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OCORRÊNCIA DE MAMÍFEROS EM AGROECOSSISTEMAS E EFEITO DE FATORES EM MULTIESCALAS NAS ASSEMBLEIAS EM PAISAGENS AGROFLORESTAIS

MAMMAL OCCURRENCE IN AGROECOSYSTEMS AND MULTI-SCALE FACTORS EFFECTS ON ASSEMBLAGES IN AGROFORESTRY LANDSCAPES

ILHÉUS – BAHIA
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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação da Biodiversidade.

Área de concentração: Ecologia e Conservação da Biodiversidade

Orientador: Dra. Camila Righetto Cassano

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Gratidão a todos!!!

Caminhos tão compridos pelas matas
Que cercam as fazendas de cacau
E na floresta, ouvem-se os micos
Os seus rostinhos mostram-se nas fotos.
E cai a noite, mas é bela a Lua
Iluminando estradas que parecem trilhas.

Pontes estreitas e compridas trilhas
A levam às câmeras nas matas
E vêem os olhos, sob a luz da Lua
A biodiversidade no cacau.
Eternizado seu registro pelas fotos
Tatus e pacas, e diversos micos.

Banana e sardinha para atrair os micos
E outros animais que andam pelas trilhas.
E longas horas tabulando as fotos
Lhe contam a história das matas
E a história da vida no cacau,
Iluminado pelo Sol e pela Lua.

Quando o Sol se põe e ergue-se a Lua
Aos seus esconderijos se retiram os micos
E se retiram os trabalhadores do cacau.
Mas outros seres andam pelas trilhas,
Silenciosas não estão as matas,
E estes seres mostram-se nas fotos.

De dia e de noite são tiradas as fotos,
Que não precisam nem da luz da Lua
Para mostrar quem vive nestas matas
E registrar os catitus e micos
E os quatis que andam pelas trilhas
E pelas folhas secas do cacau.

Cabrucas e seringas com cacau –
A sua vida mostra-se nas fotos.
Estradas esburacadas, que parecem trilhas
Ela percorre sob a luz da Lua.
Nas copas ouve-se o som dos micos
E correm raposinhas pelas matas.

Pés de cacau sob a luz da Lua –
Irão as fotos revelar os micos?
São longas trilhas, trilhas pelas matas.

Pavel Dodonov

RESUMO

Dada a grande perda de áreas nativas e crescente expansão agrícola em regiões tropicais, o futuro da biodiversidade irá depender cada vez mais de processos que afetam a viabilidade das espécies nas paisagens modificadas. Mamíferos têm importantes papéis ecossistêmicos, além de ser um grupo impactado pelas atividades humanas. O objetivo dessa tese foi investigar a ocorrência de mamíferos em matrizes agrícolas, enfatizando a resposta das assembleias de espécies a fatores atuantes em escala: local (tipo de habitat ou manejo), intermediária (heterogeneidade, cobertura florestal e densidade populacional humana no entorno) e ampla (cobertura florestal na paisagem) no Sul da Bahia, Brasil. No primeiro capítulo foi realizada uma revisão sistemática reportando o uso de agroecossistemas por carnívoros onde encontramos cerca de 40 % do total de espécies nativas em quatro tipos de sistemas agrícolas (agroflorestas, plantações florestais, perenes e anuais), nas regiões tropical e temperada. Tanto as características das espécies (massa corpórea, nível trófico e modo locomotor) quanto à qualidade do habitat predizem esse uso, embora o registro de espécies ameaçadas e predadores de topo tenham sido raros nessas matrizes. No segundo capítulo, investigamos como mamíferos de médio e grande porte respondem a fatores em diferentes escalas em paisagens cacaueiras. Nossos resultados mostram que as assembleias de mamíferos respondem aos efeitos do uso da terra nas escalas local, intermediária e ampla. As florestas e as agroflorestas de cacau apresentam alto valor de conservação para este grupo, desde que suficiente área de floresta seja mantida na paisagem ampla e que as plantações tenham um dossel diversificado. Além disso, a influência da densidade humana na estrutura das assembleias de mamíferos mostra a importância de se manter remanescentes florestais protegidos para garantir a viabilidade das espécies florestais na paisagem agrícola. No terceiro capítulo, nós investigamos como efeitos diretos (densidade de árvores nativas e estoque de carbono) e indiretos (invasão por cachorro) do manejo das agroflorestas de cacau afetam os mamíferos em paisagens com quantidade de floresta contrastantes. A quantidade de floresta na paisagem foi o principal fator a afetar a riqueza e abundância de espécies sensíveis à conversão de floresta em agroflorestas. Já a influencia do manejo agroflorestal diferiu entre as paisagens. Na paisagem dominada por floresta (Una), encontramos uma tendência ao aumento da riqueza de espécies sensíveis em agroflorestas sombreadas por maior número de nativas, enquanto na paisagem dominada por agroflorestas (Ilhéus), o aumento do estoque de carbono nas árvores de sombra foi um dos preditores da riqueza nesse grupo. Essa tese enfatiza a necessidade de conservar habitat nativo para manter espécies florestais e altamente impactadas por humanos em paisagens agrícolas. E reforça a ideia de que diferentes estratégias de manejo devem ser empregadas, considerando fatores em múltiplas escalas que afetam as assembleias de espécies. Preservar o habitat nativo é essencial para conservar espécies florestais, e as agroflorestas de cacau ampliam o valor de conservação da paisagem, promovendo conexão entre as manchas. Em paisagens dominadas por agroflorestas, é essencial que haja a restauração da floresta e que se evite a simplificação e intensificação das agroflorestas tradicionais para garantir seu papel como habitat e corredor para as espécies.

Palavras-chave: *Cabruca*. Mata Atântica. Manejo. Uso da terra. Paisagem.

ABSTRACT

Given the loss of native areas and the expansion of agriculture in tropical regions, the future of biodiversity will largely depend on the processes that affect the viability of species in modified landscapes. Mammals have important ecosystems roles, besides be a group so impacted by human activities. In this thesis, I sought to understand the occurrence of mammals in agricultural matrices, emphasizing the response of species assemblages to factors acting at different scales: local (habitat type or management), intermediates (heterogeneity, forest cover and human population density in surrounding areas) and large (forest cover in landscapes) in southern Bahia, Brazil. In the first chapter, a review was carried out reporting the use of agroecosystems by carnivores, where 40 % of total native species were found in four types of agricultural systems (agroforestry, tree plantations, perennial farmland and annual farmland) in temperate and tropical regions. Both species traits (body mass, energy trophic level and mode of locomotion) and habitat quality predict this use, although top predators and threatened species were rare in these matrices. In the second chapter, we investigated how medium to large mammals respond to factors at multiple scales in cacao' agroforestry landscapes. Our results show that mammal assemblages respond to land-use change at local, intermediate and large scales. Forest fragments and cacao agroforests show high conservation value for this group, provided that sufficiently large areas of old growth forests remain in the landscape and that the plantations have a diversified canopy. In addition, the effect of human density on mammal assemblage structure shows the importance of protected forest remainants to support forest-dwelling in agricultural landscapes. In the third chapter, we investigated how direct (native tree density and Carbon stock) and indirect (dog invasion) management of cacao agroforestry affect mammals in landscapes with contrasting amount of forest. The amount of forest in the landscape was the main factor predicting the richness and abundance of species sensitive to the conversion of forests into agroforests. Agroforestry management impacted mammals in different ways according to the landscape. In the landscape majorly covered by forest (Una), we found a tendency of greater richness of susceptible species in agroforests shaded by higher native trees density, while in the landscape dominated by cacao agroforests (Ilhéus) the increase in the carbon stock of shade trees predicted greater richness in this group. This thesis emphasizes the imperative need of native habitat to retain forest-dweling species, highly impacted by humans in agricultural landscapes. And reinforces the idea that different management strategies should be used taking into account factors in multi-scales that affect species assemblages. Native habitat is essential to ensure the permanence of forest-dwelling species, and the cacao agroforests increase the conservation value of the landscape, providing connection between patches. In landscapes dominated by cacao agroforests, it is essential to restore the forest and avoid simplification and intensification of traditional cacao agroforests, supporting its role as habitat and as a corridor for native species.

Keywords: Atlantic forest. *Cabruca*. Management. Land use. Landscape.

SUMÁRIO

1 INTRODUÇÃO

A perda de habitat e fragmentação são processos usualmente associados à redução de biodiversidade e degradação ecossistêmica (BETTS et al., 2017; HADDAD et al., 2015). Enquanto a perda de habitat esta associada à remoção de certa quantidade de habitat da paisagem, a fragmentação envolve modificação na configuração do habitat, o que pode ocasionar o aumento do número de manchas (vegetação nativa), a redução do tamanho das manchas e/ou o aumento do isolamento dessas (FAHRIG, 2003). O uso da terra para produção de alimentos, bens e outros serviços (projetos hidroelétricos, exploração de óleo, etc) tem sido identificado como principal causa da perda e fragmentação de florestas tropicais em todo o mundo (DONALD, 2004), transformando as paisagens tropicais em mosaicos onde os fragmentos florestais estão inseridos em matrizes (uso da terra dominante) (FISCHER; LINDENMAYER, 2007), como por exemplo, as plantações e pastagens (HENLE et al., 2004; PERFECTO; VANDERMEER, 2008).

Neste início de século, cerca de 40% da superfície terrestre do nosso planeta é utilizada para agricultura (RAMANKUTTY et al., 2008), e as áreas protegidas legalmente não são suficientes para garantir a conservação da biodiversidade global, abrangendo muitas vezes áreas remotas e não adequadas para atividades comerciais. Isto faz com que a conservação da biodiversidade dependa da manutenção de ecossistemas naturais com prioridade de conservação para os maiores fragmentos florestais, manutenção da conectividade entre os fragmentos menores e manejo da matriz (GARDNER et al., 2009; RIBEIRO et al., 2009), incluindo as áreas de produção agrícola e pecuária (FOLEY et al., 2011; MARGULES; PRESSEY, 2000).

Os efeitos da perda e fragmentação de habitat frequentemente têm focado nas mudanças nos padrões e processos no próprio habitat nativo, porém estudos têm mostrado a importância de entender como esses efeitos são moderados pelas características das matrizes a partir de amostragens realizadas também nesses ambientes modificados (FAHRIG, 2001; KUPFER; MALANDON; FRANKIN, 2006). A natureza da matriz têm implicações consideráveis para a a biodiversidade e deve ser considerada em práticas de manejo que visem a conservação da biodiversidade (FRANKLIN; LINDENMAYER, 2009; PRUGH et al., 2008). A matriz pode influenciar na dinâmica espacial das populações e espécies que ocorrem em paisagens fragmentadas através de efeitos associados com: 1) movimento e dispersão (de acordo com a qualidade da matriz); 2) disponibilidade de recurso (abrigo ou suplementação alimentar) e 3) condições ambientais (a matriz influência no microclima e no regime de distúrbios das manchas) (DRISCOLL et al., 2013). Sendo o contraste estrutural entre a mancha e a matriz importante para determinar muitas das funções das matrizes, como por exemplo, uso como habitat ou habitat alternativo, como fluxo (permitindo ou facilitando o movimento dos indivíduos, servindo como fonte ou dreno) ou até mesmo como barreira (KUPFER; MALANDON; FRANKIN, 2006). Além das características da matriz, a tolerância das espécies a esses ambientes modificados por humanos (i.e. características espécie-específicas) irá influenciar sua vulnerabilidade a perda de habitat e fragmentação (GASCON et al., 1999; HENLE et al., 2004).

A Mata Atlântica, distribuída originalmente na costa Atlântica brasileira, é uma das florestas tropicais mais ameaçadas globalmente (METZGER, 2009). Estima-se que no Brasil existem apenas 11,4% a 16% dos remanescentes de Mata Atlântica originais, sendo 83,4% desses fragmentos menores do que 50 ha e apenas 9% dos remanescentes florestais protegidos em unidades de conservação (RIBEIRO et al., 2009). A Mata Atlântica é reconhecida internacionalmente pelo alto número de espécies e de endemismo, com 2,7% (~300.000 espécies) do total de plantas e 2,1% (~27.298 espécies) do total de vertebrados do mundo (MYERS et al., 2000). Sendo a Bahia, a segunda sub-região de Mata Atlântica mais preservada, com 2.047.228 ha ou 17,7% da vegetação total remanescente (RIBEIRO et al., 2009), destacando-se ainda por ser um dos principais centros de endemismo do bioma (ARAUJO et al., 1998). Parte dessa vegetação florestal é composta por áreas de agroflorestas de cacau já que esses tipos de habitat não são diferenciados em imagens satélite de baixa resolução. No Sul da Bahia, aproximadamente 6000 km² de terra são compostas por cacau sombreado por árvore nativa, sistema agroflorestal regionalmente conhecido como *cabruca* (Figura 1, LANDAU; HIRSCH; MUSINKY, 2008).

As agroflorestas de cacau foram plantadas no Sul da Bahia em 1746 quando sementes de cacau trazidas do Pará substituiram o sub-bosque de florestas enquanto o raleamento (remoção) de árvores do dossel garantiu sombreamento “ideal” das árvores de cacau em sistemas tradicionais (CEPLAC, 2019). Em 1960, o governo Brasileiro através da CEPLAC (Comissão Executiva do Plano da Lavoura Cacaueira) instituiu um plano de intensificação da produção do cacau através da retirada e substituição das árvores de sombreamento. Apesar da busca por maior produção com menos sombra, essa técnica não foi aderida pelos produtores devido ao alto custo adicional de fertilizantes, inseticidas e herbicidas necessários em plantios intensificados (JOHNS, 1999). Em 1980, com o baixo preço do cacau e a introdução do fungo (*Moniliophthora perniciosa*) causador da “vassoura-de-bruxa”, muitas *cabrucas* foram substituídas por sistemas mais intensivos ou abandonadas. Porém ainda hoje, as *cabrucas* encontradas no Sul da Bahia abrigam alta diversidade florística e estrutural das ávores de sombreamento (SAMBUICHI et al., 2012). E a preservação das árvores de sombreamento nas agroflorestas de cacau contribuem para a manutenção de uma variedade de serviços ecossistêmicos como regulação climática e de pragas, polinização, fertilização do solo, disponibilidade de água e estoque de carbono (SCHROTH et al., 2016; VAAST; SOMARRIBA, 2014). Além disso, alguns estudos têm mostrado a importância das agroflorestas de cacau para a conservação da fauna no Sul da Bahia (CASSANO; BARLOW; PARDINI, 2012; CASSANO; KIERULFF; CHIARELLO, 2011; FARIA et al., 2007; RABOY et al., 2010), servindo muitas vezes como habitat alternativo e corredores ecológicos.

Figura 1 - Fotografia de um cacau sombreado (*cabrucas*) no município de Una no Sul da Bahia, Brasil.

Apesar da importância da manutenção das árvores de sombreamento nas agroflorestas de cacau, as árvores nativas têm sido substituídas por espécies em estágio sucessional inicial ou por exóticas com o objetivo de aumentar a produção (SAMBUICHI, 2006; SAMBUICHI; HARIDASAN, 2007). Além disso, de acordo ao decreto estadual n° 15.180/ 2014 e a portaria conjunta SEMA/INEMA n° 03/2017, o manejo das *cabrucas* diante autorização pode ocorrer visando "a produtividade do cacau, a conservação e o uso sustentável do agroecossistema", sendo o raleamento permitido em *cabrucas* com mais de 40 indivíduos de espécies nativas por hectare. A remoção de árvores tem comprometido a conservação da fauna em sistemas agroflorestais (BOS; STEFFAN-DEWENTER; TSCHARNTKE, 2007; CLOUGH et al., 2009; STENCHLY et al., 2011), porém faltam estudos que investiguem esse impacto sob uma maior diversidade de grupos biológicos.

Estudos desenvolvidos em agroflorestas indicam que tanto o manejo local quanto a estrutura da paisagem podem afetar as espécies associadas aos plantios (FISCHER; THIES; TSCHARNTKE, 2011; SCHMIDT et al., 2005). No que se referem à paisagem, os estudos mostraram tanto a importância da cobertura vegetal no entorno imediato das plantações (FISCHER et al., 2011), quanto à influência da cobertura florestal na paisagem ampla (FARIA et al., 2007) para a manutenção da diversidade de fauna. Porém, faltam pesquisas que avaliem a influência desses fatores em várias escalas, principalmente em mosaicos agroflorestais tropicais (para alguns exemplos ver CASSANO; BARLOW; PARDINI, 2014, CLOUGH et al., 2009).

A classe Mammalia abrange 6495 espécies globalmente (BURGIN et al., 2018) das quais 701 ocorrem no Brasil (PAGLIA et al., 2012). Mamíferos de médio e grande porte têm importantes papéis ecossistêmicos, atuando na dispersão e predação de sementes (TERBORGH et al., 2008; WRIGHT, 2003), controle populacional de presas e herbivoria (TERBORGH et al., 2001). Contudo, espécies de mamíferos em declínio têm perdido mais que 50% das suas populações segundo a IUCN (International Union for Conservation of Nature), principalmente onde as atividades humanas são intensivas (CEBALLOS; EHRLICH, 2002). Perda e fragmentação de habitat, caça, conflitos com humanos e transmissão de doenças oriundas de animais domésticos como cachorros são alguns fatores que impactam esse grupo em paisagens antrópicas (CHIARELLO, 2000; CROOKS, 2002; CULLEN JR.; BODMER; VALLADARES PÁDUA, 2000; FRIGERI; CASSANO; PARDINI, 2014; LESSA et al., 2017; WOODROFFE, 2000). Visto que as áreas protegidas não são suficientes para conservar populações viáveis de todas as espécies e estudos têm mostrado que a composição e diversidade dos mamíferos variam entre os usos da terra (DAILY et al., 2003; RAMÍREZ; SIMONETTI, 2011; HARVEY; GONZALEZ; SOMARRIBA, 2006; CAUDILL; DECLERCK; HUSBAND, 2015), é crucial entender como os mamíferos usam os agroecossistemas para que estratégias efetivas de conservação sejam criadas e implantadas. Dentro desse grupo, investigar a ocorrência de grandes carnívoros (ordem Carnivora) em matrizes agrícolas é crucial visto que são espécies sensíveis às atividades humanas que geralmente estão envolvidas em conflitos com humanos mundialmente (WOODROFFE, 2000).

Entender o papel da matriz é essencial para predizer a persistência das espécies em paisagens agrícolas (DEVICTOR; JIGUET, 2007). Sabe-se que em paisagens fragmentadas, o tipo, a quantidade e configuração da matriz frequentemente influenciam os padrões de distribuição de diferentes grupos taxonômicos (LINDENMAYER et al., 2001; PRUGH et al., 2008; UMETSU; PAUL METZGER; PARDINI, 2008). Por isso entender mais sobre como diferentes sistemas agrícolas, incluindo as agroflorestas de cacau, influenciam a distribuição dos mamíferos é essencial para conservar essas espécies e criar estratégias que evitem o impacto humano sob essas. Além disso, os processos ecológicos que determinam as espécies presentes em um dado local ocorrem em diferentes escalas (local, intermediária e ampla), portanto análises considerando diferentes escalas são de vital importância para o entendimento de padrões de distribuição de espécies (GRAF et al., 2005) e de fenômenos locais, que não podem ser totalmente compreendidos sem considerar a influência das características da paisagem (MAZEROLLE; VILLARD, 1999).

Esta tese é composta por três capítulos e tem como objetivo investigar a ocorrência de mamíferos em matrizes agrícolas e entender como fatores em multi-escalas podem afetar a distribuição desse grupo em paisagens modificadas. Consideramos ao longo da tese o termo “uso de agroecossistema” quando os indíviduos ocorreram temporalmente ou permanentemente, utilizaram esse sistema como passagem para atingir habitat nativo e/ou outro agroecossistema, e/ou utilizaram recursos alimentares (inclusive consumo de culturas comerciais) presentes nas plantações (ESTRADA; RABOY; OLIVEIRA, 2012). No primeiro capítulo dessa tese os objetivos foram: (1) avaliar como mamíferos da ordem Carnivora, cujas populações têm declinado globalmente (RIPPLE et al., 2014), usam sistemas agrícolas e (2) analisar se os traços biológicos das espécies, o estado de conservação e ou o tipo do agroecossistema predizem a ocorrência de espécies nessas matrizes. Além de investigar a ocorrência de conflitos entre carnívoros e humanos em sistemas agrícolas e identificar lacunas de conhecimento acerca do uso de agroecossistemas por este grupo animal. Já no segundo e terceiro capítulo buscamos entender mais sobre a ocorrência de mamíferos em paisagens compostas por agroflorestas de cacau (Figura 2) no Sul da Bahia, Brasil. Para isso, investigamos a influencia de fatores em escala local (tipo de habitat e manejo das agroflorestas de cacau), intermediária (heterogeneidade, cobertura florestal e densidade populacional humana no entorno) e ampla (cobertura florestal na paisagem) nas assembleias de mamíferos de médio e grande porte.

Figura 2 - Mamíferos registrados em armadilhas fotográficas em *cabrucas* situadas em Una e Ilhéus, Brasil. A) *Dasyprocta leporina* (cutia), B) *Puma concolor* (onça-parda), C) *Puma yagouaroundi* (gato-mourisco), D) *Nasua nasua* (quati), E) *Cuniculus paca* (paca), F) *Leontopithecus chrysomelas* (mico-leão-da-cara-dourada).

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2. USE OF AGROECOSYSTEM MATRIX HABITATS BY MAMMALIAN CARNIVORES (CARNIVORA): A GLOBAL-SCALE ANALYSIS

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ABSTRACT

1. Less than a quarter of Earth's terrestrial ecosystems remain intact. Protected areas (PAs) are far exceeded in area by natural habitats that have been transformed for agriculture, and PAs are too small to safeguard viable wildlife populations. It is therefore imperative to understand the use of agricultural matrix habitats by native wildlife.

2. In this study we seek to understand how the world's mammalian carnivore species (order Carnivora) use agricultural land. We assessed relationships between agroecosystem type, carnivore species traits and conservation status, and carnivore occurrence at agricultural sites, investigated the prevalent human-carnivore conflicts in anthropogenic landscapes, and identified knowledge gaps.

3. We reviewed 129 studies reporting agroecosystem use by native carnivores to understand which agroecosystem types are used by different species, and which factors may affect their occurrence in these habitats.

4. We uncovered records of 97 wild and two domesticated carnivore species within 41 types of crop in temperate and tropical regions that we classified into four agroecosystem types (agroforestry, tree plantations, perennial cropland and annual cropland).

5. Non-threatened carnivore species were more likely to use agricultural ecosystems than threatened species. Adult body mass, energetic trophic level and locomotion mode were significant predictors of carnivore occupancy in agricultural lands.

6. Our results depict a globally consistent pattern, in which the use of agroecosystem landscapes by mammalian carnivores is related to both species traits and habitat quality. We emphasise the rarity of threatened carnivore and apex predator species in agroecosystems, which strengthens the paramount importance of retaining native habitat within agricultural landscapes. Understanding the role of agricultural habitat matrices, the influence of management intensification, and the threshold areas of native habitats within anthropogenic landscapes are essential for prescribing ways to prevent further erosion of the world's carnivores in human-modified landscapes.

