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A funcionalidade ecológica das agroflorestas de cacau: revelando a influência de múltiplos fatores na chuva de sementes

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Sumário

Resumo

As florestas tropicais têm sido intensamente degradadas e desmatadas para diferentes usos antropogênicos, principalmente associados à expansão agrícola devido ao crescimento populacional. Por esse motivo, um número crescente de estudos tem defendido os benefícios de estratégias de compartilhamento de terras, como os sistemas agroflorestais, para conciliar conservação da biodiversidade com produção, porém fatores em escala de paisagem e local podem afetar os processos ecológicos e a produtividade nas agroflorestas. Aqui, usamos modelos de equações estruturais para investigar os efeitos diretos e indiretos da cobertura florestal na paisagem, animais dispersores de sementes e variáveis da vegetação local (sombreamento do dossel, riqueza e abundância das árvores), relacionadas à intensificação do manejo, na estrutura da chuva de sementes dos sistemas agroflorestais de cacau (*Theobroma cacao*) da Mata Atlântica da Bahia. Também contrastamos a composição das espécies entre sementes coletadas e espécies de árvores adultas registradas nos mesmos locais de amostragem. Nossa hipótese foi de que tanto a riqueza quanto a abundância de sementes seriam maiores em paisagens inseridas em maior quantidade de cobertura florestal e menos manejadas, e que esses fatores influenciam positivamente os dispersores que, por sua vez, afetam a chuva de sementes. Também esperávamos encontrar similaridade na composição local de árvores e sementes. Para isso, amostramos a chuva de sementes, através de coletores ao longo de um ano, além de dispersores aéreos (aves e morcegos), e medimos um conjunto de fatores da estrutura local em 15 agroflorestas de cacau com variação de cobertura florestal (2,35-74,91%) localizados no sul da Bahia. Nossos resultados indicam que a riqueza total de sementes que chegam nas agroflorestas de cacau aumenta em paisagens com maior cobertura florestal, pelo aumento da riqueza de aves frugívoras, enquanto a abundância de sementes zoocóricas e anemocóricas foi influenciada diretamente pelo maior, e menor sombreamento, respectivamente. Portanto, demonstramos que a quantidade de floresta desempenha um papel fundamental na determinação da riqueza de sementes, mas apenas afetando indiretamente a riqueza de espécies de aves frugívoras, indicando o papel central desse grupo na disseminação de sementes nas agroflorestas de cacau. Além disso, a composição das espécies de sementes reflete apenas parcialmente as espécies de árvores locais, potencialmente reforçando a importância das aves no transporte das sementes de outros locais. Dado o atual baixo retorno financeiro do cacau e o crescente abandono desses sistemas agroflorestais pelos proprietários, destacamos a importância de manter uma maior quantidade de cobertura florestal na paisagem das agroflorestas, além de coibir a extração seletiva de madeira local que fornece sombreamento para permitir a manutenção de alta diversidade de aves e potencialmente garantir o processo de dispersão de sementes e a regeneração natural nessas áreas.

Palavras-chave: Agrofloresta de cacau; Aves frugívoras; Chegada de sementes; Desmatamento; Dispersores de sementes; Regeneração florestal.

Abstract

Tropical forests have been intensively degraded and deforested for different anthropogenic uses, mostly associated to agricultural expansion due to population growth. Therefore, an emerging number of studies has advocated on the benefits of land-sharing strategies such as agroforestry systems in conciliating biodiversity conservation with production, yet features at both landscape and local scales could affect ecological processes and productivity within agroforestry. Here, we used structural equation models to investigate the direct and indirect effects of landscape forest cover, animal seed dispersers and local vegetation variables related to management intensification on the seed rain structure of cocoa (*Theobroma cacao*) agroforestry systems of the Brazilian Atlantic forest. We also contrasted species composition among collected seeds and adult tree species recorded in the same sampling sites. We hypothesized that both richness and abundance of seeds would be greater in landscapes embedded within larger amount of forest cover and less managed, and that these factors would positively influence dispersers and thus directly affect seed rain. We also expected to find similarity in local tree and seed composition. We sampled seed rain through collectors along one-year, in addition to sample aerial seed dispersers (birds and bats) and measure a set of local structure variables in 15 sites varying in forest cover amount (2.35-74.91%) located in southern Bahia. Our results indicate that the total richness of seeds that arrive in cocoa agroforestry increases in landscapes with greater forest cover, due to the increase in the richness of frugivorous birds, while the abundance of zoochoric and anemochoric seeds was directly influenced by the greater, and lesser canopy shading, respectively. We therefore demonstrate that forest amount plays a key role in determining seed arrival richness, but only through indirectly affecting the richness of frugivorous bird species, indicating the pivotal role of this group to disseminate seeds in cocoa agroforestry. In addition, the composition of the seed species only partially reflects the species of local trees, potentially reinforcing the importance of birds in transporting seeds from other locations. Given the current low financial return of cocoa and the growing abandonment of these agroforestry systems by the owners, we highlight the importance of maintaining a greater amount of forest cover in the agroforestry landscape, in addition to restraining the selective logging of local wood that provides shading to allow maintenance high bird diversity and potentially guarantee the process of seed dispersal and natural regeneration in these areas.

Keywords: Cocoa agroforestry; Deforestation; Forest management; Forest regeneration; Seed arrival; Seed dispersers.

Introdução geral

Sistema agroflorestal de cacau do sul da Bahia (Foto: Aluane Ferreira).

As florestas tropicais, além de abrigarem uma elevada diversidade de espécies (GIBSON et al., 2011), fornecem e contribuem para importantes serviços ecossistêmicos como ciclagem de nutrientes e dispersão de sementes (FERRAZ et al., 2014; MYERS, 1998; VIEIRA; GARDNER, 2012; VOEKS, 1996). No entanto, a maior parte das florestas tropicais está sendo severamente ameaçada devido ao aumento de diversas atividades antrópicas associadas à modificação do uso da terra, incluindo a conversão de florestas em cidades, pastagens e cultivos agrícolas que ocasionam perda de habitat e fragmentação das áreas naturais (BRANCALION et al., 2013; GIBSON et al., 2011). Apesar de sua importância para a produção de alimentos, grande parte dos cultivos agrícolas leva à drástica redução da biodiversidade e dos serviços ecossistêmicos tanto em áreas produtivas como também em fazendas agrícolas abandonadas, com a extinção local de espécies e de interações antes existentes, causando efeitos na funcionalidade de ecossistemas naturais (LAURANCE et al, 2014).

Uma das opções para amenizar os efeitos negativos das mudanças no uso da terra provenientes de cultivos agrícolas é a adoção de sistemas amigáveis de biodiversidade (os chamados *wildlife-friendly systems*), como os sistemas agroflorestais (SAFs), que visam integrar

a produção com a conservação da diversidade biológica (FISCHER et al., 2014; PYWELL et al., 2012). As agroflorestas são sistemas de cultivos que mantém ou introduzem plantas lenhosas perenes e por isso viabilizam uma maior complexidade estrutural quando comparada à cultivos comuns, e que devido a utilização de práticas mais sustentáveis, possuem a capacidade de reduzir os impactos antrópicos em paisagens tropicais (ABDO et al., 2008; ATANGANA et al., 2013). Deste modo, as agroflorestas representam a estratégia denominada *land-sharing* (ou compartilhamento de terras), a qual tem como princípio a integração da produção alimentícia com a manutenção da biodiversidade pelo compartilhamento da área, contrastando com a ideia *land-sparing* (separação de terras) que defende a intensificação do uso do solo estritamente para produção agrícola e separando parte da terra e destinando-a apenas para a conservação da biodiversidade (PHALAN et al., 2011). Os sistemas agroflorestais, ao abordarem a estratégia *land-sharing*, possuem elevado potencial para colaborar com o fluxo da biodiversidade na paisagem ao favorecer uma matriz amigável, que permite a manutenção de serviços ecossistêmicos enquanto atende à demanda alimentícia empregando métodos alternativos de produção (BRANCALION et al., 2013; CHAPPEL et al., 2009; PERFECTO; VANDERMEER, 2008).

Dentre os diferentes sistemas agroflorestais encontrados nas regiões tropicais, os sistemas agroflorestais de cacau (*Theobroma cacao* L.) realizam o seu cultivo sob diversas espécies arbóreas que formam uma densa camada no dossel e conseguem reter algumas características de ecossistemas naturais (BISSELEUA et al., 2009). Devido a este modo de produção e sua rentabilidade, o cacau tem destaque em vários países como Gana, Costa do Marfim e Brasil, por seus cultivos servirem de abrigo a biodiversidade e possibilitar alta produção desta *commodity* amplamente utilizada por diferentes culturas (LÄDERACH et al., 2013). No Brasil, as agroflorestas de cacau são destaques no sul da Bahia e norte do Espírito Santo, onde estão inseridas na Mata Atlântica. Este bioma compõe um dos 36 *hotspots* mundiais da biodiversidade, isto é, abriga elevada riqueza e endemismo de espécies, e se encontra severamente ameaçado devido à baixa cobertura florestal remanescente (CONSERVATION INTERNATIONAL, 2020; MYERS et al, 2000; VIEIRA; GARDNER, 2012). As agroflorestas de cacau presentes neste bioma, conhecidas localmente como cabrucas, se encontram rodeadas de Floresta Atlântica em diferentes estágios sucessionais. ~~C~~aracterizam-se pelo corte de árvores do sub-bosque e o plantio do cacau sob a sombra de 20 ou mais indivíduos de espécies nativas por hectare de árvores do dossel, promovendo certa complexidade estrutural e permitindo a manutenção de serviços ecossistêmicos

(BAHIA, 2014; PARDINI, 2004). Por isso, são consideradas um uso da terra com grande potencial para conciliar a cultura agrícola com a conservação da biodiversidade de áreas extensas na região (CASSANO et al, 2009).

A história do cacau no sul da Bahia foi iniciada com a crise da cana-de-açúcar no século XVIII, que impulsionou o cultivo do cacau, originário da Amazônia, como alternativa econômica na província da Bahia (SERRA; MARINHO, 2007). No entanto, apenas um século depois, em 1890, o Brasil ganhou evidência como grande produtor no mercado internacional, merecendo destaque a produção na região sul da Bahia (SERRA; MARINHO, 2007). Diversos pontos positivos alavancaram a produção do cacau como a criação de estradas, a alta no preço e a grande proporção de terras utilizadas para o seu cultivo na região, enquanto outros fatores levaram ao início do seu declínio em 1969, incluindo a desigualdade social, falta de políticas públicas, e interferências políticas (SERRA; MARINHO, 2007). De fato, o cultivo do cacau na região sul da Bahia teve variações na sua rentabilidade, tendo a partir dos anos 80 o marco da sua queda ocasionada pela infestação do fungo *Moniliophthora perniciosa* no fruto do cacau, responsável por causar uma doença conhecida popularmente como vassoura-de-bruxa que reduziu entre 50-90% da produção (FIORAVANTI; VELHO, 2011).

