UNIVERSIDADE FEDERAL DA BAHIA - UFBA

Programa de Pós-Graduação em Ecologia: Teoria, Aplicação e Valores

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INFLUÊNCIA DA COBERTURA FLORESTAL NATIVA E DA ESTRUTURA DA VEGETAÇÃO LOCAL NAS INTERAÇÕES TRÓFICAS EM PLANTAÇÕES DE CACAU SOMBREADAS NO SUL DA BAHIA

Salvador, fevereiro de 2020

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia: Teoria, Aplicação e Valores, como parte dos requisistos exigidos para obtenção do título de Mestre em Ecologia.

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Salvador, fevereiro de 2020

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KARLA MORATO

A Mata Atlântica é um dos habitats mais desmatados do mundo restando atualmente apenas cerca de 11,73% da sua área original. Grande parte da sua área original foi convertida em outros tipos de uso da terra, principalmente para a agricultura. No sul da Bahia, um centro de endemismo, o cacau é o produto agrícola mais comercializado e cerca de 70% da produção é realizada sob o sistema agroflorestal conhecido como cabruca. Nesse sistema árvores nativas são mantidas para sombrear os pés de cacau, então ao contrário de sistemas simplificados e intensivos, a cabruca é um modo de produção favorável à biodiversidade servindo como habitat e corredores ecológicos para várias espécies nativas. Entretanto, a crescente adoção de praticas de manejo intensificando a produção – em especial, a remoção de árvores sombreadoras – pode mudar o valor de conservação destes ambientes, reduzindo a diversidade de espécies. Ao mesmo tempo, é possível que a perda da diversidade de espécies nas cabrucas se traduza em modificações de alguns processos ecológicos nestes ambientes, alguns deles caracterizados por serviços ambientais cuja alteração pode impactar a própria lavoura. Por exemplo, a redução da capacidade local das cabrucas em abrigar aves e artrópodes pode alterar a capacidade destes grupos em controlar populações de herbívoros, muitos deles predadores de folhas do cacau. De fato, artrópodes herbívoros podem causar uma perda de 10% da produção anual do cacau, mas não sabemos ainda, se mudanças na abundância local de aves e artrópodes, desencadeadas por alterações na quantidade de floresta na paisagem ou na simplificação estrutural da lavoura cacaueira pode influenciar na taxa local de danos foliares do cacau. Portanto o objetivo desse trabalho é investigar se alterações em diferentes escalas espaciais – local e paisagem – podem influenciar os padrões de dois processos ecológicos em plantações de cacau sombreadas: a pressão de predação sobre os artrópodes herbívoros e a porcentagem de dano foliar em pés de cacau, além de avaliar

se estas alterações podem ser decorrentes da redução dos predadores de topo que exercem controle sobre as demais populações em uma escala de paisagem na Mata Atlântica do sul do Estado da Bahia. Para isso estudamos a taxa de predação em lagartas artificiais, confeccionadas com massinha de modelar dispostas por 4 dias em 18 cabrucas com cobertura florestal de 3 a 66%. Foram amostrados ainda aves de sub bosque e artrópodes em pés de cacau, além da coleta de folhas para medir a herbivoria. Foram também medidos cinco descritores locais da estrutura da vegetação de cada plantação, incluindo a estratificação vertical da floresta, área basal, sombreamento, abundância de arvores nativas e abudância de cacaueiros. A análise estatística foi feita a partir da modelagem com equações estruturais e regressão linear múltipla. O resultado mais evidente aqui é que os artrópodes predadores, e não as aves, exercem um importante controle das populações de artrópodes herbívoros. O experimento de pressão de predação mostrou que a quantidade de floresta na paisagem aumenta a pressão de predação enquanto a abundância de cacau a reduz. No entanto, embora esse experimento tenha evidenciado que o contexto local e de paisagem influenciam na pressão de predação das lagartas, a análise de caminhos não o fez. Essa discrepância pode ser resultado de diferenças nas assembléias de presas entre as diferentes abordagens. A avaliação real de artrópodes herbívoros em folhas de cacau evidenciou uma assembléia mais diversa do que as lagartas artificiais padronizadas e, portanto, é provável que envolva uma assembléia mais diversa de predadores reais. Este estudo é parte integrante de um projeto mais abrangente, o INCT-TREE, cujo objetivo é analisar a biodiversidade, serviços ecossistêmicos e a produtividade em agroflorestas de cacau.

Resumo

No sul da Bahia, um dos centros de endemismo na Mata Atlântica, o cacau é o produto agrícola mais importante e cerca de 70% da produção é realizada sob o sistema agroflorestal conhecido como cabruca. Este sistema concilia a produção do cacau com a manutenção da biodiversidade original. Apesar de sabermos que os artrópodes podem causar uma redução da produção anual do cacau, não sabemos se mudanças na abundância de aves e artrópodes predadores, desencadeadas por alterações na quantidade de floresta na paisagem ou na simplificação estrutural da lavoura cacaueira em decorrência do aumento da intensidade de manejo através da remoção da vegetação nativa para aumentar a produtividade, pode influenciar na taxa local de herbivoria. O objetivo deste estudo foi investigar o impacto do processo de desmatamento e da simplificação da estrutura da vegetação nos padrões locais de herbivoria. E testar, tanto de maneira experimental quanto através da amostragem efetiva de aves e artrópodes, se estas alterações podem ser decorrentes de um relaxamento do controle *top-down,* oriundo de mudanças na paisagem e na estrutura local da floresta. Esse estudo foi conduzido em 18 cabrucas localizadas na região Sul da Bahia, ao longo de um gradiente de cobertura florestal (3-66%). Em cada sítio amostrado, foram dispostos modelos de lagartas artificiais que foram observados durante 4 dias para verificação da taxa de predação. Foram amostradas aves de sub bosque e artrópodes presentes em folhas de cacau, além da coleta de folhas para medir o dano foliar, aqui um proxy para herbivoria. Foram também coletados dados de cinco descritores locais da floresta (estratificação vertical, área basal, sombreamento, abundância de árvores nativas e abudância de cacaueiros). A análise estatística foi feita a partir da modelagem com equações estruturais (path analysis) e regressão linear múltipla. Evidenciamos que a pressão de predação sobre os artrópodes herbívoros em folhas de pé de cacau, aqui avaliada por lagartas artificias, foi realizada principalmente por invertebrados e não por aves ou outros vertebrados. Esse controle *top-down* foi corroborado pelo resultado da *path analysis*, que indicou que o aumento da abundância real de artrópodes herbívoros nos pés de cacau não estava relacionada à abundância local de aves. No entanto ocorre como uma resposta a uma redução na abundância local de artrópodes predadores. Embora a taxa de predação em lagartas artificiais tenha aumentado com o desmatamento, enquanto diminuída sob densidades mais altas de pés de cacau, não encontramos evidências de que a paisagem ou as características locais aqui avaliadas tenham influenciado as assembléias reais de invertebrados (predadores ou herbívoros) e os danos às folhas de cacau. Embora tenhamos detectado uma cascata trófica envolvendo invertebrados ou seja, predadores que controlam herbívoros, essa interação não influenciou a quantidade de dano foliar observado nos pés de cacau.

Palavras – chave: Mata Atlântica. Cabruca. Cobertura florestal. Herbivoria. Controle *top down.* Alterações antrópicas.

Abstract

In southern Bahia, a center of endemism, cacao is the most traded agricultural product and about 70% of production is made under the agroforestry system known as cabruca. This system reconciles cacao production with maintaining the original biodiversity. Although we know that arthropods can cause a reduction in annual cacao production, we do not know if changes in the abundance of predatory birds and arthropods, triggered by changes in the amount of forest in the landscape or the structural simplification of cacao crops due to increased intensity. Management through the removal of native vegetation and the use of agrochemicals to increase productivity can influence the local herbivory rate. Therefore, the objective of this study is to investigate the impact of the deforestation process and the simplification of vegetation structure on local herbivory patterns. And test, both experimentally and through effective sampling of birds and arthropods, whether these changes may be due to a relaxation of top-down control at a landscape scale in Atlantic Forest of Southern Bahia State. This study was conducted on 18 cabrucas on a forest cover gradient (3-66%), in which dummy caterpillar were placed and observed for 4 days to verify the predation rate. We sampled understory birds and arthropods on cacao trees, and collected leaves to measure herbivory. Data were also collected from five local descriptors (vertical stratification, basal area, shading, abundance of native trees and cacao abudance). Statistical analysis was based on structural equation modeling and multiple linear regression. We reveal that predation pressure on herbivorous arthropods of cacao leaves, herein assessed by dummy caterpillars, was mainly carried out by invertebrates and not by birds or other vertebrates. Such top-down control was further corroborated by the findings of our path analysis, in which the actual increasing abundance of herbivorous artropods of cacao leaves local was not related with the local abundance of birds but rather, occurs as a response of a decreasing in the local abundance of predatory arthropods. Interesting, although predation rate of dummy catterpillars increased with deforestation while lessened under higher densities of cacao trees, we found no evidence that landscape or local features herein assessed influenced neither the actual invertebrates assemblages (predators or herbivorous) nor cacao leaf damage. Although we detected a trophic cascade involving invertebrates, i.e. predators controlling herbivorous, this interaction did not influence the actual amount of observed leaf damage in cacao trees.