Keywords: agriculture, Carnivora, land use, species traits, structural complexity

Running head: Global use of agroecosystems by carnivores

2.1 INTRODUCTION

By 2016, only 23% (≈ 30.1 million km^2) of the world's terrestrial ecosystems could be defined as intact landscapes; most other areas had already been modified by humans (Watson et al. 2016). Between 2000 and 2012, ca. 2.3 million km^2 of forest were lost globally (Hansen et al. 2013), and meeting the growing global demand for food will hinge on further natural habitat conversion into agricultural land, which is required to be at least 18% larger by 2050 than it was less than two decades ago (Tilman et al. 2001). The global effort to protect biodiversity has been largely based on protected areas (PAs), often established in regions containing a large number of endemic and threatened species (Rodrigues et al. 2004, Loucks et al. 2008). Although PAs have clearly increased worldwide over the last decades (Jenkins & Joppa 2009), they continue to be insufficient in representing regional biodiversity in all biogeographic realms (Brooks et al. 2004, Chape et al. 2005). Furthermore, most PAs are becoming increasingly isolated and surrounded by expanding areas of croplands, pastures, exotic tree plantations, and urban settlements, accompanied by burgeoning food, energy, freshwater, and fertiliser demand (Foley et al. 2005).

Given this relentless worldwide habitat conversion, almost all terrestrial regions have become dominated by landscapes where original vegetation patches are immersed within a matrix of human-modified environments (Perfecto & Vandermeer 2008). Native biotas within the remaining habitat patches then become strongly influenced by the dynamics, heterogeneity and ecological processes exerted by the dominant surrounding matrix (Kupfer et al. 2006, Driscoll et al. 2013). However, the human-modified matrix is usually not completely hostile (Tscharntke et al. 2012) and can often support resources used by native wildlife, allowing occupancy of different habitats through landscape complementation or supplementation (Dunning et al. 1992). Matrix structure and configuration often influence occupancy patterns for many taxonomic groups and ecosystems in fragmented landscapes (Lindenmayer et al. 2001, Prugh et al. 2008, Umetsu et al. 2008). While some land uses enable animal movements, others can act as complete barriers (Prevedello & Vieira 2010), so that the spillover of organisms from natural habitats to adjacent agroecosystems depends on both the matrix habitat structure and dispersal ranges (Ewers & Didham 2005, Tscharntke et al. 2012). The matrix often acts as a selective filter, and species' tolerance to human-modified environments will define their vulnerability to native habitat loss and fragmentation (Gascon et al. 1999, Henle et al. 2004).

Several studies have shown that faunal composition and diversity vary widely across most gradients of different anthropogenic land uses. Some agroecosystems, such as pasturelands, intensive cereal cropping and other annual monocultures, are highly simplified, whereas polycultural and agroforestry systems are more structurally complex, thereby supporting higher levels of biodiversity (Moguel & Toledo 1999, Tews et al. 2004). While forest habitats retain higher biodiversity than any monoculture plantation, multifunctional agroforestry systems consistently maintain intermediate levels of biodiversity (Mcneely 2004, Harvey et al. 2006, Felton et al. 2010, Ramírez & Simonetti 2011).

Designing effective strategies to conserve native species in human-modified landscapes requires an understanding of how wildlife species use agroecosystems. Matrix habitat effects have a species-specific component (Prevedello & Vieira 2010), and species traits such as trophic level, dispersal ability and degree of habitat specialisation influence their responses to fragmentation and the intervening matrix (Ewers & Didham 2005). Several biological traits have been proposed to predict the effects of fragmentation and extinction risk (Purvis et al. 2000, Cardillo et al. 2004, Kosydar et al. 2014, Pfeifer et al. 2017). Mammalian carnivore species (order Carnivora) vary widely in their sensitivity to habitat loss, degradation and fragmentation (Crooks 2002), but most wild carnivores have experienced marked population declines worldwide (Ripple et al. 2014). Biological traits such as large body size, high trophic status, low population density, and low population growth rate render these species vulnerable to native habitat conversion and degradation (Purvis et al. 2000, Cardillo et al. 2004). Carnivores often require large areas of suitable habitat due to their large home ranges (Carbone et al. 2005), and are vulnerable to high mortality in areas densely settled by humans (Woodroffe 2000). However, they can often use agroecosystems as either corridors (Beier 1993, Crooks 2002) or supplementary habitats in fragmented landscapes. Carnivores often exert strong roles in structuring ecosystems (Miller et al. 2001). For instance, they are important agents of top-down regulation via numerical or behavioural control of prey populations at several lower trophic levels (Ripple & Beschta 2012, Suraci et al. 2016); they influence plant recruitment and shape plant communities through seed dispersal and predation (Roemer et al. 2009); and they facilitate nutrient flows between adjacent ecosystems (Roemer et al. 2009, López-Bao et al. 2015). Since most PAs are not large enough to secure viable carnivore populations, and as future land-use change may further reduce native habitat availability, understanding how carnivore species use matrix environments is crucial for the prevention of further local extinctions worldwide (Di Minin et al. 2016).

We seek to understand how extant mammal species in the order Carnivora use agricultural lands in both tropical and temperate regions. We reviewed the existing literature reporting mammalian carnivores using agroecosystems, in order to summarise the evidence of the extent to which these habitats may be able to support different carnivore populations. We further synthesise the available information to guide conservation management of this iconic group of vertebrate species within agricultural landscapes. More specifically, we (1) classified all studies according to study categories (human-carnivore conflicts, diet and habitat use) and assessed the number of studies conducted over time and their main focal regions; (2) examined the degree to which morpho-ecological traits (body mass, energetic trophic level and locomotion mode) and conservation status were related to the use of agricultural lands by carnivore species; (3) compared the use of different agroecosystem types around the world by carnivores; (4) assessed relationships between agroecosystem type, conservation status and species traits and the occurrence of carnivores at agricultural sites; (5) documented human-carnivore conflicts in agroecosystems; and (6) identified knowledge gaps.

2.2 METHODS

Bibliographic search

We performed a systematic search for published papers and unpublished dissertations and reports prior to December 2017 on the use of agroecosystems by terrestrial carnivores (class Mammalia, order Carnivora). We reviewed articles within three databases of peer-reviewed literature: — ISI Web of Knowledge (www.isiwebofknowledge.com), SCOPUS (www.scopus.com) and Google Scholar (https://scholar.google.com.br/) — using the terms (in full paper, paper title, abstract, and keywords): [("mammal*" OR "carnivor*" AND "plantation" OR "monoculture" OR “agroecosystem” OR “agroforest*” OR “cocoa” OR “coffee” OR “*Eucalyptus*” OR “*Pinus*” OR “oil palm” OR “rubber”)]. We gathered papers from all years. In addition, we included undergraduate and postgraduate dissertations and theses, and conference abstracts detected by using the same terms in Google Scholar, OATD (https://oatd.org/) and Openthesis (http://www.openthesis.org/), as well as all studies that we already knew. We conducted an additional search in Google Scholar using the keywords in Portuguese and Spanish. We ensured that our data compilation effort was broadly cast, thereby encompassing all community-wide studies of mammals, rather than those studies that were strictly focused on carnivores.

We define use of agroecosystems by carnivores according to Estrada et al. (2012), as following: “(i) either temporary or permanent residency or use as passageways to reach native habitat and/or other agroecosystems, and/or (ii) use of agroecosystems as sources of food (including potential consumption of commercial crops)”. Papers obtained in our search were excluded if: (1) the species that had been recorded in any given agroecosystem or the type of agroecosystem was not specified; and (2) the paper was not based on primary empirical observational or experimental research (for example, the paper presented a simulation model). Our focus in our review was to understand the way in which carnivores use croplands, including monoculture and polyculture plantations, rather than pastoral systems associated with livestock husbandry. We did not include papers describing the use of anthropogenic pasturelands by carnivores, as there are peculiarities regarding the occurrence of carnivores in these systems, namely human-wildlife conflicts associated with livestock depredation, which could be addressed in another review. Once we applied all data filters, we retained a total of 107 published and 22 unpublished studies.

Data compilation

We placed each study in one or more study categories, depending on whether they reported human-carnivore conflicts (e.g. crop damage, crop raiding, livestock depredation, and injury to humans), diet (or feeding ecology), and/or habitat use (e.g. habitat occurrence, abundance, dispersal, habitat selection, and home range use). We recorded the geographic locality (longitude, latitude), species checklist, year of publication, and agroecosystem type considered in each study. We classified all agroecosystems according to their structural complexity, considering the vertical stratification of vegetation and crop longevity, both of which were combined into a ranked multistate degree reflecting human disturbance: (1) agroforestry (AF), including tree and shrub crops shaded by native or exotic tree species; (2) tree plantations (TP), including arborescent plantations allocated to the production of wood, pulp and other timber products; (3) perennial cropland (PC), including perennial monocultures; and (4) annual cropland (AC), including monoculture or polyculture of crops lasting over a single or a few harvests within a year (Appendix S1).

We identified all carnivore species that could potentially occur at each study site reported in studies, using the species' range polygons available at the International Union for Conservation (IUCN) spatial dataset (http://www.iucnredlist.org/technicaldocuments/spatial-data#mammals). Based on the geographic coordinates of each site, expressed as a decimal degree projection (Datum WGS 84), we performed the extraction of data points within the range of each species using a code within the R platform (R Core Team 2017), aided by the software packages *maptools* (Bivand & Lewin-Koh 2013), *maps* (Becker & Wilks 2013) and *splancs* (Rowlingson & Diggle 2017). We are aware that proposed IUCN range maps are based on limited knowledge and, therefore, the occupancy of sites by carnivores could be greatly overestimated, consequently lending support to the notion that more carnivore species are recorded at any given species pool than in reality. However, these spatial data are amply accepted and have been widely used by vertebrate conservation ecologists, particularly in global-scale studies. We obtained from literature databases (e.g. Paglia et al. 2012, Wilman et al. 2014, EOL 2016, IUCN 2017), the body mass, main dietary mode, locomotion mode, and IUCN Red List category (hereafter referred to as conservation status) for each carnivore species that potentially occurred at each site, including species that were detected and not detected within each study. We calculated the mean energetic trophic level for each species, generated as a weighted mean of the energetic level of a species' diet given the proportion of dietary items compiled by Wilman et al. (2014). The energetic levels considered here for each dietary category were assigned an ordinal sequence as follows: folivores: foliage = 1.0; frugivores: fruit pulp and nectar = 2.0; granivores: seeds = 3.0; insectivores/faunivores: invertebrates = 4.0; and carnivores: vertebrates = 5.0 (Bueno et al. 2018). We classed all carnivore species potentially occurring at each study site as either observed (present) =1, or not detected (absent), but likely to be sympatric within the overall landscape of each study = 0. In terms of conservation status, we followed the IUCN Red List (IUCN 2017) and the corresponding multiscale ranked values used by Purvis et al. (2000): Least Concern = 0, Near Threatened = 1, Vulnerable = 2, Endangered = 3, Critically Endangered = 4, and Regionally Extinct or Globally Extinct = 5. In terms of broad locomotion modes, we assigned the following mutually exclusive ranks, from most to least terrestrial, based on all available natural history information on all species: terrestrial/cursorial = 1, scansorial = 2, semi-aquatic = 3 (but this applied to only 3 of all 97species in our database), or arboreal = 4. We adopted higher values for arboreal and semi-aquatic species, assuming that species requiring greater complexity in habitat structure would be more vulnerable to habitat change.

Data analysis

We used descriptive statistics to express the prevalent species traits of all mammalian carnivores using the different types of agroecosystems worldwide, and statistically tested the effect of agroecosystem type, species trait (body mass ($\log_{10}$ x), energetic trophic level, and locomotion mode) and conservation status on the use of agricultural land by carnivores. In this analysis, we only included wild native carnivore species (thereby excluding feral, domesticated and introduced species) and those studies that strictly documented patterns of habitat occupancy across the entire local assemblage (in terms of either carnivores or mammals).

We modelled the presence/absence probability of all species at 75 sites (Appendix S2) with binomial generalised linear mixed-effect models (GLMM), using different species traits, species conservation status, and agroecosystem type as fixed factors and the study site as a random factor to control for any variation in sampling artefacts across studies. Species traits are inherently dependent on phylogeny, and treating species as independent data points in comparative analyses may increase the risk of bias and Type I errors (Felsenstein 1985). Therefore, we replicated the full model with family taxonomic identity included as a random variable, and compared the Akaike’s Information Criterion value with each respective model lacking this additional (infraorder) taxonomic information, using a chi-square test (Burnham & Anderson 2002). We used a Z test to assess the influence of the species and site variables on the use of any given agroecosystem by carnivores, using p-values generated by the full model (Zuur et al. 2009). We implemented all GLMMs using the *glmer* function in the *lme4* package (Bates et al. 2015) within the R platform version 3.3.2 (R Core Team 2017).

We performed a rarefaction curve analysis with 95% confidence intervals (Legendre & Legendre 1998, Colwell et al. 2002) based on the number of species that were either present or expected (nesting present-absent) within each of the four agroecosystem types, amounting to eight replicas. Rarefaction curves were performed using 1000 random subsampling iterations on the basis of the *rarefy* function within the *vegan* R package (Oksanen et al. 2013). Species richness (observed [present] and expected [present + absent]) was then compared based on the minimum number of individuals in the subsamples of each agroecosystem type.

2.3 RESULTS

Focus of publications

The 129 studies we included were carried out in 32 countries distributed in South America (38%), Asia (30%), Europe (10%), North America (10%), Central America (6.5%), Africa, including Madagascar (4.5%) and Oceania (1.5%), and were mainly focussed on tropical and temperate forest biomes (Fig. 1). Most studies (87%) described habitat use by different carnivore species, whereas only 9.4% reported on diet or human-wildlife conflicts involving carnivores in agroecosystems. Only 3.8% of those sources addressed more than one agroecosystem type. Most studies reporting the use of agroecosystems by carnivores were carried out in the Americas, followed by Asia, Europe, Africa and Oceania, and the same was observed for numbers of species. Brazil, the largest tropical country, contained the largest number of studies (27%) and 21% of carnivore species were reported to be using agroecosystems, followed by Malaysia (7%) with the same percentage of species using agroecosystems. In terms of agroecosystem type, almost half of all studies (46%) were conducted in tree plantations, 22% in perennial croplands, 17% in annual croplands, and 15% in agroforestry. There was a general pattern in which a growing number of carnivore studies over time reported agroecosystem use by carnivores, mainly in the last two decades; over half of all studies were published since 2010.

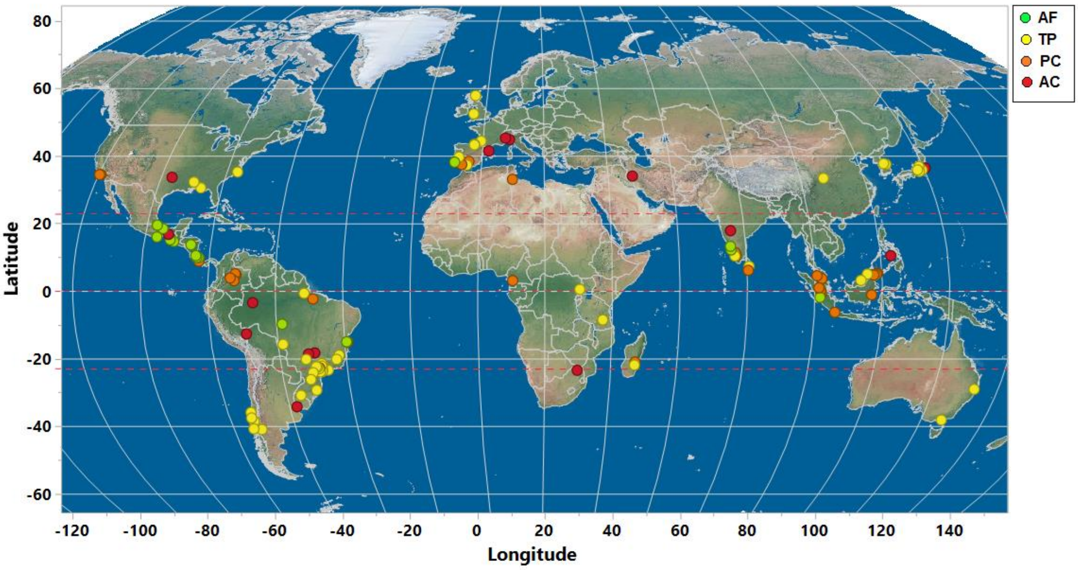

Fig. 1. Word map showing the localities where studies have been conducted and the type of agroecosystem used by carnivores, as described in each of the 129 research papers.

Agroecosystem use by carnivores

Carnivores are able to use all agroecosystem types (Appendix S1) in all temperate and tropical regions. A total of 97 carnivore species (approximately 40% of all extant terrestrial wild carnivore mammals) and two domesticated species (*Canis lupus familiaris* and *Felis catus*) were reported within 41 types of crop (Appendix S3). Of the 12 families of terrestrial carnivores, only ailurids and hyaenids were not detected in agroecosystems, whereas felids, canids and mustelids were the most frequently reported families in these systems. Representatives of almost all families of Carnivora were detected within the four types of agroecosystem. Prionodontids and euplerids were only represented in perennial croplands and tree plantations, respectively, and few families were recorded in annual croplands (Fig. 2).

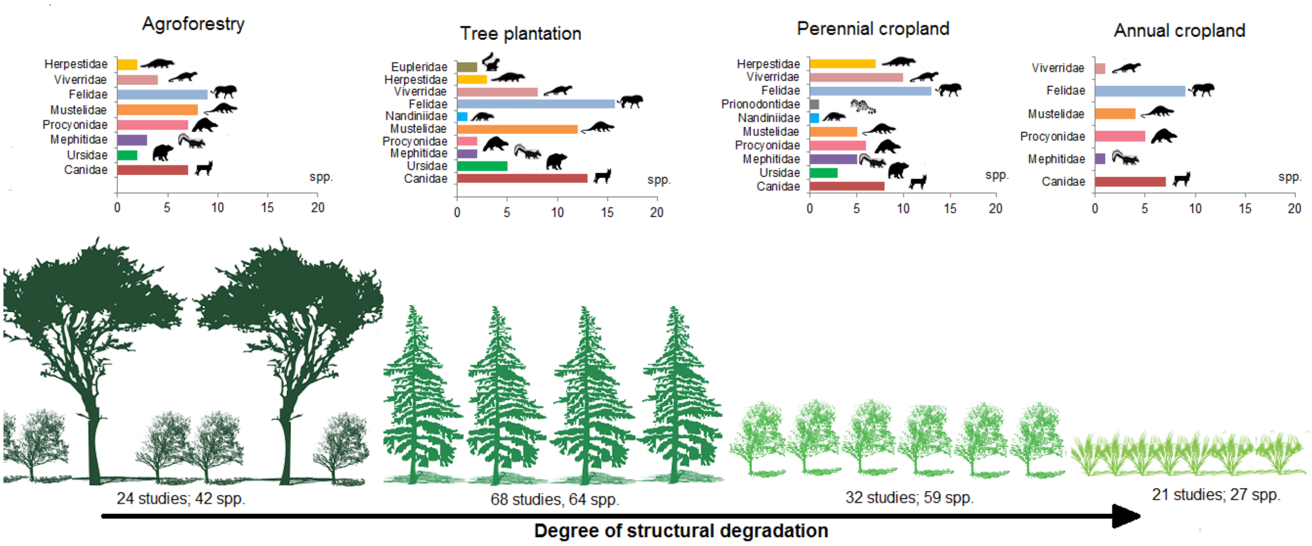

Fig. 2. Numbers of carnivore species in each family that were reported in the 129 papers we reviewed to be using the four different types of agroecosystem: agroforestry systems (AF); tree plantations (TP); perennial cropland (PC); and annual plantation (AC).

Tree plantations were associated with the highest number of species recorded (65), followed by perennial croplands (59), agroforestry patches (42) and annual croplands (28). The agricultural habitats most frequently reported as being used by carnivores were eucalyptus (25% of studies), pine (16%) and oil palm plantations (12%), with 35, 31 and 31 carnivore species, respectively (Appendix S1). Fast-growing tree plantations, particularly eucalyptus and pine, were used by many carnivore species as part of their daily home ranges or as habitat corridors linking forest patches. Some researchers pointed out that most species preferred intermediate-aged tree plantations with a well-developed understorey, rather than the final pre-cutting stage of commercial stands, where the understorey and ground vegetation had been removed by mechanised operations, herbicides, or both (Oliveira 2002, Chamberlain et al. 2003, Silveira 2005, Timo et al. 2015). Among agroforestry studies, ‘biodiversity-friendly’ land use allocated to cash crops, such as shade-coffee and shade-cacao, were the most commonly used systems (8.5% and 5.4% of all studies), thereby sustaining a higher diversity of carnivores (29 and 16 species, respectively), mainly in the Neotropics.

Perennial croplands harboured some carnivore species, and there was a particular emphasis on oil palm plantations (16 studies; 31 species), which served as transient foraging and suitable day-bed sites, or facilitated dispersal connectivity between neighbouring native habitat patches (Normua et al. 2004, Rajaratnam et al. 2007, Jennings et al. 2010, Gamage et al. 2011, Nakashima et al. 2013, Azhar et al. 2014, Jennings et al. 2015, Yue et al. 2015). In contrast, annual croplands apparently provided largely unsuitable habitat for most carnivore taxa; only sugar-cane and rice fields were used by high number of carnivores (12 and 9 species, respectively).

Conservation status and life history traits of carnivores in agroecosystems

In terms of ranked conservation status, we found that Least Concern carnivores were most likely to use agricultural matrices. Among all 249 species of terrestrial carnivores that have been assessed worldwide, 58% are classified as Least Concern (IUCN 2017), half of which (28% of the total) were observed using agricultural lands. In contrast, of the 25% of 249 carnivore species that are listed as threatened (Critically Endangered, Endangered, or Vulnerable) in the IUCN Red List, only 7% were recorded using agroecosystems. All four types of agroecosystems were dominated by species listed as Least Concern (>65%), whereas fewer than 7% were listed as Endangered; these were virtually absent from any annual cropland regardless of landscape context (Fig. 3a).