O cultivo do cacau passou por diversas formas de produção ao longo dos anos, sendo um dos métodos de manejo a derruba total, na qual ocorre a substituição de árvores nativas por árvores exóticas, como *Erythrina fusca* Lour e *Musa* spp., incentivada pela ideia de maior produtividade e recomendada pela Comissão Executiva do Plano da Lavoura Cacaueira – CEPLAC (CASSANO et al., 2009; SAMBUICHI; HARIDASAN, 2007). Devido ao maior ataque de pragas a esta última prática, a cabruca tradicional ainda é a mais utilizada na região, porém as agroflorestas variam na quantidade de árvores mantidas para o sombreamento a depender da intensidade do manejo (isto é, o adensamento da plantação devido à retirada de árvores nativas) e presença de outros cultivos como seringueiras (*Hevea* spp.) e bananeiras (CASSANO et al., 2009; SAMBUICHI, 2006). Assim, as cabrucas correspondem a um dos principais usos da terra na região do sul da Bahia, cobrindo aproximadamente, 70% da porção utilizada para o plantio do cacau e conseguindo reter 2/3 das espécies florestais de vários grupos ecológicos, indicando a importância desses sistemas economicamente produtivos para a manutenção da biodiversidade (SAMBUICHI, 2006). Porém com a queda econômica do cultivo do cacau, integração do seu espaço em áreas protegida ou para

atender a legislação ambiental, muitos proprietários têm abandonado suas fazendas, tornando-as mais propensas a ocorrer a regeneração florestal, uma vez que a ação humana do manejo deixa de existir (ROLIM et al., 2017; SAMBUICHI; HARIDASAN, 2007). Esse processo de sucessão secundária é então influenciado por diversos fatores que afetam sua trajetória sucessional, a depender do nível de sombreamento (i.e., entrada de luz), qualidade do solo (i.e, disponibilidade de nutrientes, dentre outros fatores físico-químicos), presença de dispersores (e.g., aves, mamíferos e insetos), entre outros (CHAZDON, 2012).

No sul da Bahia, os sistemas agroflorestais de cacau estão inseridos em diferentes contextos de paisagem, isto é, estão rodeados predominantemente por florestas nativas (em diferentes estágios sucessionais), pastagens, terras agrícolas e/ou plantios de eucalipto em diferentes proporções. Estudos têm demonstrado que agroflorestas de cacau rodeadas por alta quantidade de floresta nativa apresentam alto potencial para garantir a presença de determinados grupos ecológicos dependentes da presença de remanescentes florestais próximos, como aves de sub-bosque especialistas (FARIA et al., 2006). Também, tendo em vista à persistência de diferentes espécies de aves e morcegos frugívoros e insetívoros presentes nas florestas e também encontrados nestas agroflorestas (CASSANO et al., 2016; FARIA et al., 2006), este sistema produtivo difere substancialmente dos demais usos da terra, apresentando assim grande potencial para viabilizar processos ecológicos e a provisão de serviços ecossistêmicos. Por exemplo, pesquisas realizadas na região indicam a importância dessas áreas para o controle biológico realizado por aves e morcegos, tendo a quantidade de cobertura florestal na paisagem papel importante na manutenção desse serviço (CASSANO et al., 2016). Além disso, é reconhecido o papel das agroflorestas no sequestro de carbono (DE STEFANO; JACOB, 2018), sendo que em estudo realizado sobre o papel das árvores em terras agrícolas, o Brasil está entre os países que mais aumentaram o armazenamento de biomassas nesses cultivos (ZOMER et al., 2006).

Em nível local, os métodos de manejo e sua intensificação variam entre as agroflorestas e são geralmente definidos pelos proprietários (ROLIM et al., 2017). Usualmente, são utilizados pesticidas, roçagem para o corte de plântulas, árvores do sub-bosque e dossel, e manutenção das espécies arbóreas de interesse, geralmente frutíferas ou de madeira com valor econômico utilizadas para produção de móveis, lenha ou cercas. No entanto, as práticas variam na frequência e intensidade entre as fazendas produtoras de cacau (CASSANO et al., 2014; ROLIM;

CHIARELLO, 2004). Dentre estes métodos, a intensificação do manejo realizada pelo corte de árvores do dossel, conhecida como raleamento, vem resultando na diminuição de árvores e consequentemente, do sombreamento (GUIMARÃES et al., 2017; MACEDO, 2017). Apesar do Decreto Estadual nº 15180 proibir a supressão de vegetação nativa para implantação de novas cabrucas na Mata Atlântica do sul da Bahia, o manejo local visando o aumento da produtividade nas fazendas já existentes é permitido legalmente (BAHIA, 2014). Porém, a consequente simplificação estrutural destes sistemas pode induzir a mudanças abruptas na dinâmica florestal, uma vez que o sombreamento é reduzido em áreas mais intensificadas, com consequências diretas para a comunidade vegetal local. Visto que os processos de germinação e recrutamento são fortemente influenciados pela entrada de luz, é esperado que sistemas agroflorestais de cacau mais manejados apresentem mudanças diretas na dinâmica da comunidade e consequentemente na trajetória sucessional destes ambientes (CASSANO et al., 2009; ROSSI et al., 2007).

De forma geral, a etapa inicial da regeneração florestal se caracteriza pela germinação dos indivíduos presentes no banco do solo, colonização de árvores pioneiras e estabelecimento de plântulas de espécies tolerantes (CHAZDON, 2008); assim, uma vez que a ação humana para "limpeza" do sub-bosque deixa de existir, essa etapa pode enfim ser viabilizada. Em seguida, com o fechamento do dossel ocorre a substituição de espécies intolerantes a sombra pelo desenvolvimento da estrutura do sub-bosque formado por espécies tolerantes e pioneiras de vida longa. No reinício do sub-bosque há a tendência de substituição destes indivíduos em árvores do dossel, e assim se assemelhar cada vez mais estruturalmente e em termos de composição vegetal com um ambiente florestal (CHAZDON, 2008).

Nos sistemas agroflorestais de cacau abandonados do sul da Bahia, foi observado que após mais de 30 anos, estes ambientes estavam estruturalmente próximos ao original (ROLIM et al., 2017). As árvores do dossel presentes nas agroflorestas podem favorecer uma regeneração devido ao seu sombreamento impedir o recrutamento de pioneiras e favorecer espécies tolerantes à sombra (ROLIM et al., 2017). Ao mesmo tempo, o uso agrícola da terra em longo prazo também pode limitar a regeneração florestal na área, podendo tardar ou até impossibilitar esse processo (CHAZDON, 2014). Em agroflorestas produtivas do norte do Espírito Santo foi observado que a presença de árvores tardias é rara quando comparada a dominância de espécies pioneiras e secundárias iniciais, o que pode comprometer a sua regeneração (ROLIM; CHIARELLO, 2004).

Entretanto, sabe-se que a presença destas agroflorestas é importante para manter espécies de árvores onde já não há florestas preservadas na paisagem, servindo como fonte de sementes e habitat para potenciais dispersores (LOZADA et al., 2007; SAMBUICHI et al., 2012). Tendo em vista que o poder público deverá tomar ações voltadas a recomposição florística e a condução do processo de sucessão nas cabrucas abandonadas visando o estabelecimento de corredores ecológicos na Mata Atlântica, ainda há muito a ser pesquisado sobre como ocorrerá e o que irá influenciar nos estágios de regeneração florestal nestas agroflorestas em caso de abandono (BAHIA, 2014).

Dentre os processos relacionados a regeneração florestal, a dispersão de sementes tem importante papel na distribuição da estrutura espacial arbórea e, em escala local, é responsável por determinar a assembleia da comunidade juntamente com as variações das condições ambientais (CHAZDON, 2014; NATHAN; MULLER-LANDAU, 2002). Este processo, que pode ser caracterizado pela liberação dos propágulos, tem como etapa final a chegada das sementes em um determinado ambiente. Especificamente, esta chegada pode ocorrer de duas formas principais: por fatores abióticos (como água e vento), determinada a partir da liberação da árvore-mãe; ou de forma biótica, conceituada pelo movimento do animal ao consumir (ou carregar) o fruto e liberar a semente até outro espaço (SCHUPP et al., 2010). Entretanto a dispersão de sementes não representa a sua eficácia (MORANTE-FILHO; FARIA, 2017), que é determinada pela contribuição do dispersor para a dinâmica populacional e leva em consideração o número total de sementes dispersas e a probabilidade de o indivíduo atingir a fase adulta (SCHUPP et al., 2010).

Em ambientes tropicais, sabe-se que há variação sobre a capacidade de dispersão das espécies (SEIDLER; PLOTKIN, 2006), que sofre efeito de atributos morfológicos da espécie assim como de características da paisagem (OZINGA et al., 2005). Mesmo com a chegada dos propágulos, ainda pode ocorrer a limitação das sementes que ocorre devido a impossibilidade de todas conseguirem chegar a locais que possuem condições ideais para o desenvolvimento de determinada espécie, afetando as taxas da sua população (MULLER-LANDAU et al., 2002). Existem outros fatores necessários para que ocorra o sucesso do recrutamento como luminosidade, nutrição do solo, predação, além do manejo no caso das agroflorestas (CHAZDON, 2014). Este manejo realizado pelo proprietário, ainda afeta os outros fatores citados, já que influencia no nível de sombreamento pelo fechamento do dossel, quantidade de material orgânico que chega ao solo

e a ciclagem, e taxas de predação de sementes, uma vez que é esperada uma maior presença de aves granívoras em áreas agrícolas com baixa densidade de árvores (JUHRBANDT et al., 2010; SEKERCIOGLU, 2012). Pesquisas que avaliam processos como a dispersão pela chuva de sementes, apresentam relevantes informações, uma vez que este processo ecológico representa a ligação entre a última fase reprodutiva da planta com a primeira fase no recrutamento da população, influenciando consequentemente na regeneração da comunidade de plantas (BARBOSA et al, 2012).

Apesar do aumento de pesquisas relacionadas à biodiversidade nos sistemas agroflorestais de cacau nos últimos anos (CASSANO et al., 2009; CASSANO et al., 2014; DELABIE et al., 2007; FARIA et al., 2006; ROCHA et al., 2019), informações sobre a manutenção de processos ecológicos e serviços ecossistêmicos providos por estes sistemas são escassos, porém sendo extremamente necessárias para a proposição de ações de conservação na região. O amplo histórico de desmatamento da Mata Atlântica, destinados primordialmente a urbanização, agricultura e pecuária, tem induzido a perda de biodiversidade em ampla escala e levado a uma concentração de esforços para impulsionar a conservação deste bioma e a manutenção dos seus serviços ecossistêmicos. Assim, é essencial compreender o estado atual e da dinâmica desses ambientes tropicais que sofreram ações antrópicas através da implantação de cultivos agrícolas, a fim de compreender o impacto dessas atividades sobre os processos ecológicos nessas áreas e o que ocorrerá em caso de abandono. Ademais, alterações na biodiversidade ocasionada pela defaunação (i.e., extinção ou redução populacional de animais selvagens) em ambientes tropicais pode promover perdas relacionadas a estocagem de carbono, já que o desaparecimento de animais frugívoros de grande porte pode afetar negativamente a dispersão de sementes e a integridade de rede de interações, e consequentemente a regeneração da vegetação local que são importantes para a manutenção desse serviço ambiental (BELLO et al., 2015; EMER et al., 2018; GIACOMINI; GALETTI, 2013). Assim, é importante entender as fontes que ameaçam as florestas tropicais, pois a resiliência é limitada, ou seja, a capacidade das florestas de se recuperar de distúrbios antrópicos e/ou naturais não pode ser considerada infinita (CHAZDON, 2014). De modo similar, no caso das agroflorestas, que também contribuem para atenuar as mudanças climáticas por contribuir para o estoque de carbono, essas ameaças também podem ser prejudiciais a este serviço ao afetar a qualidade da dispersão de sementes e a distância de dispersão (TORRES et al., 2014).

Tendo em vista que as agroflorestas possuem capacidade de reter alguns grupos biológicos e permitir a continuação de importantes processos ecológicos, o presente estudo teve como objetivo desvendar quais são os principais fatores que afetam a chuva de sementes em agroflorestas de cacau, de modo a auxiliar na compreensão do papel funcional destes sistemas. Com o atual conhecimento da importância do contexto da paisagem, sobretudo de sua composição, e da intensificação do manejo em escala local, sabemos que esses fatores podem exercer influência positiva ou negativa, de acordo com a sua quantidade, sobre a persistência de espécies e manutenção de serviços ecológicos em ambientes tropicais (ARROYO-RODRÍGUEZ et al., 2016; CASSANO et al., 2009; FARIA et al., 2006; MORANTE-FILHO et al., 2015; ROCHA et al., 2019; ROCHA-SANTOS et al., 2016; ROCHA-SANTOS et al., 2017). Assim, realizamos amostragens da chuva de sementes por 12 meses consecutivos em 15 agroflorestas de cacau localizadas no sul da Bahia, que possuem ampla variação na quantidade de cobertura florestal ao seu redor e nível de intensificação de manejo, combinadas com amostragens de aves e morcegos (potenciais dispersores aéreos) e de árvores nestes mesmos locais. Utilizamos a análise de caminhos para analisar os efeitos diretos e indiretos da cobertura florestal na paisagem, riqueza e quantidade de dispersores e intensidade do manejo sobre a estrutura (i.e., riqueza e abundância) de sementes coletadas em cada agrofloresta amostrada. Além do melhor entendimento sobre os processos ecológicos que possivelmente ocorrem nestas áreas, este estudo tem um papel chave em ampliar o conhecimento quanto ao potencial de regeneração destas agroflorestas em caso de abandono. Com isto, buscamos ao longo do capítulo desenvolver uma perspectiva holística sobre o manejo de paisagens antropizadas levando em consideração o contexto conceitual, ecológico e espacial.

