", ylab = "", xlab = "",
cex.main = .9)
for ( k in 2:2 ) {
  points(Sp_seq , p_mean_imF[k,])
  p_PI_imF <- sapply( 1:length(p_imF) , function(i) PI(p_imF[[i]][,k]) )
  arrows(Sp_seq, p_PI_imF[1,], Sp_seq, p_PI_imF[2,], length=0.05, angle=90, code=3)
}
axis( side = 1, at = labels.at, labels = F)

plot( NULL , xlim=c(1, 20) , ylim=c(0,1) , xaxt = "n", main = "2) Random", ylab = "", xlab = "", cex.main =
.9)
for ( k in 3:3 ) {
  points( Sp_seq , p_mean_imF[k,])
  p_PI_imF <- sapply( 1:length(p_imF) , function(i) PI(p_imF[[i]][,k]) )
  arrows(Sp_seq, p_PI_imF[1,], Sp_seq, p_PI_imF[2,], length=0.05, angle=90, code=3)
}
axis( side = 1, at = labels.at, labels =labels.at)

mtext(text="Probability",side=2,line=1,outer=TRUE)
```

```
## We turn off the quartz plotting device prior to starting the next multi-panel figure.
dev.off()
```

Capítulo 3

Functional diversity of frugivorous birds and trait matching structure plant-bird interaction network and increase the functional diversity of seed rain in tropical deforested landscapes

Artigo será submetido para a Functional Ecology

Functional diversity of frugivorous birds and trait matching structure plant-bird interaction network and increase the functional diversity of seed rain in tropical deforested landscapes

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Abstract

1. Seed dispersal by animals is an important ecosystem function that shapes the diversity of tropical landscapes. However, we still poorly know how the diversity of traits of plants and frugivores match to structure the networks and the functional diversity of the seed rain that results from these interactions.
2. Here we investigated simultaneously the effects of the functional diversity of plants and birds during the process of seed dispersal in open areas within 12 fragmented landscapes in the Brazilian Atlantic Forest. We monitor the production of bird-dispersed seeds and bird abundance in forest fragments, and sampled the seed rain and the activity of birds attracted to experimental tree nuclei established in neighboring pastures.
3. With analytical approaches of functional diversity and network theory, and using structural models, we found that greater functional diversity of birds and plants created a greater trait-matching and a more connected network of plant-bird interactions. This resulted in an up to 15-fold difference in the functional richness of seed rain in pasture tree nuclei across sites.
4. The functional beta diversity between plants in adjacent forest fragments and the seed rain in pastures, caused mainly by loss of functional diversity, decreased linearly with the functional richness of frugivores.
5. Our results highlight the importance of the functional diversity of frugivores to plant-animal network assembly and for promoting a more functionally diverse seed dispersal into deforested tropical landscapes.

Keywords: animal diversity; mutualisms; forest succession; functional beta diversity; functional traits; plant diversity; plant–frugivore assemblages; seed dispersal.

Introduction

Seed dispersal is a major ecological process that plays a central role in plant community assembly in forested and deforested lands (Chazdon, 2014). To understand seed dispersal in tropical forests, we must understand the role that animals play in the process since most tropical woody plants produce fleshy fruits with seeds adapted to be dispersed by fruit-eating animals (Howe & Smallwood, 1982; Jordano, 2000). Together with frugivorous bats, birds are the main agents of seed dispersal in tropical areas due to their high abundance and diversity, mobility, and the fact that the majority of fleshy-fruited species are adapted to dispersal by birds (Sekercioglu, 2006; Pizo & dos Santos, 2011; Carlo & Morales, 2016). These animals influence the reproductive success of plants, increase forest regeneration, help to structure spatially and act on the gene flow among plant populations (Howe & Smallwood, 1982; Jordano, García, Godoy, & García-Castaño, 2007; Carlo, García, Martínez, Gleditsch, & Morales, 2013; de la Peña-Domene, Martínez-Garza, Palmas-Pérez, Rivas-Alonso, & Howe, 2014).

Previous studies have shown that the richness and abundance of frugivorous species, especially birds, are important determinants of seed dispersal patterns. For example, changes in the richness and abundance of frugivorous birds can affect the seed dispersal network interactions, lead to changes in community regeneration rates, in the genetic diversity of plant populations, and influence the extinction probability of plant species (Caughlin et al., 2015; Carvalho, Galetti, Colevatti, & Jordano, 2016, Emer, Galetti, Pizo, Jordano, & Verdú, 2019; Gardner, Bicknell, Baldwin-Cantello, Struebig, & Davies, 2019). However, frugivores vary in size, feeding behavior, foraging stratum and digestive capacity, as well as mobility and home range area, which can shape their functional roles as seed dispersers (Wheelwright, 1985; Jordano, 2000, Morales, García, Martínez, Rodriguez-Pérez, & Herrera, 2013; González-Castro, Yang, Nogales, & Carlo, 2015). Therefore, it is important to consider that the analysis

of frugivore diversity based only on species richness and abundance does not allows to predict the structure and functioning of their communities and quality of services, particularly regarding the generated seed rain (Gagic et al., 2015). This is because these traditional measures fail to capture the particularities of each species involved and do not consider redundant or complementary effects among species that may exist in a community (Cianciaruso, Silva, & Batalha, 2009; Mouchet, Villéger, Mason, & Mouillot, 2010).

Functional diversity has emerged as an alternative approach to describe the variation of species traits within a community and the ecological functions they play (Mouchet et al., 2010; Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011). In fact, functional diversity measures the range of traits that capture different aspects of the resource use and ecological requirements of species (Villéger, Mason, & Mouillot, 2008). These traits can potentially predict how species influence ecological processes such as seed dispersal (de Bello et al., 2010). For example, functional metrics describe the distribution of species and their abundance within the functional space and indicate the structuring processes of communities by limiting similarity, niche filtering, dispersal limitation and neutral processes (Villéger et al., 2008; Mouchet et al., 2010). Additionally, these functional metrics may reveal which specific functional trait in a community influences trophic interactions between species and ecosystem processes (Mokany, Ash, & Roxburgh, 2008; Gagic et al., 2015). Thus, particularly in seed dispersal mutualisms, the study of the functional diversity of frugivores and plants provides a deeper understanding of how the functional roles of the species involved act to structure the process itself and the resulting forest communities (Garnier, Navas, & Grigulis, 2016; Lavabre, Gilarranz, Fortuna, & Bascompte, 2016; Pigot et al., 2016).

The recognition of the importance of measures of functional diversity for the understanding of the influence of species traits on the structuring of communities and ecosystem processes linked to the mutualism of seed dispersal has resulted in an increasing

number of studies (e.g., Lavabre et al., 2016, Muñoz, Schaefer, Böhning-Gaese, Neuschulz, & Schleuning, 2017b; Albrecht et al., 2018; Bovo et al., 2018; Quitián et al., 2019; Camargo, Pizo, Brancalion, & Carlo, 2020; Carlucci, Brancalion, Rodrigues, Loyola, & Cianciaruso, 2020). In fact, several studies have related the functional diversity of dispersers to the quality of the dispersal service and plant-animal interaction strength (e.g. Lavabre et al., 2016; Pigot et al., 2016), shown the importance of functional traits in attracting dispersers and in the forest restoration process (Camargo et al., 2020; Carlucci et al., 2020) or how the functional diversity of plants in the community affects the outputs of the seed dispersal process (Muñoz et al., 2017b). Almost always, however, these studies focus on only one side of the relationship (*but see* Albrecht et al., 2018; Quitián et al., 2019). There is still little knowledge about how the functional diversity of plants and animals in conjunction influences the functioning of the resulting ecosystem. This is because plants also vary in functional traits such as life forms, preferred habitats, and in fruit and seed traits (e.g., sizes, color displays, shapes, and nutritional rewards) that influence fruit selection by frugivores (Jordano, 2000; Garnier et al., 2016). In addition, it is expected that the functional traits of both birds and plants will strongly affect the structural and functional composition of the resulting seed rain, since mutualistic seed dispersal networks are strongly structured by the matching of traits (Bascompte & Jordano, 2007; Schleuning, Fründ, & García, 2015; Muñoz, Schaefer, Böhning-Gaese, & Schleuning, 2007a; Morán-López et al., 2020).

Here, we carried out a replicated study at the landscape level to simultaneously study the effects of the functional diversity of plants and birds during the process of seed dispersal in deforested landscapes in the Atlantic Forest of southeastern Brazil. Specifically, we ask whether a greater functional diversity of birds and plants increases the chance of trait-matching between them, increases the number of interactions of network and allows for a more functionally diverse seed rain. By means of structural models, we predict causal

relationships in which the greater functional diversity of birds and plants allows for greater trait-matching, which leads to a greater network of interactions and generates a greater functional diversity in the seed rain. We also evaluated how the functional diversity of frugivores can influence the functional profile of seed sampled in experimental tree nuclei in pastures in relation to the functions of plants present in adjacent forest fragments. We expect that a greater functional diversity of dispersers will allow to occupy a greater functional volume in the niche of the plant community in the forest fragments. This will result in a seed rain that is functionally more similar to the forest community and therefore there will be lower functional beta diversity between forest and the seed rain that reach adjacent pastures.

Materials and methods

Study sites

We conducted the experiment in 12 sites of the Paranapanema municipality in São Paulo, southeastern Brazil (23°23' S, 48°43' W). The municipality is located at ca. 600 m a.s.l. on the watershed region of the Alto Paranapanema river (Cielo-Filho et al., 2009). Average annual rainfall is 1,407.9 mm concentrated in the wet summer season (December to March), with a mean annual temperature of 18 °C (Cielo-Filho et al., 2009). Forests cover only about 6% of the Paranapanema landscape (Fundação SOS Mata Atlântica, 2013), which is located within the second most threatened biogeographical region of the Atlantic Forest, with only 7% forest cover remaining (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Our study sites were located on private lands containing cattle pastures and fragments of primary and secondary semideciduous Atlantic Forests >30 years old, ranging from 12.2 to 98.8 hectares.

Tree nuclei in pastures

In December 2016, we established eight 4.5 x 4.5 m experimental plots in cattle pastures at each site to measure bird visits and seed rain. Except for control plots, we planted a pioneer tree at reproductive age (minimum height of 1.5 m) in the center of each plot, forming tree nuclei. We removed and mechanically controlled grasses throughout the experiment. To attract a greater diversity of birds, we planted trees with fruits offering different resources: the wind-dispersed *Heliocarpus popayanensis* Kunth with dry fruits, bird-dispersed *Acnistus arborescens* Schltdl. with fruits composed of 48.3% of carbohydrates, 7.9% of proteins and 0.04% of lipids, and *Trema micrantha* (L.) Blume, another bird-dispersed species with fruits composed of 48.8% of lipid, 10.7% of proteins and 2.2% of carbohydrates. Plots were fenced with barbwire to keep cattle out and established at 10 and 50 m from the nearest forest fragment, distances over which we found a small variation in the parameters of seed rain (Camargo et al., 2020).

Fruit abundance in forest fragments

We established 10 vegetation sampling plots of 5 x 5 m in forest fragments totalizing 250 m² in each study site. From October 2017 to November 2018 we counted monthly the number of fruits of all reproductive bird-dispersed plants in the plots, representing 187 species (38.3 ± 10.2 plant species per site). We extrapolate the average density of fruits sampled in the vegetation plots (fruits/m²) to estimate fruit availability in the entire forest fragment (fruits/ hectare). Then, we obtained the abundance of seeds in the forest by multiplying the estimated fruit density by the average number of seeds per fruit of a given species.

Bird abundance in forest fragments

We estimated the abundance of birds with 10-min point counts at the five vegetation sampling plots per forest separated from each other by at least 200 m. Bird surveys were conducted

once a month between October 2017 and November 2018 from 6:00 to 7:30 when all birds visually and acoustically detected within a 50 m radius were recorded.

Bird activity in tree nuclei

To record bird visits in all experimental tree nuclei in pastures, from October 2017 to November 2018 we did direct observations and used video recordings. Each plot was observed once a month by one observer (PHSA Camargo) using a pair of binoculars from a distance of 50 m for 20 min during morning hours (07:30 to 10:30), totalizing 13.3 h of focal observations per site. We also used 22 camera-traps from different models (ten Bushnell Trophy Cam, six Bushnell Trophy Cam HD, six Tigrinus). Each camera-trap operated 24 h/day for a total of 59,152.9 hours of filming. Finally, we also used six GoPro Hero 3 cameras that filmed for about 2 hours before batteries were depleted, totaling 193.5 hours of filming. All the cameras were rotated and the sampling efforts of the focal observations and filming were equally distributed among experimental plots and sites to prevent sampling bias.

Seed rain

We sampled the seed rain with one 0.25 m^2 seed trap lined with a 0.2 mm nylon mesh and located at the center of each tree nuclei. We smeared the support posts of traps with Formifuu® to exclude ant and covered the traps with a wire screen (2.5 x 2.5 cm mesh) to prevent vertebrate access. Trapped seeds were retrieved once a month, counted and identified to the lowest taxonomic level in the laboratory with the aid of a dissecting scope and available reference books and collections for the local flora. We disregarded grass seeds and seeds from the same experimental plant species present in the plot.