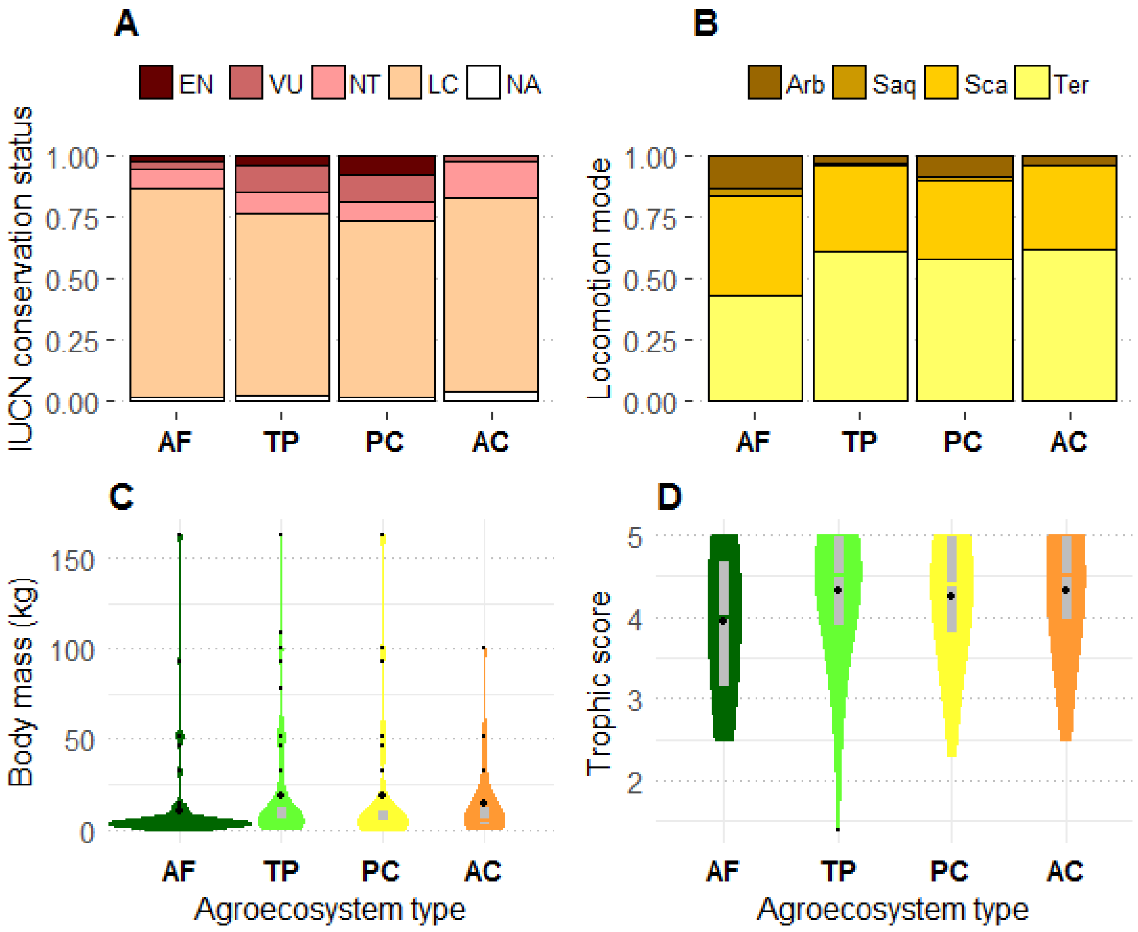

Fig. 3. Proportion of carnivores (Carnivora, Mammalia; excluding marine species) by conservation status (A; IUCN Red List) and locomotion mode (B), and distributions of carnivore body mass (C) and energetic trophic score (D) recorded in different types of agroecosystens: agroforestry (AF), tree plantations (TP) perennial cropland (PC), and annual cropland (AC), as described in the 129 papers we reviewed. IUCN Red List categories in A are: Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Not Evaluated (NA = domestic species). Locomotion modes in B are arboreal (Arb), semi-aquatic (Saq), scansorial (Sca), and terrestrial (Ter). In figures C and D, the coloured areas represent a Kernel density plot, the grey blocks represent the box plot median and quartiles, the large black dots represent the mean and the small black dots represent outliers. Energetic trophic guild scores in D are based on the sum of the proportion of each food item multiplied by its energy score: 1.0 (folivores: foliage), 2.0 (frugivores: fruit pulp and nectar), 3.0 (granivores: seeds), 4.0 (insectivore/faunivores: invertebrates), and 5.0 (carnivores: vertebrates).

The most common locomotion modes of carnivores (99 species) using agroecosystems were terrestrial (54%) and scansorial (33%). In contrast, few arboreal species (10%) were found using agricultural matrices, and those were most frequently recorded in perennial croplands and agroforestry (Fig. 3b). Only three semi-aquatic species (3%) used agricultural lands: *Aonyx cinereus* in coconut, tea and shade-coffee plantations; *Lutra lutra* in cork-oak agroforestry; and *Lontra longicaudis* in shade-banana, shade-cacao and *Pinus* plantations.

Carnivores detected in cultivated lands ranged widely in adult body mass, from a small mustelid (*Mustela frenata*, ~0.15 kg) to a large felid (*Panthera tigris*, >150 kg). However, 87% of all species were intermediate in size (body mass range = 1 - 15 kg). Only 13 species were smaller than 1 kg, and another 14 species were larger than 15 kg. Large (>50 kg) species were found primarily in tree plantations and perennial croplands (Fig. 3c).

Considering the different trophic guilds, most carnivore species using agroecosystems were generalist consumers feeding on different plant parts, invertebrates and vertebrates. Only one species, which was observed using a tree plantation, is a strict folivore with 90% of its diet based on foliage (giant panda, *Ailuropoda melanoleuca*: energetic score of 1.4). Some 50% or more of all carnivore species recorded in perennial and annual croplands and tree plantations had a high energetic trophic level (energetic scores >4.5; >90% of diets based on vertebrate prey; Fig. 3d). In contrast, species recorded within agroforestry patches were highly variable in terms of their energetic scores, and included considerable numbers of arboreal and scansorial frugivorous species (range of energetic scores = 2.5 - 2.7; >60% of diet consisting of fruit).

Predictors of the use of agroecosystems by carnivores

The full GLMM models with and without family-level taxonomic identity provided similar results [$\chi^2 = 1.24$; p = 0.27], thereby indicating that our models were unbiased in relation to phylogenetic contrasts across the species data (Appendix S4). We therefore examined which factors were most important in explaining globally reported use of agroecosystems by carnivores on the basis of sites as the only random factor. Both species traits and conservation status were significant predictors of use of agricultural lands by carnivores (Appendix S5). However, agroecosystem type was relatively unimportant in determining the overall use by all species [Z = –0.60; p > 0.1].

Of all 133 carnivore species expected to occur across all 75 sites in our database, only 87 species (65%) were actually reported using agroecosystems, and only 15% of all sites were used by more than 10 species. The percentage of all species that were either observed or expected to use the agricultural matrix differed across agroecosystem types. On the basis of rarefaction curves and their respective confidence intervals, there was a significant difference between the observed species richness (reported presences) and the expected species richness (including absent species) within tree plantation [$S_{obs} = 50$; $S_{exp} = 69.9$ (±3.8); $p < 0.05$] and perennial cropland samples [$S_{obs} = 55$; $S_{exp} = 64.0$ (±3.2); $p < 0.05$]. There were also no statistical differences between observed and expected species richness for agroforestry [$S_{obs} = 39$; $S_{exp} = 41.1$ (±2.8); $p > 0.05$] and annual cropland samples [$S_{obs} = 18$; $S_{exp} = 22$ (±2.7); $p > 0.05$] (Appendix S5). However, we observed that the mean percentage of species detected in annual cropland sites was 32% and the expected species richness was always higher than the observed species richness at those sites.

Species recorded within agroecosystems were heavily concentrated at the lowest-ranking conservation status (Least Concern) ($Z = –6.01$, $p < 0.001$; Fig.4a). Species recorded using agroecosystems were disproportionately terrestrial (or strictly terrestrial) (Fig.4b), indicating that arboreal and semi-aquatic species avoided these systems ($Z = –4.15$, $p < 0.01$). Habitat use was also significantly related to adult body mass ($Z = 4.98$, $p < 0.001$) and trophic guild ($Z = –5.59$, $p < 0.001$), showing a consistent tendency within any given local carnivore assemblage for the largest species and consumers at lower trophic levels (Fig. 4d) to use the agricultural matrix (Fig. 4c; Appendix S6).

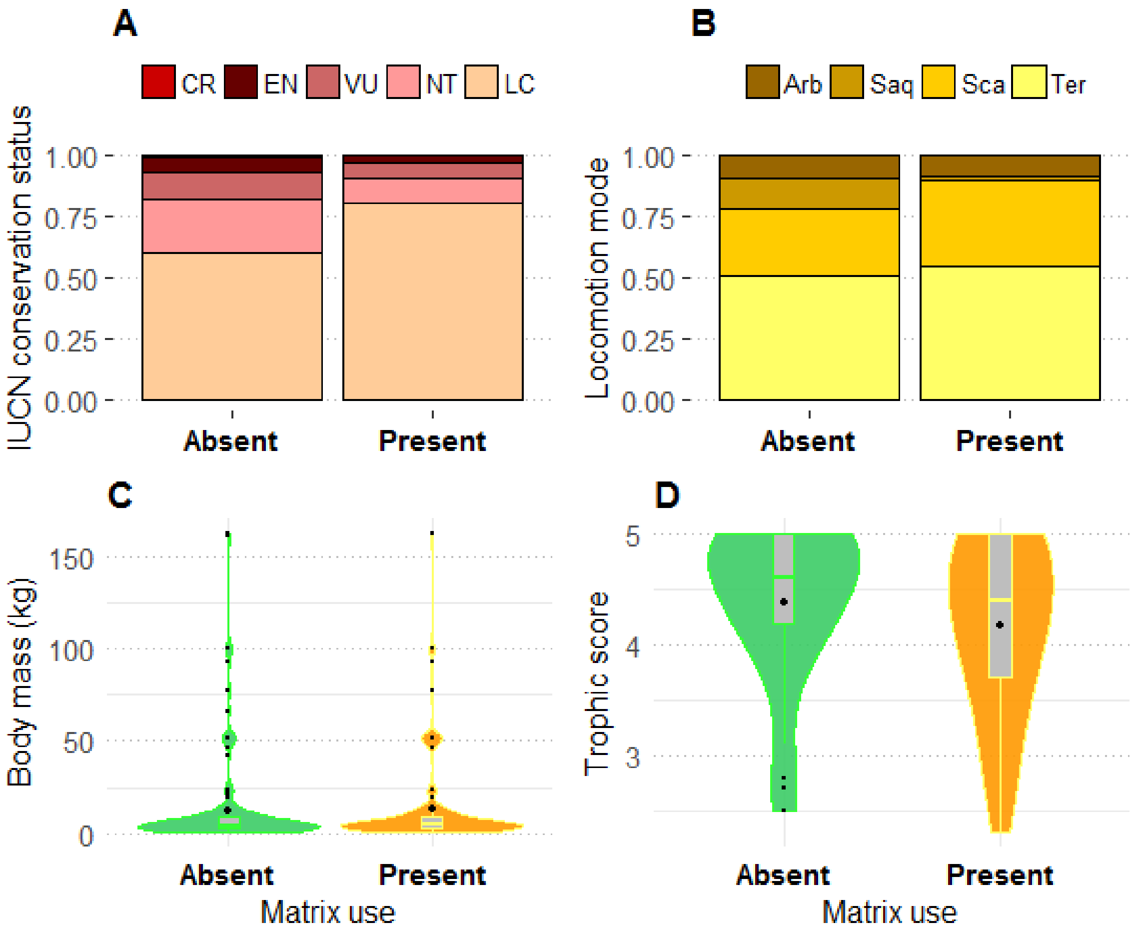

Fig. 4. Conservation status (IUCN Red List; A), locomotion mode (B), carnivore body mass (C) and energetic trophic score (D) for all wild carnivore species that potentially occurred at each of the 75 study sites, including species that were detected (present) and not detected (absent) in the four agroecosystems. IUCN Red List categories in A are: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT) and Least Concern (LC). Locomotion modes in B are arboreal (Arb), semi-aquatic (Saq), scansorial (Sca), and terrestrial (Ter). In figures C and D, the coloured areas represent a Kernel density plot, the grey blocks represent the box plot median and quartiles, the large black dots represent the mean and the small black dots represent outliers. Energetic trophic guild scores in D are based on the sum of the proportion of each food item multiplied by its energy score: 1.0 (folivores: foliage), 2.0 (frugivores: fruit pulp and nectar), 3.0 (granivores: seeds), 4.0 (insectivore/faunivores: invertebrates), and 5.0 (carnivores: vertebrates).

Does use of agroecosystems by carnivores resulted in human-wildlife conflicts?

Only 7% of all studies reported that use of agroecosystems by carnivores resulted in conflicts with local human livelihoods, including crop raiding, crop damage, livestock depredation and lethal or non-lethal injury to local people. Human encounters with large apex carnivores, such as wolves *Canis lupus*, Sumatran tigers *Panthera tigris* and Asiatic black bears *Ursus thibetanus*, can result in attacks on humans and subsequent retaliatory threats to these species (Nyhus & Tilson 2004, Takahata et al. 2013, Behdarvand et al. 2014). Human-wildlife conflicts have also resulted from damage caused by Asiatic black bears to coniferous tree plantations (Yamada & Fujioka 2010) and from crop damage in oil palm, banana and rubber plantations caused by Malay civets *Viverra tangalunga* (Jennings et al. 2010). Omnivorous mustelids, such as tayras *Eira barbara* in neotropical annual croplands including rice, maize and yucca, are often considered pests by farmers (Naughton-Treves et al. 2003). Other conflicts were documented between sun bears *Helarctos malayanus* and humans in agroforestry areas, coconut plantations and fruit orchards due to crop raiding, crop damage, livestock depredation and occasional injury (Fredriksson 2005, Wong et al. 2015).

Hunting of carnivores in plantations has not been widely reported and this threat to carnivores was recorded in only one study. Two carnivores (*Procyon lotor* and *Urocyon cinereoargenteus*) were listed as the most hunted species in coffee plantations for food, trade or medicinal use (Tlapaya & Gallina 2010). Domestic dogs associated with plantation workers pose another threat to carnivores (Frigeri et al. 2014). Crab-eating raccoons *Procyon cancrivorus* and tayras *Eira barbara* responded negatively to domestic dog rate in shade-cacao agroforestry (Cassano et al. 2014).

2.4 DISCUSSION

Our global-scale review shows that a wide range of carnivores — particularly species of Least Concern in terms of their conservation status — were recorded in the wider agricultural matrix. Systematic studies investigating the use of agroecosystems by carnivores increased rapidly around the year 2001. This marked increase seems to reflect the growing research interest in understanding the consequences of agricultural matrix habitats for biodiversity and the biotic flows between the predominantly anthropogenic matrix and native habitat patches embedded therein (Lindenmayer et al. 2008, Perfecto & Vandermeer 2008).

Most studies reporting carnivore species in agroecosystems were carried out in the Americas and Asia, mainly in Brazil and Malaysia. These countries have a considerable proportion of cropland and fast-growing tree plantations (Ramankutty et al. 2008, FAO 2017), as well as high carnivore species richness (IUCN 2017), which may explain the large numbers of both researchers and carnivore species using agricultural lands in these regions. Africa and Oceania exhibited the smallest number of carnivore species using agricultural land. Mainland Africa accounts for ~26% of all terrestrial carnivore species worldwide (IUCN 2017) and has about 2.78 million km² of land area converted into cropland (Ramankutty et al. 2008). Surprisingly, this is at odds with the relative dearth of African carnivore studies in human-modified landscapes. Metatherians largely dominate the mammal fauna of Oceania, so the small number of studies in this continent can be attributed to the fact that all terrestrial mammals there in the order Carnivora are exotic species.

We show that some carnivores can use all agroecosystem types considered here in both temperate and tropical regions. However, the number of carnivore species increases in higher-quality agricultural habitat patches, which tend to covary in structural similarity with adjacent primary habitat patches (Prevedello & Vieira 2010). The large number of species using tree plantations reflects both the ubiquitous distribution of this agroecosystem type worldwide (FAO 2017) and the arborescent cover provided by these habitats, even in exotic tree monocultures. Furthermore, tree plantations lacking periodic herbicidal or mechanical treatments may further contain a well-developed native understorey, which often harbours species-rich mammal assemblages (Umetsu & Pardini 2007). Fast-growing *Eucalyptus* and *Pinus* plantations accounted for most records of carnivores within tree plantation areas, but also reflect their undisputed dominance among tropical and sub-tropical tree plantations (Gerber 2011). These tree plantations function as valuable supplementary foraging habitat, often hosting abundant prey populations, or otherwise serving as a refuge for native carnivores (Guerrero et al. 2006, Zúñiga et al. 2009, Moreira-Arce et al. 2015). As a land-use option, agroforestry has been widely extolled as a ‘win-win’ solution to the problem of reconciling the imperatives of growing demands for food and fibre with biodiversity conservation (Izac & Sanchez 2001), and our review shows that agroforestry patches did indeed sustain a high diversity of carnivore species. For example, tropical arboreal carnivores, which are often generalist frugivores, frequently used agroforestry patches but were largely missing from other agroecosystems. This probably reflects the relatively high diversity and basal area of native trees within multifunctional shade-tree plantations, which often provides benign structural connectivity between canopy trees (Schroth & Harvey 2007, Sambuichi et al. 2012). We suggest that a structurally complex agricultural matrix can provide landscape supplementation and/or complementation (Dunning et al. 1992) for carnivores, which can increase the probability of dispersal movements across the landscape, thereby elevating local species richness (Brady et al. 2011).

Although many carnivore species have been recorded in agricultural lands, we highlight that few researchers assessed exactly how these environments are used by carnivores. A species record in an agroecosystem does not necessarily mean that sufficient resources or habitat are provided, or that the agricultural patch can ensure basic metabolic requirements and long-term population viability. Furthermore, the landscape composition surrounding agroecosystems and more detailed information on where any species is found (edge or interior) are missing from the vast majority of studies. Further understanding of the role of different agroecosystems for carnivore species may emerge from more detailed information on habitat use (e.g. for food, resting or dispersal) and the surrounding landscape context (e.g. amount of native habitat and other land use types).

Although few studies addressed the effects of local management practices within agroecosystems, the age of plantations and land-use intensification can clearly influence their use by carnivores as either habitat or dispersal corridors. Dense ground cover and the retention of native vegetation connectivity in the understorey and/or canopy in agroforestry patches typically favours larger numbers and higher diversity of carnivores by augmenting food, shelter and other structural resources. Aging tree plantations, however, often have a limited conservation potential because the understorey vegetation is typically removed to facilitate harvesting. The understorey may also be suppressed by reduced sunlight penetration through the canopy into the forest floor (Bonnington et al. 2007, Timo et al. 2015). In agroforestry, socioeconomic demands for higher yields have often forced farmers to intensify their traditional shade-tree management systems by thinning native canopy tree species, thereby greatly simplifying the habitat structure for forest wildlife (Schroth & Harvey 2007, Steffan-Dewenter et al. 2007). A lower density and diversity of canopy trees and lower canopy connectivity can greatly reduce the conservation value of agroforestry rural enterprises for carnivores, even though few studies have addressed this issue (but see Estrada et al. 1994, Cassano et al. 2014).

Our results show that both species traits and their conservation status are stronger predictors of crop patch use by carnivores than agroecosystem type.

Threatened (Critically Endangered, Endangered, or Vulnerable) species were far more likely to avoid agroecosystems than non-threatened (Least Concern and Near Threatened) species. Some studies also reported a significant preference for native habitats over agricultural land-use by threatened carnivores (Acosta-Jamett & Simonetti 2004, Bali et al. 2007). Threatened species often have small population sizes (Mace et al. 2008), are more reliant on native habitats and their resources (Lu et al. 2007, Azhar et al. 2014), and are often threatened because of primary habitat conversion and degradation. Conversely, habitat generalists often use agricultural matrix resources, and may persist in agricultural landscapes even if only very small native habitat patches are available (Andrén 1994). Baseline patterns of diversity and assemblage composition, including the persistence of habitat specialists, may collapse when habitat loss falls below a certain threshold (Fahrig 2001, Pardini et al. 2010). For example, the spillover of forest specialists into adjacent matrix areas may occur only in more forested landscapes (Estavillo et al. 2013). We therefore suggest the need to retain native habitats – whatever amount remains available -- within agricultural landscapes to enhance the viability of extinction-prone carnivore populations. In striving for a balance between agricultural yields and nature conservation, land-sparing vs. land-sharing strategies must consider the role of environmental heterogeneity on biodiversity retention, local suitability of biodiversity-friendly cropping systems, and socioeconomic factors (Grau et al. 2013). For carnivores in human-modified landscapes, both land-sparing and land-sharing strategies could be considered. Agroforestry matrices are often sufficiently structurally complex and can favour high mammal diversity, thereby representing land-sharing strategies that can optimise high biodiversity and high agricultural yields (Clough et al. 2011). However, our review shows that many species are effectively intolerant to high levels of land-use change, thereby requiring some level of land-sparing for their conservation (Green et al. 2005). These are typically species of conservation concern, for which sufficiently large areas of native habitat set-asides should be allocated.

Some species traits reflect high levels of habitat-specificity, and can be used to predict species' sensitivity to habitat fragmentation (Henle et al. 2004, Keinath et al. 2016). Traits such as dietary mode and resource specialisation contribute to species-specific responses to fragmentation effects (Crooks 2002) and have been related to extinction risk (Henle et al. 2004). Species exhibiting broad diets can fuel their metabolism from a greater fraction of the habitat mosaic in heterogeneous landscapes (Gehring & Swihart 2003), which can explain the prevalence of generalist consumers in agricultural patches. The virtual absence of hypercarnivores operating at the highest trophic level can be explained both by their low population densities and by their more discerning patterns of habitat selection in fragmented landscapes (Kosydar et al. 2014). Wide-ranging species exhibiting greater vagility can often disperse between native vegetation remnants, and so may be less affected by habitat fragmentation (Ewers & Didham 2005, Tscharntke et al. 2012). We found that terrestrial carnivores dominated agricultural patches, while arboreal and semi-aquatic species were rarely reported even in more benign agroecosystem types, probably because of severe simplification of habitat features such as vertical stratification and water resources. Maintaining vegetation complexity, including an arboreal stratum is essential to provide suitable food and shelter resources, thereby promoting agroecosystem use by carnivores (Gallina et al. 1996, García-Burgos et al. 2014, Caudill et al. 2015). We observed a tendency for the largest species to use the agricultural matrix, although species larger than 50 kg, which often occupy a high trophic level, were rarely recorded in any of these landscapes. Home range size scales to body mass in carnivores (Lindstedt et al. 1986), suggesting that larger, more mobile species can make transient use of even suboptimal habitats to meet their metabolic needs (Gehring & Swihart 2003).

Our review indicates that human-wildlife conflicts associated with carnivores either rarely occur in agroecosystems or are under-reported. Rates of crop-raiding by generalist carnivores are low, and we failed to consider retaliation mortality in pastoral systems associated with depredation of livestock. Although information on human-wildlife conflicts in agroecosystems is insufficient, the conspicuous lack of large mammals may be due to steep population declines induced by multiple human activities (Morrison et al. 2007). Local extinctions of large carnivores are intimately associated with growing co-existing human populations (Woodroffe 2000), and hunting and retaliation for livestock losses are often the main drivers of large carnivore declines (Lopes & Ferrari 2000, Peres 2001). Furthermore, there are strong indirect effects of humans on food webs that include carnivores in densely settled areas (Muhly et al. 2013), which further strengthens the research agenda on carnivore ecology in human-modified landscapes. On the other hand, there is ample evidence that large carnivores can coexist with dense human populations (Athreya et al. 2013), although there is a huge amount of cultural variance in human tolerance to potentially threatening carnivores, resulting in variable ‘social carrying capacities’ (Breitenmoser et al. 2005).