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Chapter 1

Seed rain in agroforestry is induced by effects of forest loss on frugivorous birds

Frugivorous bird (*Tangara seledon*) and seeds sampled in cocoa agroforestry sites located in southern Bahia, Brazil. Photos by: I. Araújo-Santos and J. Cabral.

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ABSTRACT

Tropical forests have been intensively degraded and deforested for different anthropogenic uses, mostly associated to agricultural expansion due to population growth. Therefore, an emerging number of studies has advocated on the benefits of land-sharing strategies such as agroforestry systems in conciliating biodiversity conservation with production, yet features at both landscape and local scales could affect ecological processes and productivity within agroforestry. Here, we used structural equation models to investigate the direct and indirect effects of landscape forest cover, animal seed dispersers and local vegetation variables related to management intensification on the seed rain structure of cocoa (*Theobroma cacao*) agroforestry systems of the Brazilian Atlantic forest. We also contrasted species composition among collected seeds and adult tree species recorded in the same sampling sites. We hypothesized that both richness and abundance of seeds would be greater in landscapes embedded within larger amount of forest cover and less managed, and that these factors would positively influence dispersers and thus directly affect seed rain. We also expected to find greater similarity in local tree and seed composition. We sampled seed rain using eight collectors per site along one-year, in addition to sample aerial seed dispersers (birds and bats) and measured a set of local structure variables in 15 sites varying in forest cover amount (2.35-74.91%) located in southern Bahia. Our results indicate that overall seed richness in cocoa agroforestry increases in more forested landscapes by the increase of frugivorous bird richness, whereas the abundance of biotic-dispersed and abiotic-dispersed seeds respectively enhanced and decreased in more shaded farms. We therefore demonstrate that forest amount and management intensification play key roles in determining seed arrival richness and zoochoric seed abundance,. Furthermore, the composition of local tree species was partially similar from seed species composition, suggesting that several seeds were actively dispersed (e.g. likely by birds) from other localities. Given the current low financial return of cocoa, and the growing abandonment of these agroforestry systems by local farmers, we thus highlight the importance of restraining tree extraction within farms and preserving large tracts of native forests around cocoa agroforest sites to enable the maintenance of high diversity and abundance of birds and the seed dispersal process, thereby facilitating the natural regeneration in these areas.

Keywords: Cocoa agroforestry; Deforestation; Forest management; Forest regeneration; Seed arrival; Seed dispersers.

Introduction

Tropical forests have been increasingly degraded and deforested for different anthropogenic uses, including urban, timber extraction, infrastructure, and mainly for agricultural expansion to attend food demand for global growing population (Curtis et al., 2018). The conversion of native forests into agriculture crops has mostly shown detrimental effects on ecosystem structure, including biodiversity loss and disruptions in ecological functioning (Lambin et al., 2001; Newbold, 2015; Turner et al., 2007), leading therefore to scientific debates on how to minimize these negative impacts. Consequently, decisions on how land can best be used to harmonize food production and biodiversity conservation have been promoting disagreements among researchers, by either advocate on land sparing or land sharing strategies (Fischer et al., 2014). The former defends increasing yield to reduce the amount of land needed for agriculture, whereas land-sharing agricultural practices incorporate elements of native ecosystems into the yield to integrate agriculture production with biodiversity conservation (Grass et al., 2019; Phalan, 2018).

Land-sharing strategies include a wide variety of agroforestry systems in tropical areas (e.g., cocoa, coffee, rubber, banana), and due to the greater structural complexity, may allow the persistence of several faunal and floristic species, and potentially the maintenance of ecological processes. Indeed, a growing number of studies and policy actions has advocated on the benefits of land-sharing strategies as wildlife-friendly systems, by increasing the amount of small farmers that use agroecological principles, and supporting social movements concerned on biodiversity maintenance (Badgley et al., 2007; Chappell et al., 2009; Perfecto and Vandermeer, 2008; Pywell et al., 2015). Yet differences at landscape and local scales of the property can influence biodiversity

patterns and processes in addition to farm productivity, with studies focused in disentangling these features being required to unveil the main characteristics required to both gain production and achieve conservation goals.

Several factors are likely to affect ecosystem functionality in agroforestry systems, with key environmental predictors explaining biodiversity patterns and ecological processes in forested sites might be applicable in these agricultural areas. For instance, the landscape context is decisive to maintain structural vegetation integrity and retain greater biodiversity in tropical fragmented forest landscapes. Specifically, the amount of forest cover at the landscape scale has strongly affected local structure, tree diversity and explained richness and abundance of forest-specialist birds, bats and small mammals in patches in the Brazilian Atlantic forest – particularly, landscapes retaining less than 40% of native forest cover exhibited degraded vegetation structure (Rocha-Santos et al., 2016) and harboured depauperate faunal assemblages (Bovendorp et al., 2018; Faria et al., 2006; Gorresen et al., 2004; Morante-Filho et al., 2016). Since these forest vertebrates act as key seed dispersers for most of tropical plants, it is expected substantial reduction in the provision of ecological processes such as seed dispersal and forest regeneration in sites surrounded by low amount of vegetation cover due to the decrease in the number of species and individuals of both trees and animal (seed) dispersers. Yet agroforestry sites embedded in deforested landscapes might experience even worse effects. In fact, studies conducted in cacao and banana agroforestry systems in Costa Rica, shade coffee plantations in India, and agroforestry landscapes in Cameroon showed high dependence of some forest bird and bat species to forest proximity (Harvey and Villalobos., 2007; Kupsch et al., 2019; Wordley et al., 2018). Thus, it is predictable that agrosystems within highly deforested landscapes are prone to retain reduced richness and

abundance of vertebrate dispersers, with subsequent negative effects on seed arrival (i.e., less diversity of seeds).

Seed arrival comprises the first in a many-phased process leading to tree establishment in tropical sites (Duncan and Chapman, 1999), embracing a fundamental step for forest regeneration. Although seed arrival does not mean survival (see Reid and Holl, 2012), the seed rain is influenced by seed limitation, which means the failure of the seeds to reach everywhere with adequate conditions (Barbosa and Pizo, 2006; Muller-Landau et al., 2002). Together with species pools and local biotic process, seed limitation drives the structure of arboreal community (Foster and Tilman, 2003). The wind, water or animal dispersers are the main agents for seed dissemination, with the propagules could come from off-site and local trees in any site, with the latter being highly associated with the intensity of local farming management through tree removal in agroforestry systems. Thus, research on seed rain (i.e. including the obtainment of seed arrival *in situ* using collectors) can enhance our understanding on ecological processes and therefore ecosystem functionality in agroforestry farms (Martins et al., 2016; da Silva et al., 2018).

In the tropics, a well-recognized wildlife-friendly system that has been expanding in different countries across the Americas, Africa and Asia is the cocoa agroforestry, in which the cocoa is cultivated under the shade of native trees (Asase and Teeth, 2010; Cassano et al, 2009; Wartenberg et al., 2018). Specifically in Brazil, cocoa is vastly cultivated in the southern Bahia region situated within the threatened Atlantic Forest, notably recognized for harbouring one of the greatest biodiversity's worldwide (see Myers 2000 and Martini et al., 2007). Cocoa plantations played a major role in local economic development in the late nineteenth century, turning Brazil as one of the major exporters worldwide. Yet, less than 100 years later, due the witches' broom fungus (*Moniliophthora perniciosa*) and political interference, the production had substantially

declined and the region consequently experienced a major economic downturn (Serra and Marinho, 2007). Nevertheless, a large part of southern Bahia is still composed of cocoa plantations, but with the reduced productivity and economic crisis, most farms owners have abandoned their crops or intensified the management (i.e., incorporating the use of pesticides or extracting native trees) to trade the timber (Cassano et al., 2009). Recent studies have demonstrated that the structural simplification caused by management intensification in cocoa agroforestry sites promotes abrupt changes in local biodiversity, including the decrease in plant density and basal area of the arboreal component (Vera-Vélez et al., 2019), in addition to the gradual loss of forest specialists birds followed by an increase in habitat generalists (Rocha et al., 2019). Therefore, the intensive management of cocoa agroforestry by cutting emergent trees is likely to affect the persistence of faunal species, such as frugivorous bats and birds, and potentially leading to cascade effects ─ i.e., precluding ecological processes that are vital to ecosystem maintenance, such as seed dispersal and forest regeneration (Muscarella and Fleming, 2007). Combining multiple factors including landscape and local features could additionally enhance our understanding on which are the main factors driving patterns of seed arrival in existing agroforestry systems, and consequently in enabling ecological functionality.

Here, we used structural equation models to investigate the direct and indirect effects of landscape forest cover, animal seed dispersers and local management on the seed rain (Appendix A) of 15 contrasted cocoa agroforestry systems sites in the Brazilian Atlantic rainforest. Our conceptual model (Fig. 1) considered the direct positive effect that landscape forest amount may have on the richness and abundance of both omnivorous/frugivorous birds and bats, which together may determine the diversity (i.e., seed richness and abundance) of immigrant seeds on these agroforests, especially zoochoric seeds. In particular, we expect to find a greater influence of

landscape context, with forest cover exerting the strongest influence, both directly and indirectly, on seed structure. We predict that seed richness and abundance would be increased in landscapes embedded within greater amount of forest cover, given the potential of surrounding areas in providing higher source of propagules required to boost seed arrival (Chazdon, 2012). We also expect that the richness and abundance of frugivorous/omnivorous birds and bats would be higher in more forested landscapes (Faria et al., 2006; Kupsch et al., 2019; Morante-Filho et al. 2015, 2016; Peter et al. 2015), and indirectly maximize seed richness and abundance giving their greater importance as vertebrate seed vectors (García and Martinez, 2012; Ingle, 2003). Additionally, we also predict a negative and both direct and indirect effect of management intensification (i.e., lower abundance and richness of adult trees and canopy shading) on seed richness and abundance, by the reduction of bird and bat richness and abundance (Faria et al., 2006; Harvey and Villalobos, 2007; Wordley et al., 2018). We finally contrasted species composition among the arrived seeds and adult tree species recorded in the same sampling sites, expecting to find a greater similarity among local communities due to the greater importance of local adult trees on seed rain (San-José et al., 2019a). By examining patterns of seed arrival in response to both landscape and local features, we intend to both enhance our understanding on the role of agroforests in guaranteeing ecological processes and ecosystem services, and predict the fate of those abandoned cocoa agroforestry systems in the threatened Atlantic forest.