Functional Diversity

To characterize the functional structure of bird and plant assemblages we used corresponding traits that reflect energy requirements, foraging behavior, movement capacity, resource utilization, and plant-bird spatial and temporal match (Table 1). In addition to the corresponding traits, we selected five plant traits that may reflect fecundity, post-dispersal survival, and establishment success (Table 1). We perform correlation tests between traits before further analysis. From the trait matrix we created a distance matrix using the Gower distance (Gower, 1971) and then calculated the functional diversity indices using the FD package (Laliberté & Legendre, 2010; Laliberté, Legendre, & Shipley, 2015) in Software R (R Core Team, 2018). To characterize the functional structure of birds and plants we used functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Laliberté &Legendre, 2010; Mason, Mouillot, Lee, & Wilson, 2005; Petchey & Gaston, 2002; Villéger et al., 2008). FRic is expressed as the volume of the convex hull of the functional trait space. High FRic indicates that there are many traits within a community (Laliberté et al., 2015). FEve measures the regularity of the distribution of the abundance of traits within the functional space, and can indicate the efficient use of resources within an ecosystem (Prescott et al., 2016). Finally, FDiv measures the distribution of the abundance of traits within this volume, increasing with extreme values of traits (Mason et al., 2005; Villéger et al., 2008; Laliberté & Legendre, 2010). We also calculated the community weighted averages (CWM) of the functional traits. CWM measures the average values of species traits for each community. Finally, we seek to assess how much of the functional diversity of birds and plants changes due to the loss and exchange of functions between forest and pasture. For this, we calculated the functional beta diversity using a functional tree (sum of branch lengths of a functional dendrogram; Petchey & Gaston, 2007) constructed with presence-absence data and Jaccard dissimilarity index. The analyses were conducted using the ‘beta’ function of the R package BAT (Cardoso, Rigal, & Carvalho, 2015).

Statistical Analyses

We compared each metric of functional diversity (FRic, FEve and FDiv) and CWM for birds and plants between forest and pasture using paired t-tests. To test the influence of the functional diversity of visiting birds on changes in functional diversity of plants between forest and pasture, we performed linear regression with the FRic of visiting birds as the predictive variable and the functional beta diversity of plants as the response variable.

To test the relationships between the traits of birds and plants (trait-matching) that interact to disperse seeds in pastures, we used an approach similar to Albrecht et al. (2018) and performed RLQ analyses (Dolédec, Chessel, Ter Braak, & Champely, 1996). The RLQ analysis is an ordination technique based on three matrices and originally proposed to relate species traits to environmental variables (Dolédec et al., 1996). Here, for each site, we use an R $(m \times p)$ matrix describing p traits for m plant species, a Q $(n \times a)$ matrix describing a traits for n bird species, and a third L $(m \times n)$ matrix containing qualitative information on the occurrence of paired interactions between m species of plants and n birds. To prepare the L matrix, we used a dataset containing a compilation of 8320 frugivory interactions among 331 vertebrate species and 788 plant species for the Atlantic Forest of Brazil (Bello et al., 2017). We also used information available in Frisch & Frisch (2005), Kuhlmann (2018a), Kuhlmann (2018b) and records of interactions made by us in field. We used as traits for matrices R and Q seven pairs of corresponding traits between birds and plants (first seven pairs in Table 1), but the binary and fuzzy variables were transformed into quantitative variables to facilitate the analysis. For example, for bird diets, we used only the percentage of fruits in the diet, while the foraging stratum, life form, forest dependence and habitat were transformed into scores, and migratory status and fruiting period were transformed into numbers of months of residence and months of fruiting, respectively. Thus, first, the interaction matrix (L) was

ordered by correspondence analysis (CA) with the aim of reducing the dimensionality of the data set and verifying the degree of association between plants and birds (Legendre & Legendre, 2012). Then, we applied principal component analysis (PCA) to R and Q matrices weighted by the number of interactions (species degrees) of each species in matrix L. Finally, we combined the three separate ordinations of R, L and Q using the RLQ approach. The significance of the relationship was investigated using a Monte Carlo permutation test with 49999 permutations (Dolédec et al., 1996). We used the fourth-corner analysis to test the relationships between plant traits and bird traits (Dray et al., 2014). The analyses were performed using the ade4 package (Dray & Dufour, 2007) for software R (R Core Team, 2018).

To explore the causal processes that link FRic (proxy for general functional diversity) of seed rain, FRic of birds and plants from the forest, FRic of birds from pastures, plant-bird trait-matching and plant-bird interaction networks, structural equation models (SEM) were adjusted using the lavaan package (Rosseel, 2012). From the path approach, we built SEM with causal relationships between FRic of birds and plants from the forest, FRic of birds from pastures, plant-bird trait-matching and plant-bird interaction networks to explain the FRic of seed rain, as well as intermediate paths between these variables. We used the FRic values as showed above. For trait-matching, we used the highest correlation value between the ordination axes of bird and plant traits in RLQ analysis, and for interaction networks we used the connectance values of the expected networks generated from the L matrix of each site. Network analyses were performed using the bipartite package (Dormann, Gruber, & Fruend, 2008). The models were visualized with the semPlot package (Epskamp, 2015). All analyses were performed in R version 3.5.1 (R Core Team, 2018).

Results

Functional diversity of birds in forests and pastures

We recorded on average 110 ± 23.3 (mean ± SD) bird species in forest fragments and 16 ± 4.2 active bird species in tree nuclei in pastures (Table S1). Regarding Functional diversity, the values obtained for FRic for the bird communities in forest fragments were on average 13 times higher than in pastures ($t = 10.26$, $df = 11$, $p < 0.001$, Fig. 1 & S1). However, the FEve was on average 1.2 times higher in pastures than in forests ($t = 10.66$, $df = 11$, $p < 0.001$). We found no difference in the values of FDiv ($t = 1.14$, $df = 11$ $p = 0.28$, Table S2). The average functional beta diversity for the bird communities at all sites was 0.81 ± 0.03, which was generated mainly by the loss of the functional diversity of pasture birds in relation to forest birds (Fig S2). As a consequence, the average CWMs differed significantly between forest and pasture for most traits evaluated (Table S3).

In both forest and pasture, bird species with a higher percentage of invertebrates in the diet predominated, followed by fruits and seeds, but the average CWM of the percentage of each item in the diet varied between habitats (Table S3). The preferred foraging stratum also differed. While birds in the forest frequently use the understory, birds that visited pastures prefer to forage on the ground (Table S3). Regarding the foraging method, gleaning predominated in both habitats. However, birds in pastures also used the pursuit method for foraging. The proportion of migrant birds was only 0.42 in the forest, while in the pasture most birds (0.76 ± 0.07) perform some type of migration. In the forest, birds with medium forest dependence predominated, while birds with low forest dependence predominated in the pasture. The average CWM for quantitative traits in forest and pasture were, respectively, 80.27 ± 8.06 and 46.05 ± 6.03 g for body mass, 9.00 ± 0.28 and 10.05 ± 0.65 mm for gape width, and 0.27 ± 0.02 and 0.21 ± 0.02 g/mm for wing loading (Table S3).

Functional diversity of plants in forests and the seed rain in pastures

We recorded on average 30.0 ± 7.1 plant species producing fleshy fruits in forest fragments, and 26.3 ± 3.7 plant species in the seed rain sampled in pastures (Table S4).

We found a positive correlation between the FRic of plant communities in the forest and FRic of plants that arrived in pastures as seeds ($r_s = 0.783$, $p = 0.004$). However, we found no difference in the values of FRic ($t = 0.04$, $df = 11$, $p = 0.971$) and FDiv ($t = 1.53$, $df = 22$, $p = 0.139$) between plants in forest and pasture (Fig. 2 & S3). The FEve values, on the other hand, were on average, 2.6 times higher in the pasture than in the forest ($t = 14.74$, $df = 11$, $p < 0.001$, Fig. 2 & S3, Table S2).

The average functional beta diversity for the plant communities at all sites was only 0.44 ± 0.08, which was generated mainly by replacement of the functional traits of seeds in pasture in relation to the forest plant community (Fig. S4). Because of this, the CWMs did not differ between forest and pasture for most traits evaluated (Table S5). However, catkins were more common in the forest, while follicle was more common in pasture (Table S5). Regarding the life form, palm and shrub were more common in the pasture, while trees were more common and hemiepiphytes were exclusive to the forest. Plant height was greater in plants sampled in the forest, but the fruit mass and seed length were greater in the pasture. Plants that arrived in pastures also had fruits richer in lipids (score 2), with higher proportion of medium-length fruiting period and higher germination rate than plants from the forest (Table S5).

The role of bird functional diversity on plant functional diversity

The RLQ analysis showed that there is a correspondence between the traits of plants and frugivorous birds in most of the sites (mean total inertia = 0.363 ± 0.216; $p < 0.05$ for nine sites; Fig. S5). In all sites, the first ordering axis explained most of the cross covariance

between spaces of plant and bird traits (69.1 ± 11.3%), while the second axis explained 22.5 ± 10.3%. The association between the first axes of the plant and bird trait space were weak and not significant for most sites (| r | = 0.36 ± 0.24). On the other hand, we found strong and significant correlations between the second axes of the trait spaces of plants and animals (| r | = 0.55 ± 0.31, Fig. S5). In all sites, the traits of birds and plants most positively correlated were body mass x fruit mass, and gape width x seed length, while the % of fruits in the diet x fruit lipid score were negatively corelated (Table S6, Fig. S5). The expected interaction networks for all study sites include 143 plant species in the forest (average per site: 30 ± 7.1 species) interacting with 39 (16.3 ± 4.4) species of visiting birds in the pasture. Combined, they comprised a total of 2087 interactions (221 ± 129.8 per site) forming highly connected networks (mean connectance = 0.43 ± 0.12, Fig. S6).

The path analysis showed an interesting sequence through which the functional richness of birds forest increases the functional richness of seed rain (Fig. 3, Table S7). The functional richness of birds and plants in the forest increases the plant-bird trait-matching. A greater functional richness of plants in forest and a greater trait-matching (although with marginal significance, Table S7) increased the connectance of interaction network. The marginal trend of explaining the interaction network by trait matching is probably due to the high number of trait combinations (seven pairs) and the lack of statistical power due to the relatively small number of samples (n = 12). Finally, the functional richness of the seed rain is positively correlated with the connectance of interaction network (Fig. 3, Table S7). We did not find any direct or indirect effects of the functional richness of birds visiting pastures on the functional richness of seed rain (Fig. 3, Table S7). Our results also show that the functional beta diversity of the seeds decreases with the FRic of birds in the pasture (Fig. 4).

Discussion

Combining extensive field study with analytical approaches to functional diversity and network theory, we show that the functional diversity of birds of forests and the plant-bird trait-matching structure the interaction network and increase the functional diversity of seed rain in deforested landscapes of the Brazilian Atlantic Forest. Our results also show that a higher functional volume (FRic) occupied by frugivores reduces the loss of functions in the seed rain and, consequently, also decreases the functional beta diversity between forest plants and the seed rain in tree nuclei in the pasture.

Functional diversity in forest and tree nuclei in pasture

In our study, functional richness showed different patterns for birds and plants between forest and tree nuclei in pasture: for birds, FRic was markedly lower in pasture plots than in forest, resulting in a narrower niche width for open-area birds compared to forest birds (Mason et al., 2005). For plants, FRic did not differ between seed rain in the pasture and the forest community (Fig. 2). This finding is not surprising within the context of birds and reflects a trend observed in other regions where losses of functional traits or FRic in anthropized and simplified environments were reported (e.g., Prescott et al., 2016, Matuoka, Benchimol, de Almeida-Rocha, & Morante-Filho, 2020). This is because the greater structural complexity and heterogeneity of forest habitats can provide a greater variety of niches compared to more simplified landscapes such as pastures (MacArthur & MacArthur, 1961). In fact, the variety of habitats and environmental characteristics existing in forest fragments (e.g., types and strata of vegetation, light gradients, food and nesting resources, PHSA Camargo, pers. obs.) may have allowed the largest spectrum of all traits analyzed (Table S3). For example, larger species and/or more specialized frugivores such as *Penelope superciliaris*, *Trogon surrucura*, *Ramphastos toco*, *Procnias nudicollis* and *Pyroderus*

scutatus were recorded only in the forest (Table S1), where we also recorded less specialized and smaller species such as *Turdus* spp., *Tangara* spp. In tree nuclei in pasture, we registered exclusively generalist and smaller species such as *Pitangus sulphuratus*, *Tyrannus melancholicus* and *Tangara* spp.