Beyond possible human-carnivore conflicts in anthropogenic landscapes, many carnivore species play important roles as agents of top-down control (Miller et al. 2001). The absence of large carnivores in agricultural systems can induce population hyperabundance of smaller carnivores through increasingly well-documented trophic cascades, including mesopredator release (Terborgh & Estes 2010). Natural predation by carnivores can also reduce monetary losses in a number of monoculture and polyculture systems by suppressing rodents and other agricultural pests (Takele et al. 2008, Puan et al. 2011). Growing populations of invasive species in agroecosystems represent yet another largely neglected phenomenon. The presence of rural workers in agroecosystems is widely known to facilitate invasions by exotic species such as free-ranging dogs (Frigeri et al. 2014), which have a direct impact on wild carnivores and other vertebrate populations through competitive displacement, predation, disease transmission and hybridisation (Vanak & Gompper 2009). Further studies on the use of agroecosystem by native carnivores can help us understand the positive ecosystem services they provide in regulating otherwise hyperdominant prey populations, many of which can result in detrimental crop-raiding or epidemiological effects.

2.5 FINAL CONSIDERATIONS AND FUTURE RESEARCH DIRECTIONS

Our results show that a growing number of studies report the presence of carnivores in agroecosystems worldwide, indicating that frequent occupancy of agricultural matrix habitats is related to both species morpho-ecological traits and habitat quality. We emphasise that the conspicuous absence from agroecosystems of threatened carnivores and species foraging at the highest trophic levels suggests the paramount importance of retaining at least some native habitat within agricultural landscapes. Moreover, some agroecosystem types, mainly those in environments retaining a complex physical structure, are able to maintain the highest taxonomic and functional diversity of residual carnivore assemblages. Moreover, fine-scale habitat use data are largely unavailable for many poorly-known small carnivore species, which could be severely disadvantaged in agroecosystems.

The future of mammalian diversity in the anthropocene depends largely on the conservation value of human-dominated landscapes (Daily et al. 2003). This includes the often thorny issue of persisting large hypercarnivore populations, which are essential for biodiversity maintenance and ecosystem functioning (Ripple et al. 2014).

Despite the large number of studies reporting carnivore occurrence in agricultural areas, we identified some glaring knowledge gaps. Future studies are necessary for a greater understanding of: (1) the extent to which agroecosystems function as either foraging habitat or as dispersal corridors, and which are the main resources used by carnivores in these systems? (2) How the use of agroecosystems by carnivore species can impact their long-term population viability; (3) the relative importance of local management intensification, and the impacts of humans and exotic commensal species on carnivore populations; (4) minimum natural habitat cover thresholds for different agroecosystem types, and the importance of landscape heterogeneity to carnivores; (5) the direct and indirect effects of humans on food webs that include carnivores in heavily modified landscapes; (6) agricultural yield benefits of pest control by carnivores; and (7) how human attitude and tolerance towards carnivores can influence their persistence in agroecosystems.

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SUPPORTING INFORMATION

APPENDIX S1

References and information on habitats within the agroecosystem types (Agroforestry - AF, Tree Plantation - FP, Perennial Cropland - PC and Annual Cropland - AC) used by carnivores in 129 studies reviewed.

Agroecosystem	**Source**	**Species number**
Agroforestry (AF)		
Albizia falcataria underplanted with *Theobroma cacao*	Stuebing (1989)	1
Allspice agroforestry: *Pimenta dioica* in pasture with coffee, cacao, and citrus	King et al. (2007)	2
Cinnamon, coffee, legume, fruit, and timber trees	Nyhus & Tilson (2004)	1
Cork oak agroforestry (*Quercus suber* with riparian vegetation, woods and orchards)	Rosalino et al. (2009)	6
Pine, coffee and addocks	Chacón et al. (2013)	1
Shaded banana (*Musa* spp.)	Guiracocha et al. (2001), Harvey et al. (2006), Soley (2012)	9
Shaded cacao (*Theobroma cacao*)	Cassano et al. (2012, 2014), Estrada et al. (1994), Frigeri et al. (2014), Guiracocha et al. (2001), Harvey et al. (2006), Soley (2012)	16
Shaded coffee (*Coffea* spp.)	Anleu (2015), Bali et al. (2007), Caudill et al. (2014, 2015), Caudill & Rice (2016), Estrada et al. (1994), Gallina et al. (1996), García-Burgos et al. (2014), Palacios-Romo et al. (2012), Prakash et al. (2012), Tlapaya & Gallina (2010)	29
Shaded teak (*Tectona grandis*)	Oliveira (2015)	2
Agroforestry system (unidentified cultivar)	Wong et al. (2015)	1
Tree Plantation (TP)		
Acacia (*Acacia mangium*)	McShea et al. (2009), Ramesh et al. (2016), Sompud et al. (2016), Sunarto et al. (2012)	12

Acacia spp., *Azadirachta indica*, Eucalyptus hybrid and *Glyricidia sepium*	Vanak & Gompper (2010)	1
Allspice (*Pimenta dioica*)	Estrada et al. (1994)	1
Coniferous plantation	Baker & Harris (2006), Caryl et al. (2012), Kaneko et al. (2006, 2009), Lantschner et al. (2012), Mello (2005), Takahata et al. (2013), Tsujino & Yumoto (2014), Yamada & Fujioka (2010), Zabala et al. (2005)	12
Eucalyptus (*Eucalyptus* spp.)	Andrade-Núñez & Aide,(2010), Ciocheti (2007), Coelho et al. (2014), Cruz et al. (2015), Dotta & Verdade (2007, 2009, 2011), Ferraz et al. (2010), Gerber et al. (2012), Haddad (2008), Hatakeyama (2015), Law et al. (2017), Lima (2012), Lima et al. (2013), Lyra-Jorge et al. (2008), Lyra-Jorge et al. (2010), Michalski et al. (2006), Minami (2010), Moreira-Arce et al. (2015), Navya et al. (2014), Oliveira (2002), Palomares et al. (2000), Ramesh et al. (2016), Rodas-Trejo et al. (2010), Silva (2001), Silveira (2005), Spínola et al. (2005), Stallings (1991), Stuebing & Gasis (1989), Timo et al. (2015), Tófoli et al. (2009), Zuberogoitia et al. (2002)	35
Larch (*Larix* spp.)	Hwang et al. (2014), Lu et al. (2007), Rhim et al. (2015), Son et al. (2017), Takahata et al. (2013)	5
Pine *(Pinus* spp.)	Acosta-Jamett & Simonetti (2004), Chamberlain et al. (2003), Dias (2010), Fournier et al. (2007), Friend (1982), Gerber et al. (2012), Guerrero et al. (2006), Jones & Pelton (2003), Kittle et al. (2014), Lu et al. (2007), Mello (2005), Moreira-Arce et al. (2015), Palomares et al. (2000), Ramesh et al. (2016), Rodas-Trejo et al.	31

	(2010), Simonetti et al. (2013), Stratman et al. (2001), Zanne et al. (2001), Zuberogoitia et al. (2002), Zúñiga et al. (2009)	
Planted stands of *Pinus* spp., Eucalyptus spp., and *Araucaria angustifolia*	Mazzolli (2010)	1
Teak (*Tectona grandis*)	Balakrishnan & Easa (1986), Bonnington et al. (2007), Faustino (2015)	13
Perennial Cropland (PC)		
Avocado (*Persea americana*)	Borchet et al. (2008), Nogeire et al. (2013)	8
Banana (Musa spp.)	Jennings et al. (2010)	1
Cacao (*Theobroma cacao*)	Massussi et al. (2009)	3
Citrus (*Citrus* spp.)	Estrada et al. (1994)	3
Coconut palm plantation (*Cocos nucifera*)	Fredriksson (2005), Nakamoto et al. (2006)	6
Coffee (*Coffea* spp.)	Daily et al. (2003), García-Burgos et al. (2014), Pacheco et al. (2006)	10
Date palms cultivation (*Phoenix dactylifera*)	Dell'Arte & Leonardi (2007)	1
Oil palm (*Elaeis* spp.)	Azhar et al. (2014), Maria (2013), Gamage et al. (2011), Jennings et al. (2010, 2015), Naim et al. (2012), Nakashima et al. (2013), Normua et al. (2004), Olarte-Gonzáles & Escovar-Fadul (2014), Pardo-Vargas & Payán-Garrido (2015), Pardo et al. (2017), Rajaratnam et al. (2007), Simijaca (2016), Sunarto et al. (2012), Wearn (2015), Yue et al. (2015)	31
Olive plantations (*Olea europaea*)	Dell'Arte & Leonardi (2007), Garrote et al. (2017), González (2011)	3
Rubber (*Hevea brasiliensis*)	Jennings et al. (2010), Soares et al. (2013), Sunarto et al. (2012)	4
Tea (*Camellia thea*)	Gokula & Thangatamil (2014),	11

	Kumara et al. (2004), Navya et al. (2014), Prakash et al. (2012)	
Tea, coffee, Eucalyptus	Navya et al. (2014)	4
Annual Cropland (AC)		
Cereal (wheat, sunflower e/ou milo)	González (2011), Matlack et al. (2000)	2
Corn/maize (*Zea*)	Balestrieri et al. (2004), Canova & Rosa (1994)	2
Herbaceous crops, fruit trees and vines, abandoned fields and common thatching grass (*Hyparrhenia hirta*) meadows	Camps & Alldredge (2013)	1
Maize, groundnut and other pulses	Vanak & Gompper (2010)	1
Manioc (*Manihot esculenta*)	Abrahams et al. (2018)	6
Pickets, acahuales and maize cultivation	Chacón et al. (2013)	3
Potato and Corn/maize	Behdarvand et al. (2014), Ramesh et al. (2016)	2
Rice (*Oryza* spp.)	Alves et al. (2012), Kaneko et al. (2009); Lorica & Heaney (2013), Soares et al. (2010), Soares & Peña (2015)	9
Rice, maize and yucca	Naughton-Treves et al. (2003)	4
Soybean (*Glycine max*)	Peirano (2016)	2
Sugar cane (*Saccharum*)	Dotta & Verdade (2007, 2009, 2011), Ferraz et al. (2010)	12

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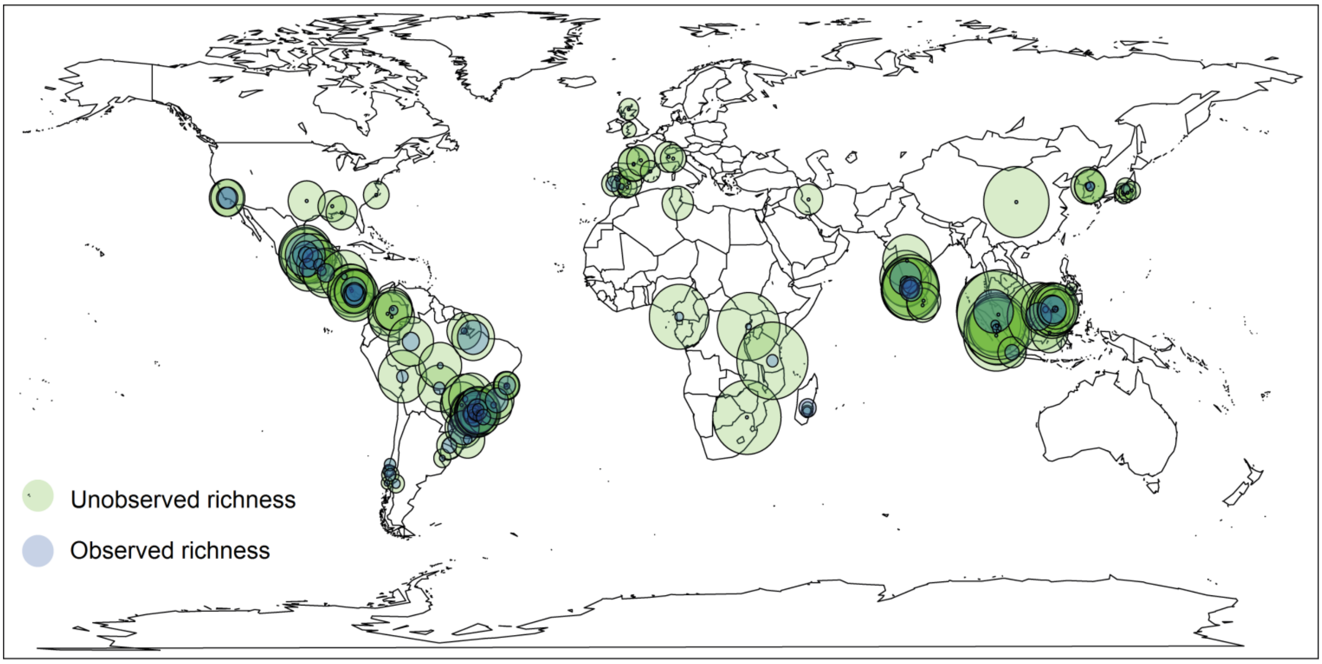
APPENDIX S2.

Observed carnivores' richness (indicating by the size of blue circles) and expected richness (indicating by the size of green circles) based on the number of species that were either present and absence (could potentially occur at site but was not observed) at 75 agricultural sites of studies reviewed.



APPENDIX S3.

References (see in Appendix S1) and information on mammalian carnivores reported in agroecosystems: Agroforestry (AF), Tree Plantation (FP), Perennial Cropland (PC) and Annual Cropland (AC) in 129 studies reviewed. Conservation status (Cons.), Locomotion mode (Loc.), Energetic trophic level (Diet) and Body Mass in grams (BM) of species are shown.

Region/Taxa	**Common name**	**Cons.** [a]	**Loc.** [b]	**Diet** [c]	**BM(g)**	**AF** [d]	**TP** [e]	**PC** [f]	**AC** [g]	**Source**
America										
Bassaricyon gabbii	Olingo	LC	Ar	2.7	1250			24		Pacheco et al. (2006)
Bassariscus astutus	Ringtail	LC	Sc	2.7	1130	8				Gallina et al. (1996), Tlapaya & Gallina (2010)
Bassariscus sumichrasti	Cacomistle	LC	Ar	2.7	900	7,8		22	36	Chacón et al. (2013), Estrada et al. (1994), García-Burgos et al. (2014)
Canis latrans	Coyote	LC	Te	5	13406	8		19		Borchert et al. (2008), Gallina et al. (1996), Nogeire et al. (2013), Tlapaya & Gallina (2010)
Canis lupus familiaris	Domestic dog	NA	Te	5.0	32183	7	14	19	41	Borchert et al. (2008), Cassano et al. (2014, 2012),

										Dotta & Verdade (2011), Frigeri et al. (2014), Timo et al. (2015)
Cerdocyon thous	Crab-eating fox	LC	Te	4.5	5240	7, 9	14, 16, 18	26, 28	38, 41	Alves et al. (2012), Andrade-Núñez & Aide (2010), Cassano et al. (2014, 2012), Coelho et al. (2014), Dias (2010), Dotta & Verdade (2011, 2007), Faustino (2015), Ferraz et al. (2010), Haddad (2008), Hatakeyama (2015), Lyra-Jorge et al. (2008), Maria (2013), Michalski et al. (2006), Oliveira (2002), Oliveira (2015), Pardo-Vargas & Payán-Garrido (2015), Simijaca (2016), Silveira (2005), Soares et al. (2010), Soares et al. (2013), Soares & Peña (2015), Spínola et al.

										(2005), Timo et al. (2015)
Chrysocyon brachyurus	Maned wolf	NT	Te	4,2	23250		14, 18		38, 41	Ciochete (2007), Dotta & Verdade (2011, 2007), Faustino (2015), Lima (2012), Lyra-Jorge et al. (2008, 2010), Minami (2010), Soares et al. (2010), Soares & Peña (2015), Spínola et al. (2005), Timo et al. (2015)
Conepatus chinga	Molina's hog-nosed skunk	LC	Te	3.9	1918		13, 14, 16	24	40, 41	Acosta-Jamett & Simonetti (2004), Andrade-Núñez & Aide (2010), Daily et al. (2003), Dotta & Verdade (2011, 2007), Lantschner et al. (2012), Peirano (2016), Simonetti et al. (2013)
Conepatus leuconotus	American hog-nosed skunk	LC	Te	3.9	3500	8				Gallina et al. (1996), Palacios-Romo et al. (2012)
Conepatus semistriatus	Striped hog-nosed skunk	LC	Te	3.9	1200	2, 6, 7, 8	12, 14	22, 24		Estrada et al. (1994), Guiracocha et al. (2001), King et al. (2007), Lyra-Jorge

										et al. (2008), Pacheco et al. (2006)
Eira barbara	Tayra	LC	Te	4.7	3910	2, 6, 7	14, 16 18	24, 26	35, 39	Abrahams et al. (2018), Cassano et al. (2014, 2012), Daily et al. (2003), Dias (2010), Dotta & Verdade (2011, 2007), Faustino (2015), Guiracocha et al. (2001), Haddad (2008), Harvey et al. (2006), Hatakeyama (2015), King et al. (2007), Lyra-Jorge et al. (2008, 2010), Maria (2013), Michalski et al. (2006), Minami (2010), Naughton-Treves et al. (2003), Pacheco et al. (2006), Silva (2001), Soley (2012), Stallings (1991), Timo et al. (2015)

Felis catus	Domestic cat	NA	Sc	5.0	2885				41	Dotta & Verdade (2011)
Galictis cuja	Lesser grison	LC	Te	4.2	1000		14, 16		41	Dias (2010), Dotta & Verdade (2007, 2011), Mello (2005), Zúñiga et al. (2009)
Galictis vittata	Greater grison	LC	Te	4.2	3200	6, 7		26		Estrada et al. (1994), Harvey et al. (2006), Maria (2013)
Leopardus geoffroyi	Geoffroy's cat	LC	Te	5.0	5158		14			Andrade-Núñez & Aide (2010)
Leopardus guigna	Kodkod	VU	Sc	5.0	5158		14, 16			Acosta-Jamett & Simonetti (2004), Guerrero et al. (2006), Moreira-Arce et al. (2015), Simonetti et al. (2013), Zúñiga et al. (2009)
Leopardus pardalis	Ocelot	LC	Te	5.0	11900	6, 7, 8	14, 16, 18	24, 26	35, 38, 39, 41	Abrahams et al. (2018), Alves et al. (2012), Ciochete (2007), Daily et al. (2003), Dias (2010), Dotta & Verdade (2007, 2009, 2011), Faustino (2015), Haddad (2008), Harvey et al. (2006), Hatakeyama (2015), Lyra-

										Jorge et al. (2008, 2010), Maria (2013), Minami (2010), Naughton-Treves et al. (2003), Oliveira (2002), Pacheco et al. (2006), Palacios-Romo et al. (2012), Pardo-Vargas & Payán-Garrido (2015), Silva (2001)
Leopardus tigrinus	Northern tiger cat	VU	Sc	5.0	2250		14, 16		41	Dias (2010), Dotta & Verdade (2009), Timo et al. (2015)
Leopardus wiedii	Margay	NT	Sc	4.4	3250	7, 8	16	26, 28	35, 41	Abrahams et al. (2018), Anleu (2015), Dias (2010), Dotta & Verdade (2009), Gallina et al. (1996), Harvey et al. (2006), Maria (2013), Palacios-Romo et al. (2012), Soares et al. (2013), Tlapaya & Gallina (2010)
Lontra longicaudis	Neotropical otter	Te	As	4.9	6555	6, 8	16			Dias (2010), Gallina et al.

										(1996), Harvey et al. (2006)
Lycalopex culpaeus	Culpeo	LC	Te	4.6	8616		13, 14, 16			Acosta-Jamett & Simonetti (2004), Guerrero et al. (2006), Lantschner et al., (2012), Moreira-Arce et al. (2015), Simonetti et al. (2013)
Lycalopex fulvipes	Darwin's fox	EN	Te	4.2	5147		14, 16			Moreira-Arce et al. (2015)
Lycalopex griseus	South American grey fox	LC	Te	3.9	5147		14, 16			Guerrero et al. (2006), Moreira-Arce et al. (2015), Rodas-Trejo et al. (2010), Zúñiga et al. (2009)
Lycalopex gymnocercus	Pampas fox	LC	Te	3.3	4543		14		40	Andrade-Núñez & Aide (2010), Peirano (2016)
Lycalopex vetulus	Hoary fox	LC	Te	3.9	4233		14			Haddad (2008), Minami (2010)
Lynx rufus	Bobcat	LC	Sc	5.0	8904		16	19		Borchert et al (2008), Chamberlain et al. (2003), Nogeire et al. (2013)
Mephitis	Hooded skunk	LC	Te	3.2	801	8				Anleu (2015), Gallina et al.

macroura										(1996), Tlapaya & Gallina (2010)
Mephitis mephitis	Striped skunk	LC	Te	3.2	2085			19		Borchert et al (2008), Nogeire et al. (2013)
Mustela frenata	Long-tailed weasel					6,7,8		24		Daily et al. (2003), Estrada et al. (1994), Gallina et al. (1996), García-Burgos et al. (2014), Harvey et al. (2006), Pacheco et al. (2006), Tlapaya & Gallina (2010)
Nasua narica	White-nosed coati	LC	Sc	2.8	4030	5, 6, 7, 8,		24		Anleu (2015), Chacón et al. (2013), Daily et al. (2003), Estrada et al. (1994), Gallina et al. (1996), García-Burgos et al. (2014), Guiracocha et al. (2001), Harvey et al. (2006), Pacheco et al. (2006), Tlapaya & Gallina (2010)
Nasua nasua	South American	LC	Te	2.8	3794	7, 9	13,	26	38,	Cassano et al. (2012, 2014),

	coati						14, 16		39, 41	Dias (2010), Dotta & Verdade (2007, 2011), Hatakeyama (2015), Maria (2013), Mello (2005), Minami (2010), Naughton-Treves et al. (2003), Oliveira (2015), Silveira (2005), Soares et al. (2010), Spínola et al. (2005), Timo et al. (2015)
Panthera onca	Jaguar	NT	Te	5.0	100000		14	26	35, 39	Abrahams et al. (2018), Coelho et al. (2014), Hatakeyama (2015), Lima et al. (2013), Maria (2013), Naughton-Treves et al. (2003)
Potos flavus	Kinkajou	LC	Ar	2.5	3000	7, 8			36	Cassano et al. (2014), Chacón et al. (2013), Estrada et al. (1994), Gallina et al. (1996), Harvey et al. (2006), Palacios-Romo et al. (2012), Tlapaya & Gallina

										(2010)
Procyon cancrivorus	Crab-eating raccoon	LC	Sc	4.0	6950	7	14, 16	26	38, 41	Alves et al. (2012), Andrade-Núñez & Aide (2010), Cassano et al. (2012, 2014), Dias (2010), Dotta & Verdade (2007, 2011), Haddad (2008), Hatakeyama (2015), Maria (2013), Mello (2005), Oliveira (2002), Soares et al. (2010), Stallings (1991)
Procyon lotor	Raccoon	LC	Sc	3.6	5525	6, 7, 8		19, 22, 24	36	Anleu (2015), Borchert et al (2008), Caudill et al. (2015), Caudill & Rice (2016), Chacón et al. (2013), Estrada et al. (1994), Gallina et al. (1996), García-Burgos et al. (2014), Guiracocha et al. (2001), Harvey et al. (2006), Nogeire et al. (2013), Pacheco et al. (2006),

										Palacios-Romo et al. (2012), Tlapaya & Gallina (2010)
Puma concolor	Puma	LC	Te	5.0	51600	7, 8	13, 14, 16, 17	19, 26	35, 38	Abrahams et al. (2018), Alves et al. (2012), Anleu (2015), Ciochete (2007), Dias (2010), Dotta & Verdade (2007, 2009, 2011), Gallina et al. (1996), Guiracocha et al. (2001), Haddad (2008), Hatakeyama (2015), Lantschner et al. (2012), Lyra-Jorge et al. (2008, 2010), Maria (2013), Mazzolli (2010), Minami (2010), Nogeire et al. (2013), Olarte-González & Escovar-Fadul (2014), Oliveira (2002), Pardo et al. (2017), Rodas-Trejo et al. (2010), Soares et al. (2010), Spínola et al. (2005), Timo et al.