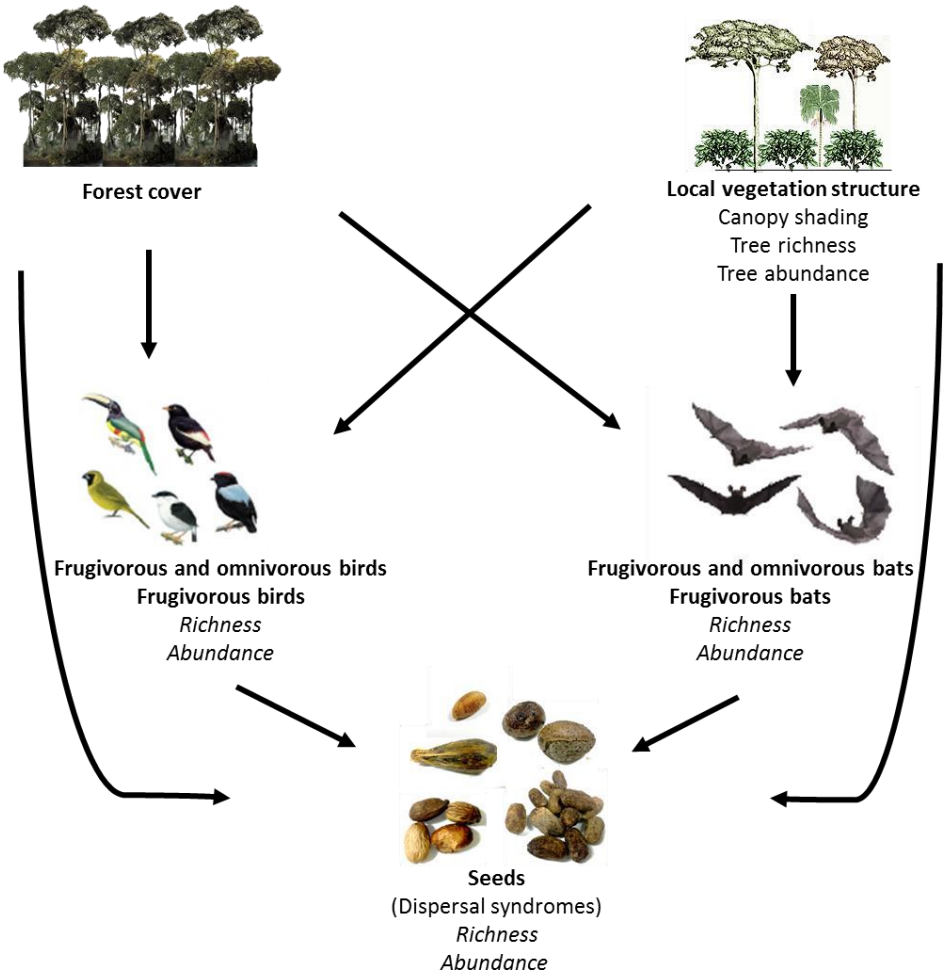


Figure 1. Conceptual model to test the direct and indirect effects of landscape composition (i.e., forest cover) and local features (i.e., management intensification through local vegetation structure, including canopy shading and adult tree species richness and abundance, and richness and abundance of animal dispersers) on the seed rain structure (all seeds and dispersal syndromes - zoochoric, anemochoric and ornithochoric). Positive hypothetical pathways are indicated by black lines.

Materials and methods

Study area

We conducted this study in 15 cocoa agroforestry systems located in the southeastern Bahia state of Brazil, specifically in the municipalities of Una (15 ° 17'36 "S and 39 ° 04'31"W), Uruçuca (14 ° 35'35"S and 39 ° 17'04"W) and Belmonte (15 ° 51'47 "S and 38 ° 52'58"W). The climate is type Af in the classification of Köppen, hot and humid, with an annual average temperature of

25ºC and rainfall of 1200-1800 mm (Mori et al., 1983). We adopted a hybrid patch-landscape approach (Tischendorf and Fahrig, 2000) by sampling independent cocoa agroforestry systems in non-overlapping landscapes with a 1 km buffer from the centre of each sites. We firstly used high resolution satellite images (Landsat from 2011, QuickBird [J1] and WorldView, from 2011; RapidEye, from 2009-2010), covering a total area of 4548 km² in the southern region of Bahia, to create digital maps with a 1:10,000 scale, which is suitable for identifying landmarks based on visual inspection of differences in colour, texture, shape, location and context to map all land use types. The remaining fragments were classified according to the different forest types, following the typologies provided by IBGE (2006). We thus used ArcGIS 10.2 (ESRI, 2014) to measure the amount of native forest cover (hereafter, FC) at the landscape-scale, i.e., the percentage of native FC within a radius of 1000 m surrounding each agroforestry. We considered only mature and secondary native forests (excluding shade cocoa and rubber plantations) in our FC estimates. From a total of 80 identified cocoa agroforest systems, we randomly selected a set of 15 sites with at least 2 km distance between them, with a gradient of FC, to conduct our surveys. For these landscapes, land use corrections were made after on-site visits with the help of Google Earth images. Specifically, the chosen sites covered a wide variation of FC at the landscape-scale (2.35-74.9%), and were equally distributed in all three municipalities (i.e., 5 in Una, 5 in Uruçuca and 5 in Belmonte; Fig. 2).

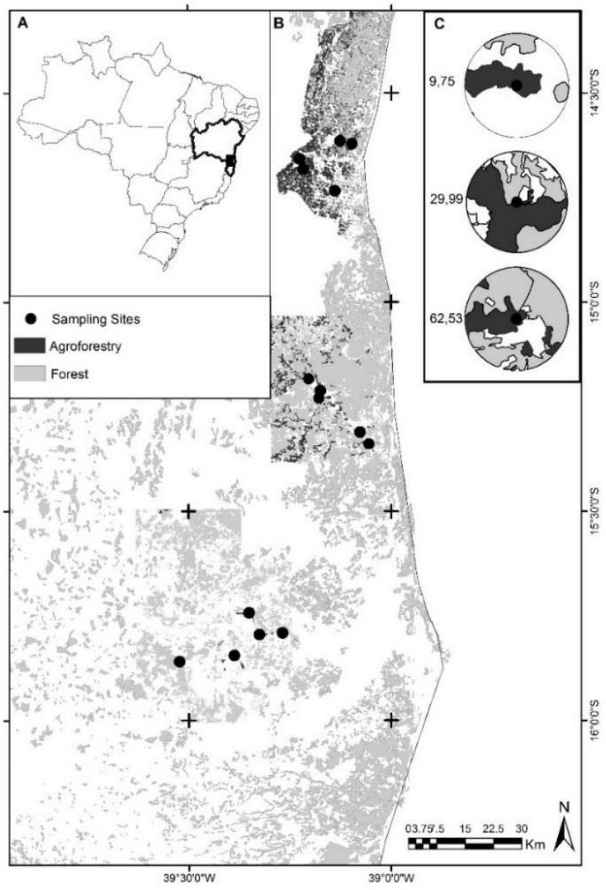


Figure 2. Study area in Bahia, Brazil (A), showing the location of each 15 sampled sites (black dots) along the southern Bahia, from Una (five northern dots), Uruçuca (five middle dots) and Belmonte (five lower dots) (B). In (C) are exhibited three surveyed agroforestry sites embedded within a wide range of landscape native forest cover within a 1000 m radius.

Seed rain sampling

In each sampling site, we established 8 seed collectors starting from the centre of each agroforestry site at 0.5 m from the ground, with a minimum distance of 50 m between each other and between the nearest edge (planned sampling effort = 15 X 8 = 120 traps). Maximum distance among more distant collectors was 414,75 m (274,58 ± 83,94). The collectors were made with PVC pipe, nylon net and wire, with a screen size of 1 m². Every 45 days during 12 consecutive months (October 2018-September 2019), the contents of each trap were collected and packed in

paper bags for later laboratory screening. Although we are aware that seed predation and their removal from traps were likely to occur, we considered that seed loss was uniform across the temporal and spatial gradient (see also Piotto et al., 2019).In the laboratory, the collected material was dried and all seeds were separated, counted and identified to the lowest possible taxonomic level (APG IV, 2016) using either field guides (Lorenzi, 2002; Souza Júnior and Brancalion, 2016) or by consulting botanists from the *Universidade Estadual de Santa Cruz* and *Universidade Federal do Sul da Bahia*. We thus obtained data on species composition, richness and abundance of each sampling site by combining all seeds obtained in the collectors during 12 months. In the case of very abundant and small-sized seed species that did not enable us to count the total number of seeds, we firstly weighted the minimum set of seeds, and thus weighted the total of seeds collected to obtain an approximately estimate of seed number (abundance). Finally, we classified each species according to the dispersion syndrome – abiotic (wind, gravity and/or autochoric dispersion), and zoochoric (dispersed by animals and mixed dispersion syndromes), using the criteria of Van der Pijl (1982). Given that some collectors were stolen or damaged in some of the sampling sites, we used the density estimates of each attribute for further analyses ─ i.e. total sampled area (94,5 m^2 ± 1,7, minimum 89 m^2, maximum 96 m^2).

Landscape and local predictors

At the landscape scale, we measured FC at different spatial scales given that multi-scale analysis is considered the most appropriate approach for deciding a landscape size when the fitting scale is unknown (Jackson and Fahrig, 2015; Thompson and McGarigal, 2002). We thus tested seven different scales (400, 500, 600, 700, 800, 900 and 1000 m), based on both biological and spatial aspects. Firstly, previous studies conducted in forest sites in the same region demonstrated

that birds (Morante-Filho et al., 2018) and adult trees (Rocha-Santos et al., 2017) best responded to scales of 600 and 1000 m of FC, respectively, for richness and abundance patterns. Additionally, we avoided scales larger than 1000 m due to overlapping and potentially non-independence among landscapes, and did not include smaller scales than 400 m given that this was the greatest distance among collectors within a sampling site. We thus compared the coefficients of determination between FC and total seed richness and abundance. The 400 m radius presented the best determination coefficient values for total seeds and seed richness analyzed separately by dispersion syndrome, and 1000 m radius was the best for the abundance of all seed groups classified through syndromes.

At local scale, we established one 100 x 25 m forest-plot (0.25 ha) in the centre of each selected agroforestry sampling site, in order to obtain local structure variables. This plot size was chosen given that some agroforests were too small to allocate more plots at spaced distances. Although some collectors were established outside these plots, we assume that local variables therein collected well characterize the sampling site. Inside each plot, we counted and identified all native and exotic trees (excepting cocoa tree) with diameter at breast height (DBH) $\geq$ 10 cm, obtaining therefore the species composition, richness and abundance of adult trees, we also classified each species according to the dispersion syndrome (zoochoric and ornithochoric). We calculated the percentage of canopy shading using hemispheric photographs that were taken using a cell phone camera (android) and the GLAMA application. We took five hemispheric photos of the canopy over the cocoa trees, every 20 m, at 1.30 m from the ground, and always starting from the centre line of the plot (12.5 m). Adult tree richness, abundance and canopy shading are assumed to be directly related to the management intensification within the agroforestry ─ i.e., the lesser is

the tree richness and abundance and lower the canopy shading, higher is the human management intensification in the farm. In total, we obtained 485 individuals of trees from 91 species.

We also obtained data on bird and bat communities' structure, given their potential effect on seed arrival. We deployed ten mist nests (12 m long, 2.5 m high, 31 mm nesh, total of 120 m) to collect bird and bat species within each agroforestry, either inside or nearby the central plot. For bird surveys, mist-nets were opened during two periods (morning and afternoon) for three consecutive days in two different times (January and June 2019), totaling 48 hours/site, which enables the capture of only understory bird species. All individuals were identified at species-level, following the scientific nomenclature of the South American Classification Committee, with the assistance of the Sigrist Identification Guide (2014). Then, following Wilman et al. (2014), species were classified according to its dietary as frugivorous, granivorous, omnivorous and insectivorous. For subsequent analyses, we considered total richness and abundance of combined frugivorous and omnivorous bird species, and only frugivorous birds, per sampling site. We also opened mist-nets during two consecutive nights (January and June 2019), either inside or nearby the central plot, to collect bats in each sampling site (totalizing 10 hours/site). The captured bats were identified at species-level (Reis et al., 2013), marked and released at the end of the night. Subsequently, individuals were classified according to their diet in omnivorous, frugivorous, nectivorous and insectivorous (Reis et al., 2013), and for subsequent analyzes, we used species and individuals data from only frugivorous bats, also combined frugivorous and omnivorous. License for birds and bats captures were properly obtained from CEUA, the Animal Ethics Committee (021/18 and 026/17, respectively). In total, we captured 285 birds belonging to 21 species, and 1429 bats from 18 species.