In fragmented landscapes, such as our study sites, some ecological functions can be lost or replaced in pastures (Newbold et al., 2013; Matuoka et al. 2020), as we have actually observed, resulting in a high functional beta diversity (Fig. S2). Even with functional simplification (Devictor et al. 2008), the birds visiting pastures still perform well the seed dispersal function as the functional richness of the plants reaching the pastures via seed rain was similar to that of the plants in nearby forests, indicating that the bird-mediated seed dispersal allows an equivalent niche width for both habitats. In addition, we observed low functional beta diversity caused by loss of functional traits between pastures and forest (Fig. S4). The low functional beta diversity recorded for plants was caused mainly by replacement of functions, which may come from seeds from other communities (immigrant seeds, Jordano et al. 2007). In general, the spectrum of functional traits of plants was similar between forest and pasture (Table S5).

Our results also show that for both birds and plants, functional divergence (FDiv) was similar between forest and pasture, suggesting similar levels of niche differentiation between communities in both habitats for both groups (Prescott et al. 2016). On the other hand, functional evenness (FEve) showed significant differences between the two habitats. For both birds and plants, communities recorded in pastures have greater functional evenness than forest communities (Figs. 1-2). It may seem contradictory and contra intuitive that more simplified environments have a higher FD based on the FEve metric. Functional evenness measures the uniformity of species in the multidimensional traits space and is strongly influenced by species abundances (Laliberté & Legendre, 2010; Prescott et al., 2016). In this

sense, in community ecology, it is known that communities with greater species richness are generally more likely to have rare species (e.g., Hubbell, 2013). When using the same principle for functional diversity, it is possible to assume that the increase in functional volume will result in some traits being underrepresented in the community, while others will be overrepresented. Thus, in our study, it is possible that the increase in the spectrum of functional traits in the forest (FRic) also increased the asymmetry in the distribution of these traits, leading to a decrease in the functional evenness of birds and plants in forests (Mason et al., 2005). Functional evenness, therefore, can be compared to taxonomic evenness (Pielou's evenness). In this sense, recently Carlo & Morales (2016) demonstrated that frugivorous birds can equalize the abundance of dispersed seed species in relation to the availability of seeds in the environment. Here, since seed dispersal and, consequently, the dissemination of plant traits are highly mediated by frugivores (see discussion in the next section), it is possible that seed dispersers also play an important role in the equalization of functional traits.

Plant and frugivore functional diversity and trait-matching

As we expected, functional richness and trait-matching between birds and plants were the main drivers of changes in the network structure in our communities and in the functional diversity of the resulting seed rain. The variation in the functional diversity of bird communities, however, did not reflect directly in differences in the connectance of interaction networks or in the functional diversity of the seed rain, but only indirectly in the trait-matching with plants (Fig. 3).

The increase in the functional richness of plants increased the spectrum of traits in the community, allowing for a greater number of foraging niches for frugivorous birds (Dehling et al., 2016). Likewise, the functional richness of birds increased the spectrum of traits linked to the use of these resources, enabling greater trait-matching with plants (Albrecht et al.,

2018). Studies have often shown that interactions between fleshy-fruited plants and frugivorous birds are influenced by morphological traits, especially linked to the size of birds and plants, which promote or restrict fruit consumption (Muñoz et al., 2017a; Bender et al., 2018). Here, we found that functional traits not only related to size matching, but also related to energy requirements, resource utilization, and plant-bird spatial match were strongly associated with the connectance of seed dispersal networks.

Gape size may constrain fruit consumption when the fruit/seed is too big to be swallowed (Wheelwright, 1985; González-Castro et al., 2015). Here, seed size was highly correlated with gape size of avian communities, which corroborates with other studies that found a similar pattern in several locations (e.g. Dehling et al., 2014; Vollstädt et al., 2017; Albrecht, et al. 2018; Bender et al., 2018), suggesting this as a general phenomenon in plant-frugivorous bird networks, and that the loss of bird species with large gapes can have important functional consequences related to seed dispersal (see Galetti et al., 2013). Fruit mass and bird body mass, which can predict supply and energy requirements, were also closely related. This can be explained by the optimal foraging theory (Pyke, Pulliam, & Charnov, 1977) in that larger bird species, which have greater energy needs, should prefer spatially grouped resources (e.g. larger fruits) to reduce energy costs (Petchey, Beckerman, Riede, & Warren, 2008). The degree of frugivory was negatively correlated with the lipid score. This means that more frugivorous birds choose fruits that are lower in lipids due possibly to metabolic constraints that reduces the assimilation efficiency of lipids (Levey & Martínez del Rio, 2001). Finally, our results showed a match between forest dependence on birds with the preferential habitat of plants. Although it is known that birds can cross habitat boundaries to track resources (Neuschulz, Brown, & Farwig, 2013), our data indicate that the location of the resource can be an important restriction for their interactions with fruiting plants.

The trait-matching related to the foraging stratum with plant life form and bird mobility with plant height as well as related to the migration period and fruiting period were more variable among our communities (Fig. 3, Table S6). Although vertical stratification in tropical forests is known to directly influence the niche partition in seed dispersal networks (e.g., Schleuning et al., 2011), it is possible that some birds often move between strata to obtain resources and, therefore, these species are not strictly restricted to a given stratum. Likewise, the low matching of traits related to migration period of birds and the phenology period of plants may be related to less seasonality and high irregularity of fruiting in tropical forests (Morellato et al., 2000). In addition, in the tropics the repertoire of migratory behavior developed by birds is wide (Boyle & Conway, 2007), and many species can migrate only partially (Sekercioglu, 2010, Somenzari et al., 2018). Frugivorous birds also have the ability to track fruits and respond directly to the temporal availability of fruits (Hampe, 2008), and therefore, these traits may not be an impediment to interaction in the community.

Despite the significant general relationships in most pairs of traits, the degree of trait-matching differed among sites due to difference in the spectrum of functional traits existing at each site (Fig. 3). The result of the degree of distinct trait-matching among the sites, together with the functional diversity of plants existing in forest fragments generated different degrees of network connectance among sites. Sites with high functional richness of plants and high plant-bird trait-matching also had high connectance in the expected interaction networks. This is particularly important in the context of our study in fragmented landscapes, because highly connected networks present a lower risk of secondary losses of species resulting from the local extinction of interacting species, and can present a high rate of ecosystem processes (Tylianakis, Laliberté, Nielsen, & Bascompte, 2010). In fact, particularly in mutualistic plant-frugivorous networks, greater disperser diversity is associated with greater seed dispersal effectiveness (Schleuning et al., 2015). Here, connectance was the only variable to positively

influence the functional richness of seed rain on tree nuclei in pastures. A high functional diversity in seed rain can increase the spectrum of traits associated with reproductive and establishment success (e.g. germination percentage, desiccation resistance; Table S5), or simply maintain the functional composition of the source forest community.

Our study demonstrates that trait-matching is a driving force in the assembly of seed dispersal networks in fragmented landscapes, and that the functional diversity of birds is important to expand the spectrum of traits that mediates their interactions with fruits and can translate functional consequences to the seed rain. We also demonstrate that frugivores can equalize the functional diversity of seed rain, just as they do with taxonomic diversity (Carlo & Morales, 2016), as well as that the functional richness of frugivores can prevent loss of functions in the seed rain. We, therefore, highlight the importance of considering the functional diversity of frugivores in plant-animal network studies for a deeper understanding of how the functional roles of the species involved act to structure the seed dispersal process and the resulting forest communities in tropical landscapes.

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Figure captions

Fig. 1. Comparative values of functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) obtained for bird communities in forest fragments and pastures in the 12 study sites. Note that the FRic values for forest bird communities were on average 13 times higher than for pasture communities. Despite this, the FEve values were higher in pastures. There was no difference in the mean values of FDiv.

Fig. 2. Comparative values of functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) obtained for plant communities in forest fragments and in seeds that were dispersed to pastures in the 12 study sites. Although there were no differences in the values of FRic and FDiv, the values of FEve were, on average, almost three times higher in pastures than in the forests.

Fig. 3. Standardized path coefficients among variables determining functional richness of seeds dispersed to pastures adjacent to forest fragments in the 12 study sites. The independent variables are functional richness from forest and pasture birds, and functional richness of plants from forest (represented by convex hulls), plant-bird trait matching obtained from the RLQ analysis (represented by the ordination axes), and plant-bird interactions network (network diagram). The arrows represent unidirectional relationships between variables and the variation in the tint of lines (from lightest to dark) indicates the strength of the effect. See also Table S7.

Fig. 4. The functional beta diversity of plant species in the seed rain decreases with the functional richness of visiting birds in pastures ($r^2 = 0.42$, $p = 0.022$).

Table 1. Summary of traits used to calculate the functional diversity of birds and plants. Numbers below bird and plant traits refer to the sources of trait values, which are listed in the footnote of the table.

Bird trait	**Categories**	**Plant trait**	**Categories**	**Explanation**
Body mass (g) 1	Continuous	Fruit mass (g) 8	Continuous	Bird body mass and fruit mass are related to birds' energy requirements (Moermond & Denslow, 1985; Blendinger & Villegas, 2011)
Gape width 1	Continuous	Seed length (mm) 2	Continuous	Gape width and seed length are related to seed dispersal because a lack of trait matching may constrain fruit consumption (Wheelwright, 1985; González-Castro et al., 2015)
Wing loading 1, 2	Continuous	Plant height (m) 2, 9-13	Continuous	Wing-loading is a proxy for the bird movement capacity, flight performance, and foraging ability, and may be related to plant height (Sullivan, Meyers, & Arzt, 2019)

Diet [3]	Invertebrates	Fuzzy	Lipid score [8, 14-15]	1	Binary	Associated with foraging and resource utilization. In general birds with a high percentage of fruits in the diet prefer fruits with a low lipid concentration, while insectivorous-generalist birds may prefer lipid-rich fruits (Levey & Martínez del Rio, 2001)
	Vertebrates (amphibian, reptiles)	Fuzzy		2	Binary	
	Vertebrates (mammals, birds)	Fuzzy		3	Binary	
	Vertebrates (Unknown)	Fuzzy		4	Binary	
	Fish	Fuzzy				
	Scavenger	Fuzzy				
	Fruits	Fuzzy				
	Nectar	Fuzzy				
	Seeds	Fuzzy				
	Plants (others)	Fuzzy				
Foraging stratum [3]	Water (below)	Fuzzy	Life form [2, 8-13]	Liana	Binary	The vegetation strata used influence the habitat where birds forage and may be related to plant life forms.
	Water (around)	Fuzzy		Hemiparasite	Binary	
	Ground	Fuzzy		Shrub	Binary	
	Understory	Fuzzy		Palm	Binary	
	Mid high	Fuzzy		Tree	Binary	
	Canopy	Fuzzy		Hemiepiphyt	Binary	
	Aerial	Fuzzy				
Migratory status [4-6]	Migrant	Binary	Fruit period length	Short (<2 months)	Binary	The mismatch between the migratory and fruiting phenology

	Resident	Binary	2, 9-13, 16-22	Medium (2-4 months) Long (> 4 months)	Binary Binary	of bird and plants, respectively, may constrain fruit consumption and reduce seed dispersal (Plein et al., 2013)
Forest dependence 4, 6-7	High Medium Low Not occur		Habitat 9-13, 16-22	Forest Semi-forest Open landscapes	Fuzzy Fuzzy Fuzzy	Species preferential habitat can determine habitats where birds look for resources and with which plants can interact
Foraging method 4	Pursuit Gleaning Pouncing Grazing Scavenging Probing	Binary Binary Binary Binary Binary Binary	Fruit type 12-13, 15-22	Berry Drupe Capsule Catkin Syconium Compound (Others) Nucoid Follicle Legume	Binary Binary Binary Binary Binary Binary Binary Binary Binary	The bird foraging method can constraint or facilitate access to certain fruit types
			Number of seeds per fruit		Continuous	Related to plant fecundity

	12-14, 16-22			
	Desiccation resistance 23-24	Hight Medium Low	Binary Binary Binary	A proxy for the chance of seed mortality due to desiccation after dispersal, depending on the deposition site
	Expected germination 9-13, 23-24	Hight Moderate Low	Binary Binary Binary	Help to estimate the plant reproductive success and the chance of successful establishment
	Growth rates 9-13	Slow Moderate Fast	Binary Binary Binary	Related to the chance of successful establishment
	Succession type 9-11, 23	Pioneer Secondary Climax	Binary Binary Binary	May be used to infer the life strategies of plants and their role in the succession and recovery of deforested areas.

Bird traits: 1 – Rodrigues et al. (2019), 2 – Measured or calculated by us, 3 – Wilman et al. (2014), 4 – Del Hoyo et al. (2019), 5 – Sick (2001), 6 - BirdLife International (2019), 7 – Stotz et al. (1996); **Plant traits:** 8 – Bello et al. (2017), 9 – Lorenzi (1992), 10 – Lorenzi (1998), 11 – Lorenzi (2009), 12 – Kuhlmann (2018a), 13 – Kuhlmann (2018b), 14 – Galetti et al. 2011, 15 – Pessoa et al. (2017), 16 – Wanderley et al. (2002), 17 – Wanderley et al. (2003), 18 – Wanderley et al. (2005), 19 – Melhem et al. (2007), 20 – Martins et al. (2009), 21 – Wanderley et al. (2012), 22 – Tozzi et al. (2016), 23 – Mori et al. (2012), 24 – Souza Junior & Brancalion (2016).