										(2015), Zúñiga et al. (2009)
Puma yagouaroundi	Jaguarundi	LC	Te	4.6	6875	4, 7, 8	14, 16	26	35, 38, 41	Abrahams et al. (2018), Caudill & Rice (2016), Ciochete (2007), Dias (2010), Gallina et al. (1996), Dotta & Verdade (2009), Guiracocha et al. (2001), Hatakeyama (2015), Lyra-Jorge et al. (2010), Maria (2013), Michalski et al. (2006), Oliveira (2002), Pardo-Vargas & Payán-Garrido (2015), Soares et al. (2010), Spínola et al. (2005), Tófoli et al. (2009)
Speothos venaticus	Bush dog	NT	Te	5.0	6000			26		Maria (2013)
Spilogale putorius	Eastern spotted skunk	VU	Te	3.5	341			24		Daily et al. (2003)
Urocyon cinereoargenteus	Grey fox	LC	Te	3.1	3834	8		19, 24		Anleu (2015), Borchert et al. (2008), Caudill & Rice

										(2016); Daily et al. (2003), Gallina et al. (1996), García-Burgos et al. (2014), Nogeire et al. (2013), Pacheco et al. (2006), Palacios-Romo et al. (2012), Tlapaya & Gallina (2010)
Ursus americanus	American black bear	LC	Sc	2.3	99949		16	19		Borchert et al. (2008), Jones & Pelton (2003), Nogeire et al. (2013), Stratman et al. (2001)
Vulpes velox	Swift fox	LC	Te	4.9	2198				31	Matlack et al. (2000)
Africa										
Canis lupus familiaris	Domestic dog	NA	Te	5.0	32183		14,16			Gerber et al. (2012)
Canis mesomelas	Black-backed jackal	LC	Te	3.7	8500		18			Bonnington et al. (2007)
Caracal caracal	Caracal	LC	Te	5.0	13750		10, 14, 16		37	Ramesh et al. (2016)

Civettictis civetta	African civet	LC	Te	3.5	12000		16, 18	21		Bonnington et al. (2007), Massussi et al. (2009), Zanne et al. (2001)
Crossarchus obscurus	Cusimanse	LC	Te	3.8	1250			21		Massussi et al. (2009)
Galidia elegans	Ring-tailed mongoose	LC	Sc				14,16			Gerber et al. (2012)
Galidictis fasciata	Malagasy road-striped mongoose	VU	Sc	4.7	550		14, 16			Gerber et al. (2012)
Martes zibelina	Sable	LC	Sc	4.5	1130		18			Bonnington et al. (2007)
Nandinia binotata	African palm civet	LC	Ar	2.5	2000		16	21		Massussi et al. (2009), Zanne et al. (2001)
Panthera pardus	Leopard	VU	Te	5.0	52038		18			Bonnington et al. (2007)
Vulpes vulpes	Red fox	LC	Te	4.5	5476			25, 27		Dell’Arte & Leonardi (2007)
Asia				Fo/On						
Ailuropoda melanoleuca	Giant panda	VU	Sc	1.4	108400		15, 16			Lu et al. (2007)
Aonyx cinereus	Asian small-clawed otter	VU	As	4.2 Ca	3528	8		23, 29		Nakamoto et al. (2006), Prakash et al. (2012)

Arctictis binturong	Binturong	VU	Ar	3.3	9875			26		Azhar et al. (2014)
Arctogalidia trivirgata	Small-toothed palm civet	LC	Ar	4.2	2250		10	26		Azhar et al. (2014), Sompud et al. (2016)
Canis aureus	Golden jackal	LC	Te	4.6	10345	8		29		Bali et al. (2007), Caudill et al. (2014), Kumara et al. (2004)
Canis lupus	Gray wolf	LC	Te	5.0	32183				37	Behdarvand et al. (2014)
Canis lupus familiaris	Domestic dog	NA	Te	5.0	32183			26		Wearn (2015)
Cuon alpinus	Dhole	EN	Te	5.0	14173	8	14, 18	29, 30		Balakrishnan & Easa (1986); Bali et al. (2007), Kumara et al. (2004), Navya et al. (2014)
Felis chaus	Jungle cat	LC	Sc	5.0	7393	8		29		Bali et al. (2007), Gokula & Thangatamil (2014), Kumara et al. (2004)
Helarctos malayanus	Sun bear	VU	Sc	3.7	46500	x	10	23, 26		Azhar et al. (2014), Fredriksson (2005), McShea et al. (2009), Normua et al. (2004), Wearn (2015), Wong

										et al. (2015), Yue et al. (2015)
Hemigalus derbyanus	Banded palm civet	NT	Te	4.0	2323		10	26		McShea et al. (2009), Wearn (2015), Yue et al. (2015)
Herpestes brachyurus	Short-tailed mongoose	NT	Te	4.4	1854		10	26		McShea et al. (2009), Wearn (2015), Yue et al. (2015)
Herpestes edwardsii	Indian grey mongoose	LC	Te	4.5	1305	8		29		Caudill et al (2014), Gokula & Thangatamil (2014)
Herpestes fuscus	Indian brown mongoose	LC	Te	4.4	1985			30		Navya et al. (2014)
Herpestes javanicus	Small Asian mongoose	LC	Te	4.4	750			23		Nakamoto et al. (2006)
Herpestes semitorquatus	Collared mongoose	NT	Te	4.4	1916		10	26		McShea et al. (2009), Wearn (2015), Yue et al. (2015)
Herpestes vitticollis	Stripe-necked mongoose	LC	Te	On	2576		14	29, 30		Kumara et al. (2004), Navya et al. (2014)
Martes flavigula	Yellow-throated marten	LC	Sc	4.6	1843		10	26		McShea et al. (2009), Wearn (2015), Yue et al. (2015)
Martes melampus	Japanese marten	LC	Sc	3.5	1000		13			Tsujino & Yumoto (2014)

Meles meles	European badger	LC	Sc	3.6	1300		13, 15			Kaneko et al. (2006), Rhim et al. (2015), Son et al. (2017)
Melursus ursinus	Sloth bear	VU	Sc	3.2	93130	8	14, 18	29		Balakrishnan & Easa (1986), Bali et al. (2007), Gokula & Thangatamil (2014), Navya et al. (2014)
Mustela itatsi	Japanese weasel	NT	Te	3.8	531		13		38	Kaneko et al. (2009)
Mustela sibirica	Siberian weasel	LC	Te	5.0	405		15			Hwang et al. (2014), Rhim et al. (2015), Son et al. (2017)
Mydaus javanensis	Sunda stink-badger	LC	Te	3.4	2500			26		Wearn (2015), Yue et al. (2015)
Neofelis nebulosa	Clouded leopard	VU	Sc	5.0	19676			26		Azhar et al. (2014)
Nyctereutes procyonoides	Raccoon dog	LC	Sc	3.7	4040		15			Hwang et al. (2014), Rhim et al. (2015), Son et al. (2017)
Paguma larvata	Masked palm civet	LC	Sc	4.2	4300		13	26		Azhar et al. (2014), Tsujino & Yumoto (2014), Wearn (2015)
Panthera pardus	Leopard	VU	Te	5.0	52038	8	16,	26,		Azhar et al. (2014),

							18	29		Balakrishnan & Easa (1986), Bali et al. (2007), Gokula & Thangatamil (2014), Kittle et al. (2014), Kumara et al. (2004)
Panthera tigris	Tiger	EN	Sc	Ca	162564	3, 8	10, 18	26, 28, 29		Azhar et al. (2014), Balakrishnan & Easa (1986), Bali et al. (2007), Gokula & Thangatamil (2014), Kumara et al. (2004), Nyhus & Tilson (2004), Sunarto et al. (2012)
Paradoxurus hermaphroditus	Asian palm civet	LC	Ar	3.8	3157	1 8	10, 14, 18	23, 26		Azhar et al. (2014), Balakrishnan and Easa (1986), Bali et al. (2007), Caudill et al. (2014), Jennings et al. (2015), McShea et al. (2009), Naim et al. (2012), Nakamoto et al. 2006), Nakashima et al. (2013), Sompud et al.

										(2016), Stuebing & Gasis (1989), Yue et al. (2015)
Paradoxurus jerdoni	Jerdon palm civet	LC	Ar	3.8	2781	8				Bali et al. (2007)
Pardofelis marmorata	Marbled cat	NT	Ar	5.0	2854		10			McShea et al. (2009)
Prionailurus bengalensis	Leopard cat	LC	Sc	5.0	3300	8	10	23, 26, 29	38	Azhar et al. (2014), Bali et al. (2007), Jennings et al. (2015), Kumara et al. (2004), Lorica & Heaney (2013), McShea et al. (2009), Naim et al. (2012), Nakamoto et al. (2006), Rajaratnam et al. (2007), Wearn (2015), Yue et al. (2015)
Prionailurus planiceps	Flat-headed cat	EN	Te	5.0	6750			26		Azhar et al. (2014)
Prionailurus rubiginosus	Rusty-spotted cat	NT	Sc	5.0	1384	8				Bali et al. (2007)
Prionodon linsang	Banded linsang	LC	Sc	Ca				26		Azhar et al. (2014)

Ursus thibetanus	Asiatic black bear	VU	Sc	2.5	77500		13, 15			Takahata et al. (2013), Tsujino & Yumoto (2014), Yamada & Fujioka (2010)
Viverra tangalunga	Malay civet	LC	Te	4.2	6885		10	20, 26, 28		Azhar et al. (2014), Jennings et al. (2010, 2015), McShea et al. (2009), Naim et al. (2012), Wearn (2015), Yue et al. (2015)
Viverra zibetha	Large Indian civet	LC	Te	4.6	9500			26		Azhar et al. (2014)
Viverricula indica	Small Indian civet	LC	Te	4.1	2908	8	14, 18	23, 26, 29, 30		Azhar et al. (2014), Balakrishnan & Easa (1986), Bali et al. (2007), Caudill et al. (2014), Rice (2014), Gamage et al. (2011), Kumara et al. (2004), Nakamoto et al. (2006), Navya et al. (2014)
Vulpes bengalensis	Bengal fox	LC	Te	4.2	2726		11		34	Vanak & Gompper (2010)
Europe										

Genetta genetta	Common genet	LC	Sc	4.9	1800	4	14, 16	27	33	Camps & Alldredge (2013), González (2011), Rosalino et al. (2009), Zuberogoitia et al. (2002)
Herpestes ichneumon	Egyptian mongoose	LC	Te	4.4	5175	4				Rosalino et al. (2009)
Lutra lutra	European otter	NT	Sa	4.7	8785	4				Rosalino et al. (2009)
Lynx pardinus	Iberian lynx	EN	Sc	5.0	9400		14, 16	27		Garrote et al. (2017), Palomares et al. (2000)
Martes foina	Beech marten	LC	Sc	4.0	1541	4	14			Cruz et al. (2015), Rosalino et al. (2009)
Martes martes	European pine marten	LC	Sc	3.8	1300		13			Caryl et al. (2012)
Meles meles	European badger	LC	Sc	3.6	13000	4	14		31, 32	Balestrieri et al. (2004), Canova & Rosa (1994), Cruz et al. (2015), González (2011), Rosalino et al. (2009)
Mustela putorius	European polecat	LC	Te	4.9	915		13, 16			Fournier et al. (2007), Zabala et al. (2005)
Vulpes vulpes	Red fox	LC	Te	4.5	5476	4	13, 14		32	Baker & Harris (2006), Canova & Rosa (1994), Cruz

										et al. (2015), Rosalino et al. (2009)
Oceania										
Canis lupus dingo	Dingo	VU	Te	5.0	32183		14			Law et al. (2017)
Felis catus	Domestic cat	NA	Sc	5.0	2885		16			Friend (1982)
Vulpes vulpes	Red fox	LC	Te	4.5	5476		16			Friend (1982)
Number of domestic species						1	2	1	2	
Number of wild species						41	63	58	26	

[a] Conservation status: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), NA = not available;

[b] Locomotion mode: Ar (arboreal), Sc (scansorial), As (Semi-aquatic) and Te (terrestrial);

[c] Diet: score based on the sum of the proportion of each food item multiplied by its energy score (1 – grass, ground vegetation, seedlings, weeds, lichen, moss, small plants, reeds, cultivated crops, forbs, vegetables, fungi, roots, tubers, legumes, bulbs, leaves, above ground vegetation, twigs, bark, shrubs, herbs, shoots, aquatic vegetation, aquatic plants, 2 - fruits, drupes, nectar, pollen, exudate or gum, 3 - seed, maize, nuts, spore, wheat or grains 4 - invertebrates and 5 - vertebrates)

[d] Agroforestry (AF) codes: 1, *Albizia falcataria* underplanted with *Theobroma cacao*; 2, Allspice agroforestry (*Pimenta dioica* in pasture with coffee, cacao, and citrus); 3, Cinnamon, coffee, legume, fruit, and timber trees; 4, Cork oak agroforestry (*Quercus suber* with riparian vegetation, woods and orchards); 5, Pine, coffee and addocks; 6, Shade banana (*Musa* spp.); 7, Shade cacao (*Theobroma cacao*); 8, Shade coffee (*Coffea* spp.) ; 9, Shade teak (*Tectona grandis*)

[e] Tree Plantation (TP) codes: 10, Acacia (*Acacia mangium*); 11, *Acacia* spp., *Azadirachta indica*, eucalyptus hybrid and *Glyricidia sepium*; 12, Allspice (*Pimenta dioica*); 13, Coniferous plantation; 14, Eucalyptus; 15, Larch (*Larix* spp.); 16, Pine *(Pinus* spp.); 17, Planted stands of *Pinus* spp., eucalyptus spp., and *Araucaria angustifolia*; 18, Teak (*Tectona grandis*)

[f] Perennial Cropland (PC) codes: 19, Av, Avocado (*Persea americana*); 20, Banana (Musa spp.); 21, Cacao (*Theobroma cacao*); 22, Citrus (*Citrus* spp.); 23, Coconut palm plantation (*Cocos nucifera*); 24, Coffee (*Coffea* spp.); 25, Date palms cultivation (*Phoenix dactylifera*); 26, Oil palm (*Elaeis* spp.); 27, Olive plantations (*Olea europaea*); 28, Rubber (*Hevea brasiliensis)*; 29, Tea (*Camellia thea*); 30, Tea, coffee, eucalyptus

[g] Annual Cropland (AC): 31, Cereal (wheat, sunflower and/or milo); 32, Corn/ Maize (*Zea*); 33, Herbaceous crops, fruit trees and vines, abandoned fields and common thatching grass (*Hyparrhenia hirta*) meadows; 34, Maize, groundnut and other pulses; 35, Manioc (*Manihot esculenta*); 36, Pickets, acahuales and maize cultivation; 37, Potato and corn/maize; 38, Rice (*Oryza* spp.); 39, Rice, maize and yucca; 40, Soybean (*Glycine max);* 41, Sugar cane (*Saccharum*); x, unidentified (used only for conflicts)

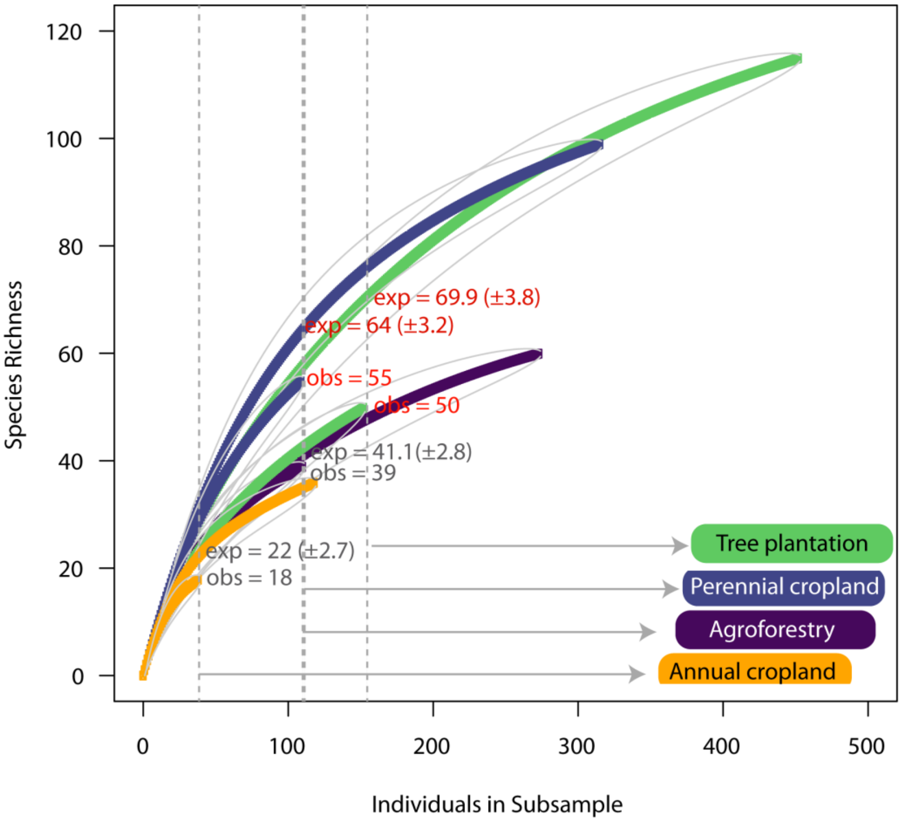
APPENDIX S4

Akaike's information criterion (AIC) of the saturated model (occurrence ~ Log body mass + Energetic Trophic Level + Locomotor Habitat rank + IUCN Red List rank + Agroecossystem Type + (1|sitio)) with and without family taxonomic information included as a random variable

Model description	**AIC**	**K**	**Chisq**	**P**
Saturated model with family	1362.4	8	1.241	0.2652
Saturated model without family	1361.6	7		

APPENDIX S5

Rarefaction curves and 95% confidence intervals (gray lines) for carnivore species richness based on the number of species that were either present and expected (nesting presence and absence) within 75 agricultural sites across four agroecosystem types. Dashed lines represent the minimum number of individuals within each subsample per agroecosystem type. Significant differences [at $p < 0.05$] between observed and expected species richness in each agroecosystem type are highlighted in red.



APPENDIX S6

Binomial Generalized Linear Mixed Model results for the most parsimonious model.

Term	**Estimate**	**Std. Error**	**Z value**	**Significance**
(Intercept)	0.2973	0.7096	0.419	0.675
IUCN Red List rank	-0.6246	0.1039	-6.009	$1.86\ e^{-09}$
Energetic Trophic Level	-0.6164	0.1103	-5.588	$2.30\ e^{-08}$
Log Body Mass (g)	0.2966	0.0595	4.984	$6.21\ e^{-07}$
Locomotion Mode	-0.3512	0.0846	-4.151	$3.31\ e^{-05}$

3. MULTI-SCALE MAMMAL RESPONSES TO LAND USE IN CACAO AGROFORESTRY LANDSCAPES IN THE BRAZILIAN ATLANTIC FOREST

Submitted to Journal of Applied Ecology

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ABSTRACT

1. Growing human populations and food demand will continue to transform landscapes so that the future of tropical forest biodiversity will largely depend on retaining species assemblages in highly human-modified landscapes.
2. We investigated how mammals in agroforestry landscapes respond to factors at local (habitat type), intermediate (land-use heterogeneity, forest cover and human population density in surrounding area) and large spatial scales (forest cover within landscapes). We surveyed medium-sized to large mammals using camera traps in traditional cacao agroforests (*cabrucas*), intensified cacao agroforests and forest remnants within two landscapes of southern Bahia, Brazil, exhibiting contrasting amounts of forest and agroforest cover.
3. Mammal assemblages responded to environmental factors at all scales considered. At local scale, habitat types differed in their potential to harbour mammal species, with forest remnants and *cabrucas* showing high conservation value, mainly in the high forest cover landscape, whereas intensified cacao agroforests contained less diversified species assemblages in both landscapes. At intermediate scales, the amount of surrounding forest elevated mammal species-richness in forest and intensified cacao agroforests, but this was reversed in *cabrucas*. Human population density affected mammal assemblage structure, with some species having higher abundances at sparsely settled sites, whereas others persisted in heavily-settled areas. At the largest scale, we highlight the importance of largely forested landscapes in supporting species-rich assemblages, including forest-dwelling species.
4. *Synthesis and applications*. Mammal assemblages responded to land-use change at multiple scales. Cacao agroforests contribute to mammal assemblage integrity provided that sufficiently large areas of secondary and old-growth forest at the landscape and canopy tree cover of traditional *cabrucas* are retained. We emphasise the imperative of maintaining forest remnants, to retain forest-dwelling mammals in human-dominated landscapes. Both land-sparing and land-sharing strategies should be

considered to conserve diverse mammal assemblages in agroforestry landscapes, as some species are impacted by human settlements and are highly dependent of forest remnants while others are highly tolerant of agroforestry habitats.

Keywords: agriculture, agroecosystem, forest cover, habitat type, heterogeneity, human density.

Running head: Mammal responses to agroforestry landscapes

3.1 INTRODUCTION

Several studies have advocated for biodiversity conservation in natural landscapes exposed to low levels of human activity (Fazey, Fischer, & Lindenmayer, 2005). However, one-tenth of all largely intact areas has been lost globally since the 1990s (Watson et al., 2016), with cropland and anthropogenic pastures covering almost 40% of the world's land surface (Foley et al., 2011). Growing human population, food and biofuel demands will boost further agricultural expansion and intensification, affecting mainly tropical ecosystems, where human populations are projected to grow most rapidly, through loss and/or structural changes in forest habitat (Laurance, Sayer, & Cassman, 2014). The future of biodiversity will thus largely depend on processes that affect species viability in human-modified landscapes (Chazdon et al., 2009; Gardner et al., 2009).