Data Analyses

We used structural equation models (hereafter, SEM) to investigate which indirect and direct factors influence attributes of local seed rain. SEM is a very flexible method that can be used to promote causal understanding through the use of various independent and dependent variables, and is useful for testing the general fit of complex networks (Eisenhauer, 2015; Grace, 2006). Also, it presents the strength of the relationship by separating the multiple paths generated by the direct and indirect influences of the predictors (Eisenhauer, 2015). Our models had as exogenous variables 'FC' and 'local vegetation structure' (richness and abundance of trees, and canopy shading), and as endogenous variables the 'richness' and 'abundance' of dispersers (frugivorous birds and bats, frugivorous + omnivorous birds and bats) and seeds. To analyze the seed rain of seeds dispersed zoochorically, abiotic or by birds, we used only data from the identified species of seeds and trees. Based on previous research on the effects of landscape and local scales on ecological attributes as dispersal syndromes, quality of ecosystem services, and diversity of seed dispersers and seed rain in tropical forests (Chazdon, 2012; Faria et al., 2006; García and Martinez, 2012; Morante-Filho et al., 2018; Pivello et al., 2006; San-José et al., 2019a, 2019b), we designed a set of SEMs in order to understand the influence of FC and local vegetation structure on animal dispersers and seed structure in our study area. We developed a theoretical SEM (Fig. 1) with FC, management intensification (tree abundance or tree richness or canopy shading), dispersers (frugivorous + omnivorous bird richness or frugivorous + omnivorous bird abundance or frugivorous bird richness or frugivorous bird abundance or frugivorous + omnivorous bats richness or frugivorous + omnivorous bats abundance or frugivorous bats richness or frugivorous bats abundance) and seed rain (richness or abundance for total species, animal-dispersed species, bird-dispersed species and abiotic-dispersed species). The local vegetation structure and disperser

variable were replaced in each model (Appendix C).

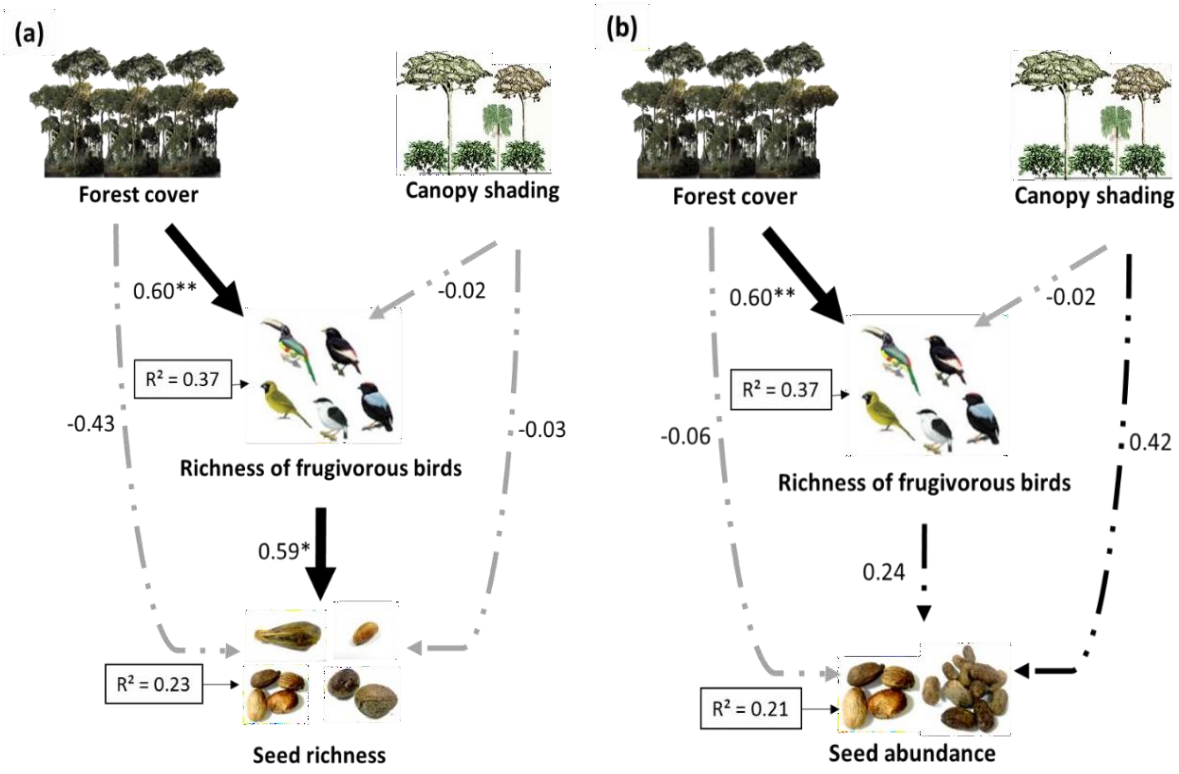
We tested and confirmed the normality among all variables using the Mardia's multivariate normality test, which is necessary since SEM admits a normal multivariate distribution. Then, we created separately SEM for seed richness and seed abundance of all species and each group-mediated dispersal using *lavaan* package, being each model composed of four variables and 15 observations. We evaluated the adjustment coefficients of all models (Appendix D) using test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), and root mean square error of approximation (RMSEA). A well-fitting model should has (1) a non-significant x^2 test (P-value > 0.05), (2) CFI and LTI > 0.9, and (3) lower 90% confidence intervals of RMSEA < 0.05 (Zhang et al., 2013). We thus performed a model selection approach using the value of Akaike's Information Criterion (AIC), and selected the smallest value from those tested that presented a good fit for each response variable. We used P-values and β coefficients (standardized path) to check if there is significance between the individually analyzed paths of the best model, and the R^2 as coefficient of determination to evaluate the variance of endogenous variable caused by the effect of its predictor variables (Appendix E). Finally, in order to contrast composition patterns among the arrived seeds and adult tree species recorded in the sampling sites, we performed Non-Metric Multidimensional Scaling (NMDS) ordinations using the Bray-Curtis dissimilarity matrix based on qualitative (presence/absence data). We further tested the similarity in floristic composition among seeds and adult trees recorded in each cocoa agroforestry system using a Procrustes analysis; a useful technique that tests the correlation using a rotation minimizing the reference-space model between two arrays (Perez-Sala et al., 2007). All analyses were performed using the software R 3.4.0 software (R Core Team, 2015) and Past (Hammer et al., 2001).

Results

We recorded a total of 28,435 seeds belonging to 77 morphotypes from 26 identified families, considering all 15 cocoa agroforestry sites (Appendix B). In total, we identified 29 morphotypes at the species level, 17 at the genus level, and nine at the family level. The mean richness and abundance of all seeds were, respectively, 10,2 ± 4,30 and 1895,67 ± 1215,09 per site. The majority number of seed species (75,32%) and abundance (94,89%) consisted of zoochoric species, which presenting based on density estimates an average richness of 0,08/m² ± 0.04, and abundance of 19,15/m² ± 13,73. The most abundant family was Moraceae (N=21,850 individuals), with the most abundant species being *Ficus clusiifolia* (55,8%), followed by *Ficus gomelleira* (19,7%) and Matayba sp (4,22%). Some species occurred just at one site, such as *Eschweilera ovata* and *Joannesia princeps*.

We detected that most models of SEM showed good adjustments (Appendix D). Among the models that did not present good adjustments, most contained abundance of dispersers. For seed richness, only one model was parsimonious ($\Delta AIC \leq 2$), while for seed abundance two models were parsimonious. The best model (lowest AIC), for most of the analyzed paths, included FC, canopy shading and frugivorous bird richness (Fig. 3). However, for the abundance of seeds dispersed by birds, none of the models presented showed good adjustments. Yet, only FC and richness of frugivorous birds were significant variables explaining total seed richness arrival, via indirect and direct ways, respectively (Fig. 3a). Specifically, FC positively affected frugivorous bird richness ($\beta = 0,60$), which in turn positively affected seed richness ($\beta = 0,59$). Contrary to our expectations, none of the paths significantly explained patterns of total seed abundance (3b), zoochoric seed richness (3c), ornitochoric seed richness and abundance (3e), and abiotic seed richness. We found only FC exerting a significant influence on the number of frugivorous birds,

and omnivorous + frugivorous birds species (Fig. 3a, 3b, 3c, 3d, 3e), or seed rain according to dispersion or disperser syndrome (Fig. 3c, 3d, 3e, 3f, 3g). We also detected the influence of canopy shading was significant for the abundance of zoochoric seeds and for the abundance of abiotic seeds. For both all seed richness and abundance, the best model explained 37% of frugivorous birds, 23% of seed richness, and 21% of the seed abundance. The best model explained 37% of frugivorous birds, and 22% of zoochoric seed richness, while for zoochoric seed abundance the model explained 36% of richness of frugivorous + omnivorous birds, and 24% of the seed abundance. For ornithochoric seed richness, the best model explained 37% of frugivorous birds, and 2% of seed richness. For abiotic seeds, the richness was explained 2% while the percentage for abundance was 21%.



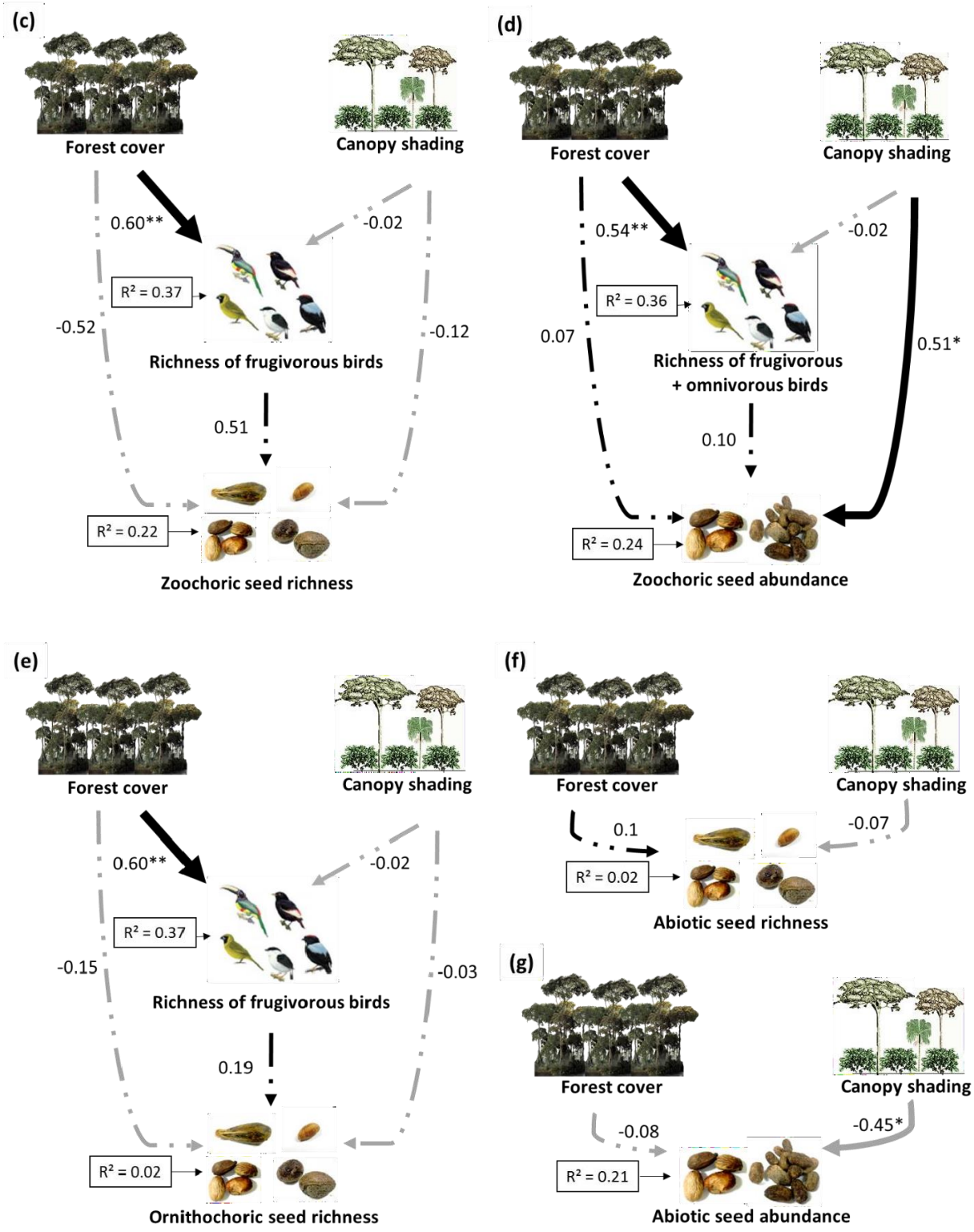


Figure 3. Best-fitted path model showing the direct and indirect effects of landscape forest cover on the richness and abundance of all seeds (a,b), zoochoric seeds (c,d), ornithochoric seeds (e), abiotic seeds (f,g) collected in cocoa agroforestry sites located in southern Bahia, Brazil. Positive

and negative pathways are indicated by black and gray lines, respectively. Arrow thickness exhibits the relative strength of effects. Dashed arrows show no significant relationship. Significant coefficients are indicated with asterisks (*P ≤ 0.05; **P < 0.01). The black squares show the coefficient of determination (R^2) for all endogenous variables (i.e., richness of frugivorous birds and richness/abundance of seeds).