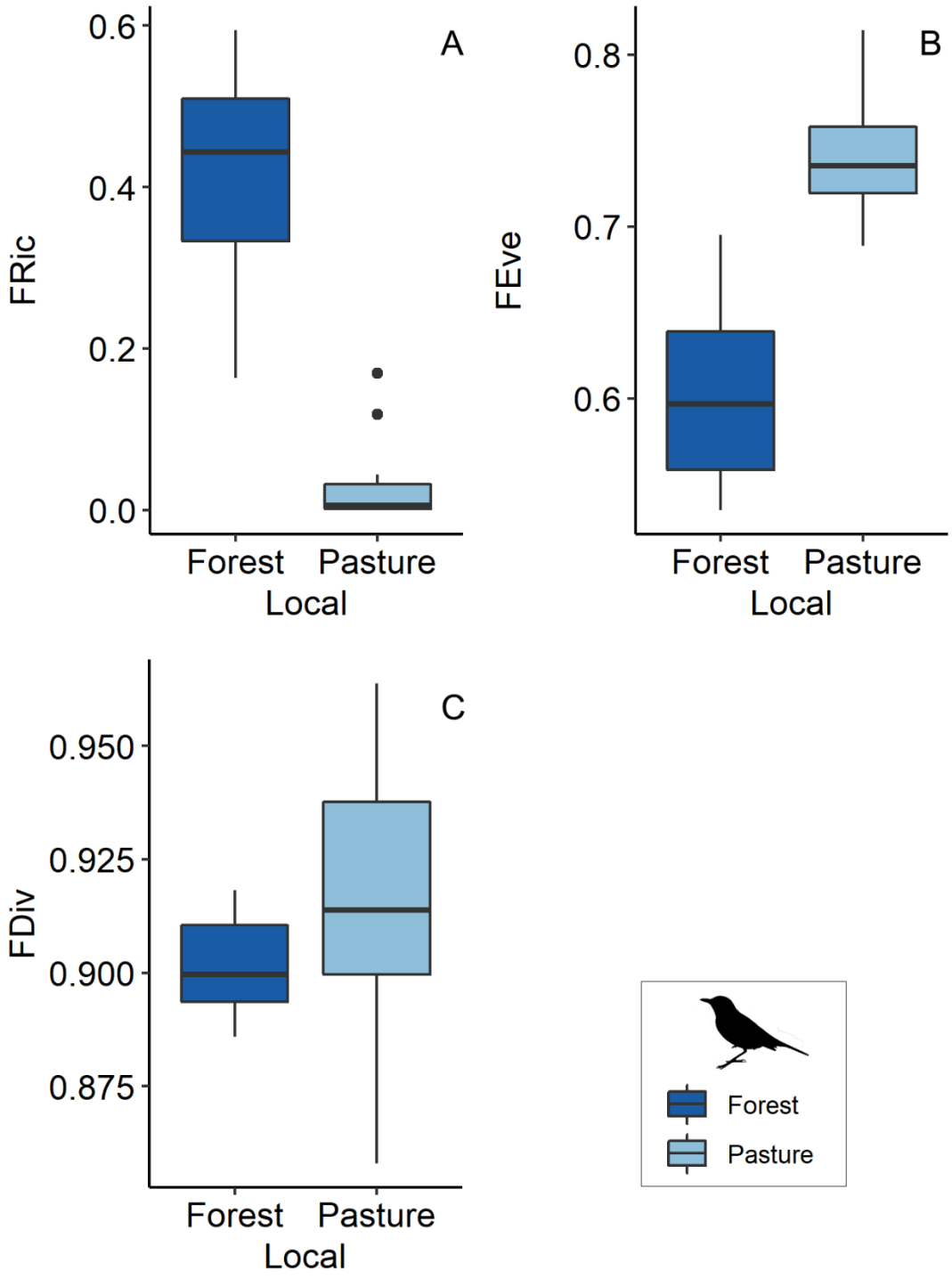

A
FRic
0.6
0.4
0.2
0.0
Forest
Pasture
Local
B
FEve
0.8
0.7
0.6
Forest
Pasture
Local
C
FDiv
0.950
0.925
0.900
0.875
Forest
Pasture
Local
Forest
Pasture

Fig. 1

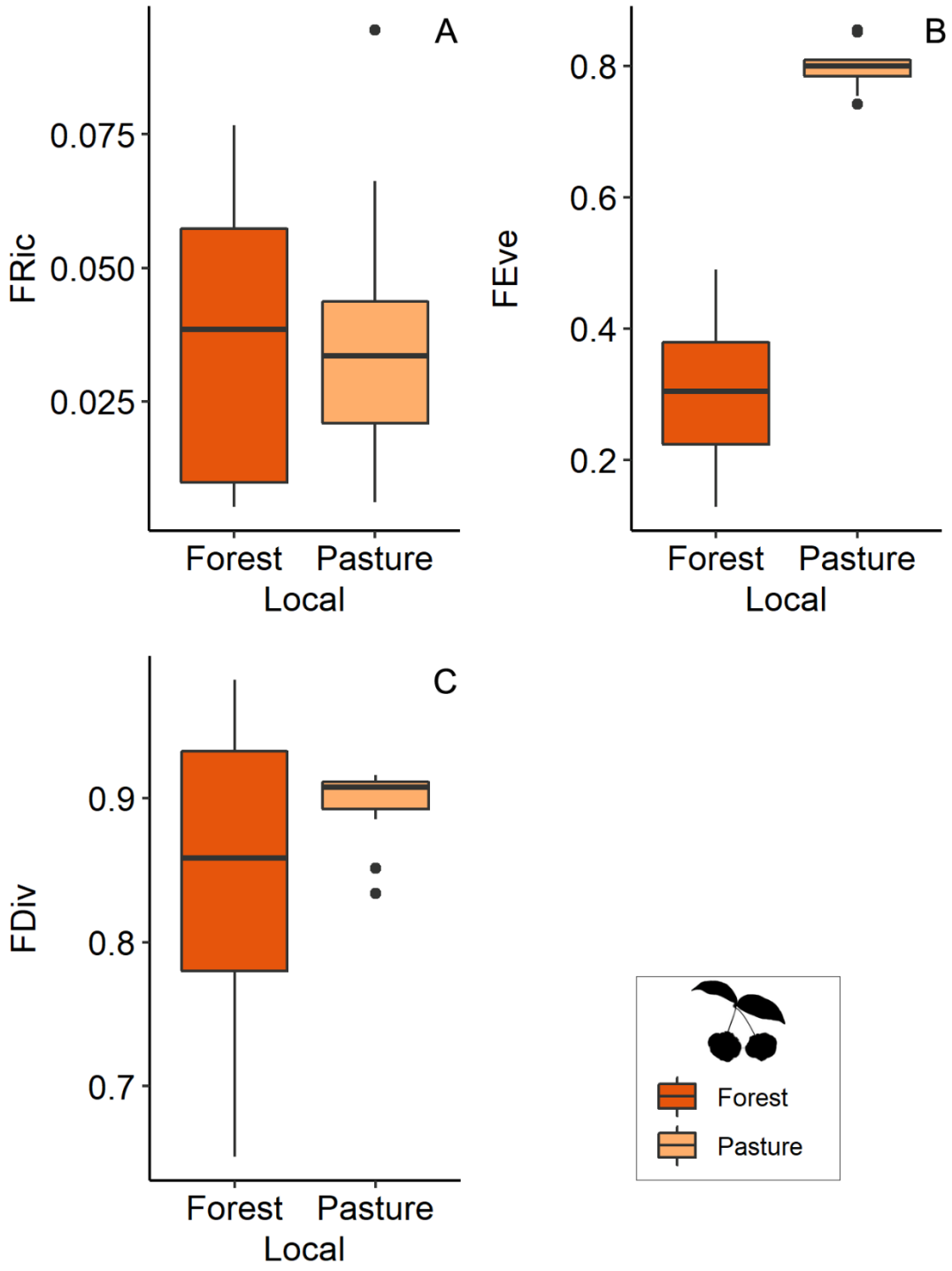
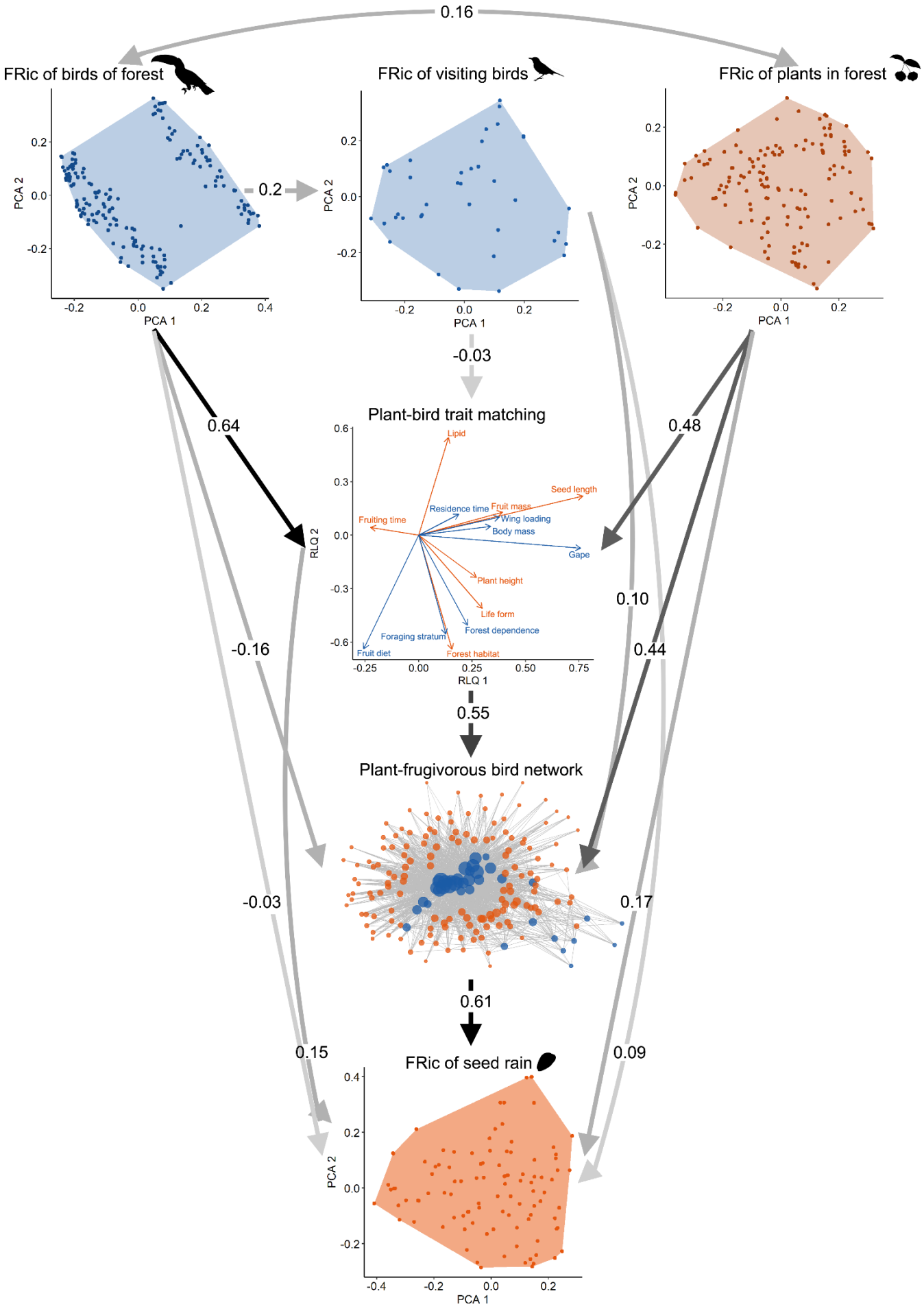

A
FRic
0.075
0.050
0.025
Forest
Pasture
Local
B
FEve
0.8
0.6
0.4
0.2
Forest
Pasture
Local
C
FDiv
0.9
0.8
0.7
Forest
Pasture
Local
Forest
Pasture

Fig. 2


0.16
FRic of birds of forest
FRic of visiting birds
FRic of plants in forest
PCA 2
PCA 1
0.2
-0.03
Plant-bird trait matching
RLQ 2
RLQ 1
Lipid
Seed length
Residence time
Fruit mass
Fruiting time
Wing loading
Body mass
Gape
Plant height
Life form
Forest dependence
Foraging stratum
Fruit diet
Forest habitat
0.64
0.48
-0.16
0.10
0.44
0.55
Plant-frugivorous bird network
-0.03
0.17
0.61
0.15
0.09
FRic of seed rain

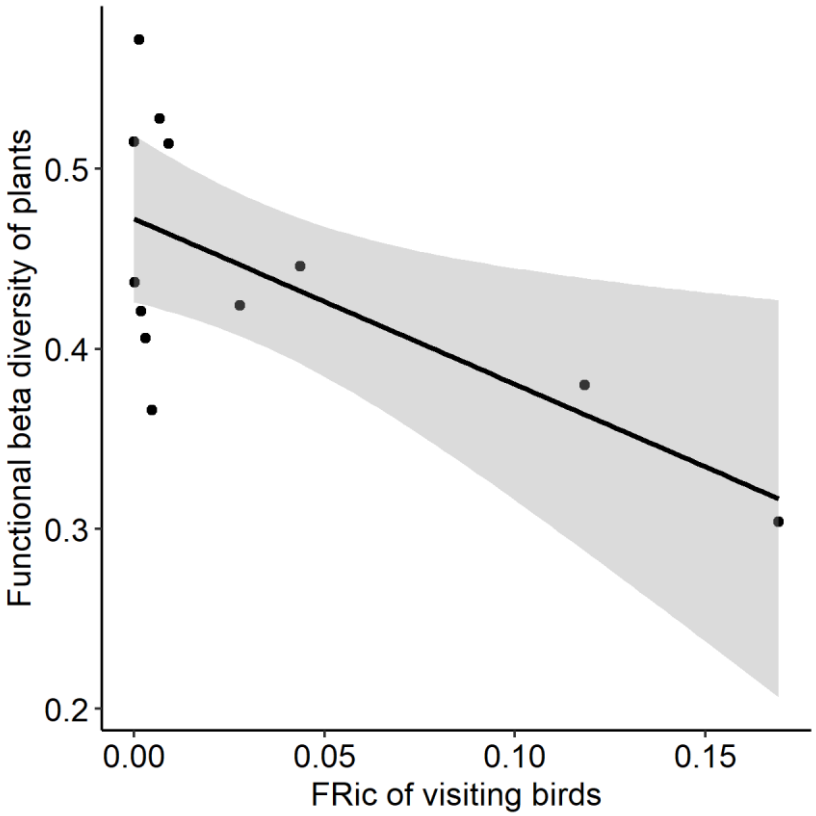

Functional beta diversity of plants
0.5
0.4
0.3
0.2
0.00
0.05
0.10
0.15
FRic of visiting birds

Fig. 4.