Keywords: Atlantic forest. Cabruca. Forest cover. Herbivory. Top-down control. Anthropogenic changes.

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Estrutura da dissertação

A presente dissertação está estruturada em um capítulo que investiga se alterações em diferentes escalas espaciais – paisagem e local – podem influenciar os padrões de dois processos ecológicos em plantações de cacau sombreadas no sul da Bahia: a pressão de predação sobre os artrópodes herbívoros e a porcentagem de dano foliar em pés de cacau. O capítulo está estruturado no formato de um artigo, já em língua inglesa, que será submetido a uma revista (Acta Oecologica, IF: 1,17). O estudo foi executado em 18 plantações de cacau que variam em relação a porcentagem de cobertura florestal em escala de paisagem (3-66%) e níveis de simplificação estrutural da lavoura. Inclui a condução de um experimento para avaliar a pressão de predação usando lagartas artificiais para simular artrópodes herbívoros e a amostragem conjunta das assembleia de aves, de artrópodes predadores e herbívoros, além dos danos em folhas de pés de cacau. Os resultados auxiliam na compreensão das relações multitróficas complexas que caracterizam sistemas agrícolas complexos como os sistemas agroflorestais. Os quais imitam sistemas florestais nativos e tem implicações para a conservação das paisagens antrópicas da Mata Atlântica, uma vez que a complexidade estrutural local e a quantidade de floresta na paisagem tem influência sobre a biodiversidade da região.

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Introdução geral

Os ecossistemas tropicais, principalmente florestas, abrigam uma grande parcela da biodiversidade global. Juntas, esta grande quantidade de espécies interage de maneira complexa, mediando importantes processos ecológicos que em sua totalidade regulam o funcionamento destes ecossistemas. Com uma composição bastante heterogênea, e considerada um *hotspot* mundial, a Mata Atlântica, abrange uma ampla faixa de climas e formações vegetais (TABARELLI *et al.,* 2005). No entanto, apesar de níveis elevados de endemismismo, a Mata Atlântica brasileira é um dos habitats mais desmatados do mundo (MYERS *et al.,* 2000). Originalmente foi uma das maiores florestas tropicais das Américas, cobrindo cerca de 150 milhões de hectares em condições ambientais altamente heterogêneas (RIBEIRO *et al*., 2009) se estendendo de forma contínua ao longo da costa brasileira, penetrando até o leste do Paraguai e nordeste da Argentina em sua porção sul (TABARELLI *et al.,* 2005). No entanto, após a chegada dos europeus à costa brasileira à 500 anos atrás, a Mata Atlântica passou a sofrer um alto nível de desmatamento que foi seguido por anos de exploração (JOLY *et al.,* 2014) e atualmente restam apenas cerca de 12% da sua área original (RIBEIRO *et al.,* 2009).

Uma das principais causas do desmatamento nas florestas tropicais é o uso da terra para a produção agrícola. Geralmente estes usos são compostos por monoculturas intensivas e extensivas como soja, cana e por outras commodities. Em contraste a esta drástica simplificação estrutural, no sul da Bahia – um dos três grandes centros de endemismo da Mata Atlântica – o cacau (*Theobroma cacau*), maior produto agrícola da região, é plantado na sua maioria em um sistema agroflorestal conhecido localmente como cabruca. Nele, são mantidas por hectare, de 20 a 35 espécies nativas de árvores para sombrear os pés de cacau (OLIVEIRA *et al*., 2014). Ao contrário de sistemas simplificados e intensivos, as cabrucas conciliam a produção agrícola com a manutenção de parte significativa da biodiversidade regional, uma vez que a permanência de árvores nativas permite abrigar espécies de flora e fauna e possivelmente contribuem para a manutenção de processos ecológicos.

Em particular, as cabrucas abrigam e protegem um grande número de artrópodes, como por exemplo as formigas, que podem ter efeitos benéficos no cultivo de cacau (DELABIE *et al*., 2007). As árvores que tem copas estruturalmente mais complexas

podem suportar mais espécies de artrópodes do que as copas mais simples que fornecem habitat e outros recursos essenciais (ULYSHEN, 2011). Portanto, as cabrucas que contêm espécies arbóreas mais estratificadas têm maior capacidade de fornecer habitats para essas formigas em geral, bem como para espécies relacionadas (DELABIE *et al.,* 2007). As plantações de cacau com maior densidade de arvores sombreadoras, também conseguem manter uma maior diversidade de aves (SCHROTH; HARVEY, 2007). Entretanto, esses sistemas agroflorestas variam em intensidades de manejo, através do raleamento da densidade de espécies arbóreas, sendo dependentes do tipo de solo, do clima local (GROSS; MELLO, 2013) e da cobertura florestal. Desde a ultima crise da lavoura cacaueira, causada pela introdução da doença vassoura de bruxa (*Moniliophtora perniciosa*) no final da década de 1980, a produção despencou. Entre as estratégias de recuperação da lavoura está a tendência de maior intensificação, em particular o adensamento do cacau aliado à remoção de parte do componente arbóreo para reduzir os altos níveis de sombreamento. Este raleamento massivo da lavoura, no entanto, desconsidera o valor das árvores nativas para conservação (SAMBUICHI, 2006). No entanto as diferenças no manejo da camada de sombra e do estrato herbáceo nas propriedades impactam fortemente as plantações de cacau (BISSELEUA *et al*., 2013), afetando negativamente a riqueza e a abundância da vegetação nativa (BOS *et al*., 2007, CLOUGH *et al.* 2009), e consequentemente os serviços ecossistêmicos, como o controle biológico de pragas (BISSELEUA *et al*., 2013, MAAS *et al*., 2013).

Dentre os serviços ecossistêmicos importantes para as lavouras está o controle de herbívoros (BETTS *et al*., 2019). A herbivoria é uma interação inter-específica com grande capacidade de influenciar o funcionamento de sistemas agroflorestais (WIRTH *et al*., 2008). Há evidências de que a herbivoria, como uma interação trófica, pode ser regulada tanto pela oferta de recursos (controle *bottom-up*) quanto por predação (controle *top-down*) (BAGCHI *et al.,* 2018), ambos componentes alterados pelo desmatamento. As alterações na disponibilidade de nutrientes, luz, umidade e calor em decorrência do desmatamento, podem, por exemplo, causar alterações nos recursos disponíveis. Isso pode ocorrer através das mudanças na disponibilidade e na distribuição das plantas (URBAS *et al.,* 2007) e consequente alterações na comunidade de insetos, uma vez que a configuração espacial das plantas hospedeiras na paisagem pode moldar a abundância local de insetos (GRIPENBERG; ROSLIN, 2007).

Por outro lado, predadores podem influenciar diretamente no tamanho das populações de espécies de presas atuando na pressão total de forrageamento em espécies de plantas específicas ou comunidades vegetais inteiras (RIPPLE; BESCHTA, 2004). Por sua vez, as espécies de predadores costumam ser negativamente influenciadas pelo desmatamento, sendo que a ausência deste grupo trófico pode desencadear uma cascata trófica. Portanto, a redução ou a ausência destes predadores pode aumentar a abundância de insetos e, consequente, aumentar a taxa de herbivoria (MORRISON; LINDELL, 2012; MÄNTYLÄ; KLEMOLA; LAAKSONEN, 2011; VAN BAEL *et al.*, 2008). Desta forma, a estrutura da paisagem, em especial a composição de habitats remanescentes pode ter grande influência na distribuição dos herbívoros em várias escalas espaciais (GRIPENBERG; ROSLIN, 2007). Isso, portanto enfatiza o papel do contexto espacial e mostra que o desmatamento em escala de paisagem pode mediar alterações nos padrões locais de herbivoria, que é um processo ecológico essencial em florestas tropicais (DODONOV *et al.*, 2016), através de mudanças na oferta de recursos ou na presença de predadores, respectivamente, controle *bottom-up* ou *top-down*.

É evidente que a intensificação do manejo nesses sistemas agroflorestais visando o aumento da produção pode causar diversas alterações na biodiversidade local. A questão que se coloca é como projetar densidades ideais de espécies vegetais que proporcionem as condições mais adequadas para a produtividade do cacau, bem como para a manutenção da biodiversidade e dos serviços ecossistêmicos (DEHEUVELS *et al.*, 2014). Portanto a compreensão das consequências das alterações na estrutura da vegetação local devido a intensificação do manejo e do contexto da paisagem sobre os processos ecológicos, torna-se fundamental para auxiliar em medidas de conservação a longo prazo.

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Justificativa

As alterações antrópicas associadas a mudanças na cobertura florestal e a perda da biodiversidade podem desencadear mudanças abruptas e irreversíveis (CHAKRAVARTY *et al*., 2012) e o impacto do desmatamento contínuo na biodiversidade é muito maior em áreas com pouca floresta remanescente e altos níveis de endemismo, como a Mata Atlântica (FEARNSIDE, 2005). Esse bioma, embora tenha sido amplamente destruído, ainda é o lar de mais de 8000 espécies endêmicas de plantas vasculares, anfíbios, répteis, aves e mamíferos (MYERS *et al.* 2000). Além disso essas florestas promovem serviços ecossistêmicos essenciais como prevenção de erosão, controle de enchentes, polinização, tratamento da água, dentre outros que são particularmente de interesse de toda a humanidade (CHAKRAVARTY *et al*., 2012).