To understand the role of anthropogenic disturbance on biological diversity, effects should be assessed at different scales. At a local scale, factors such as vegetation structure influence local conditions and resource availability, and hence habitat quality. Anthropogenic land uses are often not entirely hostile for wildlife (Tscharntke et al., 2012), and human-modified landscapes are usualy comprised of environments with varying degrees of habitat suitability for native species (Daily, Ceballos, Pacheco, Suzán, & Sánchez-Azofeita, 2003; Harvey, Gonzalez, & Somarriba, 2006). Complex plantations, with a dense understorey and canopy layer, enhance biotic diversity compared to monocultures. Traditional agroforests, for example, are complex plantations where agricultural crops are shaded by trees and are identified as potential wildlife-friendly system (McNeely & Schroth, 2006). They play an important role in conserve biodiversity in agricultural landscapes, serving as habitats outside protected land, connecting reserves and alleviating resource-use pressure on conservation areas (Bhagwat, Willis, Birks, & Whittaker, 2008). For instance, traditional agroforests, for example, cacao and coffee, have been identified as a valuable ecosystem for retaining biodiversity in tropics (Caudill, DeClerk, Husband, 2015; Rice &Greenberg, 2000; Schroth & Harvey, 2007). However, agroforests are structurally simpler than native forests due to lower tree diversity and density, replacement of the native understorey with crops, and high variation in canopy structure and species composition among farms (Sambuichi, 2002).

Local phenomena cannot be fully understood without considering the influence of surrouding characteristics (Mazerolle & Villard, 1999). These features frequently correlated with species assemblages include the amount of native vegetation, prevalence of anthropogenic edges, degree of landscape connectivity, and structure and heterogeneity of modified habitats (Fischer & Lindenmayer, 2007). Landscapes providing low habitat availability support fewer individuals (Fahrig, 2003), and loss of native vegetation around habitat remnants leads to native species declines worldwide (Andrén, 1994; Estavillo, Pardini, & Rocha, 2013; Pardini, Nichols, & Püttker, 2017). Conversely, greater land-use heterogeneity may increase biodiversity (Benton, Vickery, & Wilson, 2003), as the diversity of land-uses ensures accumulation of species requiring different habitats across the surrounding areas (Fahrig et al., 2011). Human population density is another strong indicator of threats to biodiversity (Luck, 2007) related to habitat loss, spread of exotic species, and overhunting (Cardillo et al., 2004).

The amount of native habitat surrouding any given patch often determines the dispersal capacity of native species (Fahrig, 2003), but few studies have addressed the importance of native habitat cover at large scales (but see Faria, Laps, Baumgarten, & Cetra, 2006; Martensen, Ribeiro, Banks-Leite, Prado, & Metzger, 2012; Pardini, Bueno, Gardner, Prado, & Metzger, 2010). The role of scale in ecology is recognized as vitally important to understand ecological patterns and processes (Graf, Bollmann, Suter, & Bugmann, 2005; Jackson & Fahrig, 2015), and the scale at which modelling is performed can strongly influence model outputs (Cushman & McGarigal, 2004).

Large mammals play important ecosystem roles through seed dispersal, predation (Terborgh et al., 2008; Wright, 2003), prey population control, and herbivory (Terborgh et al., 2001). Declining mammal species have lost over 50% of their continental populations, and extinctions are most prevalent in densely settled landscapes (Ceballos & Ehrlich, 2002). However, mammals have been recorded in agricultural matrixes worldwide (Ferreira, Peres, Bogoni, & Cassano, 2018; Ramírez & Simonetti, 2011), with emphasis on traditional agroforests that compared with others plantations sustain a high diversity of species due maintenance of multifunctional shade-trees (Caudill & Rice, 2016; Harvey, Gonzalez, & Somarriba, 2006). Understand more about the distribution of mammals and land use effects on this group in agroforestry landscapes is crucial to avoid future extinctions, given this relentless worldwide habitat conversion (Perfecto & Vandermeer, 2008)

Here we investigate how medium-sized to large mammal assemblages respond to land use change at different spatial scales: local (habitat type: old-growth and mid-successional forest, *cabruca* and intensified cacao agroforest), intermediate (surrounding land-use heterogeneity, percentage of forest cover and human population density), and large (forest cover across the landscape). We hypothesized that the large scale would be the strongest predictor of mammals' distribution (Faria, Paciencia, Dixo, Laps, & Baumgarten, 2007) and can modify the effects in smaller scales. In other scales, we expected that mammal species richness, abundance and biomass would increase with habitat quality (forest > *cabruca* > intensified cacao agroforest), forest cover and land-use heterogeneity and decrease with human population density. We also expected that the same direction of the variables influences on assemblage structure, with higher impacts on species that are sensitive to anthropogenic disturbance.

3.2 MATERIAL AND METHODS

Study area and sampling design

This study was carried out in southern Bahia, Brazil, where approximately 600,000 ha of land are occupied by cacao plantations (Landau, Hirsch, & Musinsky, 2008). We surveyed the medium-sized to large mammals within two large landscapes that are approximately 80 km apart: one largely covered by mature and late secondary forest in Una (66.822 ha with 50% old-growth and mid-successional forest cover, 15% cacao agroforestry; 15°03′–15°16′ S, 39°00′–39°17′ W), including the "Una Biological Reserve" (18.715 ha) and at least 14.216 ha of privately owned forest fragments contiguous to the reserve (Araujo, Alger, Rocha, & Mesquita,1988); and another in Ilhéus, mainly occupied by cacao farms (29.264 ha with 5% old-growth and mid-successional forest cover, 60% cacao agroforestry; 14°35′–14º46′ S, 39°08′–39°17′ W) and with few and very small forestry patches ranging from 1 to 300 ha (Fig.1). These landscapes, referred, hereafter, as high forest cover (HFC) and low forest cover (LFC), show similar aspects related to climate, original vegetation (Mori & Boom, 1983; Thomas, 2003) and mammal group (Prado et al., 2003), being the land use the main difference taken into account.

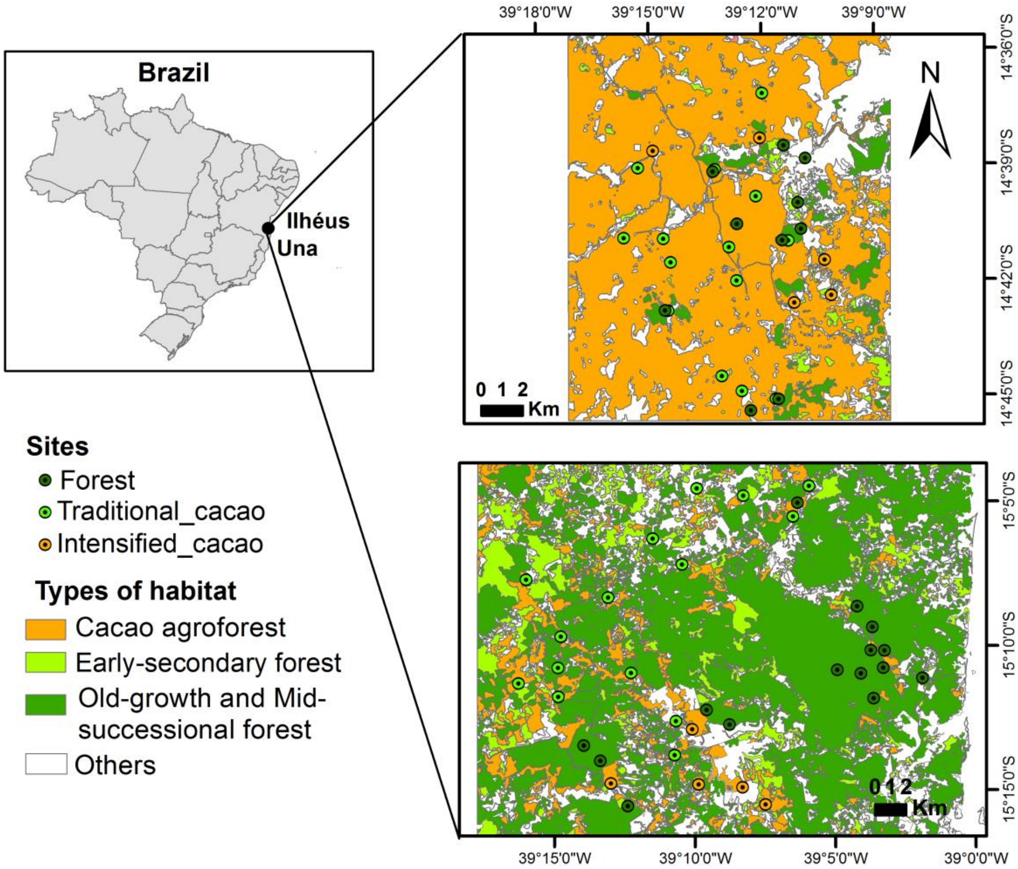

Fig. 1. Distribution of sampling sites along the Atlantic forest, including 30 traditional cacao agroforests, 10 intensified cacao agroforests and 20 forest sites in Ilhéus (top panel) and Una (bottom panel), southern Bahia, Brazil.

The study was conducted at 30 *cabrucas* (15 sites in each landscape), 10 intensified cacao agroforests (five sites in each landscape) and 25 old-growth and mid-successional forests (15 sites at Una and 10 at Ilhéus; Fig. 2). *Cabrucas* are complex agroforestry stands where small cacao (*Theobroma cacao*) trees are shaded by diverse canopy trees species (Rice and Greenberg 2001). Intensified cacao agroforests are structurally simpler systems, with understorey cacao trees largely or entirely shaded by exotic species, such as caja (*Spondias mombin*), *Erythrina* spp., jackfruit (*Artocapus heterophyllus*), palms (*Euterpe oleracea*), rubber trees (*Hevea brasiliensis*), and others.

Fig. 2. General structural profile of surveyed habitats: 1) native old-growth forest, 2) traditional cacao agroforest (*cabrucas*), and 3) intensified cacao agroforest, shaded by rubber trees (*Hevea brasiliensis*) in Una, southern Bahia, Brazil.

Sampling sites were spaced apart by a minimum distance of 800 m, with exception of four forest sites at Ilhéus, which were spaced apart by 120 – 293 m from *cabrucas*. *Cabruca* sites were repeatedly sampled during four surveys, representing two seasons (warmest season: January-March; and coolest season: June-August) in different years. Forest sites were surveyed up to four times, whereas intensified agroforest sites were surveyed only once in the warmest season. Sites at Una were surveyed in 2016 and 2017 and those at Ilhéus between 2013 and 2017.

Data acquisition

Mammal sampling

We deployed one camera-trap (Trapa Camera or Bushnell) at each sampling site, 30 cm above ground, baited with sardine and banana to surveying medium-sized to large terrestrial mammals. We also included *Didelphis aurita* (small mammal) and some arboreals, that were attracted by bait in the ground, because this method is efficient to record these species (Cassano, Barlow, & Pardini, 2012; 2014) and they are game (Castilho, De Vleeschouwer, Milner-Gulland, & Schiavetti, 2017), endemic and/or threatened species (i.e. *Callithrix kuhlii* and *Sapajus xanthosternos*) following IUCN red list. One record of *Lontra longicaudis* was excluded from analysis because the sample design used was not efficient to record semi-aquatic species. During each survey, cameras remained active for 30 days continuously and were checked weekly for maintenance and rebaiting. Due to camera-trap malfunction and different sampling effort between habitats, we obtained a total of 1569, 3382 and 290 camera-trap-days for forest, *cabrucas* and intensified cacao agroforest, respectively. Our analyses, however, explicitly account for differences in sampling effort.

Extraction of variables in intermediate scale and scale setting

Maps of both landscapes were obtained from a mix of high-resolution images (Geoeye-1, WorldView-1 e WorldView-2) between 2010 and 2011. We used ArcGIS 10.1 to calculate the percentage of old-growth and mid-successional secondary forest cover (hereafter, forest cover) and land-use heterogeneity (calculated as Shannon’s diversity index, [exp. (H’)]) within circular buffers around the sampling sites. We used the *diversity* function in the *vegan* package (Oksanen et al. 2016) in R 3.3.2 (R Core Team 2017) to calculate land-use heterogeneity. Both variables were quantified for buffer areas of 500 m, 1000 m, 1500 m and 2000 m, often used in studies on medium-sized to large mammals (Beca et al., 2017; Benchimol & Peres, 2015; Regolin et al., 2017).

To assess the spatial scales at which variables best explained estimates of mammal abundance, biomass and species richness, we constructed generalized linear models (GLMs) and used the McFadden's pseudo R^2 statistic to assess the predictive strength of the generalized model (Hu, Shao, & Palta, 2006). The 2000-m radius was selected because it produced the highest McFadden's pseudo-R^2 values for most models considering both surrounding variables (Table S1-1).

We estimated neighbouring human population density (HPD, per km²) using circular areas of 2000-m and 3000-m radius overlapping a spatial projection of census data from the Instituto Brasileiro de Geografia e Estatística (IBGE 2010). We considered HPD within a 3000-m radius because (i) it produced stronger correlations with response variables in GLMs (Table S1-1); and (ii) local residents in our study areas moved widely on foot or motorized vehicles. However, we avoided radii larger than 3000 m to maximize spatial independence among neighbouring sites.

Data analysis

We excluded images of the same species at the same camera-trapping station within a period of 24 h and calculated sampling effort (trap-days) excluding intervals of camera-trap malfunction to estimate four response variables: species richness, abundance, biomass, and assemblage structure. We estimated species richness using rarefaction or extrapolation, with Hill numbers ^{0}D (Chao et al., 2014), considering a standard effort of 50 photos, using the *iNEXT* package (Hsieh, Ma, & Chao. 2016). We used this threshold because this was approximately twice the average number of photos per site, and most sites reached an asymptote between 40 and 50 photos (Fig. S1-1). We calculated abundance as the sum of independent records of a given species at each site weighted by the sampling effort. For biomass and community structure, we considered species capture rates (abundance/sampling effort *30) that represented the number of records expected for a 30-day period, corresponding to one survey period. We calculated biomass per site by summing the species-specific capture rates multiplied by the corresponding mean adult body mass (Gonçalves et al., 2018; Wilman et al., 2014).

We used GLMs to examine the influence of habitat type (forest, traditional and intensified agroforests) at the local scale; forest cover, land-use heterogeneity and, HPD at intermediate scales; and landscapes (HFC e LFC) at large scale on mammal species richness, abundance, and biomass. HPD was log transformed and mean biomass was sqrt-transformed prior to analyses. We examined the spatial autocorrelation in the residuals of the full model using a variogram computed with the *gstat* package (Pebesma, 2004) (Fig. S1-2) and used the Generalized Variance Inflation Factor to test for multicollinearity (GVIF > 3) between independent variables using the *car* package (Fox & Weisberg, 2011) (Table S2-1). We applied stepwise multivariate regression analysis with backward selection until all remaining covariates had *P* values < 0.05, based on the likelihood ratio test. We began selection with the full model and used the functions *drop1* and *anova* to select the final model for each dependent variable (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Models were validated using graphs to verify homogeneity, normality and independence (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Given our prior expectations, we included interactions between landscape and habitat type, landscape and forest cover, and habitat type and forest cover in the full models. As survey effort varied among sampling sites, effort was included as an offset term in models constructed to explain mammal abundance. The negative binomial distribution was used for the abundance models because of over-dispersion, but we used a Gaussian distribution for biomass and estimated species richness.

We used non-metric multidimensional scaling (NMDS) with the function *metaMDS* of the *vegan* package (Oksanen et al., 2016) to summarize the assemblage structure, using the Bray-Curtis dissimilarity index on the basis of species capture rates. We used Permutational multivariate analysis of variance (Permanova: Anderson, 2017) with 999 permutations to test if independent variables affected assemblage structure, using the *adonis* function in the *vegan* package. All analyses were performed in R 3.3.2 (R Core Team 2017).

3.3 RESULTS

We recorded a total of 23 native and six exotic mammal species. Domestic dogs were the most ubiquitous species, recorded at 47 sites in agroforests (27 in traditional and 7 in intensified cacao agroforests) and in about half of forest sites (13). The most widespread native species was *Cerdocyon thous* (40 sites), followed by *Didelphis aurita* (33), *Eira barbara* (33) and *Callithrix kuhlii* (30). *Puma yagouaroundi* and *Sylvilagus brasiliensis* were the most restricted species, with only one record each at traditional cacao agroforests.

Observed native species richness per site ranged from 0 to 11. Species richness responded to landscape, proportion of forest cover and habitat type, with a significant interaction between habitat type and both landscape ($p < 0.01$), and forest cover ($p < 0.01$; Fig. S2-1). Within landscapes, mean estimated richness was similar between forest and *cabrucas* (HFC landscape: forest = 6.9 (± 2.4), *cabruca* = 6.9 (± 2.7); LFC landscape: forest = 4.0 (± 2.5), *cabruca* = 5.2 (± 2.7)), but *cabrucas* at HFC landscape contained more species than forests at LFC landscape, and intensified cacao agroforests had the lowest species richness [HFC landscape = 1.8 (± 2.9), LFC landscape = 1.8 (± 1.8)]. The highest species richness was recorded at forests surrounded by higher amounts of forest cover, but the opposite was observed for *cabrucas* (Table 1; Fig. 3).

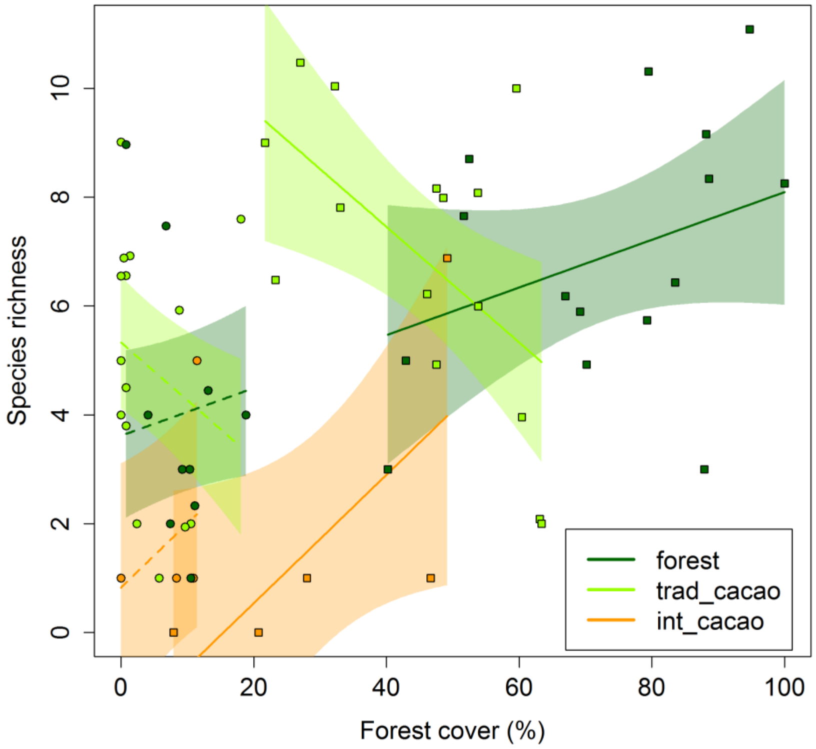

Fig. 3 Relationship between estimated species richness and percentage of forest cover surrounding 65 sites surveyed at two landscapes in southern Bahia, Brazil: Low forest cover landscape (dashed lines, circles) and High forest cover landscape (solid lines, squares). Mid-successional and old-growth forest (forest), *cabrucas* (trad_cacao) and intensified cacao agroforests (int_cacao) are colour-coded in dark green, light green and orange, respectively.

Table 1: Coefficients and *p*-values of selected models based on 65 survey sites explaining estimated species richness, abundance and biomass of medium-sized to large mammals, which were generated by backward selection. McFadden's pseudo-R^2 values are indicated for final models.

	Richness		**Abundance**		**Biomass**	
	estimate	*p*-value	estimate	*p*-value	estimate	*p*-value
Intercept	**3.61**	**< 0.01**	**-0.84**	**< 0.01**	**164.76**	**< 0.01**
Landscape (HFC)	0.10	0.96	0.23	0.71	-64.39	0.22
Habitat: intensified cacao	-2.79	0.05	**-1.67**	**< 0.01**	-4.47	0.89
Habitat: traditional cacao	1.71	0.09	**-1.26**	**< 0.01**	**-57.44**	**0.03**
Forest cover	0.04	0.18	-0.00	0.94	-3.21	0.13
Landscape (HFC): habitat (intensified cacao)	-2.75	0.37	**-3.19**	**< 0.01**	-61.13	0.22
Landscape (HFC): habitat (traditional cacao)	6.27	0.04	0.99	0.22	**95.55**	**0.01**

Landscape (HFC): forest cover	NA	NA	NA	NA	**4.83**	**0.03**
Habitat intensified cacao: forest cover	0.07	0.31	**0.10**	**< 0.01**	NA	NA
Habitat traditional cacao: forest cover	**-0.15**	**< 0.01**	0.00	0.74	NA	NA
McFadden's pseudo-R^2	0.13		0.10		0.07	

NA: not included in selected models

Mammal abundance was also affected by landscape, forest cover, and habitat type (Table 1; Fig 4; Fig. S2-2), with an interaction between habitat type and both landscape ($p < 0.01$) and forest cover ($p < 0.01$). Mammal abundance was lower in intensified and traditional agroforests compared to forests, with a positive effect of forest cover on mammal abundance only in intensified agroforests.

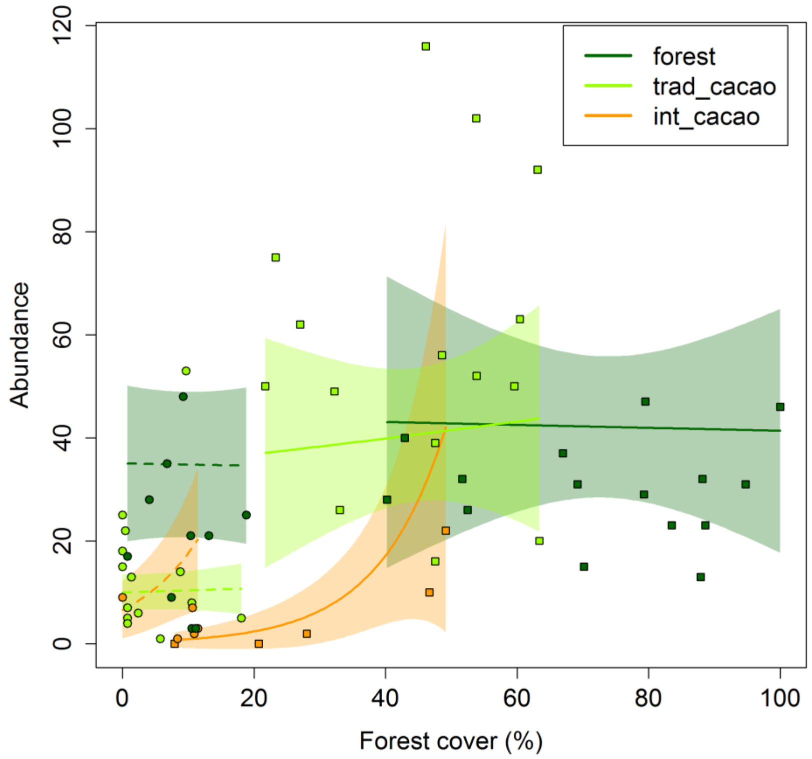

Fig. 4 Relationships between abundance and the amount of forest cover surrounding 65 sites across different habitat types [(forests (forest), traditional cacao agroforests (trad_cacao) and intensified cacao agroforests (int_cacao)] in Low forest cover landscape (dashed lines, circles) and High forest cover landscape (solid lines, squares), southern Bahia, Brazil.