Supplementary material

Table S1. Bird species recorded at point counts in forest fragments (F) and in experimental plots on open pastures (P) in the 12 study sites

Species	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
Amazilia lactea	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Amazilia versicolor	1	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Amazona aestiva	1	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Ammodramus humeralis	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0
Anthracothorax nigricollis	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Anthus lutescens	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aramides saracura	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Attila rufus	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Automolus leucophthalmus	1	1	0	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Baryphthengus ruficapillus	0	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Basileuterus culicivorus	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Brotogeris chiriri	0	1	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Bubulcus ibis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Buteo brachyurus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campephilus robustus	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Camptostoma obsoletum	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Caracara plancus	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Cariama cristata	1	1	1	1	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Cathartes aura	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Celeus flavescens	1	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Certhiaxis cinnamomeus	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chiroxiphia caudata	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Chloroceryle amazona	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chloroceryle americana	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlorostilbon lucidus	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Chrysomus ruficapillus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coereba flaveola	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1	0	1	0	0
Colaptes campestris	1	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Colaptes melanochloros	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Colonia colonus	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Columbina squammata	1	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Columbina talpacoti	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Conirostrum speciosum	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Conopophaga lineata	1	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Coragyps atratus	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Coryphospingus cucullatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	1	1	0	0
Corythopis delalandi	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Cranioleuca pallida	1	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Crotophaga ani	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Crypturellus parvirostris	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Cyanocorax chrysops	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1
Cyanocorax cristatellus	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0
Cyclarhis gujanensis	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Dacnis cayana	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0	1	0	0	0
Dryocopus lineatus	1	1	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Dysithamnus mentalis	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Elaenia flavogaster	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1
Elaenia sp	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	0	1
Elanus leucurus	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Emberizoides herbicola	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Empidonomus varius	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1
Estrilda astrild	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eupetomena macroura	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Euphonia chlorotica	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	1
Euphonia cyanocephala	1	1	0	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	1	0	0	1	1	1
Euphonia violacea	0	1	0	0	1	0	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Eupsittula aurea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Falco sparverius	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Florisuga fusca	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forpus xanthopterygius	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Furnarius rufus	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Geothlypis aequinoctialis	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranoaetus albicaudatus	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnorimopsar chopi	1	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Guira guira	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Habia rubica	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Herpetotheres cachinnans	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterospizias meridionalis	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hirundinea ferruginea	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hirundo rustica	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Icterus pyrrhopterus	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0
Ictinia plumbea	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Knipolegus cyanirostris	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathrotriccus euleri	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Legatus leucophaius	0	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidocolaptes angustirostris	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Leptopogon amaurocephalus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Leptotila rufaxilla	0	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Leptotila sp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Leptotila verreauxi	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Lochmias nematura	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Machetornis rixosa	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1
Malacoptila striata	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Megarynchus pitangua	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	1	1	1
Melanerpes candidus	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Micrastur semitorquatus	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Milvago chimachima	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Mimus saturninus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0
Mionectes rufiventris	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Molothrus bonariensis	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myiarchus ferox	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0
Myiarchus sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Myiarchus swainsoni	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Myiarchus tyrannulus	1	1	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Myiodynastes maculatus	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1
Myiothlypis flaveola	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Myiothlypis leucoblephara	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Myiozetetes similis	0	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Nemosia pileata	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0
Nothura maculosa	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Nyctidromus albicollis	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachyramphus polychopterus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachyramphus validus	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Patagioenas cayannensis	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Patagioenas picazuro	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1
Penelope superciliaris	1	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Phaethornis pretrei	0	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Phyllomyias fasciatus	1	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Phylloscartes ventralis	0	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Piaya cayana	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Picumnus temminckii	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Pionus maximiliani	0	1	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Pipraeidea melanonota	1	1	1	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Pitangus sulphuratus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Platyrinchus mystaceus	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Podager nacunda	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poecilotriccus plumbeiceps	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Procnias nudicollis	1	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Progne chalybea	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Progne tapera	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psarocolius decumanus	1	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudoleistes guirahuro	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacara leucophthalmus	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Pygochelidon cyanoleuca	0	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pyriglena leucoptera	1	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Pyrocephalus rubinus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyroderus scutatus	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Ramphastos toco	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Ramphocelus carbo	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Rupornis magnirostris	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Saltator similis	0	1	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Serpophaga subcristata	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Setophaga pitiayumi	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Sicalis flaveola	1	0	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sicalis luteola	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sittasomus griseicapillus	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Spinus magellanicus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sporophila caerulescens	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Sporophila lineola	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Sturnella superciliaris	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synallaxis frontalis	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Synallaxis ruficapilla	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Synallaxis spixi	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Syrigma sibilatrix	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tachyphonus coronatus	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1	0	0	1
Tangara cayana	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1
Tangara palmarum	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	1	0	0	1	1	1
Tangara sayaca	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tapera naevia	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Tersina viridis	0	1	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalurania glaucopis	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Thamnophilus caerulescens	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Thamnophilus doliatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Thamnophilus ruficapillus	1	0	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Theristicus caudatus	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Thlypopsis sordida	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Todirostrum cinereum	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Todirostrum poliocephalum	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Tolmomyias sulphurescens	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Trichothraupis melanops	1	1	1	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Troglodytes musculus	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Trogon surrucura	0	1	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Turdus albicollis	1	0	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Turdus amaurochalinus	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1
Turdus leucomelas	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0
Turdus rufiventris	1	1	0	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	1	0	0	0	0	0
Turdus subalaris	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyrannus melancholicus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tyrannus savana	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1
Vanellus chilensis	1	1	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Veniliornis spilogaster	0	0	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Vireo chivi	1	1	1	1	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Volatinia jacarina	1	0	1	1	0	0	1	1	0	1	0	1	1	1	1	1	0	1	1	1	1	0	0	0

Xenops rutilans	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Xolmis cinereus	1	0	1	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Xolmis velatus	1	0	0	0	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	0	0
Zenaida auriculata	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Zonotrichia capensis	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	1	1	1	0	0	0

Table S2. Values of functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) obtained for bird and plant communities in forest fragments and pastures in the 12 study sites.

	FRic				FEve				FDiv			
	Birds		Plants		Birds		Plants		Birds		Plants	
Site	Forest	Pasture	Forest	Pasture	Forest	Pasture	Forest	Pasture	Forest	Pasture	Forest	Pasture
1	0.520	0.028	0.030	0.043	0.564	0.724	0.128	0.854	0.911	0.933	0.922	0.909
2	0.470	0.118	0.052	0.047	0.595	0.742	0.279	0.809	0.898	0.913	0.726	0.911
3	0.315	0.009	0.009	0.006	0.546	0.689	0.204	0.798	0.918	0.878	0.867	0.913
4	0.163	0.000	0.047	0.027	0.637	0.709	0.230	0.794	0.915	0.858	0.902	0.910
5	0.381	0.003	0.075	0.066	0.640	0.814	0.351	0.754	0.893	0.872	0.801	0.895
6	0.339	0.005	0.012	0.031	0.695	0.788	0.329	0.808	0.910	0.907	0.651	0.851
7	0.445	0.169	0.010	0.023	0.638	0.758	0.490	0.801	0.910	0.914	0.732	0.916
8	0.269	0.002	0.005	0.010	0.560	0.751	0.181	0.742	0.901	0.913	0.796	0.834
9	0.594	0.001	0.008	0.015	0.535	0.758	0.438	0.770	0.892	0.953	0.849	0.885
10	0.584	0.000	0.060	0.041	0.599	0.723	0.258	0.789	0.895	0.964	0.965	0.916
11	0.441	0.007	0.077	0.036	0.555	0.691	0.384	0.852	0.894	0.954	0.962	0.896
12	0.506	0.044	0.057	0.095	0.650	0.729	0.377	0.809	0.886	0.921	0.982	0.906

Table S3. Comparative values of the community-weighted means (CWM) of the functional traits obtained for bird communities in forest fragments and pastures in the 12 study sites.