Portanto ao destruir as florestas, colocamos em risco a nossa própria qualidade de vida e ameaçamos a sobrevivência de diversas outras espécies (CHAKRAVARTY *et al*., 2012). A extinção de espécies endêmicas resulta na perda das funções ecológicas que somente essas espécies fornecem (BANKS-LEITE *et al*., 2014). Para manter essas funções ecológicas rurais como por exemplo controle de pragas e polinização nas áreas em um nível semelhante ao observado em áreas protegidas é importante manter ou restaurar a cobertura florestal da Mata Atlântica acima de um limite de 30% (BANKS-LEITE *et al*., 2014). No entanto, parte das florestas tropicais ainda está sendo continuamente desmatada, principalmente para usar a terra a produção agrícola.

No sul da Bahia a comercialização do cacau passou a ser uma das principais formas de subsistência da população da região e partir do século XXI, o Brasil passou a conquistar um papel de destaque no mercado externo e passou a participar dos mercados de qualidade do cacau e chocolate com direito a produção e reconhecimento do cacau fino e do aroma brasileiro (ESTIVAL; CORRÊA; PROCÓPIO, 2019). Porém, no decorrer do seu desenvolvimento o sistema agroindustrial do cacau tem enfrentado novas pressões, devido ao crescimento e diversificação das demandas dos mercados consumidores mundiais, para intensificar a produtividade aliada a qualidade e inovação (ESTIVAL; CORRÊA; PROCÓPIO, 2019). Então apesar dos benefícios do sistema cacau-cabruca, ainda existem grupos que defendem a prática de manejo intensivo com a

remoção da vegetação nativa que sombreia o cacau e uso de agroquímicos para aumentar a produtividade do cacau (PIASENTIN; SAITO, 2014). Entretanto a redução dessa floresta nativa na paisagem reduz a diversidade de espécies presentes nas cabrucas (FARIA *et al*., 2006, 2007).

A complexidade estrutural local proporcionada pelas árvores nativas que sombreiam os pés de cacau aumenta a diversidade local de animais e o contexto da paisagem, particularmente a representação de florestas nativas, também é um preditor da biodiversidade local (FARIA *et al*. 2006, 2007). Além disso as interações bióticas variam significativamente ao longo de um gradiente de intensificação de manejo (BISSELEUA; MISSOUP; VIDAL, 2009). A simplificação da lavoura causa uma redução de habitats e isso pode gerar mais danos às plantas através da redução do controle natural de pragas (PUMARIÑO *et al.,* 2015). Isso pode resultar em uma perda de 10% da produção anual, estimada em cerca de 67 milhões de dólares (OLIVEIRA *et al*., 2014).

BISSELEUA *et al*., (2013) mostrou que o número de teias de aranha e ninhos de vespas aumentou significativamente com o aumento da densidade de árvores de sombra nativas. E embora já tenha sido mostrado a importância funcional das aves e morcegos na supressão das densidades de artrópodes em sistemas agroflorestais, além de um aumento da produção de cacau em quase um terço (MAAS *et al*., 2013), no sul da Bahia o nível de sombreamento não influenciou a capacidade reguladora de artrópodes por morcegos e aves e o dano foliar (CASSANO *et al.,* 2016). Não sabemos ainda, se mudanças na abundância local de aves e de artrópodes, desencadeadas por alterações na quantidade de floresta na paisagem ou na simplificação estrutural da lavoura cacaueira pode influenciar na taxa local de danos foliares do cacau.

A manutenção das cabrucas é dependente da sustentabilidade econômica de cada fazenda e das estratégias adotadas para aumentar sua rentabilidade, o que muitas vezes pode culminar em alterações no seu valor de conservação evidenciando a necessidade de discutir e promover estratégias que conciliem a conservação e rentabilidade (SAMBUICHI *et al.*, 2012). Políticas e incentivos destinados a ajudar os produtores de cacau a fazerem a transição de sistemas de baixa diversidade para sistemas com alta diversidade, podem gerar aumentos simultâneos na biodiversidade e no lucro líquido (BISSELEUA; MISSOUP; VIDAL, 2009). No entanto, para isso é fundamental compreender como estas práticas de manejo atuam sobre processos ecológicos fundamentais para garantir a conservação da biodiversidade nestes sistemas

agroflorestais. Cerca de 80% dos estudos que buscaram entender como os sistemas agroflorestais influenciam o controle de pragas, foram realizados em plantações de café ou milho (PUMARIÑO *et al.,* 2015) existindo uma grande lacuna na literatura a respeito dos sistemas agroflorestais de cacau.

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Objetivos

Objetivo Geral

Os objetivos desse estudo foram

1. investigar o impacto do processo de desmatamento e da simplificação da estrutura da vegetação nos padrões locais de herbivoria e

2. testar, de maneira experimental, se estas alterações podem ser decorrentes de um relaxamento do controle *top-down* em uma escala de paisagem na Mata Atlântica do sul do Estado da Bahia.

Objetivos específicos

Através da amostragem em agroflorestas de cacau com diferentes níveis de manejo e inseridas em paisagens com diferentes níveis de cobertura florestal (3-66%), pretende-se especificamente:

1. avaliar se a perda de cobertura em escala de paisagem e a estrutura da vegetação local afetam a pressão de predação em hebrivoros (através de lagartas artificiais);

2. testar se a porcentagem de dano foliar observada em pés de cacau pode ser resultante de uma cascata trófica – controle *top-down* – direta ou indiretamente desencadeada por alterações nos níveis de cobertura florestal na paisagem e na estrutura da vegetação local.

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Capítulo I

Landscape-scale forest cover and local vegetation structure mediate multitrophic relationships but not the leaf damage by herbivores in cacao trees

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Capítulo I

LANDSCAPE-SCALE FOREST COVER AND LOCAL VEGETATION STRUCTURE MEDIATE MULTITROPHIC RELATIONSHIPS BUT NOT THE LEAF DAMAGE BY HERBIVORES IN CACAO TREES

[1]

Abstract:

Cacao is the most important agricultural product in the southern region of Bahia state, Brazil with 70% of its production occuring under the traditional agroforestry system. In this system, locally known as cabruca, cacao trees are grown under the shade of native trees. While this system makes it possible to reconcile the production with the maintenance of the original biodiversity. However there is a variation in the intensity of management aiming only the productivity which can lead to reduced biodiversity in the landscape and ecological functions that species provide, such as control of economically damaging arthropod species. The aim of this paper is to investigate the impact of the deforestation process on local herbivory patterns and to experimentally test whether these changes are due to a relaxation of top-down control on a landscape scale. This study was conducted at 18 sites in southern Bahia along a gradient of forest cover. We assessed predation rate using artificial caterpillars , sampled understory birds and arthropods and collected leaves to analyse damage by herbivory. We also measeured vertical stratification, basal area, shading, abundance of native and cacao trees. Most predation pressure was exerted by arthropods and was positively related to the amount of forest in the landscape and negatively related to the local abundance of cacao trees. In accordance with this result, path analysis showed that the main controllers of herbivorous arthropod assemblages are predatory arthropods and not birds, however in the model the landscape

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[1] A autoria será determinada após a defesa da dissertação e após o envio do manuscrito a aprovação e contribuição dos potenciais co-autores

did not influence any of the variables. We suggest that the discrepancy between the results of the two analyzes reveals important differences in the evaluated communities. The actual evaluation of herbivorous arthropods on cacao leaves provided a more diverse assemblage than standardized artificial caterpillars and thus is likely to involve a more diverse assemblage of real predators. Although in this study we have not obtained evidence revealing the direct mechanisms that affect herbivory.

Keywords: Atlantic forest. Cabruca. Forest cover. Herbivory. Top-down control. Anthropogenic changes.

Introduction

Tropical forest ecosystems harbor a large part of terrestrial biodiversity, an important asset that provides diverse benefits to humanity through goods and ecosystem services (GARDNER *et al.,* 2009). Due to its great diversity of species and its high degree of endemism, the Atlantic Forest is considered a global biodiversity hotspot (MYERS *et al.*, 2000). However, much of the original vegetation has been lost due to conversion to other types of land use. Selective cutting, poaching, fragmentation and deforestation due to agriculture and various anthropogenic disturbances affect the structure of biological communities and ecosystem functions at multiple scales (JOLY *et al.*, 2014).

Along most of the Atlantic Forest, the original vegetation has been converted to homogeneous and structurally simplified monocultures such as soy, cane and other commodities. Nevertheless, in southern Bahia, northeastern Brazil, since the early XIX centrury a large extend of the native vegetation has been replaced by agroforests of cacao (*Theobroma cacao*) (SCHROTH and HARVEY, 2007). Almost 70% of the cultivation is carried out under the agroforestry system locally known as cabruca, where 20 - 35 native tree species are kept per hectare to shade cacao trees (OLIVEIRA *et al.*, 2011). Cabrucas are often considered as biodiversity-friendly production mode, as they harbor a major part of the regional biota, which in southern Bahia is known to comprise such high levels of endemism that is considered a hotpoint of diversity in the biome (MARTINI *et al.,* 2007). By serving as temporary or permanent habitat for several species of native animals, this system also acts as ecological corridors or stepstones linking remaining forest fragments (SCHROTH *et al.*, 2011), thus promitong gene flow in the region (SAATCHI *et al.* 2001).