Habitat type ($p < 0.01$) and the amount of surrounding forest ($p = 0.03$) both affected the biomass of mammal assemblages but this depended on the landscape context (Table 1, Fig. S2-3). In general, mammal biomass was lower in traditional agroforests than in old-growth forests, but *cabrucas* at HFC landscape had higher biomass than forests at LFC landscape. Moreover, biomass increased with forest cover at HFC landscape but decreased at LFC landscape (Fig. 5).

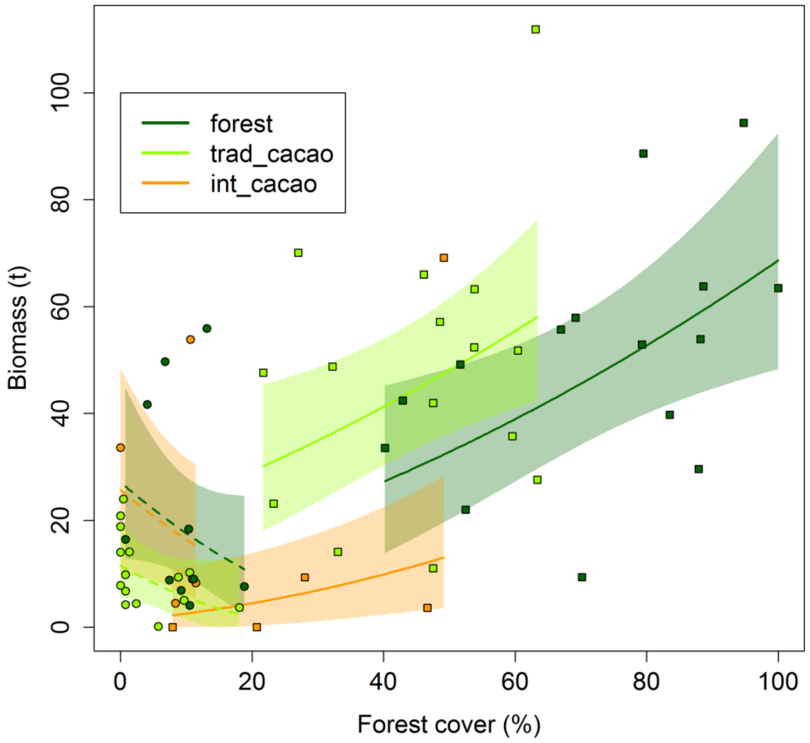

Fig. 5. Relationships between a measure of aggregate biomass and the amount of forest cover surrounding 65 sites across different habitat types [(forests (forest), traditional cacao agroforests (trad_cacao) and intensified cacao agroforests (int_cacao)] in Low forest cover landscape (dashed lines, circles) and High forest cover landscape (solid lines, squares), southern Bahia, Brazil.

The structure of medium-sized to large mammal assemblages differed across landscapes (R^2 = 0.09, p < 0.01), habitat types (R^2 = 0.10, p < 0.01), and along the human population density gradient (R^2 = 0.03, p < 0.01) (Table S2-2). We also detected an effect of forest cover on assemblage structure, depending on habitat type (R^2 = 0.04, p = 0.02). Eight forest-dwelling species (*Dasyprocta leporina*, *Mazama gouazoubira*, *Pecari tajacu*, *Potos flavus*, *Puma concolor*, *Puma yagouaroundi*, *Sciurus aestuans* and *S. brasiliensis*) were only recorded at HFC landscape, whereas one species (*Mazama americana*) was recorded only at LFC landscape. *Euphractus sexcinctus* was more common at LFC landscape, whereas *Cuniculus paca*, *Didelphis aurita*, *Eira barbara* and *Tamandua tetradactyla* were more common at HFC landscape (Table S3). Only nine species were recorded in intensified cacao agroforests, compared to 19 species in *cabrucas* and 20 in forests. Four species were entirely restricted to forest (*Cabassous tatouay*, *Potos flavus*, *Sapajus xanthosternos* and *Sciurus aestuans*), or only recorded once or twice in *cabrucas* (*M*. *americana*, *P*. *yagouaroundi* and *S*. *brasiliensis*) (Fig. S3). *D*. *leporina*, *E*. *barbara*, *Nasua nasua* and *P*. *tajacu* were more abundant in forest sites, but were also recorded in other habitats. Species responses to human population density were variable. For example, *P*. *tajacu*, *P*. *flavus*, *P*. *concolor*, *S*. *aestuans* and *T*. *tetradactyla* were most abundant at sparsely settled sites, whereas commensal species such as *C*. *thous* and *C*. *kuhlii* were most abundant in heavily settled areas (Fig. 6).

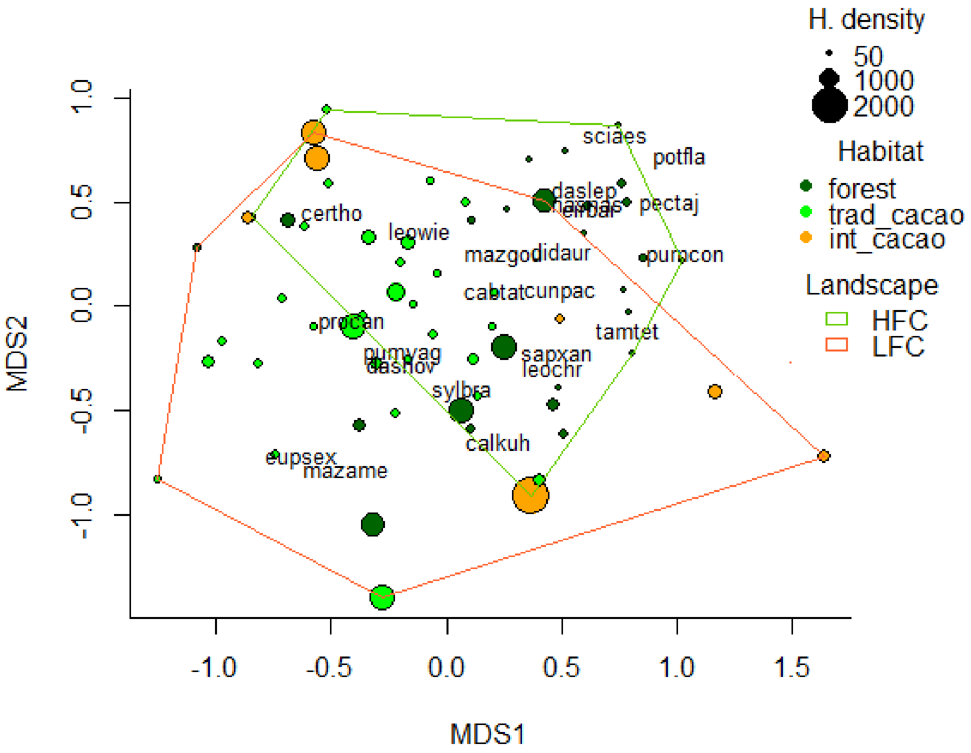

Fig. 6 Multi-dimensional scaling biplot showing 63 sampling sites in southern Bahia, Brazil, ordered by large and medium-sized mammal assemblage structure. Symbols are sizes according to human population density and coloured according to habitat types [(forests (forest), traditional cacao agroforests (trad_cacao) and intensified cacao agroforests (int_cacao)]. The two landscapes sampled are included within convex hulls (HFC: High forest cover and LFC: low forest cover landscapes). Species Latin binomial codes can be found in Table S5 -1.

3.4 DISCUSSION

Although tropical agroforestry systems have the potential to sustain native biodiversity in human-dominated landscapes (Bhagwat, Willis, Birks, & Whittaker, 2008), we show that it entirely depends on the degree to which previously undisturbed forests have been modified. Similar to other studies (e.g. Cassano et al., 2012; Estrada et al., 1994; Harvey et al., 2006), our results indicate that traditional cacao agroforests retain a high conservation value for mammals, even in landscapes that are heavily dominated by this land use, benefiting from little habitat subsidies from adjacent old-growth forests. However, intensified cacao agroforests, with a low diversity of shade trees, were used by very few mammal species, corroborating previous findings that only structurally complex vegetation containing high floristic diversity favours animal diversity in Neotropical cacao agroforests (Schroth & Harvey, 2007).

In general, complex agroforests maintain higher levels of species diversity than others agroecosystems, but lower comparable measures of diversity than natural forests (cf. Leakey, 2014; Pardini et al., 2009). In general, we found similar species richness between forests and *cabrucas* but lower biomass in *cabrucas*. At the HFC landscape, however, *cabrucas* showed higher richness and biomass than remaining forest patches at LFC landscape because some species occurred only in HFC landscape. Further some generalist species, such as *C*. *kuhlii*, *C*. *thous* and *Procyon cancrivorus*, obtained higher abundance in traditional agroforests at HFC landscape compared with the forests at LFC landscape, adding biomass in these sites. We showed that *cabrucas* can harbour a diversified mammal assemblage, including regionally rare species, some of which were recorded only once. Nevertheless, forest-dwelling species were largely restricted to, and occurred at their highest abundances in forests, and were predominantly retained at the HFC landscape, indicating the irreplaceability of native habitat for the persistence of forest-dwellings in tropical landscapes.

Predicting species persistence in agricultural landscapes requires an understanding of the surrounding habitat patches (Devictor & Jiguet, 2007). Most studies have found a positive correlation between land-use heterogeneity around sites and faunal species diversity (e.g. Tews et al., 2004), but this is at odds with our results. This can be attributed to the relatively low contrast between habitat quality (especially between forests and *cabrucas*) in addition to the fact that landscapes sharing the same degree of heterogeneity, as measured by the Shannon diversity index, can differ widely in spatial configuration.

In relation to the role of habitat amount in terms of surrounding forest cover, our findings were largely consistent with previous studies reporting higher vertebrate species richness and abundance in sites surrounded by high amount of forest (Cassano, Barlow, & Pardini, 2014; Martensen et al., 2012). Forest landscapes containing larger and more connected patches are less likely to be overhunted (Peres, 2001), also ensuring higher occupancy by large-bodied vertebrates (Magioli et al., 2016; Prugh, Hodges, Sinclair, & Brashares, 2008), and this seems to be the case of our forest sites. In intensified cacao agroforests, the positive effect of surrounding forest cover on mammal abundance may result from source proximity (Diffendorfer, 1998) and a generally more benign context acting as corridors and/or stepping stones (Baum, Haynes, Dillemuth, & Cronin, 2004) in connecting individuals between forest patches. The opposite pattern, however, was evident for species richness at all *cabrucas* and biomass estimates at *cabrucas* within LFC landscape. Although *cabrucas* are widely considered as suitable habitat for many mammal species (Cassano et al., 2012; Oliveira, Neves, Raboy, & Dietz, 2011), they were more species-poor when surrounded by higher levels of forest cover due to the absence of some forest-dwelling species. We suggest that the positive influence of forest cover on biomass at HFC landscape, but not at LFC landscape, can be attributed to differences in species composition and abundance between landscapes. As overall forest cover increased at HFC landscape, some species, such as *M. gouazoubira*, *P. tajacu*, *E. barbara*, *T. tetradactyla,* were clearly favoured, but this was not the case at LFC landscape, where large-bodied species such as *C. thous* and *P. cancrivorus* were less abundant. These carnivore species are typically described as habitat and dietary generalists, and tolerant to anthropogenic environments (Magioli, de Barros Ferraz, & Rodrigues, 2014), often thriving in agricultural habitats (Alves, Fonseca, & Engel, 2012; Cassano et al., 2014; Dotta & Verdade, 2011).

Despite the importance of habitat complexity and surrounding context in maintaining mammalian diversity, little attention has been given to the characteristics of wider landscapes (but see Anand, Krishnaswamy, Kumar, & Bali, 2010; Faria et al., 2007). Our study clearly shows that natural forests and *cabrucas* at HFC landscape harbour more forest-dwelling species and more species-rich assemblages that on average are comprised of larger-bodied species. This is consistent with a study on birds and bats in the same study areas, which emphasizes the imperative of retaining native forest remnants to support biodiversity persistence in landscapes dominated by cacao agroforestry (Faria et al., 2006). Yet the opposite pattern of lower mammal species richness, abundance and biomass was observed in intensified cacao agroforests even in the HFC landscape. This was almost certainly due to the monodominance of rubber trees used as overstorey shade at HFC landscape, whereas the canopy layer in intensified cacao agroforests at LFC landscape was comprised of more than one exotic species. This highlights the necessity of maintaining the diversity of shade trees in traditional agroforests for guarantee conservation of biodiversity and consequently of ecosystems services (Santos, Crouzeilles, & Sansevero, 2019).

Human-wildlife conflicts are often emphasised in a land-sharing context where wildlife coexists with agropastoral systems (Crespin & Simonetti, 2018). Mammal assemblages fare poorly in close proximity to human settlements due to habitat loss, overhunting, resource competition with humans and livestock, and diseases sourced from exotic animals such as domesticated dogs (Chiarello, 2000; Cullen Jr., Bodmer, & Valladares Pádua, 2000; Frigeri, Cassano, & Pardini, 2014; Lessa, Ferreguetti, Kajin, Dickman, & Bergallo, 2017; Woodroffe, 2000). Although we failed to detect any effects of human population density on mammal species richness, abundance and biomass, mammal assemblage structure was clearly affected due to changes in species composition and abundance in more heavily settled areas. Hunting for subsistence by rural dwellers is still widespread in southern Bahia and several species that were absent or virtually absent in the most heavily-settled areas (*C. paca*, *D. aurita*, *D. leporina*, *M. gouazoubira*, *N. nasua* and *P. tajacu*), are important game species (Castilho, De Vleeschouwer, Milner-Gulland, & Schiavetti, 2017), two of which (*C. paca* and *P. tajacu*) are also pursued by either domestic or feral dogs in traditional cacao agroforests (dos Santos et al., 2018). Conversely, species such as *C. thous* and *C. kuhlii* were more common in heavily populated areas, attesting to the disturbance-tolerance of those species. These species show high levels of ecological and/or behavioural plasticity, are often human commensals, and may be favored by the absence of strict forest-dwelling species, as they side-step resource competition

(Ferraz, Siqueira, Martin, Esteves, & Couto, 2010; Ferreira, Le Pendu, & Martinez, 2018).

Our study shows that agroforestry landscapes can harbour considerable diversity of medium-sized to large mammals in the Atlantic Forest biome, with patterns of land-use predicting mammal assemblage structure at multiple scales. We highlight the potential for traditional agroforests to support mammalian assemblages, as long as traditional shade management and sufficient areas of natural forests are retained within any given landscape. From a policy perspective, it is critical to note that agroforestry systems are currently permitted to replace native forests in privately protected areas in Brazil (namely in Legal Reserves within private landholdings; Nº 12.651, 25th May 2012). We here emphasise that the effects of traditional agroforestry on forest vertebrates largely depend on the type of agroforestry management used. Moreover, more widespread use of agroforestry systems at the expense of native vegetation will likely detrimentally affect mammal assemblages.

We claim that both land-sparing and land-sharing strategies (Green, Cornell, Scharlemann, & Balmford, 2005) should be considered to retain diverse mammal assemblages within agroforestry landscapes. In a land-sharing context, some mammal species can routinely use agroforests as foraging or connecting habitat and coexist with high human population densities, otherwise, in a land-sparing context, forest patches are essential to guarantee the persistence of game and forest-dwelling species. We therefore highlight the critical importance of native forest remnants and traditional agroforests underneath a diversified overstorey if forest species are to persist in these human-modified landscapes.

3.5 AUTHORS’ CONTRIBUTIONS

ASF, CRC and CAP conceived the ideas and designed the methodology; ASF collected the data; ASF and PD analysed the data; ASF, CRC, CAP and PD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

3.6 DATA ACCESSIBILITY

Data will be available from Mendeley dataset (https://data.mendeley.com/).

3.7 ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

APPENDIX 1

Table S1-1

Coefficient of determination (McFadden's pseudo-R^2) and *p*-values for generalized linear models of abundance, biomass and estimated species richness as a function of percentage of forest cover (forest), exponential Shannon's index - exp. (H') - and human population density (HPD) around survey sites using different buffers. The highest value from each independent variable is highlighted in bold. McFadden's pseudo-R^2 values were calculated using the *pscl* package (Jackman, 2017) in R 3.3.2 (R Core Team 2017).

	Abundance		**Biomass**		**Richness**	
Forest	*pseudo R^2*	*p-value*	*pseudo R^2*	*p-value*	*pseudo R^2*	*p-value*
500	0.025	0.046*	0.017	0.00038***	0.017	0.020*
1000	0.030	0.0047**	0.029	$5.21e^{-6}$***	0.024	0.0062**
1500	0.037	0.00028***	0.040	$7.97e^{-8}$***	**0.028**	0.0027**
2000	**0.041**	0.000082***	**0.043**	$2.75e^{-8}$***	0.027	0.0034**
Exp. H'						
500	0.019	0.57	0.00032	0.63	**0.0039**	0.27
1000	0.020	0.36	0.000068	0.82	0.00042	0.71
1500	0.022	0.17	0.00077	0.46	0.000034	0.92
2000	**0.025**	0.050*	**0.0026**	0.17	0.0013	0.52
HPD						
2000	0.19	0.61	0.0080	0.016*	0.023	0.0068**
3000	**0.022**	0.11	**0.14**	0.0014**	**0.055**	0.000031***

Significance codes: 0.001 '***' 0.01 '**' 0.05 '*'

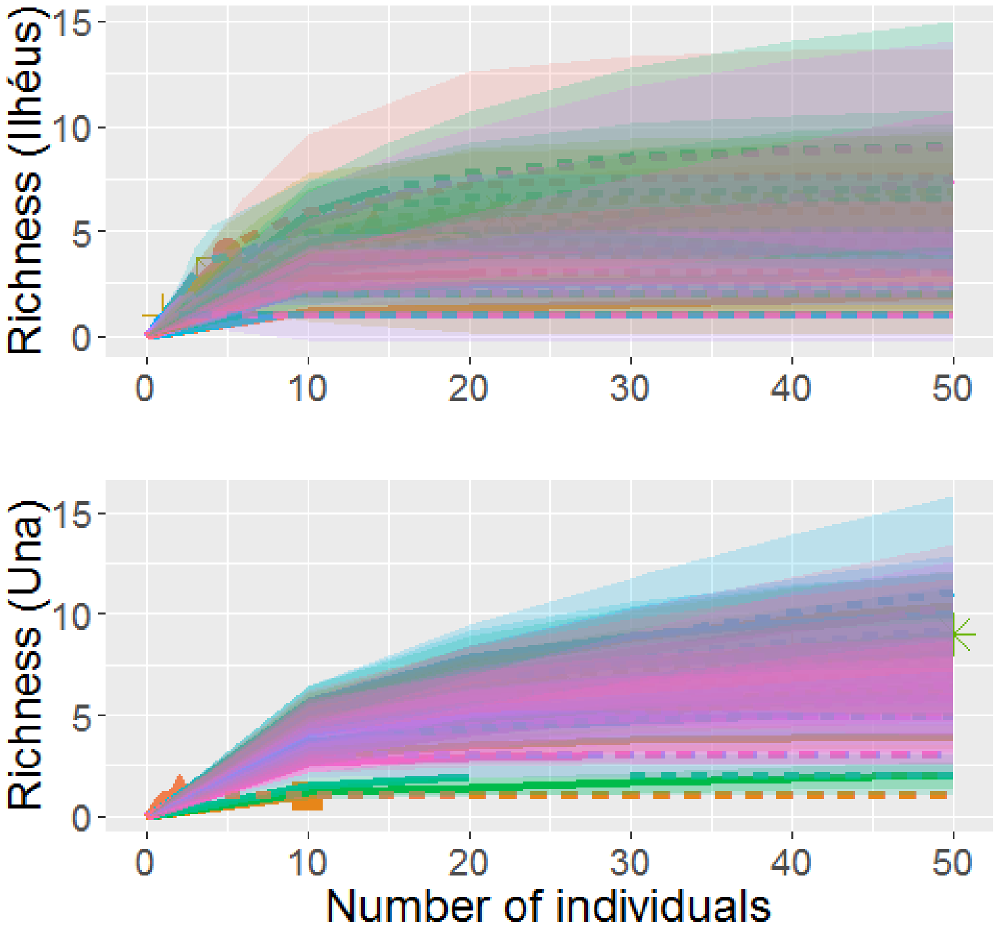

Figure S1-1 Estimated mammal species richness on the basis of 50 photos at 65 sites surveyed using camera-traps in the Ilhéus and Una study landscapes, southern Bahia, Brazil. Estimated species richness was generated using rarefaction and extrapolation with Hill numbers ^0D (Chao et al., 2014) based on abundance at 50 independent photos using the *iNEXT* package (T. C. Hsieh, K. H. Ma, & Anne Chao. 2016) in R 3.3.2 (R Core Team 2017).

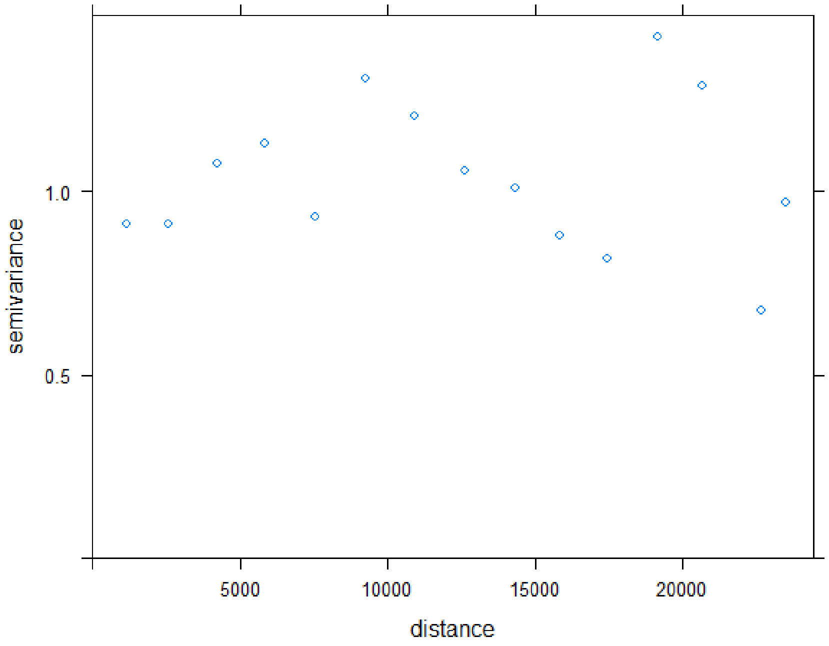

Figure S1-2 Experimental spatial variogram of full model residuals showing lack of spatial autocorrelation among survey sites.