Traits	Forest	Pasture	t	p
Diet.Inv	54.02 ± 1.705	50.24 ± 5.143	2.505	**0.029**
Diet.Vend	1.025 ± 0.288	2.798 ± 0.551	9.248	< **0.001**
Diet.Vect	1.452 ± 0.444	3.034 ± 0.69	5.954	< **0.001**
Diet.Vfish	0.372 ± 0.108	2.798 ± 0.551	13.492	< **0.001**
Diet.Vunk	0.316 ± 0.116	0.171 ± 0.264	1.524	0.156
Diet.Fruit	22.781 ± 1.173	27.543 ± 6.318	2.949	**0.013**
Diet.Nect	2.971 ± 0.376	1.201 ± 1.062	6.211	< **0.001**
Diet.Seed	14.158 ± 1.414	11.024 ± 3.976	2.763	**0.018**
Diet.PlantO	2.68 ± 0.499	1.19 ± 0.758	5.872	< **0.001**
ForStrat.ground	24.598 ± 2.138	33.416 ± 10.273	2.919	**0.014**
ForStrat.understory	29.084 ± 1.16	22.015 ± 2.161	12.881	< **0.001**
ForStrat.midhigh	28.149 ± 1.55	22.772 ± 4.777	4.257	**0.001**
ForStrat.canopy	17.452 ± 1.254	21.383 ± 4.895	2.310	**0.041**
ForStrat.aerial	0.516 ± 0.094	0.392 ± 0.271	1.310	0.217
ForMet.Porsuit	0.318 ± 0.037	0.629 ± 0.109	8.683	< **0.001**
ForMet.Probing	0.142 ± 0.021	0.017 ± 0.02	12.154	< **0.001**
ForMet.Gleaning	0.935 ± 0.008	0.843 ± 0.038	8.342	< **0.001**
ForMet.Digging	0.006 ± 0.005	0.001 ± 0.003	2.807	**0.017**
ForMet.Poucing	0.113 ± 0.015	0.316 ± 0.032	20.853	< **0.001**
Migrant	0.423 ± 0.045	0.763 ± 0.07	13.002	< **0.001**
ForDep.Hight	0.102 ± 0.031	0.009 ± 0.011	12.314	< **0.001**
ForDep.Medium	0.42 ± 0.032	0.121 ± 0.054	33.836	< **0.001**

ForDep.Low	0.377 ± 0.047	0.709 ± 0.083	9.664	< **0.001**
ForDep.notoccur	0.101 ± 0.023	0.16 ± 0.12	1.894	0.085
BodyMass.Value	80.269 ± 8.065	46.051 ± 6.028	16.203	< **0.001**
Gape	8.996 ± 0.285	10.046 ± 0.647	7.295	< **0.001**
Wing.loading	0.272 ± 0.016	0.211 ± 0.015	13.782	< **0.001**

Table S4. Plant species recorded producing fleshy fruits at vegetation plots in forest fragments (F) and in seed rain in experimental plots on open pastures (P) in the 12 study sites

Species	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12
Abuta selloana	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Actinostemon concepcionis	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Actinostemon concolor	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Aegiphila integrifolia	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	0
Alchornea glandulosa	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0
Alibertia concolor	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Allophylus edulis	1	0	1	1	1	1	1	0	0	1	0	1	1	0	0	1	1	1	1	0	0	1	0	1
Amaioua intermedia	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Annona sylvatica	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Aparisthmium cordatum	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Byrsonima laxiflora	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cabralea canjerana	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Calyptranthes clusiifolia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Calyptranthes concinna	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Calyptranthes sp	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campomanesia guaviroba	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
Campomanesia guazumifolia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campomanesia xanthocarpa	1	0	1	0	0	1	0	1	1	0	0	0	1	0	1	1	0	1	0	1	1	0	0	1

Casearia decandra	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Casearia gossypiosperma	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Casearia sylvestris	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cecropia pachystachya	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Celtis iguanaea	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0
Chrysophyllum gonocarpum	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Chrysophyllum marginatum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cissus erosa	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cissus serroniana	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Citrus limon	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Citharexylum myrianthum	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0
Colubrina glandulosa	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copaifera langsdorffii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cordia ecalyculata	0	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	0
Cordia sellowiana	0	1	0	0	1	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	1	1	0	1
Cordia superba	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Croton floribundus	0	1	0	0	1	1	0	1	0	0	0	1	0	1	0	0	1	1	0	1	1	0	1	1
Cupania vernalis	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dendropanax cuneatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Diospyros inconstans	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	1	1	0
Endlicheria paniculata	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enterolobium contortisiliquum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erythroxylum deciduum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0

Erythroxylum pelleterianum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Eugenia blastantha	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Eugenia hiemalis	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eugenia involucrata	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Eugenia myrcianthes	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eugenia sp3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Eugenia subterminalis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eugenia uniflora	1	1	0	0	1	1	0	0	0	1	0	0	1	1	0	1	1	0	1	0	1	1	0	1
Euterpe edulis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1
Faramea montevidensis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ficus citrifolia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ficus enormis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ficus luschnathiana	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ficus pulchella	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Ficus trigona	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geissanthus ambiguus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Guarea guidonia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Guapira hirsuta	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Guarea kunthiana	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Guarea macrophylla	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Guatteria nigrescens	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Guapira opposita	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Guapira sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Guazuma ulmifolia	1	0	1	1	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	1
Holocalyx balansae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hybanthus bigibbosus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyeronima alchorneoides	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Ilex dumosa	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ilex sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Inga edulis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inga striata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ixora venulosa	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Jacaratia spinosa	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lacistema hasslerianum	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Lauraceae 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Lauraceae 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Lauraceae 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lauraceae 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Lithraea molleoides	1	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	1	0	0
Maclura tinctoria	0	1	1	1	1	0	1	1	1	0	0	1	0	1	0	1	1	0	1	1	1	0	0	0
Magnolia ovata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Maprounea guianensis	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0
Margaritopsis cephalantha	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Matayba elaeagnoides	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maytenus evonymoides	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maytenus gonoclada	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0

Melastomataceae 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Melastomataceae 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Melastomataceae 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Miconia albicans	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Miconia ligustroides	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Mollinedia widgrenii	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	1
Myrtaceae 1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0
Myrtaceae 2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Myrtaceae 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Myrtaceae 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Myrtaceae 7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Myrciaria floribunda	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Myrsine lancifolia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrcianthes pungens	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrcia rostrata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrcia tomentosa	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Myrsine umbellata	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Nectandra cuspidata	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Nectandra lanceolata	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Nectandra megapotamica	1	0	1	1	0	0	0	1	1	1	0	0	1	0	1	1	0	0	0	1	0	1	0	1
Nectandra oppositifolia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ocotea corymbosa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Ocotea nutans	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Ocotea silvestris	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Ocotea velutina	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Ormosia arborea	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ouratea spectabilis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Paullinia meliifolia	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pera glabrata	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1
Persea willdenovii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoradendron crassifolium	1	1	1	1	1	0	1	0	0	1	1	0	1	1	0	0	1	0	1	0	0	1	1	0
Piper amalago	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Piper arboreum	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piper gaudichaudianum	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Piper sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1
Plinia rivularis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prockia crucis	0	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Protium heptaphyllum	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0
Prunus myrtifolia	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0
Psidium guajava	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	0	0	1	0	1	1	0	0
Psychotria carthagenensis	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Psychotria leiocarpa	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Psychotria sp	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0
Randia calycina	1	1	1	0	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1
Rauvolfia sellowii	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnidium elaeocarpum	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0

Rubus bogotensis var. brasiliensis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Rudgea jasminoides	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schoepfia brasiliensis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Schefflera morototoni	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schinus terebinthifolia	1	0	1	0	0	1	1	1	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	0
Schefflera vinosa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sebastiania brasiliensis	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
Siparuna guianensis	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Smilax sp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Solanum argenteum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Solanum pseudoquina	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Solanum sp	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Solanum sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sorocea bonplandii	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1
Strychnos brasiliensis	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Styrax acuminatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Syagrus romanzoffiana	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1
Tabernaemontana hystrix	0	1	0	1	0	1	0	1	1	1	0	1	0	1	0	1	0	1	1	1	1	1	0	1
Tapirira guianensis	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Trema micrantha	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichilia casaretti	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Trichilia catigua	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0

Trichilia elegans	1	0	0	0	1	0	0	1	0	1	0	1	1	0	0	1	1	1	0	1	0	1	0	1
Trichilia pallida	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1
Trichilia sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Vitex megapotamica	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0
Xylosma pseudosalzmanii	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Zanthoxylum acuminatum	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Zanthoxylum caribaeum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Zanthoxylum fagara	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0
Zanthoxylum monogynum	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
Zanthoxylum rhoifolium	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0

Table S5. Comparative values of the community-weighted means (CWM) of the functional traits obtained for plant communities in forest fragments and pastures in the 12 study sites.

Traits	**Forest**	**Pasture**	**t**	**p**
FruType.Berry	0.186 ± 0.231	0.22 ± 0.074	0.579	0.574
FruType.Drupe	0.148 ± 0.234	0.269 ± 0.078	2.107	0.059
FruType.Capsule	0.421 ± 0.254	0.375 ± 0.077	0.753	0.467
FruType.Catkin	0.004 ± 0.006	0.026 ± 0.032	2.425	**0.033**
FruType.Syconium	0.15 ± 0.243	0.022 ± 0.053	1.873	0.088
FruType.CompOthers	0.082 ± 0.159	0.026 ± 0.031	1.344	0.206
FruType.Nucoid	0.0001 ± 0.0003	0.005 ± 0.013	1.370	0.198
FruType.Legume	0.006 ± 0.022	0.006 ± 0.013	0.110	0.914
FruType.Follicle	0.003 ± 0.004	0.051 ± 0.036	4.883	< **0.001**
LifeForm.Palm	0.0003 ± 0.0004	0.031 ± 0.018	5.849	< **0.001**
LifeForm.Tree	0.969 ± 0.032	0.81 ± 0.062	8.552	< **0.001**
LifeForm.hemiepiphyt	0.098 ± 0.213	0	*	*
LifeForm.Shurb	0.168 ± 0.246	0.306 ± 0.106	2.298	**0.042**
LifeForm.Liana	0.0002 ± 0.00003	0.004 ± 0.015	0.998	0.340
LifeForm.Hemiparasite	0.008 ± 0.015	0.013 ± 0.017	0.756	0.465
LipidScore.1	0.549 ± 0.278	0.547 ± 0.094	0.033	0.974
LipidScore.2	0.015 ± 0.026	0.092 ± 0.039	5.524	< **0.001**
LipidScore.3	0.204 ± 0.224	0.129 ± 0.054	1.213	0.251
LipidScore.4	0.232 ± 0.294	0.232 ± 0.058	0.004	0.997
SeedNumber	31.224 ± 39.587	46.921 ± 67.131	0.825	0.427
FruitMass	1.375 ± 1.213	9.263 ± 12.401	2.417	**0.034**
SeedLenght	4.691 ± 1.148	6.686 ± 0.521	5.341	< **0.001**
PlantHeight	10.369 ± 2.088	8.454 ± 1.156	2.917	**0.014**

FruTime.Short	0.192 ± 0.235	0.116 ± 0.052	1.220	0.248
FruTime.Medium	0.165 ± 0.171	0.349 ± 0.076	3.657	**0.004**
FruTime.Long	0.643 ± 0.269	0.535 ± 0.082	1.471	0.169
Hab.Forest	65.412 ± 12.456	63.279 ± 4.782	0.573	0.578
Hab.Semiforest	27.961 ± 9.378	26.724 ± 3.392	0.472	0.646
Hab.Open	6.621 ± 4.752	9.878 ± 2.026	2.092	0.060
Germ.Low	0.239 ± 0.255	0.223 ± 0.093	0.207	0.840
Germ.Moderate	0.7 ± 0.24	0.591 ± 0.089	1.337	0.208
Germ.High	0.061 ± 0.067	0.186 ± 0.104	3.040	**0.011**
Des.Res.High	0.35 ± 0.307	0.476 ± 0.093	1.672	0.123
Des.Res.Medium	0.13 ± 0.163	0.057 ± 0.034	1.714	0.115
Des.Res.Low	0.52 ± 0.294	0.467 ± 0.071	0.652	0.528
Growth.Slow	0.139 ± 0.242	0.144 ± 0.06	0.093	0.928
Growth.Moderate	0.438 ± 0.339	0.4 ± 0.089	0.450	0.661
Growth.Fast	0.432 ± 0.341	0.458 ± 0.09	0.296	0.773
SucPioneer	0.572 ± 0.37	0.435 ± 0.099	1.605	0.137
SucSecondary	0.299 ± 0.299	0.444 ± 0.08	2.020	0.068
SucClimax	0.129 ± 0.232	0.121 ± 0.04	0.120	0.906

Table S6. Combination of fourth-corner and RLQ results for all sites. Above is shown the fourth-corner tests between the first two RLQ axes for plant traits (AxR1/AxR2) and bird traits. Below is shown the fourth-corner tests between the first two RLQ axes for bird traits (AxQ1/AxQ2) and plant traits. Significant ($P < 0{\cdot}05$) associations are represented by grey cells.

Bird traits	AxR1	AxR2
Foraging stratum	0.029	-0.120
Fruit-eating diet	-0.059	-0.138
Time of residence	0.043	0.025
Forest dependence	0.053	-0.109
Body mass	0.077	0.011
Gape width	0.174	-0.016
Wing loading	0.087	0.022

Plant traits	AxQ1	AxQ2
Life form	0.060	-0.080
Lipid score	0.028	0.107
Fuiting period length	-0.045	0.008
Forest habitat	0.032	-0.125
Fruit mass	0.079	0.025
Seed lenght	0.155	0.043
Plant height	0.055	-0.046

Table S7. Summary of path analysis of the relationships among variables determining functional richness of dispersed seeds in plots in pastures adjacent to forest fragments in the 12 study sites.