Besides the conservation of animal and plant species, this forest biota is also pivotal for the maintenance of key ecological processes (SCHROTH *et al.,* 2011). For

instance, cabrucas comprise most of the carbon stocks in southern Bahia (SCHROTH *et al.,* 2015), and as other agricultural system, they show a high potential to help in the recovery of degraded areas, reduce erosion and conserve soil and water, benefits that transcend from local to global level (NAIR, 2011). However, the potential of a plantation to host biodiversity and, possibly, to provide ecosystem services is likely to be mediated by processes at different scales. For instance, while the structural complexity providing by many and diverse assemblage of shade trees can increase local animal diversity, landscape context, particularly the representation of native forests, is also an important feature explaining locally high levels of biodiversity (FARIA *et al*. 2006, 2007).

Nevertheless, the dynamic of land use is changing both local and landscape context of this crop in the region. The national technical report of the forest remnants of the Atlantic Forest published by INPE and the Fundação SOS Mata Atlântica (2017) showed that Bahia was leading in deforestation among the states within the Atlantic Forest biome between 2015 and 2016 . Meanwhile, due to economic pressures, many farmers are intensifying their management practices, drastically reducing the abundance of shading native trees and increasing the density of cacao tree (SCHROTH *et al.,* 2011). The understanding of the consequences of the joint effect of landscape-scale deforestation and the local management intensification of cabrucas on ecological processes becomes pivotal not only for long-term conservation measures, but also for the maintenance of important ecosystem services (SCHROTH *et al*., 2011).

In cacao agroforestry systems, ants reduce the abundance of herbivorous arthropods and therefore affect plant growth and leaf and fruit development (GRAS *et al*., 2016). Ants can provide plant defense by either displacing or preying on herbivores (WIELGOSS *et al.* 2013).These changes in commercial income influenced by the ant community may occur due to complex processes not assessed here as it involves fruit set, abortion and herbivore interference, as well as pest and disease control (WIELGOSS *et al.* 2013). The shaded agroforestry that has the lower canopy dominated by cacao trees contributes to the conservation of ant and beetle species diversity, depending on the intensity and variety of management techniques, with forest species usually disappearing according to a canopy reduction. In addition, the conversion of forests to agroforestry systems generates habitat changes that may result in community changes due to the loss of forest-dependent species (BOS; STEFFAN-DEWENTER; TSCHARNTKE, 2007a).

For instance, that cacao plantations in Brazil suffer an estimated US$67 million annually in losses due to damages caused by insects pre-harvest (Olveira *et al.* 2014) and birds and other apex predators are important to reduce some pests in cacao plantations (MAAS *et al.,* 2015). Rich and abundant bird communities are negatively affected by both landscape-scale deforestation (MORANTE-FILHO *et al.* 2015) and cacao intensification (VAN BAEL *et al.,* 2007), although the link between local diversity and the potential of top-down control remains unclear.

This study aims to disintangle the role of the percentage forest cover in the surrounding landscape and the local structural complexity on pest control in cabruca systems. First, we experimentally assess the influence of landscape-scale forest cover and local characteristics of cacao agroforestry on the predation pressure on herbivorius arthropods in cacao leaves,using dummy caterpillars as proxies for herbivorous insects. Second, we study to what degree changes in the landscape and local characteristics of cacao agroforestry explain the actual amount of leaf damage in cacao trees, as a cascading effect of multi-trophic relationships encompassing local avian diversity and diversity of predatory and herbivorous artropods. Overall, we expect to provide information on the mechanisms and impacts of anthropogenic action on the landscape in order to reconcile profitable farming and the maintenance and conservation of biodiversity and ecosystem services.

Materials and Methods

1. Study area

This study was conducted in southern Bahia, in the central corridor of the Atlantic Forest. This region contains large forest reserves with old growth remnants and large proportions of secondary forest (PIOTTO *et al*., 2009), but also large areas of cacao agroforests. Remnant Atlantic Forest in southern Bahia is characterized by two different physiognomies, the hygrophilic forest located closer to the coast, thus having more sandy soils, and the mesophytic forest, which occurs further inland, with more nutrient-rich soils (GOUVÊA *et al*., 1976).This regions present an average annual temperature of 24°C and 1500 mm of precipitation, with no defined seasonality (MORI *et al*., 1983).

2. Sampling design

We maped the region using satellite images (QuickBird [J1] and WorldView, 2011; RapidEye, 2009-2010) that enabled the identification of land use categories. We classified the fragments following the typologies provided by IBGE (2006). From this, we selected the three regions including the municipalities of Una, Ilhéus and Belmonte. Within the municipality of Una lies two conservation units (Una Biological Reserve and the Una Wildlife Refuge) with a total area of 34,804 ha. This area contains a larger amount of native forest cover than the other two municipalities, with a heterogeneous matrix composed of ancient old-growth forest, native secondary forest, cacao agroforestry systems and rubber plantations. The municipality of Ilhéus has several cacao agroforestry systems interspersed with native remnants, while Belmonte contains a more homogeneous matrix composed mainly of Eucalyptus plantations, cacau agroforestry systems and a large amount of pastures. From this map, we selected 80 cacao agroforestry systems and calculated the proportion of native forests (herein, forest cover) within a landscape with a radius of 1 km drawn from the center of each plantation. We subsequently selected 18 farms, six in each municipality, located at least 2 km distance between them, as sampling sites (Figure 1).
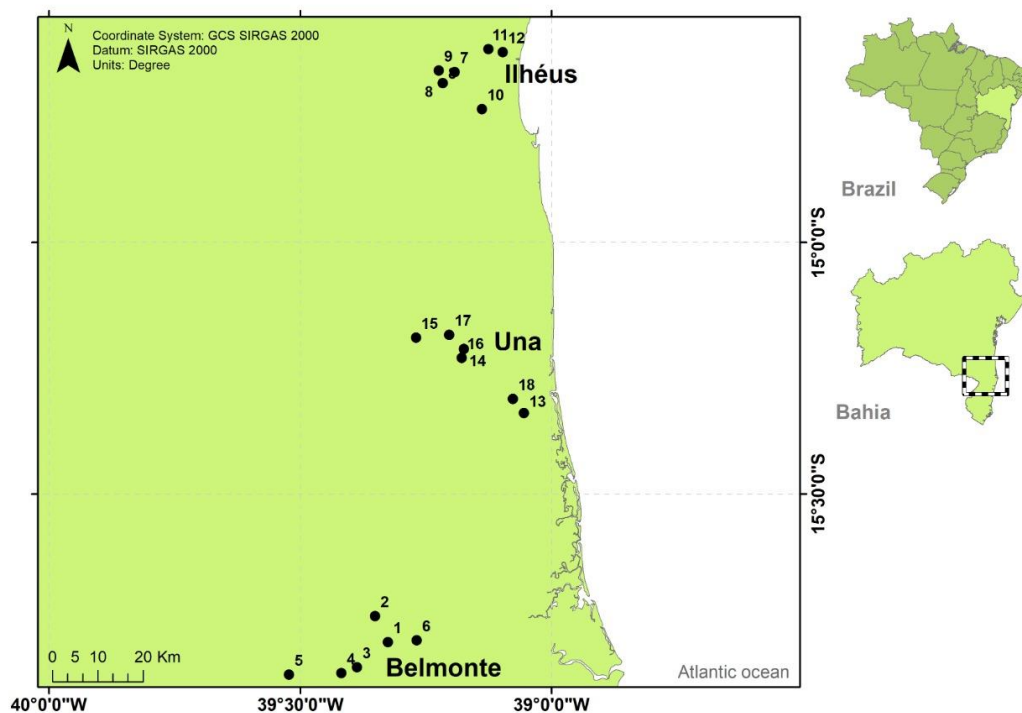

Figure 1 - Study location map indicating sampling points.

2.1. Vegetation structure

In each sampling site we established a 100m x 25m plot to assess the vegetation structure. Within each plot were counted the number of cacao trees, the abundance of shade trees (native/exotic, except cacao) with DBH ≥ 10 cm, and estimated the sum of the basal area of all trees (DBH ≥ 10 cm), adjusted to hectares (m^2/ha). Within each plot, we randomly selected five points to assess the vertical profiles by estimating the length (cm) occupied by the foliage in an imaginary vertical line in eight forest strata (0-1m; 1; 1-2m; 2.1-3m; 3.1-4m 4.1-5m; 5.1-10m; 10.1-15m and >15.1m) (HUBBELL; FOSTER, 1986). The average values of foliage length in each stratum were reduced to two dimensions using the first two axis of a Principal Component Analysis (PCA). Axis 1 explained 37% of the total variation and represented a decreasing gradient of dense cacao strata and high dense forest canopy above 5m high, or rather a variable describing an increasing structuiral simplification of the local canopy while a increasing density of foliage on the forest strata in which the cacao grows. This axis was thus used as a single variable describing the simplification of the vertical profile (Appendix S1). To measure the canopy shading over the cacao trees, within each plot, five points with at least 20 m from each other and 1.30 m from the ground. At each point a photograph was taken using the GLAMA application. To take the picture the cacao leaves were moved aside to account only for the canopy.