Considering the NMDS ordinations on the qualitative species composition among the seeds and adult trees, we detected that sampling sites exhibited great similarity of seed composition among each other and lower similarity with adult tree species composition (Fig. 4). Procrustes analyses demonstrated a significant but moderate correlation between each pair (i.e., within the same site) of seeds and tree species composition (R^2= 0,533; P=0,003).

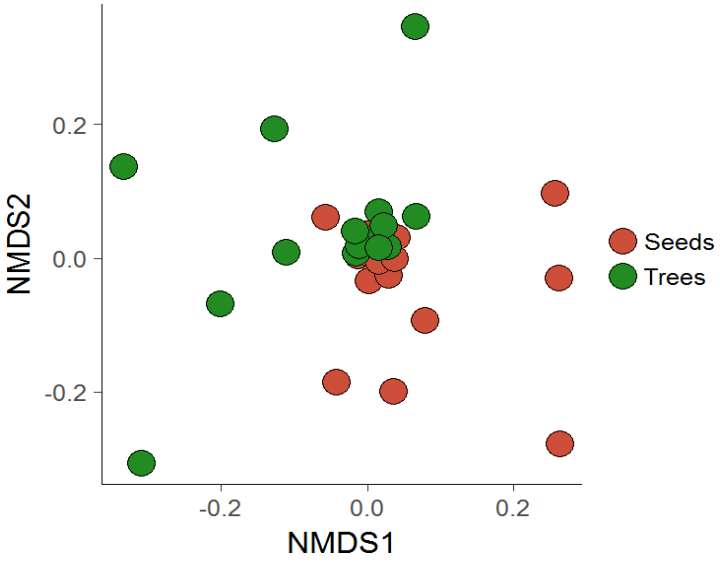


Figure 4. Non-Metric Multidimensional Scaling (NMDS) ordinations on the qualitative species composition of arrived seeds and adult tree species recorded in 15 cocoa agroforestry systems located in southern Bahia, Brazil.

Discussion

Our results clearly show that the number of overall seed species arriving in cocoa agroforestry is mostly explained by the indirect effects of forest cover on the richness of frugivorous birds, whereas the management intensification directly affected the abundance of both

animal-dispersed and abiotic-dispersed seeds. As expected, forest cover amount has substantially explained patterns of frugivorous bird richness, which in turn positively affected the number of seed species. This indicates that cocoa agroforests surrounded by highly forested landscapes are prone to attract these key seed disperser agents, which will therefore propagate a great number of seed species (Jordano et al, 2007). Furthermore, only one local management predictor (i.e, shading) showed a substantial effect on the seed rain, but only when examined the abundance of seed groups separately (i.e., biotic-dispersed and abiotic-dispersed seeds). Interestingly, we observed that the composition of dispersed (immigrant) seeds slightly reflected the adult tree species composition within each sampling site, which provides evidence that seeds are coming from off-sites. Our study demonstrates that cocoa agroforestry does not only retain biodiversity, as previous studies pointed out (Cassano et al., 2009; Faria et al., 2006), but is also likely to provide key ecological processes (e.g., seed dispersal and forest regeneration) as long as the farms are surrounded by forested landscapes and exhibited lower degree of intensification, demonstrating to be indeed *wildlife* (and *ecosystem*)-*friendly* environments. Thus, we provide additional support on the benefits of land-sharing strategy (Chappell et al., 2009; Perfecto and Vandermeer, 2008) of shaded cocoa farms, which are prone to conciliate productivity with biodiversity conservation.

We unveil that landscape composition is exerting an indirect effect on seed richness arrival of overall species in agroforestry systems, by affecting frugivorous birds. Specifically, our results demonstrate that cocoa agroforestry systems surrounded by reduced forest amount are indirectly losing species on seed arrival, via the erosion of its key aerial dispersers. Similar results about the influence of forest cover on frugivorous birds was found in forest remnants of the same region, suggesting that severely deforested landscapes retain depauperate bird assemblages, with potential detrimental consequences on seed dispersal (Morante-Filho et al., 2015). Birds are indeed key seed

dispersers in tropical forests (Sekercioglu, 2006), comprising the main group that disseminates zoochoric seeds. In fact, the majority (75,32%) of our collected diaspores are zoochorically dispersed, which is comparable to patterns found in tropical forests worldwide, where ~ 90% of total tree species are dispersed by animals (Howe and Smallwood, 1982). Among those animals that consume fruits, frugivorous are highlighted for exerting an important role in spreading seeds, mostly associated with their dietary specialization (Mello et al., 2015). Differently, despite the recognized role of bats in acting as important seed dispersers (Mello et al., 2011), this group was irrelevant for influencing patterns of seed arrival in cocoa agroforests sites.

Studies have indeed found that frugivorous birds interact with more plant species and disperse more seed species than frugivorous flying mammals (Ingle, 2003; Mello et al., 2011), highlighting the greater importance of birds for seed arrival in tropical forests. Of utmost importance, frugivorous birds are likely to be attracted by the great diversity of trees bearing fleshy fruits that are commonly recorded in agroforestry systems (Oke and Odebiyi, 2007), such as *Spondias venulosa* and *Tapirira guianensis*, which were recorded as adult trees and seeds in our studied sites. We presume that several frugivorous bird species inhabiting nearby forest sites forage in cocoa farms, and will thus disperse differently seed species by defecation or eventual dropping of the seed (Chazdon, 2014; Corlett, 1998). However, caution is needed, given that the high number of seeds arriving in those agroforest sites does not mean that seed dispersal effectiveness is occurring, i.e., that the arrived seeds are certainly reaching the adult stage (Morante-Filho and Faria, 2017; Schupp et al., 2010). Additionally, despite the importance of forest amount for indirectly explaining the arrival of seed species, this landscape predictor was unimportant for predicting overall seed abundance. Conversely, canopy shading was a substantial and direct predictor explaining abundance patterns of specific seed-dispersal modes – while

agroforestry sites exhibiting greater shade positively lead to greater biotic-dispersed species, these sites exerted a negative influence on the arrival of abiotic-dispersed seeds. Considering that higher shade levels in cacao agroforest tend to occur in areas exhibiting greater tree basal area (Silva et al., 2020), this suggest that more shaded environments offer more resources for animals, including fruit availability for feeding and branches for resting, ultimately resulting in higher locally precipitation of seeds. The significant and negative influence of canopy shading on the abundance of seeds dispersed by the wind, added to the scarcity of information of this type of syndrome in specialized articles, highlights the need for studies that involve the relationship between the variables analyzed for more evidences.

In addition to the key contribution of frugivorous birds in seed arrival in cocoa agroforests, this specific group is also potentially contributingto forest regeneration in those abandoned farms – i.e., in sites where the landowners abdicated to continually invest in cocoa production and the forest can thus be naturally recovered. Conversely, in those managed agroforestry sites, the farmer periodically clean the understory stratum, hampering the plants growth and consequently the forest succession in the entire property (Rolim and Chiarello, 2004). In fact, seed arrival comprises the first step of forest regeneration, and combined with abiotic factors including luminosity, nutrient and water availability, will determine the success of plant establishment, growth and reproduction (Chazdon, 2014; Duncan and Chapman, 1999). Therefore, our results indicate that in those agroforestry sites embedded within highly forested landscapes, the forest regeneration are prone to naturally occur due the presence of the pivotal presence of bird dispersers. Given that several farmers are abandoning their cocoa agroforests in southern Bahia region, due to low productivity and financial return from cocoa (Rolim et al., 2017; Serra and Marinho, 2007), it is possible that the number of areas naturally regenerating region will increase in the next years.

Our results further show that species composition was slightly similar in between local adult trees and the collected seeds within the same site. Particularly, 53% of the overall variation in seed species composition was predicted by adult trees (i.e., local seeds), indicating that the seed arrival is partially explained by local trees species whereas the other fraction comes from off-sites (i.e., immigrant seeds). For example, we found *Eriotheca macrophylla*, *Garcinia mangostana* and *Parkia pendula* only as adult trees, whereas *Euterpe edulis, Eschweilera ovata, Pera glabrata, Plathymenia reticulata* Benth, *Syzygium aromaticum* and *Tibouchina granulosa* were species solely recorded as seeds. This result indicates that seed arrival is partially mirroring local trees, indicating that immigrant seeds are pivotal in determine seed species assemblage with subsequent effects on forest regeneration. It therefore emphasizes the importance of nearby forest remnants to serve as a source of seeds and ensure the dispersion process (Chazdon, 2012; Pivello et al., 2006; Tres et al., 2007). Likewise, a study comparing degraded primary forest with abandoned and actively managed coffee agroforestry systems in Ecuador found great dissimilarity among juvenile (i.e., seedlings and saplings) and adult trees, also suggesting the influence of bird seed dispersers on regeneration (Lozada et al., 2007).

Conservation Implications

Our study shows that a great number of seed species can arrive in cocoa agroforest embedded within highly forested landscapes in southern Bahia, mainly due to the visit of frugivorous bird species in these areas. Although the number of seed species recorded in the collectors were lower than recorded in forest sites of the same studied region (see Coelho 2016; Piotto 2009), we recorded some seeds of tolerant and valuable timber species including *Plathymenia reticulata* Benth, *Jacaranda* sp. and *Macrolobium latifolium*. In addition, seeds from

Euterpe edulis, a vulnerable species to extinction exhibiting great economic importance for human consumption (Martinelli and Moraes, 2013), were commonly recorded in surveyed sites, which would have potentially come from the nearby forest sites and disseminated by birds, given this group comprises its main disperser. In addition, a greater number of animal-dispersed seeds can be found in more shading environments (i.e., exposed to lower farm intensification), suggesting the importance of the maintenance of local adult trees as resource for faunal groups and therefore enhanced probability of seed germination. These results act as an ecological sign of ecosystem functionality and reaffirms the status of cocoa agroforest sites as wildlife-friendly systems (Rice and Greenberg, 2000; Schroth et al., 2011).