	Estimate	SE	z	p	Std.lv	Std.all
FRic of dispersed seeds in pastures ~						
Interections network	**0.128**	**0.055**	**2.318**	**0.02**	**0.128**	**0.605**
Plant-bird trait matching	0.019	0.041	0.48	0.632	0.019	0.153
FRic of plants from forest	0.154	0.214	0.721	0.471	0.154	0.168
FRic of birds from forest	-0.005	0.047	-0.117	0.907	-0.005	-0.028
FRic of birds from pasture	0.043	0.07	0.617	0.537	0.043	0.094
Interactions network ~						
Plant-bird trait matching	0.332	0.189	1.76	0.078	0.332	0.553
FRic of plants from forest	**1.919**	**0.971**	**1.977**	**0.048**	**1.919**	**0.442**
FRic of birds from forest	-0.145	0.241	-0.599	0.549	-0.145	-0.157
FRic of birds from pasture	0.215	0.362	0.593	0.553	0.215	0.099
Plant-bird trait matching ~						
FRic of plants from forest	**3.484**	**1.094**	**3.185**	**0.001**	**3.484**	**0.481**

FRic of birds from forest	**0.984**	**0.236**	**4.165**	**0**	**0.984**	**0.642**
FRic of birds from pasture	-0.12	0.553	-0.216	0.829	-0.12	-0.033
FRic of birds from pasture ~						
FRic of birds from forest	0.084	0.119	0.708	0.479	0.084	0.2

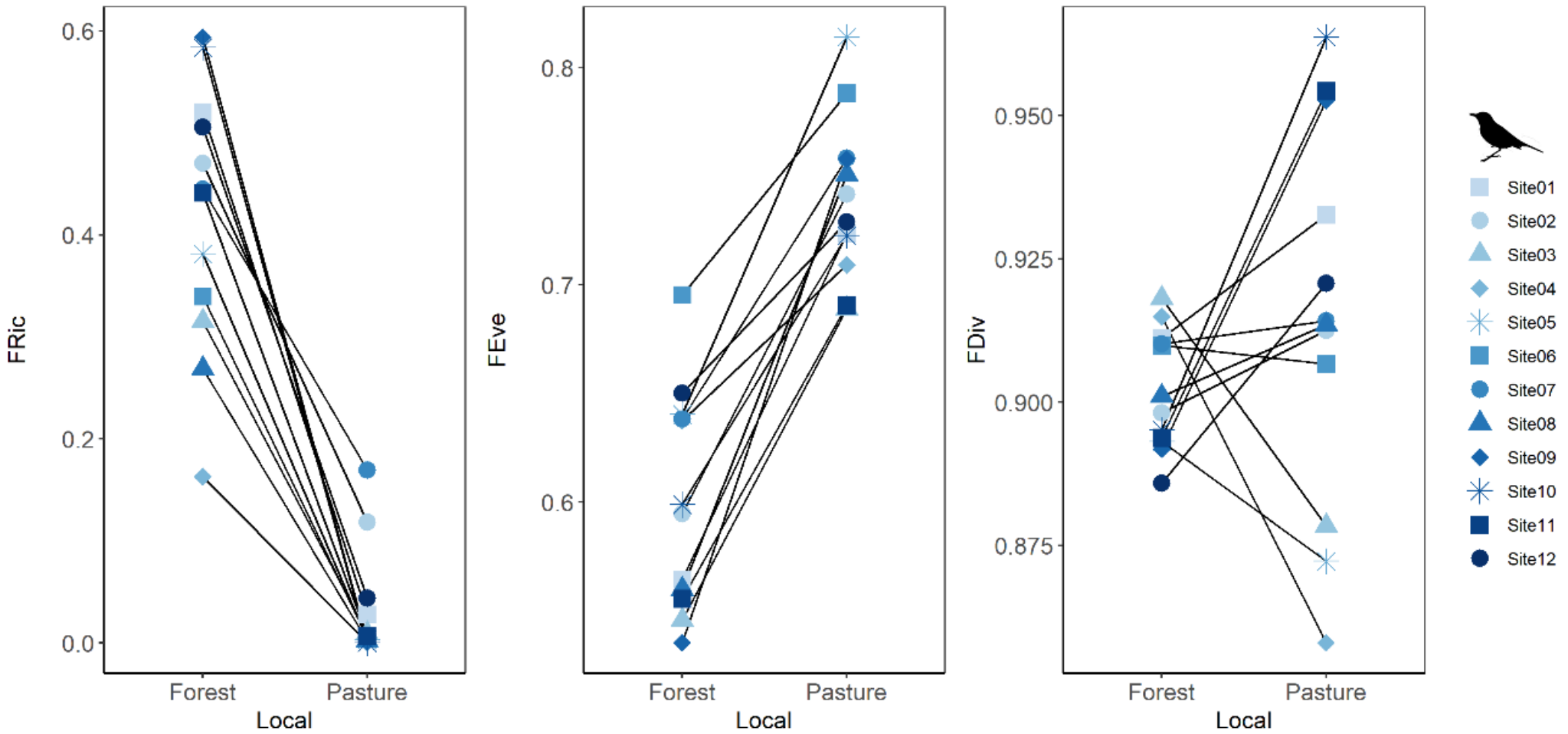


Fig. S1. Comparative values of functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) obtained for bird communities in forest fragments and adjacent pastures on each of the 12 study sites.

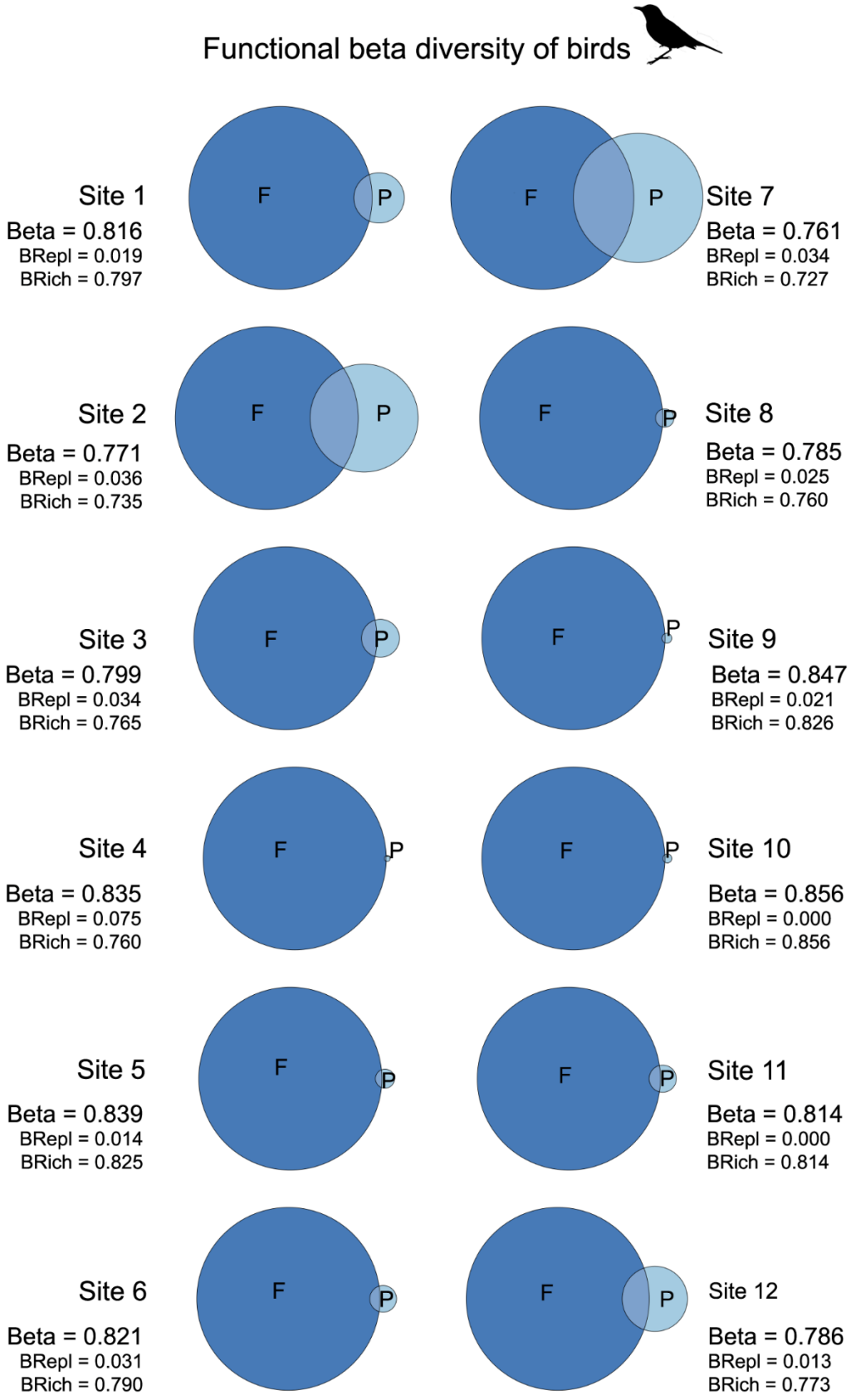


Fig. S2. Functional beta diversity of bird communities generated from loss or gain of richness (BRich) and replacement of functions (BRepl) between forest and adjacent pastures on each of the

12 study sites. The size of the circles represents the relationship between the FRic of birds in the forest (F) and in the pasture (P) and the overlapping area represents the proportion of functions shared between these locations.

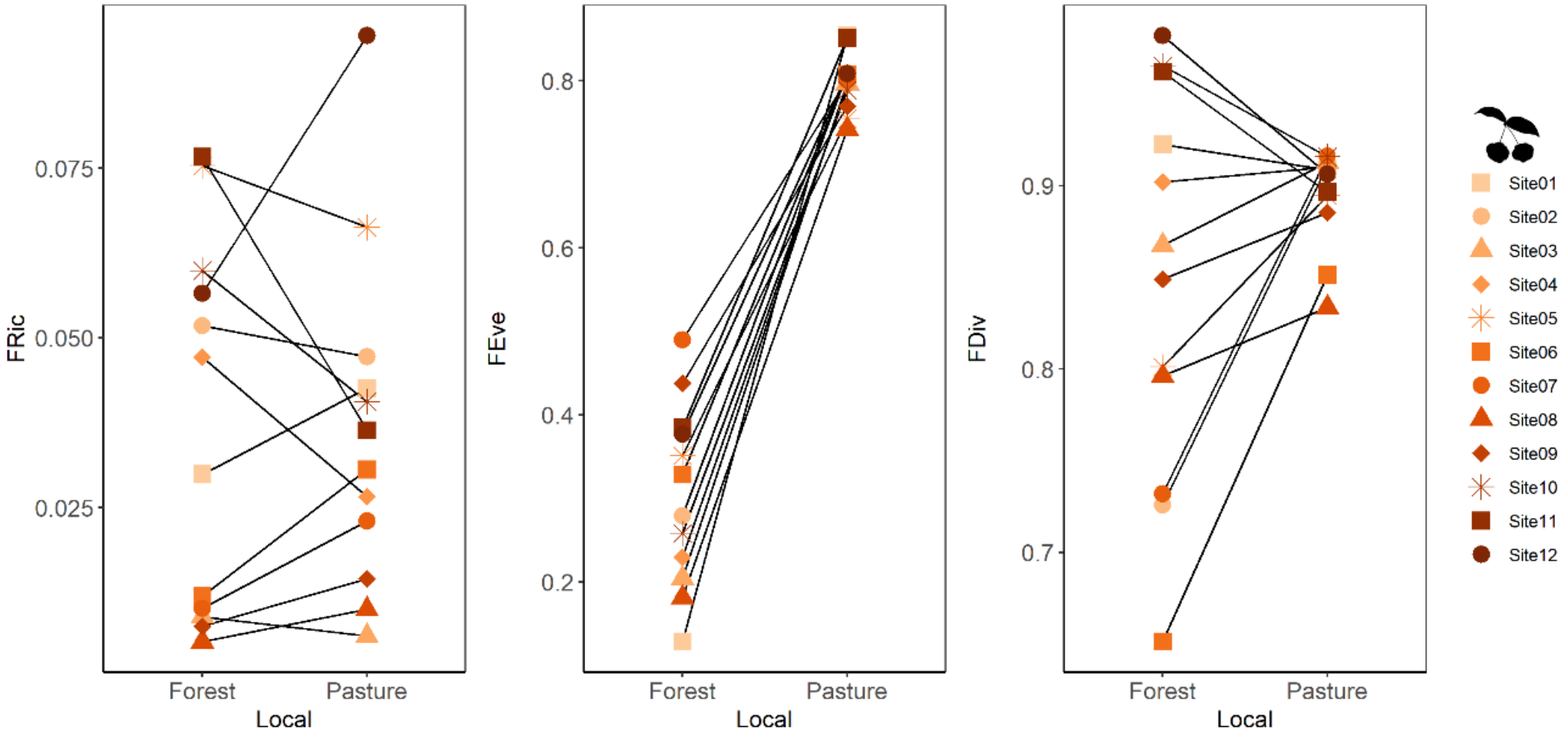


Fig. S3. Comparative values of functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) obtained for plant communities in forest fragments and in seed rain in adjacent pastures on each of the 12 study sites.