2.2. Experiment of predation pressure

We used the rate of predation of dummy caterpillars as a proxy for predation of invertebrate herbivory on cacao leaves. The molds were made with non-toxic modeling clay in a 1:1 ratio blend of the ACRILEX® green and white colors. This coloration was chosen because it resembled the most abundant group of Lepidoptera found all over the world and were made in such a way as to have a standard size and shape (2.5 x 30mm) modeled in a looping position, which is characteristic of an adopted geometrid caterpillar while resting (ROSLIN, T. *et al.*, 2017). We know that the models do not present many of the characteristics of real caterpillars, such as chemical tracks, movement or even characteristics that help predators to identify them as potential prey. Nonetheless, it comprises a suitable method to document the interaction between predator and prey (LELES *et al.,* 2017; RICHARDS; COLEY, 2007) and is widely used successfully in other studies (MENEZES *et al.,* 2016; MORENO, FERRO, 2012; ROSLIN, T. *et al.*, 2017; TVARDIKOVA; NOVOTNY, 2012).

Following the methodology proposed by Roslin *et al*. (2017), we installed five 3x4m grids in and around each plot. The individual grids were at least 50 m apart (Figure 2) and all grids in the same location were set up on the same day. Twenty uniformly spaced (1m) cacao trees were selected in each grid, and on each cacao tree we placed 1 caterpillar on leaves located at least 1 m above the ground, totaling 20 dummy caterpillars in each grid and 100 for each sampling site.
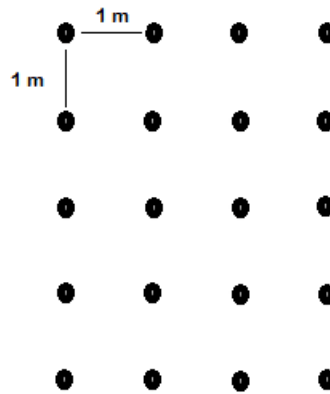

Figure 2 - Depiction of a grid showing the spatial position of each 25 cacao tree (black dots) used to allocate a model of dummy caterpillar in sites of cacao plantations in Southern Bahia, Brazil.

The molds were only placed on undamaged leaves that were not touching the ground. All leaves with molds were sequentially numbered on the bottom usin a non-toxic pen, and signaling tape was used to assist in locating the leaves.

The caterpillars were exposed for 4 days, observed every 48 hours and after the end of the experiment the caterpillars with signs of predation were taken to the laboratory for analysis and the others were discarded. Caterpillars that were found in the soil or disappeared were not considered as predated, as we could not prove that the disappearance was caused by predation, and they haven't been replaced either. Using a magnifying glass and available literature (LOW *et al*., 2014) it was possible to identify the marks and classify them according to the main predator groups (arthropods, birds, lizards or mammals) others were identified as damaged by snail feeding.

2.3. Arthropod survey

To estimate the composition of the local arthropod commity, five cacao trees with dummy caterpillars were randomly chosen from each grid. On these trees, the arthropods

were sampled manually, at a height of 50 to 200 cm, during the same period of the predation pressure survey, following the methodology of Morante-Filho *et al*. (2016). The collected arthropods were identified by specialists and classified into predators, herbivores, omnivores, detritivores, saprophages and xylophages based on the morphology of their oral apparatus.

2.4. Bird survey

Birds were surveyed using mist nets (12 m long, 2.5 m high with 31 mm mesh size) (KARR, 1981). Nets were and open from 6:00 to 16:00 and inspected every 30 minutes (BANKS-LEITE *et al*., 2010). In each sampling site, 10 mist nets were arranged with a total of 120 m in length . These nets were open for 3 consecutive days at each site, except for the days when there were no ideal conditions for bird capture or movement, such as rainy days. As a way to avoid double counting, after capture we marked each bird on theprimary feathers of the right wing using temporary ink. The names of species follow the scientific nomenclature of the South American Classification Committee (REMSEN *et al*. 2013). We used the available literature to classify species into food guilds (CAZETTA *et al*., 2002; FADINI; MARCO Jr, 2004; PASCOAL *et al*., 2016; COSTA e SILVA; SOUZA; LIMA *et al*., 2010).

2.5. Assessment of leaf damage

The cacao trees selected for arthropod sampling were also analyzed for leaf damage over the same period as arthropod sampling and exposure of dummy caterpillars. The area of leaf damage was estimated by collecting five leaves per cacao tree, in five cacao trees per grid, totaling 25 leaves per grid, 125 leaves per sampling site and 2,250 for the entire study area. The collected leaves were scanned and images analyzed using the software ImageJ1.52a (MORANTE-FILHO *et al*., 2016). Leaf damage caused by herbivorous insects was quantified as a percentage of the lost leaf area, calculated by subtracting the amount of damaged leaf area from the total leaf area. For leaves that showed damage on their edges, the potential leaf area was estimated by drawing the leaf perimeter based on leaf symmetry (MORANTE-FILHO *et al*., 2016; VAN BAEL *et al*., 2003; CASSANO *et al.,* 2016). The mean loss of leaf area per site was used as a direct measure for insect herbivory (MORANTE-FILHO *et al*., 2016).

2.6. Data analysis

First, we used multiple linear regression to test whether predation of dummy caterpillars by different predators is influenced by remnant forest cover at the landscape scale as well as each of the five local descriptors (i.e. vertical stratification, shading, basal area and abundance of native trees and abundance of cacao trees). We then investigated whether and how landscape and local scale variables affect leaf damage of cacao trees using Structural Equations Modeling (SEMs). This statistical technique allows for the inclusion of variables that are measured not only directly, but also through their effects , while simultaneously estimating several relations of interdependence. In addition, these equations allow a variable that is dependent (response variable) at a given stage, to be independent (predictor variable) in the subsequent step and to incorporate measurement errors (AMORIM *et al*., 2012). Within the SEM, Path Analysis was used as a way to evaluate the direct and indirect effects of the independent variables on the dependent variable. In general, Path Analysis solves a set of simultaneous regression equations that establish the relationship among the observed variables (SCHUMACHER; LOMAX, 2010).

For the path analysis we built a theoretical model using forest cover (landscape variable) and vertical stratification, shading, basal area and abundance of native trees and abundance of cacao trees (local variable) as exogenous predictors, while (1) vertebrate predatory richness and abundance (birds), (2) predatory invertebrate abudance, and (3) abundance of herbivorous invertebrates were defined as endogenous predictors for the damage in cacao leaves. From this theoretical model we tested different combinations of variables using five local vegetation structure descriptors (vertical stratification, shading, basal area and abundance of native trees and abundance of cacao trees) and five characteristics of potential predators (abundance and richness considering all bird species, abundance and richness of insectivorous birds and abundance of predatory arthropods). So we were able to select the variables that optimized the overall performance of the model because the number of observations limited us to simple model structures containing few pathways.

As SEM requires normally distributed data, so we tested each variable using Mardia's multivariate normality test (MORANTE-FILHO *et al*., 2016). Variables with a non-normal distribution (abundance data for arthropods, including omnivores, herbivores and predators, insectivorous birds and native trees) were transformed using logarithmic

transformation, and stratification data using the arcsine transformation according to the data distribution adjustment.