Given the low financial return of cocoa mainly caused by the fungus *Moniliophthora perniciosa* (Serra and Marinho, 2007), and the consequently potential of enhancing the number of abandonment farms (Rolim et al., 2017), our results show the potential of natural recovery of these sites. Yet is required the maintenance of both forest remnants in their surroundings and the persistence of local emergent trees to providing higher level of shading. Both farm characteristics are likely to attract frugivorous birds expected to promote the arrival of seeds in these abandoned farms, and speed-up of forest regeneration (Chazdon, 2014; Morante-Filho et al., 2015). We therefore strongly emphasize the importance of retaining native vegetation cover around the cocoa agroforestry, by either preserving the existing forest remnants or promoting restoration programs for forested and deforested landscapes, respectively, in addition to curb the extraction of emergent trees within these farms. These simple conservation measures are likely to not only retain the biodiversity, but also guarantee the ecosystem functionality.

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Appendix

Appendix A. Hypotheses analyzed in our research.

Table A.1. Tested hypotheses of the direct (one arrow) and indirect influence of landscape and local predictors on seed rain attributes (i.e., richness and abundance) in 15 cocoa agroforestry surveyed in southern Bahia. FC = forest cover; CS = canopy shading; TR = tree richness; TA = tree abundance; DR = dispersers richness ; DA = dispersers abundance.

Predictor	Hypothesis	Prediction
Forest cover	Sites embedded within landscapes with great amount of FC would have greater seed richness and abundance because the adjacent forest remnants act as a source of seeds.	FC → Seed rain
	High percentage of forest cover in the landscape positively influences the presence and quantity of seed dispersers in cocoa agroforestry systems influencing the seed rain.	FC → Dispersers → Seed rain
Canopy shading	Greater canopy closure indicates more shadow environments, which possibility the establishment of more species and individual of shade-tolerant tree species that bear flesh fruits	CS → Seed rain
	Greater canopy closure indicates more shadow environments, which possibility the establishment of more species and individual of shade-tolerant tree species that bear flesh fruits that positively influences the presence and quantity of seed dispersers in cocoa agroforestry systems influencing the seed rain.	CS → Dispersers → Seed rain
Tree richness	The greater the richness of trees present in the area, the larger the amount of species and number of seeds collected due to their direct contribution to the area.	TR → Seed rain
	A greater variety of trees contributes to the presence of different dispersers in cocoa agroforestry systems, which contributes to seed rain.	TR → Dispersers → Seed rain
Tree abundance	The greater the number of trees present in the area, the greater the amount of species and number of seeds collected due to their direct contribution to the area.	TA → Seed rain
	The greater the number of trees in the area, the more likely they are to serve as food sources and attract potential seed dispersers influencing seed rain.	TA → Dispersers → Seed rain
Disperser's richness	The greater the variety of disperser species present in the area, the greater the chances of different species and larger amount of seeds reaching the site through dispersal.	DR → Seed rain
Disperser's abundance	The greater the amount of dispersers present in the area, the greater the chances of different species and larger number of seeds reaching the site through dispersal.	DA → Seed rain

Appendix B. Seeds collected in 15 cocoa agroforestry sites of southern Bahia.

Table B.1. Total number of collected seeds per species, considering all 15 cocoa agroforestry sampling sites. Information on family and dispersion syndrome are also provided.

Family/specie	Dispersion	Abundance
Anacardiaceae		
Spondias venulosa Mart.	zoochoric	49
Tapirira guianensis Aubl.	zoochoric	13
Annonaceae		
Annona montana Macfad.	zoochoric	1
Annonaceae sp1	abiotic	52
Araliaceae		
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	zoochoric	586
Arecaceae		
Elaeis guineensis Jacq.	zoochoric	12
Euterpe edulis Mart.	zoochoric	574
Bignoniaceae		
Jacaranda sp.	abiotic	60
Bignoniaceae 1	abiotic	1
Malvaceae		
Pachira glabra Pasq.	zoochoric	3
Boraginaceae		
Cordia sp.	zoochoric	132
Cucurbitaceae		
Cucurbitaceae 1	zoochoric	1
Ebenaceae		
Diospyros sp.	zoochoric	124
Euphorbiaceae		
Hevea brasiliensis Muell. Arg.	abiotic	26
Joannesia princeps Vell.	zoochoric	4
Euphorbiaceae 1	zoochoric	10
Fabaceae		
Albizia polycephala (Benth.) Killip	abiotic	14
Albizia sp2	abiotic	3
Andira sp1	zoochoric	435
Andira sp2	zoochoric	13
Bauhinia sp.	abiotic	18
Dioclea sp.	abiotic	10
Erythrina poeppigiana (Walp.) O.F.Cook	zoochoric	39
Erytrina fusca Lour	abiotic	35
Inga edulis Martius	zoochoric	275
Macrolobium latifolium Vogel	zoochoric	1
Plathymenia reticulate Benth.	abiotic	23

Family/specie	Dispersion	Abundance
Senna multijuga (Rich.) Irwin et Barn.	abiotic	8
Swartzia sp.	zoochoric	4
Vatairea sp.	abiotic	4
sp5	zoochoric	1
Clusiaceae		
Clusiaceae 1	zoochoric	4
Lamiaceae		
Aegiphila sellowiana Cham.	zoochoric	12
Aegiphila verticillata Vell.	zoochoric	4
Lecythidaceae		
Eschweilera ovata (Cambess) Miers	zoochoric	44
Lecythidaceae 1	zoochoric	11
Malpighiaceae		
Byrsonima sp.	zoochoric	5
Malvaceae		
Theobroma cacao L.	zoochoric	24
Melastomaceae		
Miconia sp.	zoochoric	23
Centronia sp.	zoochoric	2
Tibouchina granulosa Cogn.	abiotic	900
Meliaceae		
Azadirachta indica A. Juss	zoochoric	15
Cedrela odorata L.	abiotic	139
Moraceae		
Artocarpus heterophyllus Lam.	zoochoric	5
Ficus clusiifolia Schott	zoochoric	16562
Ficus gomelleira Kunth	zoochoric	5283
Myrtaceae		
Syzygium aromaticum (L.) Merr. & Perry	zoochoric	39
Peraceae		
Pera glabrata (Schott) Poepp.	zoochoric	2
Rhamnaceae		
Gouania sp.	abiotic	126
Rubiaceae		
Genipa americana L.	zoochoric	1148
Rubiaceae 1	zoochoric	111
Rutaceae		
Citrus sp.	zoochoric	1
Sapindaceae		
Matayba sp.	zoochoric	1132

Family/specie	Dispersion	Abundance
Sapotaceae		
Pouteria sp.	zoochoric	7
Sapotaceae 1	zoochoric	3
Morphospecies		
sp1	zoochoric	39
sp2	zoochoric	1
sp3	zoochoric	1
sp3	zoochoric	1
sp4	zoochoric	28
sp5	abiotic	1
sp6	zoochoric	13
sp7	abiotic	23
sp8	zoochoric	2
sp9	abiotic	8
sp10	zoochoric	1
sp11	zoochoric	19
sp12	zoochoric	1
sp13	zoochoric	8
sp14	zoochoric	3
sp15	zoochoric	25
sp16	zoochoric	1
sp17	zoochoric	27
sp18	zoochoric	3
sp19	zoochoric	29
sp20	zoochoric	62
sp21	abiotic	6
Total		**28,435**

Appendix C. All models analyzed for investigating which landscape and local variables best direct and indirectly affect the attributes of seed rain structure (richness and abundance) in 15 cocoa agroforestry sites surveyed in southern Bahia.

Table C.1. All model combinations used for each response variable.

Model	Landscape	Disperser	Trophic Guild	Disperser variable	Vegetation structure
1	Forest cover	Bird	Frugivorous + omnivorous	Richness	Tree richness
2	Forest cover	Bird	Frugivorous + omnivorous	Richness	Canopy shading
3	Forest cover	Bird	Frugivorous + omnivorous	Richness	Tree abundance
4	Forest cover	Bird	Frugivorous	Richness	Tree richness
5	Forest cover	Bird	Frugivorous	Richness	Canopy shading
6	Forest cover	Bird	Frugivorous	Richness	Tree abundance
7	Forest cover	Bat	Frugivorous + omnivorous	Richness	Tree richness
8	Forest cover	Bat	Frugivorous + omnivorous	Richness	Canopy shading
9	Forest cover	Bat	Frugivorous + omnivorous	Richness	Tree abundance
10	Forest cover	Bat	Frugivorous	Richness	Tree richness
11	Forest cover	Bat	Frugivorous	Richness	Canopy shading
12	Forest cover	Bat	Frugivorous	Richness	Tree abundance
13	Forest cover	Bird	Frugivorous + omnivorous	Abundance	Tree richness
14	Forest cover	Bird	Frugivorous + omnivorous	Abundance	Canopy shading
15	Forest cover	Bird	Frugivorous + omnivorous	Abundance	Tree abundance
16	Forest cover	Bird	Frugivorous	Abundance	Tree richness
17	Forest cover	Bird	Frugivorous	Abundance	Canopy shading
18	Forest cover	Bird	Frugivorous	Abundance	Tree abundance
19	Forest cover	Bat	Frugivorous + omnivorous	Abundance	Tree richness
20	Forest cover	Bat	Frugivorous + omnivorous	Abundance	Canopy shading
21	Forest cover	Bat	Frugivorous + omnivorous	Abundance	Tree abundance
22	Forest cover	Bat	Frugivorous	Abundance	Tree richness
23	Forest cover	Bat	Frugivorous	Abundance	Canopy shading
24	Forest cover	Bat	Frugivorous	Abundance	Tree abundance

Appendix D. Results of the adjustment coefficients of all models (Appendix C) analyzed for investigating which landscape and local variables best direct and indirectly affect the attributes of seed rain (richness and abundance) in 15 cocoa agroforestry sites of southern Bahia.

Table D.1 Seed richness results. For each model, we show the degrees of freedom (DF), test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the greatest.

Model	X^2	DF	P-VALUE	AIC	Δ AIC	CFI	TLI	RMSEA
5	10,782	5	0,056	75,479	0,000	1	1	0
1	10,378	5	0,057	84,291	8,812	1	1	0
3	6,440	5	0,266	88,589	13,110	1	1	0
2	6,402	5	0,269	88,627	13,148	1	1	0
12	5,517	5	0,356	92,117	16,638	1	1	0
10	4,166	5	0,526	93,468	17,989	1	1	0
11	3,504	5	0,623	94,130	18,651	1	1	0
9	6,415	5	0,268	98,888	23,409	1	1	0
7	5,527	5	0,355	99,775	24,296	1	1	0
8	4,798	5	0,441	100,504	25,025	1	1	0
14	11,87	5	0,037	137,518	62,039	1	1	0
22	10,188	5	0,070	169,912	94,433	1	1	0
23	9,931	5	0,077	170,170	94,691	1	1	0
19	10,195	5	0,070	171,041	95,562	1	1	0
20	10,044	5	0,740	171,192	95,713	1	1	0
4	14,310	5	0,014	71,951	-3,528	1	1	0
6	12,501	5	0,029	73,760	-1,719	1	1	0
18	15,591	5	0,008	131,745	56,266	1	1	0
17	14,075	5	0,015	133,262	57,783	1	1	0
16	13,984	5	0,016	133,352	57,873	1	1	0
15	13,165	5	0,022	136,22	60,741	1	1	0
13	12,491	5	0,029	136,893	61,414	1	1	0
24	12,528	5	0,028	167,573	92,094	1	1	0
21	12,344	5	0,030	168,892	93,413	1	1	0

Table D.2 Seed abundance results. For each model, we show the degrees of freedom (DF), test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the greatest.