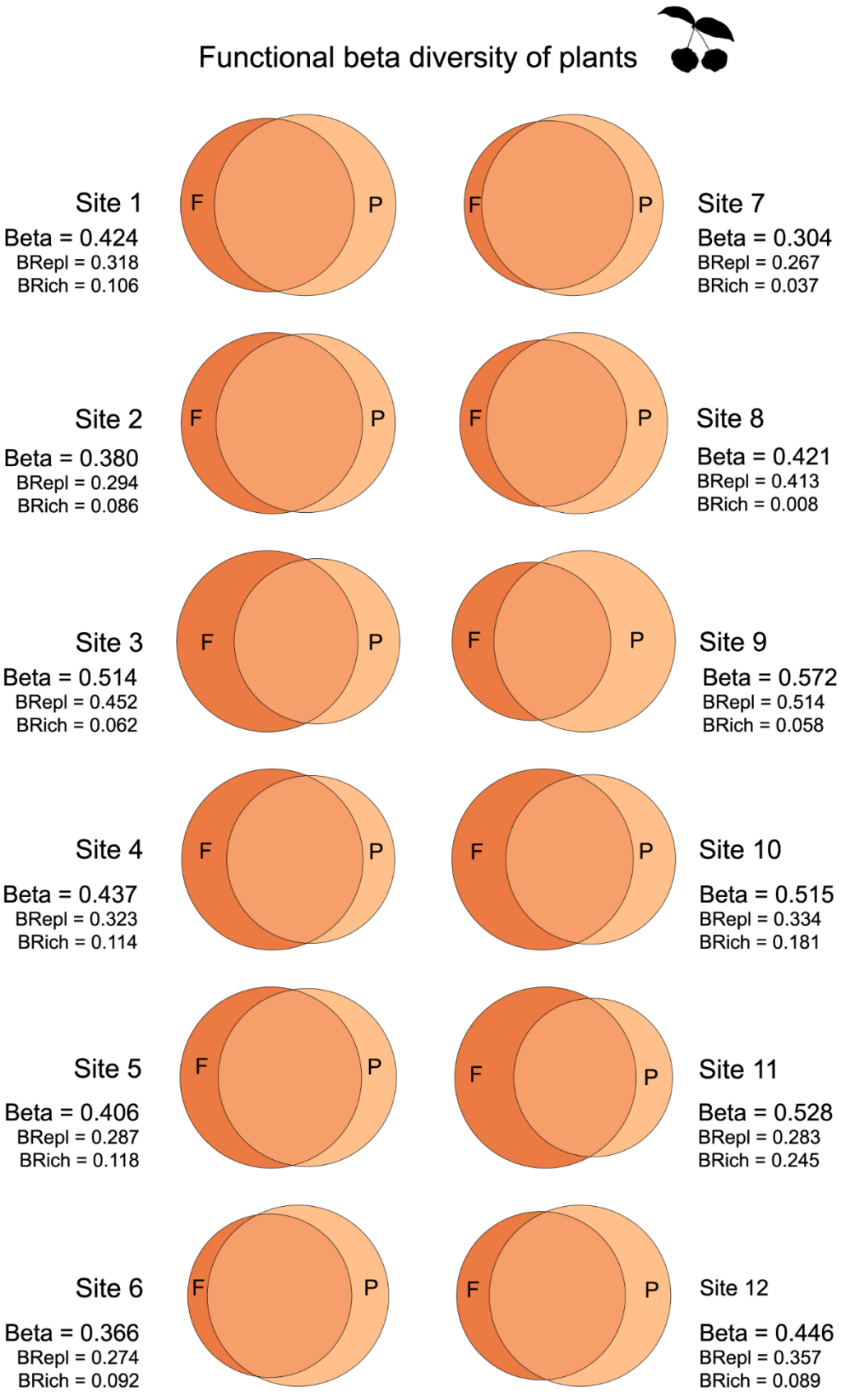

Functional beta diversity of plants
Site 1
Beta = 0.424
BRepl = 0.318
BRich = 0.106
F
P
Site 2
Beta = 0.380
BRepl = 0.294
BRich = 0.086
Site 3
Beta = 0.514
BRepl = 0.452
BRich = 0.062
Site 4
Beta = 0.437
BRepl = 0.323
BRich = 0.114
Site 5
Beta = 0.406
BRepl = 0.287
BRich = 0.118
Site 6
Beta = 0.366
BRepl = 0.274
BRich = 0.092
Site 7
Beta = 0.304
BRepl = 0.267
BRich = 0.037
Site 8
Beta = 0.421
BRepl = 0.413
BRich = 0.008
Site 9
Beta = 0.572
BRepl = 0.514
BRich = 0.058
Site 10
Beta = 0.515
BRepl = 0.334
BRich = 0.181
Site 11
Beta = 0.528
BRepl = 0.283
BRich = 0.245
Site 12
Beta = 0.446
BRepl = 0.357
BRich = 0.089

Fig. S4. Functional beta diversity of plant communities generated from loss or gain of richness (BRich) and replacement of functions (BRepl) between forest and adjacent pastures on each of the 12 study sites. The size of the circles represents the relationship between the FRic of plant in the forest (F) and in the pasture (P) and the overlapping area represents the proportion of functions shared between these locations.

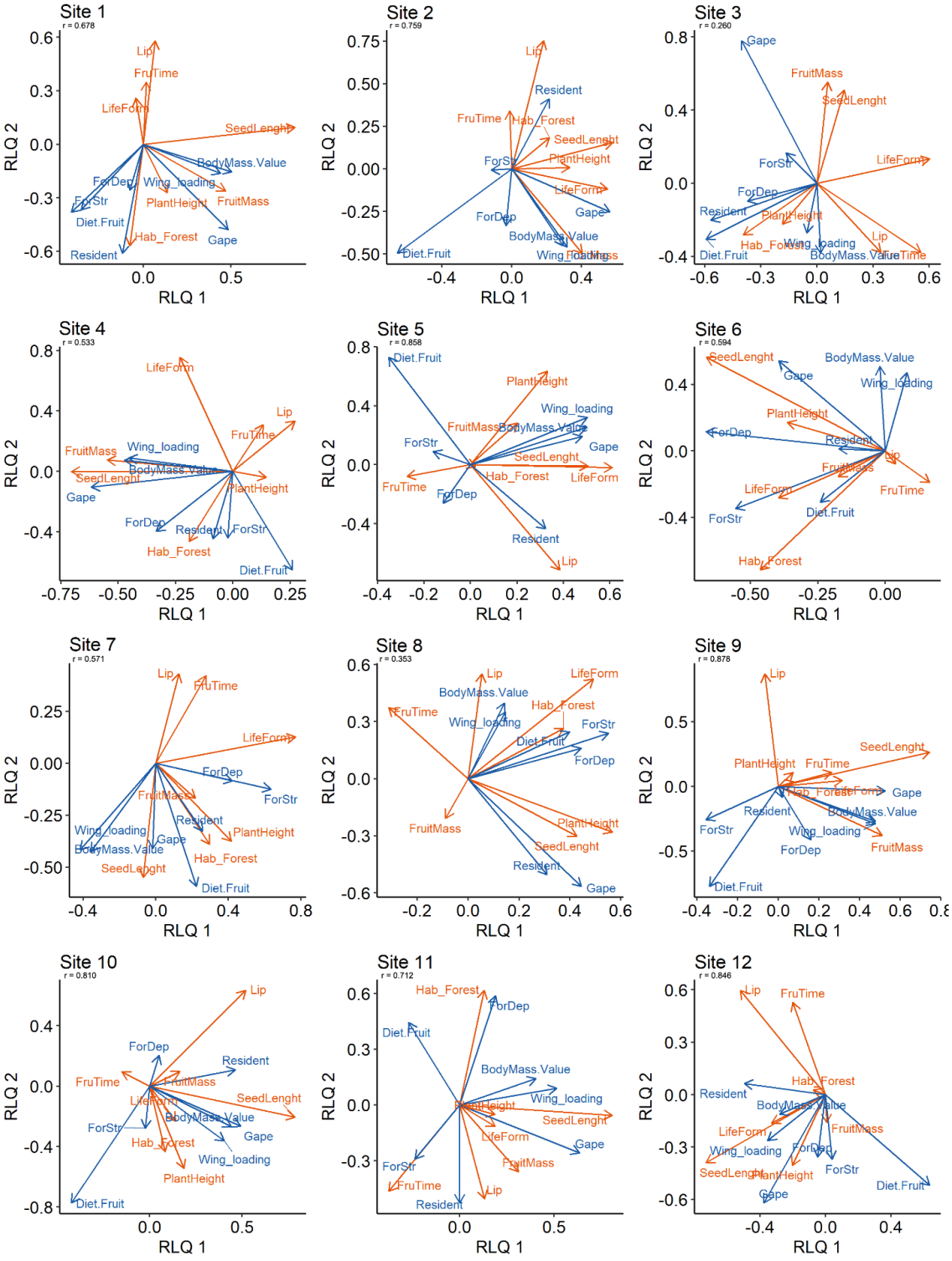


Fig. S5. Matching of functional traits of frugivorous birds and plants resulting from the combination of RLQ and fourth corner analyses. For each of the 12 study sites we show the variation of the space of traits of birds (blue vectors) and plants (orange vectors) based on

plant-animal interaction networks. The long vectors of birds and plants pointing in the same direction indicate a high positive correlation between traits, while in opposite directions they indicate negative correlations. Pearson's correlation coefficient between the first or second axes (the highest value) of ordinations of the traits of birds and plants is also provided.

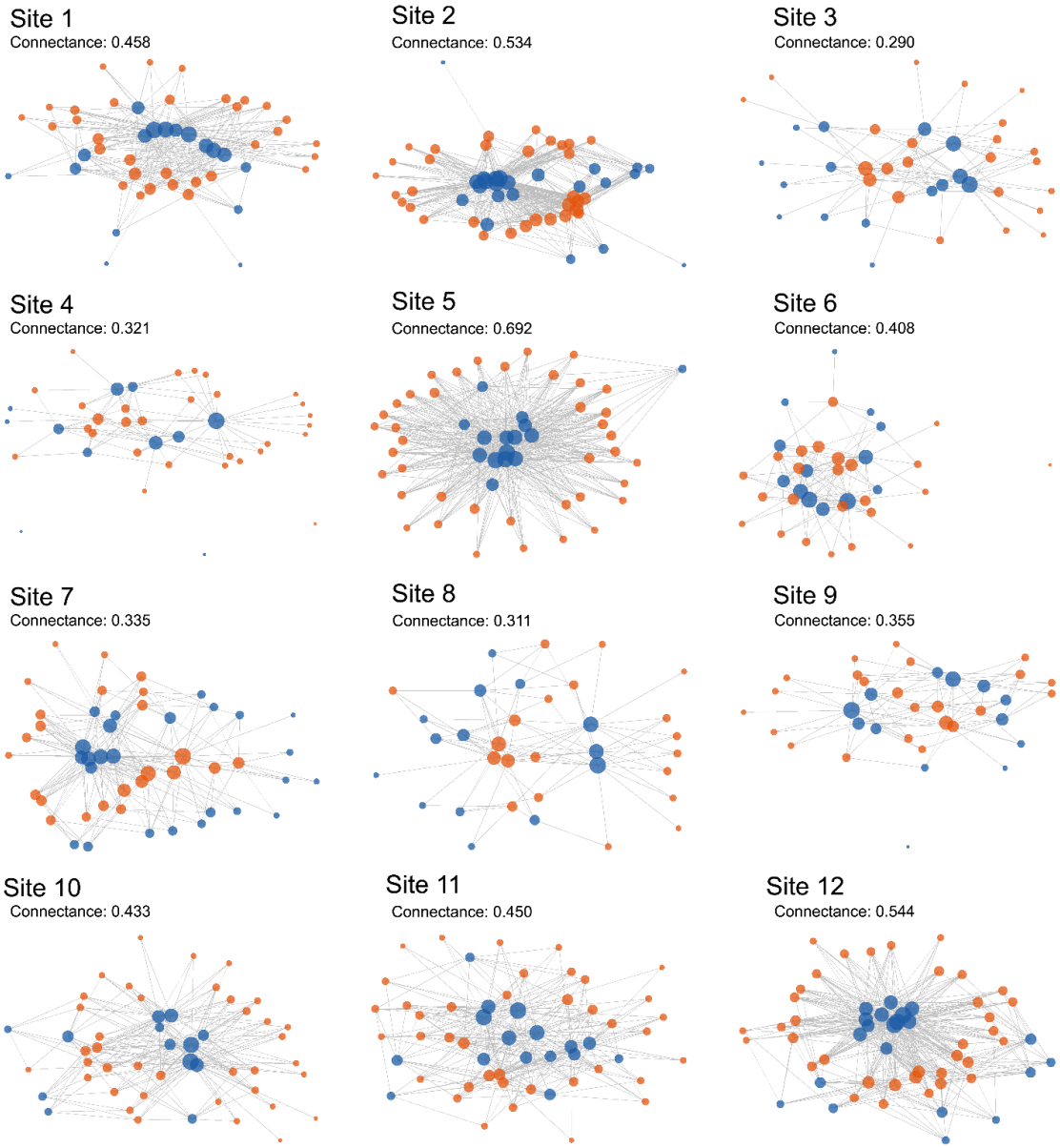


Fig. S6. Interaction networks involving plants (orange circles) and frugivorous birds (blue circles) expected for each of the 12 study sites from literature data. The size of the circles indicates the degrees of each species involved. Network connectance values are also provided.

Conclusões finais

Ao final dessa tese, chegamos às seguintes conclusões

- Compreender os efeitos da correspondência de características entre aves e plantas sobre a chuva de sementes em um gradiente de distância que separa áreas desmatadas de fragmentos florestais é fundamental para melhorar os esforços de restauração, especialmente no contexto de nucleação aplicada em paisagens tropicais desmatadas. Neste sentido, a dispersão de sementes de aves pode ser manipulada em projetos de restauração a fim de aumentar a conectividade e acelerar a recuperação da floresta e a provisão de vários serviços ecossistêmicos que se seguem após a sucessão da floresta.
- Nossos resultados mostram que os frutos proporcionalmente raros em fragmentos de Mata Atlântica têm uma probabilidade maior do que o esperado de dispersão de sementes devido ao efeito equalizador promovido por aves frugívoras, que é um mecanismo importante e geral Dependente da Densidade Negativa que promove a coexistência e a resiliência das comunidades de plantas tropicais. Além disso, há efeito positivo da riqueza de frugívoros no tamanho desse efeito equalizador resultante da dispersão de sementes, o que ressalta a urgência de reduzir a perda de espécies de aves e a simplificação de suas comunidades em paisagens tropicais.
- Descobrimos que uma maior diversidade funcional de aves e plantas permite uma maior correspondência de características entre plantas e aves e uma rede de interações mais conectada. Isso pode gerar uma maior riqueza funcional na chuva de sementes. Nossos resultados destacam a importância da diversidade funcional de frugívoros para a montagem das redes de interação planta-animal e a promoção de uma dispersão de sementes funcionalmente mais diversa em paisagens tropicais.

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