Each model consisted of six variables and 18 observations.The parameters used to evaluate the quality of the fit of the models were: $\chi 2$ goodness-of-fit test of the difference between the observed date and the hypothetical model, Tucker-Lewis Fit Index, Comparative Fit Index (CFI) and the root mean square error of approximation (RMSEA). Among the models that presented a good fit, the model with the lowest AIC value was selected (MORANTE-FILHO *et al*., 2016). The model was considered to have a good fit when the χ^2 goodness-of-fit test showed P> 0.05 (GRACE, 2006), CFI and LTI> 0.9 and RMSEA <0.08 (HAIR *et al*., 2005). We used the standardized path coefficients (β) and the P values to evaluate the significance of the individual variables in the final model (GRACE, 2006). The coefficient of determination (R^2) shows the variation of each endogenous variable due to the effect of the other variables. All analyzes and statistical graphs were performed using the software R (Version 3.6.2), using the lavaan.survey, lavaan, lavaanPlot and MVN packages.
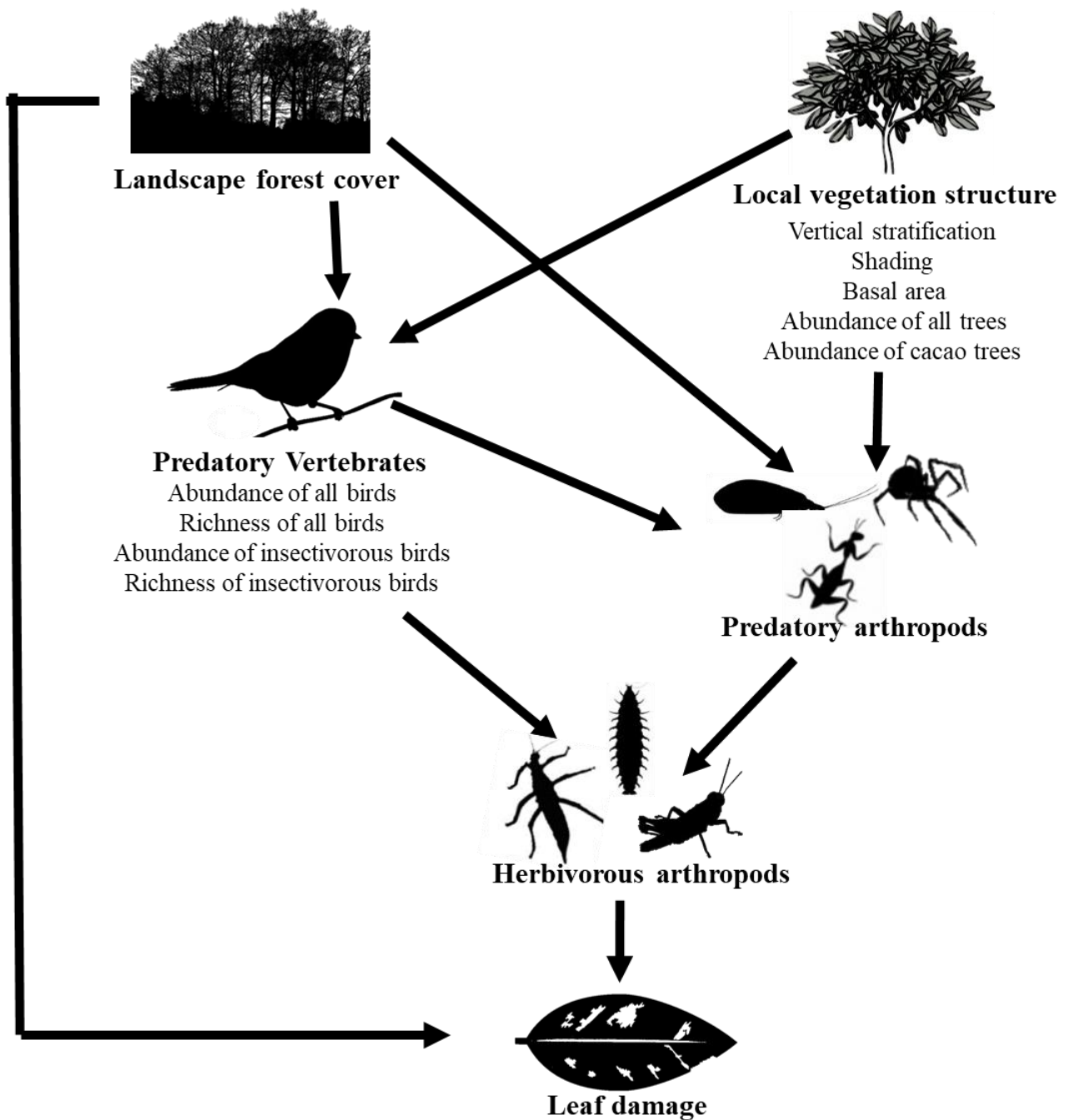
Figure 3 - Conceptual model predicting that leaf damage as a result of possible causal direct and indirect relationships between exogenous variables (landscape and local-scale variables) and a series of variables directly describing trophic relations, such as the local diversity of birds, predatory and herbivorous anthropods

Results

Of the 1800 dummy caterpillars placed along the 18 sampling sites, 21.8% showed signs of predation. Among the predated caterpillars, 79.1% showed signs compatible with arthropod predation, 9.7% by birds, 5.1% by mammals, 0.5% reptiles, while for the remaining 5.4% it was not possible to identify the nature of predation. Forest cover and

cacao tree abudance affected the rate of predation on cacao trees (R^2 = 0.42, P = 0.007). The percentage of forest cover in the landscape positively affected predation pressure, while cacao abudance negatively affected predation pressure. Multiple regressions using the percentage of forest cover with each of the other local variables (tree abundance, vertical stratification, shading and basal area) were not statistically significant (see Appendix S2).

Of the 2225 cacao leaves collected and analysized, 82.8% presented leaf damage (n = 1842) with an average of 4.1% of herbivory per leaf. Among the 968 arthropods collected 10.4% were predators, 15.1% were herbivores, 72.4% were omnivores and 2.1% were detritivores, xylophages and saprophages. We also captured 406 birds of 53 species,, 51 individuals were insectivores (12.6%), belonging to 16 species.

The path model with the lowest AIC was composed of the percentage of forest cover in the landscape, abundance of cacao trees, abundance of insectivorous birds, abundance of predatory arthropods, abundance of herbivorous arthropods and leaf damage (see Appendices S3-S5). Of the nine paths present in the model with the best fit, only two were statistically significant and one was consistent with our predictions. The model explained 21% of insectivorous bird abundance, 18% of predatory arthropod abundance, 36% of herbivorous arthropod abundance and 10% of leaf damage. The abundance of insectivorous birds was positively related to the abundance of cacao trees (β = 0.46), while the abundance of herbivorous arthropods was negatively affected by the abundance of predatory arthropods (β = – 0.51).
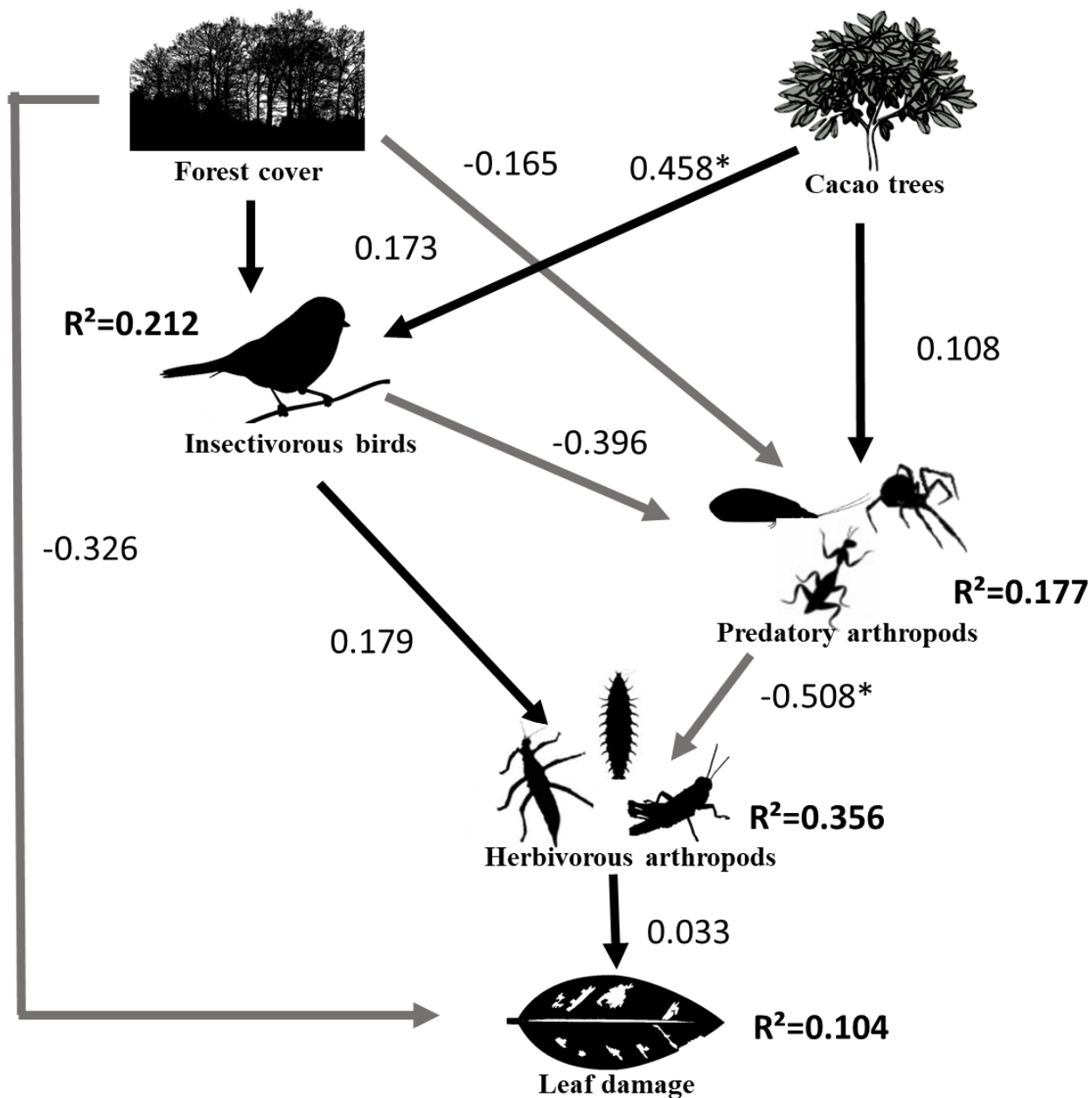
Figure 4 - Path analysis model with the best fit (see Appendices S3 and S4). Significant coefficients are indicated with asterisks (* P <0.05).

Discussion

Our results elucidated three important aspects of the multitrofic relationships within a biodiversity-friendly crop system. First, we found that the main predators of herbivorous arthropods of cacao leaves, as assessed using dummy caterpillars, were invertebrates as opposed to birds or other vertebrates. Such top-down control was further corroborated by the result of the path analysis, in which the actual increasing abundance of herbivorous artropods of cacao leaves was not related with the local abundance of birds

but rather, occured as a response to a decrease in local abundance of predatory arthropods. Second, even though predation rate of dummy caterpillars increased with forest cover while decreased under higher densities of cacao trees, we found no evidence that landscape or local features influenced neither the actual invertebrate assemblages (predators or herbivorous), nor cacao leaf damage. Third, the reported trophic cascade involving invertebrates, i.e. predators controlling herbivores, did not influence the actual amount of observed leaf damage in cacao trees.