Model	X^2	DF	P-VALUE	AIC	Δ AIC	CFI	TLI
5	10,297	5	0,067	178,153	0,000	1	1
4	9,215	5	0,101	179,235	1,082	1	1
6	7,922	5	0,161	180,528	2,375	1	1
2	7,936	5	0,160	189,282	11,129	1	1
1	7,442	5	0,190	189,776	11,623	1	1
11	7,660	5	0,176	192,163	14,010	1	1
3	4,300	5	0,507	192,917	14,764	1	1
12	5,879	5	0,318	193,944	15,791	1	1
10	5,237	5	0,388	194,586	16,433	1	1
8	9,464	5	0,092	198,027	19,874	1	1
9	7,190	5	0,207	200,301	22,148	1	1
7	6,937	5	0,225	200,554	22,401	1	1
13	10,963	5	0,052	240,611	62,458	1	1
17	16,160	5	0,006	233,365	55,212	1	1
18	14,849	5	0,011	234,676	56,523	1	1
16	12,903	5	0,024	236,621	58,468	1	1
14	13,431	5	0,020	238,143	59,990	1	1
15	11,836	5	0,037	239,738	61,585	1	1
23	14,825	5	0,011	267,464	89,311	1	1
24	13,419	5	0,020	268,870	90,717	1	1
20	14,488	5	0,013	268,936	90,783	1	1
22	11,760	5	0,038	270,529	92,376	1	1
21	12,498	5	0,029	270,927	92,774	1	1
19	11,206	5	0,047	272,219	94,066	1	1

Table D.3 Zoochoric **s**eed richness results. For each model, we show the degrees of freedom (DF), test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the greatest.

Model	X^2	DF	P-VALUE	AIC	Δ AIC	CFI	TLI	RMSEA
5	10.564	5	0.061	5.27	0	1	1	0
2	9.298	5	0.098	15.31	10.04	1	1	0
10	9.829	5	0.08	17.384	2.074	1	1	0
11	8.417	5	0.135	18.797	1.413	1	1	0
7	10.696	5	0.058	24.185	5.388	1	1	0
8	8.365	5	0.137	26.516	2.331	1	1	0
23	11.087	5	0.05	98.592	72.076	1	1	0
20	10.693	5	0.058	100.122	1.53	1	1	0
1	16.441	5	0.006	8.167		1	1	0
4	19.54	5	0.002	-3.7		1	1	0

13	17.38	5	0.004	61.584		1	1	0
14	16.155	5	0.006	62.81		1	1	0
16	17.722	5	0.003	59.194		1	1	0
17	16.806	5	0.005	60.11		1	1	0
19	12.22	5	0.032	98.595		1	1	0
22	12.629	5	0.027	97.051		1	1	0

Table D.4 Zoochoric seed abundance results. For each model, we show the degrees of freedom (DF), test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the greatest.

Model	X^2	DF	P-VALUE	AIC	Δ AIC	CFI	TLI	RMSEA
2	10.984	5	0.052	186.739	0	1	1	0
11	7.392	5	0.193	192.936	6.197	1	1	0
10	3.737	5	0.588	196.591	3.655	1	1	0
8	8.22	5	0.145	199.777	3.186	1	1	0
7	5.212	5	0.391	202.784	3.007	1	1	0
23	9.551	5	0.089	273.243	70.459	1	1	0
20	9.103	5	0.105	274.827	1.584	1	1	0
22	4.874	5	0.431	277.921	3.094	1	1	0
19	4.233	5	0.516	279.697	1.776	1	1	0
1	16.341	5	0.006	181.382		1	1	0
4	17.855	5	0.003	171.101		1	1	0
5	11.734	5	0.039	177.221		1	1	0
13	12.344	5	0.03	239.735		1	1	0
14	15.762	5	0.008	236.407		1	1	0
16	11.881	5	0.036	238.149		1	1	0
17	16.263	5	0.006	233.767		1	1	0

Table D.5 Ornitochoric seed richness results. For each model, we show the degrees of freedom (DF), test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the greatest.

Model	X^2	DF	P-VALUE	AIC	Δ AIC	CFI	TLI	RMSEA
5	10.782	5	0.056	75.479	0	1	1	0
2	6.402	5	0.269	88.627	13.148	1	1	0
1	12.889	5	0.024	82.14		1	1	0
4	20.797	5	0.001	65.464		1	1	0
13	14.356	5	0.014	135.029		1	1	0

14	11.687	5	0.037	137.518	1	1	0
16	16.351	5	0.006	130.985	1	1	0
17	14.075	5	0.015	133.262	1	1	0

Table D.6 Ornitochoric **s**eed abundance results. For each model, we show the degrees of freedom (DF), test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the greatest.

Model	X^2	DF	P-VALUE	AIC	Δ AIC	CFI	TLI	RMSEA
4	18.465	5	0.002	170.141		1	1	0
5	12.162	5	0.033	176.625		1	1	0
1	13.934	5	0.016	183.62		1	1	0
2	11.868	5	0.037	185.686		1	1	0
17	16.316	5	0.006	233.546		1	1	0
14	16.13	5	0.006	235.78		1	1	0
16	11.667	5	0.04	238.194		1	1	0
13	12.133	5	0.033	239.777		1	1	0

Table D.7 Abiotic **s**eed richness results. For each model, we show the degrees of freedom (DF), test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the greatest.

Model	X^2	DF	P-VALUE	AIC	Δ AIC	CFI	TLI	RMSEA
1	0.351	2	0.839	-72.615	0	1	1	0
3	0.287	2	0.866	-72.552	0.019	1	1	0
2	0.307	2	0.858	-72.571	0.044	1	1	0

Table D.8 Abiotic **s**eed abundance results. For each model, we show the degrees of freedom (DF), test statistic (minimum function chi-square, X^2), model *P*-value, comparative fit index (CFI), Tucker-Lewis fit index (TLI), Akaike Informaton Criterion (AIC), difference in AIC between the best model and the *i*-th model (ΔAIC), and root mean square error of approximation (RMSEA). Models are ranked by their AIC values, from the lowest to the greatest.

Model	X^2	DF	P-VALUE	AIC	Δ AIC	CFI	TLI	RMSEA
2	3.471	2	0.176	70.045	0	1	1	0
1	0.163	2	0.922	73.353	3.308	1	1	0
3	0.08	2	0.961	73.436	0.083	1	1	0

Appendix E. Coefficients of the variables included in the best model explaining patterns of seeds richness and abundance in 15 cocoa agroforestry sites of southern Bahia.

Table E.1. Coefficients β, P-value and R^2 of the variables of the best model for seed richness. Significant values are highlighted in bold.

Variables	β	P-value	R^2
Frugivorous bird richness			0,367
FC	0,602	**0,004**	
Canopy shading	-0,024	0,906	
Seed richness			0,230
FC	-0,428	0,134	
Canopy shading	-0,031	0,894	
Frugivorous bird richness	0,595	**0,037**	

Table E.2. Coefficients β, P-value and R^2 of the variables of the best model for seed abundance. Significant values are highlighted in bold.

Variables	β	P-value	R^2
Frugivorous bird richness			0,367
FC	0,602	**0,004**	
Canopy shading	-0,024	0,906	
Seed abundance			0,205
FC	-0,058	0,841	
Canopy shading	0,42	0,071	
Frugivorous bird richness	0,238	0,411	

Table E.3. Coefficients β, P-value and R^2 of the variables of the best model for zoochoric seed richness. Significant values are highlighted in bold.

Variables	β	P-value	R^2
Frugivorous bird richness			0,367
FC	0,602	**0,004**	
Canopy shading	-0,024	0,906	
Zoochoric seed richness			0,219
FC	-0,516	0,073	
Canopy shading	-0,125	0,587	
Frugivorous bird richness	0,508	0,076	

Table E.4. Coefficients β, P-value and R^2 of the variables of the best model for zoochoric seed abundance. Significant values are highlighted in bold.

Variables	β	P-value	R^2
Frugivorous + omnivorous bird richness			0,364
FC	0,545	**0,008**	

Canopy shading	-0,226	0,274	
Zoochoric seed abundance			0,244
FC	0,074	0,785	
Canopy shading	0,501	**0,032**	
Frugivorous + omnivorous bird richness	0,101	0,720	

Table E.5. Coefficients β, P-value and R^2 of the variables of the best model for ornithochoric seed richness. Significant values are highlighted in bold.

Variables	**β**	**P-value**	**R^2**
Frugivorous bird richness			0,367
FC	0,602	**0,004**	
Canopy shading	-0,024	0,906	
Ornithochoric seed richness			0,025
FC	-0,146	0,649	
Canopy shading	-0,03	0,906	
Frugivorous bird richness	0,193	0,546	

Table E.6. Coefficients β, P-value and R^2 of the variables of the best model for abiotic seed richness.

Variables	**β**	**P-value**	**R^2**
Abiotic seed richness			0,023
FC	0,105	0,711	
Canopy shading	-0,074	0,794	

Table E.7. Coefficients β, P-value and R^2 of the variables of the best model for abiotic seed abundance. Significant values are highlighted in bold.

Variables	**β**	**P-value**	**R^2**
Abiotic seed abundance			0,207
FC	-0,082	0,722	
Canopy shading	-0,452	**0,050**	

Appendix F. Photos referring to the materials and methods used in this research.

Figure 1. Photo of a seed collector installed in a cacao agroforestry sampled in south Bahia.

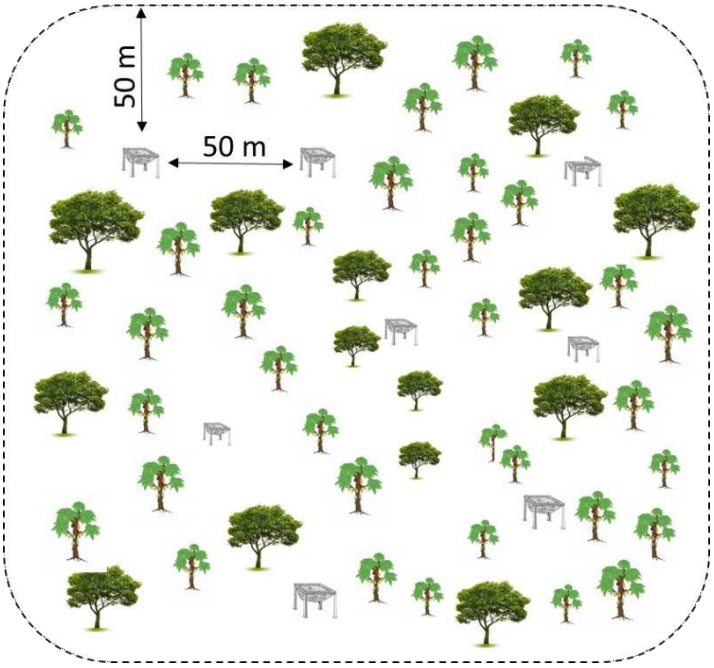

Figure 2. Example of a collector arrangement scheme in cocoa agroforestry sampled in southern Bahia.

CONCLUSÕES GERAIS

Os resultados do nosso trabalho elucidam sobre os principais fatores que influenciam na chuva de sementes em sistemas agroflorestais de cacau encontrados no sul da Bahia. Pela análise de múltiplos fatores em escalas de paisagem e local, conseguimos determinar a influência indireta que a perda de cobertura florestal na paisagem possui sobre a riqueza das sementes ao induzir negativamente a riqueza de espécies de aves frugívoras, assim como a influência direta do sombreamento sobre o aumento de número de sementes dispersas por animais e redução de sementes dispersas de forma abiótica. Assim, adicionamos conhecimento sobre a relevância das aves como dispersores de sementes ao afetar a riqueza das espécies de sementes que estão chegando nas agroflorestas, e assim possivelmente nos processos de dispersão de sementes e regeneração florestal dessas áreas em caso de abandono. Finalmente, mostramos que fazendas expostas à uma maior intensificação de manejo, através da extração das árvores emergentes que fornecem sombreamento, são propensas a receberem uma menor quantidade de sementes dispersas pelos animais, com efeitos subsequentes nos processos de dispersão efetiva de sementes e regeneração florestal. De tal modo, o nosso trabalho indica a necessidade de elaboração de estratégias de conservação que preservem as áreas florestais existentes, que visem a restauração florestal do entorno e que reduzam as ações de intensificação de manejo localmente nas fazendas de cacau, a fim de assegurar a manutenção da biodiversidade e a continuidade de processos ecológicos na região cacaueira do sul da Bahia