Previous studies conducted in southern Bahia have shown that both local vegetation structure and forest cover at the landscape scale are powerful predictors of local diversity of many biological groups and ecological processes in both forests (MORANTE-FILHO *et al.* 2015, 2016; DODONOV *et al*., 2016; MENEZES *et al*., 2016; PESSOA *et al.,* 2017) and cabruca systems (FARIA *et al.* 2006;; 2007, Cassano et al. 2009). Indeed, studies show that more complex habitats within largely forested landscapes can harbor a large diversity of predators that are able to exploit a series of different microhabitats (VAN BAEL *et al.,* 2008), consequently controlling some subsets of preys (CASSANO *et al*., 2016). Accordingly, we did report that predation rates on dummy caterpillars increased in more forested landscapes but decreased in farms with under intensified management (i.e with higher density of cacao trees). This result suggests the possibility that herbivory levels could be mediated by processes acting at both spatial scales.

Indeed, other studies using this methodology to quantify predation pressure also found a higher predation rate exerted by arthropods (SEIFERT *et al.,* 2015; LELES *et al.,* 2017; ROSLIN *et al*., 2017; FÁVARELI; VASCONCELOS; DIRZO, 2008; SAM; REMMEl; MOLLEMAN, 2015). In addition, previous studies show that bird and predatory arthropod diversity in forest fragments in this region are directly influenced by both forest cover and structural complexity of the forest (MORANTE-FILHO *et al*., 2016). Nevertheless, we found no evidence that landscape directly influenced the actual abundance of predators (birds or arthropods) or leaf damage. In addition, only birds were affected by local characteristics. We suggest that such discrepancies between our two assessments reveal key differences about the composition of the assemblages actually measured. When using dummy caterpillars, we focused on a smaller subset of preys that eventually can be detected and consumed by a smaller subset of predators. By contrast, the actual assessment of herbivorous arthropods on cacao leaves provided a more diverse

assemblage than the standardized caterpillars, and thus are likely to involve more diverse and complex interactions among a more varied assemblage of preys and predators, that in turn may respond more idiosyncratically to both local and landscape-scale change. Therefore, our study suggests that although predation pressure can be affected at both local and landscape scales, neither variables seem to mediate the more complex interactions encompassing a larger variety of predators and preys observed on actual cacao leaves.

And yet, the most evident result here is that arthropods, not vertebrates, exert an important top-down control over herbivorous assemblages. It is surprising because 1. such pattern emerged from both experimental and real assessment on cacao plantations 2. they are known to exert a top-down control of many pests (VAN BAEL; BICHIER; GREENBERG, 2007; MÄNTYLÄ; KLEMOLA; LAAKSONEN, 2011; VAN BAEL *et al.*, 2008; POCH; SIMONETTI, 2013) and 3. bird assemblages are directly affected at both landscape and local scales (MORANTE-FILHO *et al.* 2016). Indeed, the bird assemblage in cacao agroforest systems in southern Bahia is often characterized as an ecotone, comprising of the juxtaposition of generalists from more open and disturbed areas and a subset of the species inhabiting the surrounding forests (FARIA *et al.,* 2006).

However, we found no evidence that the local abundance of insectivorous birds – including the generalists – in cacao plantations varied according to the remaining forest cover but rather, increased with the density of cacao trees. This result possibly reflects a compensatory dynamics of bird assemblage, as shown by Morante-Filho *et al.* (2015) for native forests, where the abundance of generalists increase and specialists decrease as deforestation progresses, thus maintaining biodiversity regardless landscape-scale deforestation. It is also possible that, as noticed by Cassano *et al.* (2016), birds are exerting biological control over a small number of leaf-chewing insects that are not the main vectors causing leaf damage on this specific plant species.

In addition, our study did not account for the potential top-down control of bats, another important vertebrate group that is known to exert top-down control in many agricultural systems including cacao (VAN BAEL *et al*., 2008; KARP and DAILY, 2014; MAAS *et al.,* 2013). Indeed, as CASSANO *et al.,* (2015) pointed out, the joint effect of predation by birds and bats on artropods is very complex and poorly known and such information gap can prevent us from fully understanding trophic relationships. Morante-

Filho *et al*,. (2017) also fail to provide evience for a top-down control of local herbivory in understory plants within forest fragments, and suggest bottom-up control.

In our study, arthropods were able to significantly deplete the abundance of herbivorous species on cacao leaves. While arthropods are often perceived by farmers as dangerous pests, they can also perform pest control, intraguild predation can be significant and thus generate benefits for agriculture (PHILPOTT; ARMBRECHT, 2006). The ability of these organisms to provide both ecosystem services that are beneficial to agriculture can also generate disservices, the prevalence of these services over disservices is evident, and the loss or reduction of predatory arthropods can lead to a 27% reduction in commercial yield (WIELGOSS *et al.* 2013).

In cacao agroforestry systems, ants reduce the abundance of herbivorous arthropods and therefore affect plant growth and leaf and fruit development (GRAS *et al*., 2016). Ants can provide plant defense by either displacing or preying on herbivores (WIELGOSS *et al.* 2013).These changes in commercial income influenced by the ant community may occur due to complex processes not assessed here as it involves fruit set, abortion and herbivore interference, as well as pest and disease control (WIELGOSS *et al.* 2013). The shaded agroforestry that has the lower canopy dominated by cacao trees contributes to the conservation of ant and beetle species diversity, depending on the intensity and variety of management techniques, with forest species usually disappearing according to a canopy reduction. In addition, the conversion of forests to agroforestry systems generates habitat changes that may result in community changes due to the loss of forest-dependent species (BOS; STEFFAN-DEWENTER; TSCHARNTKE, 2007a).

Despite the top-down control of herbivores by predators , we found no significant relationship between the abundance of such herbivorous arthropods and leaf damage. Indeed, Cassano *et al.* (2016) provide evidence that when bats and birds were experimentally excluded from cacao trees, the releasing of measopredators arthropods cascade to decrease leaf damage. Therefore, intraguild predation may be an important mechanism to control herbivory levels in the absence of apex predators, a situation not assessed here. In addition, our assessment of leaf damage represented the accumulated damage over a larger time frame, and not necessarily the damage occurring only during the experiment period, a mismatch that could hide actual top-down control (SCHMITZ; HAMBÄCK; BECKERMAN, 2000). Another important aspect to consider is that, among other things, we were unable to control key procedures of management that may influence

the observed patterns, such as the use of fertilizers and pesticides. This may have caused the apparent lack of trophic control.

In addition, herbivores not only cause damage to leaves, but also to cacao flowers, which can influence cacao crop development as observed by Maas, Clough and Tscharntke (2013). The authors also did not find a significant relationship between leaf damage and abundance of herbivorous arthropods, but observed several groups of arthropods in flowers during the study period and pointed out that this is a mechanism that needs further study. Therefore, the reduction of predatory arthropods such as ants in cacao plantations may result in an increase in herbivore abundance and, consequently greater damage to leaves and flowers (GRAS *et al.,* 2016). This observation was corroborated by Wielgoss *et al.* (2013) who showed that due to the complexity of the direct and indirect relationships these organisms have with cacao plantations, the exclusion of ants resulted in a reduction of fruit weight (WIELGOSS e*t al,.* 2013).

Limitations

This study should be viewed with caution, as in addition to the already mentioned limitations with regard to the predation pressure experiment, the dimensions adopted may have influenced this difference between bird and arthropod predation. Predatory arthropods, such as ants and spiders, are known to attack smaller prey, while birds prefer larger prey (VAN BAEL *et al.,* 2008; PHILPOTT *et al.,* 2004; VAN BAEL; BICHIER; GREENBERG, 2007). In addition, ants, the most abundant arthropods in our sampling, usually attack anything unusual in their territory and this methodology with fictitious caterpillars does not allow us to differentiate the marks left on artificial caterpillars by ants or other arthorpods (SAM; KOANE; NOVOTNY, 2014). Nevertheless, despite these limitations and the inability of this experiment to measure predation itself, it was successful as a proxy for predation (LELES *et al*. 2017; ROSLIN *et al*., 2017; ZVEREVA *et al.,* 2019; SAM; KOANE; NOVOTNY, 2014).

While we have not found a consistent effect of certain characteristics of these agroforestry systems on the abundance of arthropods, cabrucas seem to host a diverse arthropod fauna (BOS; STEFFAN-DEWENTER; TSCHARNTKE, 2007a) and these communities exert a significant control over herbivorous arthropods populations. However, we still do not know if other aspects not addressed here, such as the use of

fertilizers and pesticides, distance between cabrucas and forest fragments and the diversity of native trees, for example, can influence this biological control service.

Conclusion

Although the functional importance of birds in arthropod suppression and consequently increased cacao production in tropical agroforestry systems has already been documented (MAAS; CLOUGH; TSCHARNTKE, 2013), in this study we found that in cacao agroforestry systems in southern Bahia, it is predatory arthropods and not insectivorous birds that exert top-down control on herbivorous arthropods . Instead, we highlighted that arthropods are key elements in agroforests and, as predators this group can locally deplete herbivores shown by an experiment using dummy caterpillars, as well as actual fauna sampled on cacao leaves.

A smaller subset of the actual predation pressure on a small subset of herbivore assemblages could possibly be affected at landscape and local scale, but we found no evidence that changes in such features – directly or indirectly - affect the actual abundance of herbivores, possibly indicating more complex and idiosyncratic responses. Interestingly, this occurs despite the fact that both vertebrate and artrhopod diversity are highly influenced by changes at both scales (CASSANO *et al.,* 2009, 2016; FARIA *et al* 2006; 2007; MORANTE-FILHO *et al.* 2015, 2016; DODONOV *et al.*, 2016; GONZÁLEZ; SALVO; VALLADARES, 2017).

Therefore, although in this study we have not obtained evidence revealing the direct mechanisms that affect herbivory, it is therefore important to unravel the mechanisms that affect biodiversity and consequently the trophic interactions within agroforestry systems. For a better understanding of how local and landscape variables affect top-down control and consequently herbivory in cabrucas, further study using methodologies to monitor leaf damage from the beginning of the experiment along with monitoring production rates, and other ecosystem services such as pollination, so that we can better understand the trade-off between maintaining biodiversity and increasing production.

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ANEXOS

Appendix S1. Principal Component Analysis using the dataset of vertical stratification

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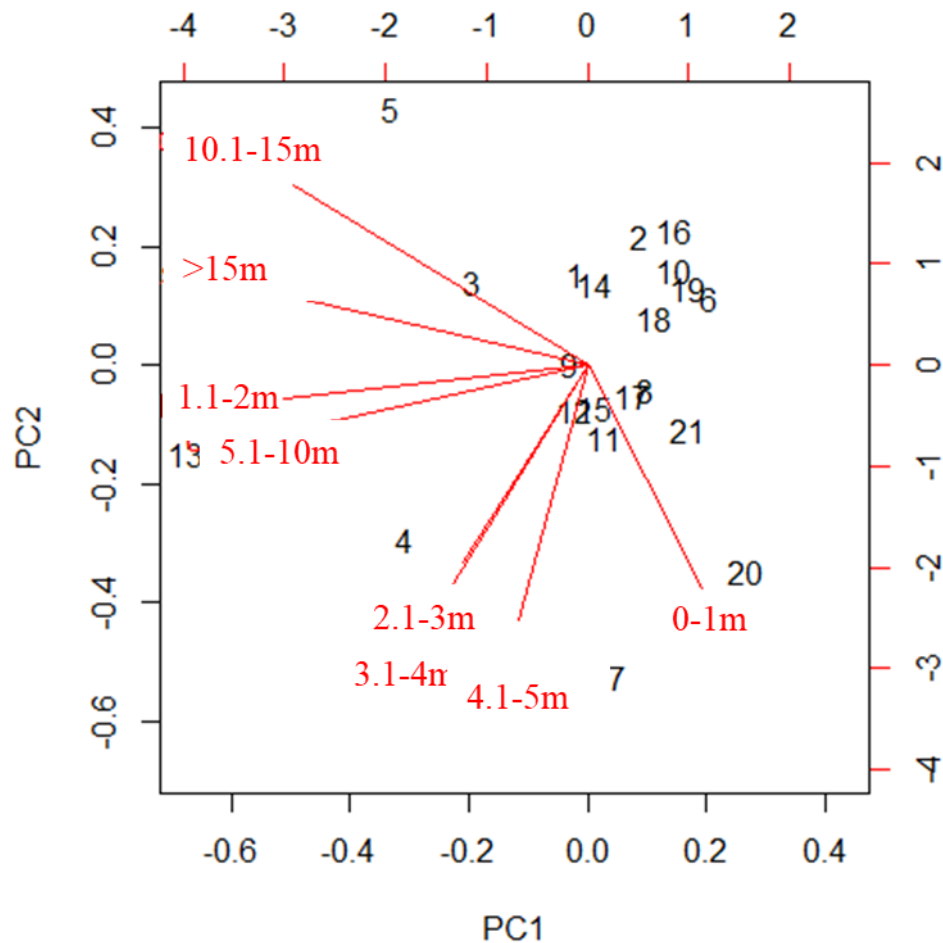
Figure S1. Biplot representation of the two first axes of a PCfor organizing average foliage length values for each of the eight strata (0-1m; 1.1-2m; 2.1-3m; 3.1-4m 4.1-5m, 5.1-10m, 10.1-15m, > 15.1m) . The first axis captures about 37% of the original variation. The numbers indicate the height classes around each of the 18 sampling sites.

Appendix S2. Results of multiple regressions

Table S1. We show the R^2 and *P*-value for each multiple regression.

Regressions	R^2	P
Predation pressure ~ Forest cover + Shading	0.2492	0.04556
Predation pressure ~ Forest cover + Abundance of trees	0.2639	0.03929
Predation pressure ~ Forest cover + Abundance of cacao trees	0.4135	0.007148
Predation pressure ~ Forest cover + Basal Area	0.2332	0.05336
Predation pressure ~ Forest cover + Vegetal stratification	0.22	0.06071

Appendix S3. Results of the adjustment coefficients of all models (Appendix S5).

Table S1. For each model we show the degrees of freedom (DF), test statistic (minimum function chi-square, χ^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 largest

Model	DF	X2	P-value	CFI	TLI	AIC	ΔAIC	RMSEA
1	5	0.783	0.196	1.000	2.682	215.401	1.949	0
2	5	0.812	0.181	1.000	2.672	214.855	1.403	0
3	5	0.980	0.186	1.000	3.653	213.452	0	0
4	5	0.910	0.358	1.000	8.462	217.402	3.950	0
5	5	0.925	0.282	1.000	4.988	216.044	2.592	0
6	5	0.851	0.117	1.000	2.313	241.472	28.020	0
7	5	0.824	0.129	1.000	2.310	242.048	28.596	0
8	5	0.986	0.139	1.000	3.132	240.841	27.389	0
9	5	0.888	0.265	1.000	4.255	244.781	31.329	0
10	5	0.904	0.238	1.000	3.853	244.127	30.675	0
11	5	0.595	0.049	1.000	1.376	317.070	103.618	0
12	5	0.770	0.101	1.000	1.980	318.666	105.214	0
13	5	0.935	0.018	1.000	1.780	311.183	97.731	0
14	5	0.736	0.061	1.000	1.701	316.978	103.526	0
15	5	0.814	0.098	1.000	2.079	318.250	104.798	0
16	5	0.698	0.132	1.000	1.937	277.587	64.135	0
17	5	0.879	0.238	1.000	3.697	278.947	65.495	0
18	5	0.973	0.146	1.000	3.101	275.851	62.399	0
19	5	0.892	0.274	1.000	4.484	279.519	66.067	0
20	5	0.778	0.218	1.000	2.864	279.236	65.784	0

*The variables that compose each model are showed in Appendix S2.

Appendix S4. Test statistic for the best path model.

Table S1. We show the unstandardized path coefficients (Coef.), the related standard error (SE), Z-value, *P*-value and standardized path coefficients (β) based on the results of the best model.

Regressions	Coef	SE	Z	P	β
Abundance of insectivorous birds~ Abundance of cacao trees	0.007	0.003	2.155	0.031	0.458
Forest cover	0.005	.006	0.815	0.415	0.173
Predatory arthropods~ Abundance of cacao trees	0.002	0.005	0.443	0.657	0.108
Forest cover	-0.006	0.009	-0.747	0.455	-0.165
Abundance of insectivorous birds	-0.508	0.309	-1.642	0.101	-0.396
Herbivorous arthropods~ Abundance of insectivorous birds	0.246	0.279	0.880	0.379	0.179
Predatory arthropods	-0.543	0.217	-2.500	0.012	-0.508
Leaf damage~ Herbivorous arthropods	0.047	0.324	0.145	0.885	0.033
Forest cover	-0.020	0.014	-1.448	0.148	-0.326

Appendix S5. Models used for path analysis.

Table S1. Path models constructed using different combinations of variables (see Fig 3). Each model was composed of six variables and 18 observations (sites) nested in three regions

Model	Variables
1	FC, ANT, AIB, AP, AH, LD
2	FC, S, AIB, AP, AH, LD
3	FC, ACT, AIB, AP, AH, LD
4	FC, BA, AIB, AP, AH, LD
5	FC, EST, AIB, AP, AH, LD
6	FC, ANT, RIB, AP, AH, LD
7	FC, S, RIB, AP, AH, LD
8	FC, ACT, RIB, AP, AH, LD
9	FC, BA, RIB, AP, AH, LD
10	FC, EST, RIB, AP, AH, LD
11	FC, ANT, AB, AP, AH, LD
12	FC, S, AB, AP, AH, LD
13	FC, ACT, AB, AP, AH, LD
14	FC, BA, AB, AP, AH, LD
15	FC, EST, AB, AP, AH, LD
16	FC, ANT, RB, AP, AH, LD
17	FC, S, RB, AP, AH, LD
18	FC, ACT, RB, AP, AH, LD
19	FC, BA, RB, AP, AH, LD
20	FC, EST, RB, AP, AH, LD

*FC = forest cover; EST = first axis of the PCA to the data of vertical stratification; S= shading; BA = basal area; ANT = native tree abundance; ACT = cacao tree abundance; RB = bird species richness; AB = bird abundance; RIB = insectivorous bird richness; AIB = insectivorous bird abundance; AP = predatory arthropods abundance; AH = herbivorous arthropods abundance; LD = leaf damage.