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APPENDIX 2

Table S2-1

Generalized variance Inflation Factor (GVIF) showing if there is multicollinearity (GVIF > 3) between the independent variables [Percentage of forest cover in a buffer of 2000 m, habitat type (forest, traditional cacao agroforest and intensified cacao agroforest), human population density (HPD) in a buffer of 3000 m (number of dwellers), landscapes (Una: high forest cover and Ilhéus: low forest cover) and exponential Shannon's index (land-use heterogeneity within a buffer of 2000 m)] in full models with abundance, biomass (sq-rt x) and estimated species richness of medium-sized to large mammals at 65 survey sites as dependent variables. This was developed using the *car* package (Fox & Weisberg, 2011) in the R platform 3.3.2 (R Core Team 2017).

Abundance	**df**	**GVIF (1/(2*df)) (richness)**	**GVIF (1/(2*df)) (abundance)**	**GVIF (1/(2*df)) (biomass)**
Forest cover	1	2.02	2.46	2.45
Habitat	2	1.16	1.16	1.16
Log_{10}(HPD)	1	1.55	1.55	1.55
Landscape	1	2.45	2.04	2.03
Exponential Shannon's index	1	1.06	1.07	1.06

Fig. S2

Figures show the estimates, 95% confidence intervals and *p*-value significance (0.001 ***, 0.01** and 0.05*) of the final models generated by backward selection (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) in terms of estimated species richness (1), abundance (2) and sq-rt of mean biomass (3) of medium-sized to large mammals at 65 survey sites. McFadden's pseudo R^2 are shown for final models.

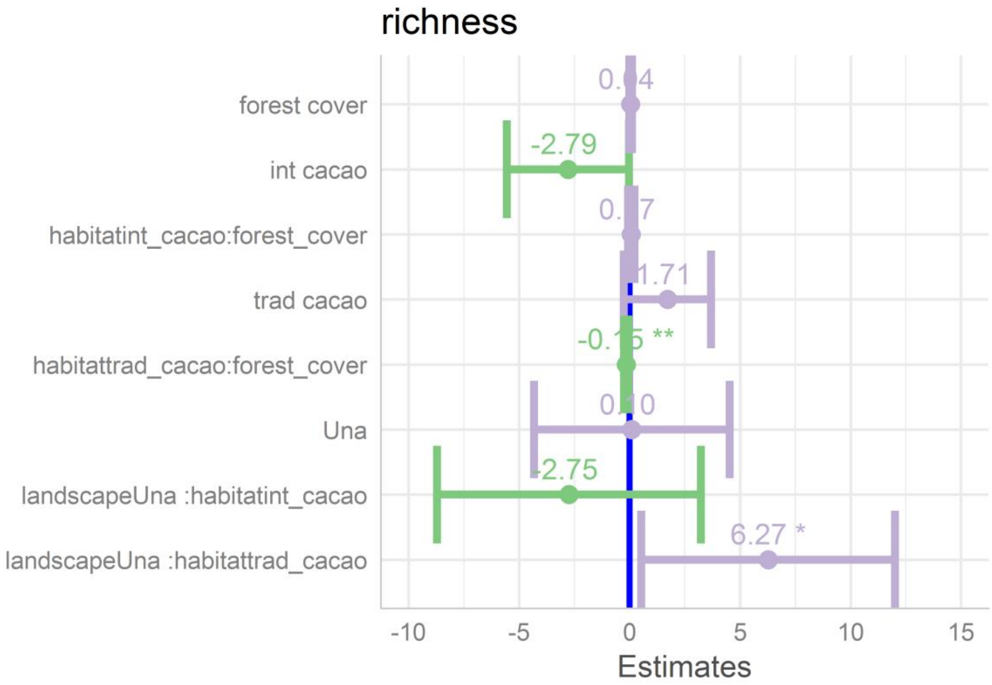

Fig S2 - 1 Model: Richness ~ landscape + habitat + forest cover + landscape:habitat + landscape:forest cover. McFadden's pseudo-R^2 = 0.13.

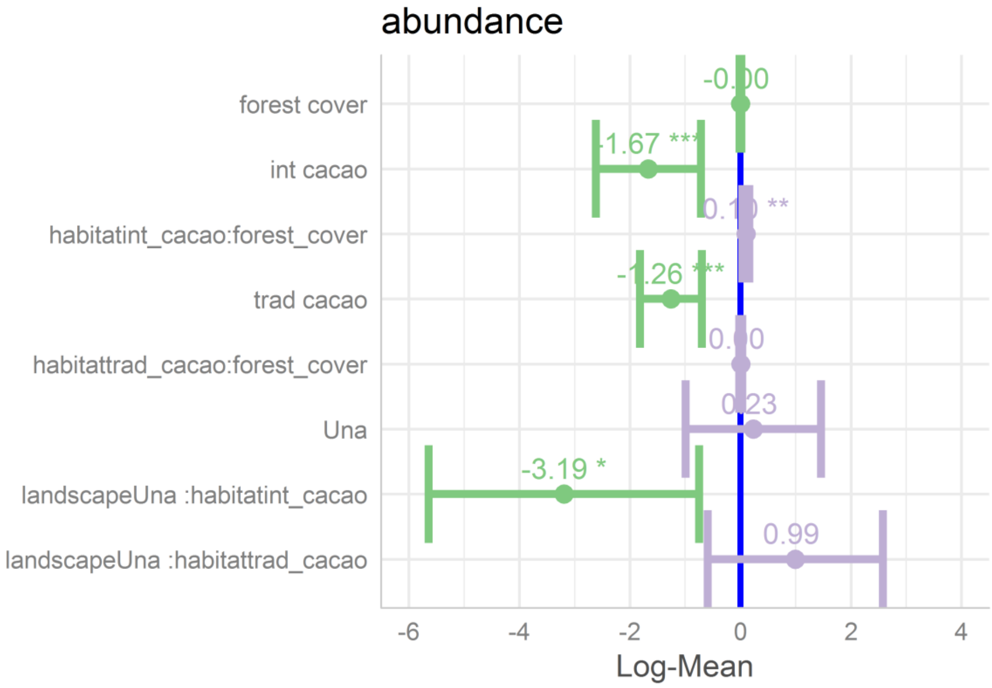

Fig. S2 – 2 Model: Abundance ~ ladscape + habitat + forest cover + landscape:habitat + habitat:forest cover + offset (log(effort)). McFadden's pseudo-R^2 = 0.10

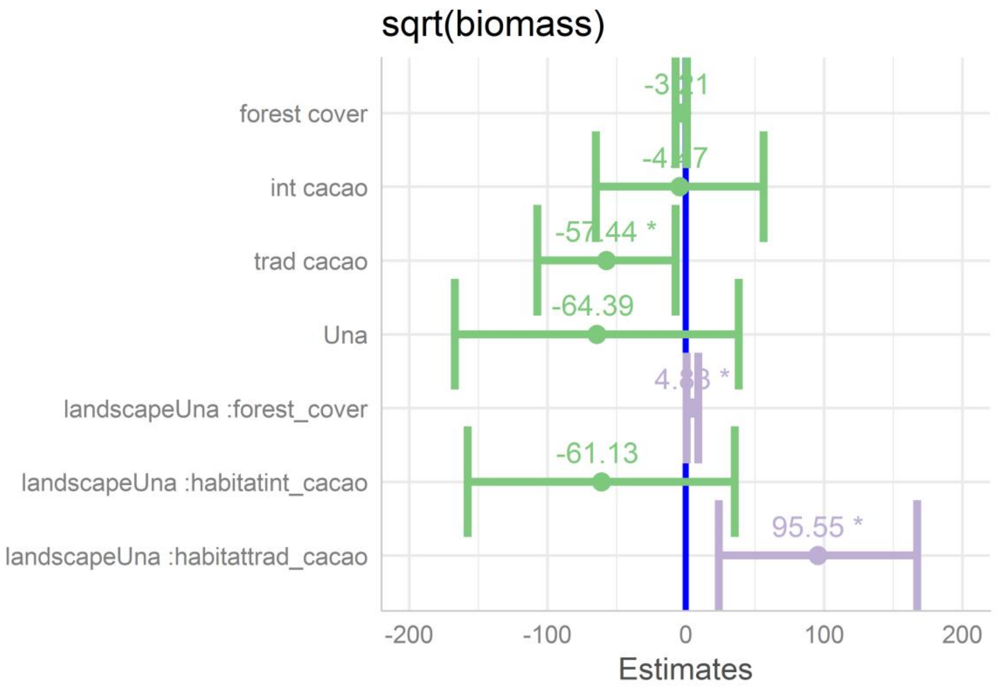

Fig. S2 – 3 Model: Sq-rt (biomass) ~ landscape + habitat + forest cover+ landscape:habitat + landscape:forest cover. McFadden's pseudo-R^2 = 0.07

Table S2-2

Results of mammalian species structure analysis (Permutational multivariate analysis of variance, PERMANOVA), using the Bray-Curtis method for record rate with 999 permutations. Analysis was performed using the *adonis* function in the *vegan* package (Oksanen et al., 2016) in R 3.3.2 software (R Core Team 2017).

Model: Community ~ landscape + habitat + forest cover + log10(human p. density) + exponential Shannon's index + landscape:habitat + landscape:forest cover + habitat: forest cover

	DF	F.model	R2	*P*
Landscape	1	7.19	0.09	0.001***
Habitat	2	3.85	0.10	0.001***
Log_{10}(HPD)	1	2.45	0.03	0.008**
Forest cover (%)	1	1.30	0.02	0.21
Exponential Shannon's index	1	1.87	0.02	0.05
Landscape:habitat	2	1.53	0.04	0.06
Landscape:forest cover	1	1.52	0.02	0.11
Habitat:forest cover	2	1.75	0.04	0.02*

Significance codes: 0.001 '**' 0.01 '*' 0.05 '*'

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APPENDIX S3

Table S3

Average of species capture rates over a 30-day period (abundance/sampling effort *30) at 25 forests (15 in a high forest cover landscape: Una and 10 in a low forest cover landscape: Ilhéus), 30 traditional cacao agroforests (15 in each landscape), and 10 intensified cacao agroforests (five in each landscape) in Southern Bahia, Brazil.

		Record rate					
Species / Latin binomial codes	**Common name**	**Forest**		**Traditional**		**Intensified**	
Order Arctiodactyla		**Ilhéus**	**Una**	**Ilhéus**	**Una**	**Ilhéus**	**Una**
Mazama americana (mazame)	South American Red Brocket	0.00	0.00	0.04	0.00	0.00	0.00
Mazama gouazoubira (mazgou)	South American Brown Brocket	0.00	0.20	0.00	0.16	0.00	0.00
Pecari tajacu (pectaj)	Collared Peccary	0.00	0.67	0.00	0.03	0.00	0.00
Order Carnivora							
Cerdocyon thous (certho)	Crab-eating Fox	1.49	0.69	0.84	5.95	4.43	0.43
Eira barbara (eirbar)	Tayra	1.53	4.05	1.14	0.83	0.00	1.07
Nasua nasua (nasnas)	South American Coati	0.03	1.25	0.00	0.22	0.00	0.00
Leopardus wiedii (leowie)	Margay	0.00	0.03	0.04	0.10	0.00	0.00
Potos flavus (potfla)	Kinkajou	0.00	0.81	0.00	0.00	0.00	0.00
Procyon cancrivorus (procan)	Crab-eating Raccoon	0.14	0.00	0.36	0.86	0.00	0.00
Puma concolor (pumcon)	Cougar	0.00	0.07	0.00	0.02	0.00	0.00
Puma yagouaroundi (pumyag)	Jaguarundi	0.00	0.00	0.00	0.02	0.00	0.00
Order Cingulata							
Cabassous tatouay (cabtat)	Greater Naked-tailed	0.09	0.14	0.00	0.00	0.00	0.00

Dasypus novemcinctus (dasnov)	Armadillo	0.47	0.14	0.09	0.42	0.00	0.21
Euphractus sexcinctus (eupsex)	Nine-banded Armadillo	0.00	0.03	0.12	0.00	0.17	0.00
	Six-banded Armadillo						
Order Didelphimorphia							
Didelphis aurita (didaur)	Big-eared Opossum	1.22	3.14	0.20	1.47	0.17	0.86
Order Lagomorpha							
Sylvilagus brasiliensis (sylbra)	Tapeti rabbit	0.00	0.00	0.00	0.02	0.00	0.00
Order Pilosa							
Tamandua tetradactyla (tamtet)	Southern tamandua	0.12	0.25	0.02	0.17	0.37	0.00
Order Primates							
Callithrix kuhlii (calkuh)	Wied’s Marmoset	6.27	0.83	1.51	3.25	0.00	3.21
Sapajus xanthosternos (sapxan)	Golden-bellied Capuchin	1.14	0.24	0.00	0.00	0.00	0.00
Leontopithecus chrysomelas (leochr)	Golden-headed Lion Tamarin	0.85	1.95	0.38	1.05	0.00	0.21
Order Rodentia							
Cuniculus paca (cunpac)	Lowland Paca	0.14	0.47	0.04	0.32	0.00	1.29
Dasyprocta leporina (daslep)	Red-rumped Agouti	0.00	0.56	0.00	0.29	0.00	0.00
Sciurus aestuans (sciaes)	Guianan Squirrel	0.00	0.13	0.00	0.00	0.00	0.00

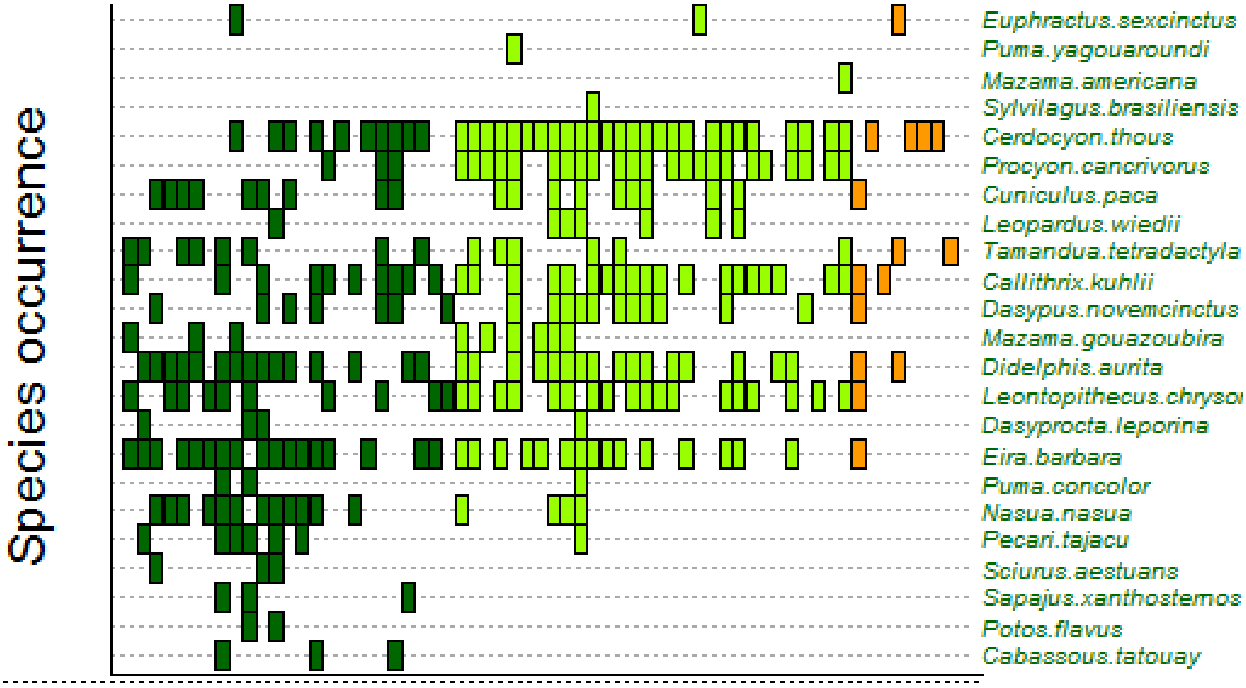

Fig. S3 Mammal species occurrence across 65 survey sites in the Ilhéus and Una study landscapes, Southern Bahia, Brazil. Sites were ordered by habitat type (forests in dark green, traditional cacao agroforests in green and intensified cacao agroforests in orange).

4 MAMMALS IN CACAO AGROFORESTS: IMPLICATIONS OF MANAGEMENT INTENSIFICATION IN TWO CONTRASTING LANDSCAPES IN THE ATLANTIC FOREST, BRAZIL

This manuscript will be submitted to the Agriculture, Ecosystems & Environment journal after review by examiners and co-authors

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ABSTRACT

The future of tropical biodiversity will largely depend on the effective management of modified landscapes, aiming at both agricultural production and environmental conservation. Cacao agroforestry systems (CAFS) have been identified as a potential wildlife-friendly farming and play an important role in enhancing biodiversity and providing ecosystem services. We investigate how direct (native tree density and Carbon stock) and indirect (dog invasion) outputs of local management of CAFS affect medium to large-sized mammals in landscapes with contrasting amount of forest. Species were classified in two groups: sensitive and non-sensitive to the conversion of forests into cacao agroforests, using species' capture rates in both habitats. Landscape forest amount was the main factor predicting higher richness and abundance of sensitive mammals in CAFS, while local management impacted this group in different ways, according to the landscape. In the landscape dominated by native forests, the richness of sensitive species tends to increase in agroforests with higher number of native trees, while in a landscape dominated by human-modified environments the increase of C stock of shade trees predicted higher richness of sensitive species in these systems. We did not find influence of dog invasion on assemblages sampled. We reinforce the idea that conservation strategies in agroforestry landscapes should prioritize the maintenance and restoration of native habitat to ensure the permanence of forest-dwelling mammals. And we suggest that the thinning in CAFs should be restricted (avoiding the removal of a high number of native trees and individuals that store high values of carbon) and punctual to avoid the intensification of CAFS over large extents of land in landscapes dominated by agroforests, which impact on fauna can be higher than the effect observed at a local scale. Future studies should look for best management practices to ensure cacao yield considering the impact on biodiversity.

Keywords: *cabrucas*, carbon stock, domestic dog invasion, landscape context, native tree density, shade management

Running head: Effect of management intensification on mammals in contrasting landscapes

4.1 INTRODUCTION

With the reduction of global wilderness areas (3.3 million km² lost since 1990) and projected 50% increase in global population and food demand by 2050 (Tilman et al., 2001; Watson et al., 2016), the future of tropical forest biodiversity will largely depend on the effective management of modified landscapes (Gardner et al., 2009). Focusing in biodiversity and overall environmental conservation only inside large blocks of pristine tropical forests, while ignoring agricultural landscapes, has been seen as a failed strategy (Bhagwat et al., 2008; Perfecto and Vandermeer, 2008). And a growing recognition of human-modified landscapes as a component of any conservation strategy has emerged in the last decades (Melo et al., 2013). To attain biodiversity conservation in human-modified landscapes, the management of "working lands" must support biodiversity while providing goods and services for humanity, complementing protected areas by providing habitats and resources in buffer zones (Kremen and Merenlender, 2018).

Deforestation can result in the isolation of habitat patches within expanding agricultural matrixes (Deheuvels et al., 2014). In these areas, understanding how agricultural land use affects the native species and ecosystem functioning is critical for successful conservation in the future (Tscharntke et al., 2005). Two strategies have been proposed to resolve the trade-off between wildlife conservation and farming: (1) adoption of wildlife-friendly systems, which boosts densities of wild populations on farmland but may decrease agricultural yield, i.e land-sharing system and (2) local land use intensification, which minimizes demand for farmland by increasing local yield, concomitant to the sparing of land for conservation, i.e land-sparing system (Green et al., 2005). Agroforestry systems – intentional management of shade trees with agricultural crops - have been identified as a potential wildlife-friendly system, sustaining biodiversity, the associated ecosystem services and food production in human-dominated landscapes (Bhagwat et al., 2008; Santos et al., 2019; Steffan-Dewenter et al., 2007). Agroforests have potential to provide habitat outside protected lands, connect landscapes components, maintain landscape heterogeneity, reduce pressure on formally protected forest due the presence of trees, allow better nutrient cycling, soil conservation, as well as carbon (C) storage (Bhagwat et al., 2008; McNeely and Schroth, 2006; Schroth et al., 2015, 2001).

The cacao tree (*Theobroma cacao*) is commonly cultivated in agroforests, under the shade of thinned forests (where the understory and some of the canopy trees have been removed) or interspersed between planted mono- or poly-cultural shade system (Rice and Greenberg, 2000; Schroth et al., 2011). Cacao covers about 10 million-ha in the world (FAO, 2016), and cacao agroforestry systems (CAFS) represent 50 to 60% of this area (Jagoret et al., 2017) in the humid tropics in South and Central America, West and Central Africa, Southeast Asia and the Pacific Islands (Wood and Lass, 2001). CAFS vary in tree composition, which changes the value of these systems for seed availability, wood and fruit value and ecosystem services provision (Braga et al., 2018).

CAFS (shaded mainly by native trees and regionally referred as *cabrucas*) are found in areas originally occupied by the Brazilian Atlantic Forest (Piasentin and Saito, 2014; Rolim et al., 2017), a global hotspot with only 11 to 16% of its original forest cover, mostly (80%) remaining in fragments smaller than 50 ha (Ribeiro et al., 2009). *Cabrucas* harbor a high structural and floristic diversity of shade trees (Sambuichi et al., 2012), contribute to 59% of the regional carbon stock in tree vegetation (Schroth et al., 2016), and can serve as secondary habitat or corridor for different groups of fauna (Cassano et al., 2012; Delabie et al., 2007; Faria et al., 2006). In the 1980's, low cocoa prices and the introduction of the "witches broom" disease caused the replacement of *cabrucas* by more intensive cultivation systems and the abandonment of other areas in southern Bahia (Sambuichi et al., 2012). Studies have also shown that current management practices favor early successional trees and exotic species of economic value in order to increase overall plantation yield (Sambuichi, 2006; Sambuichi and Haridasan, 2007). Recently, shade reduction is an ongoing process in the tropics (Tscharntke et al., 2011) and it is not different in southern Bahia where the ordinance number 03/2017 (Portaria Conjunta SEMA/INEMA Nº03/2017; Bahia State) set the legal grounds to enable commercialization of shade trees removed from cacao agroforest, previously forbidden. For the purpose of thinning, the native tree density in *cabrucas* (mean of 121 ind ha^{-1} in southern Bahia, Sambuichi et al., 2012) can be reduced to 40 ind ha^{-1}.

The management intensification of CAFS, mainly associated with reduction of shade, has reduced the value of these systems for both biodiversity conservation and ecosystems services provision (De Beenhouwer et al., 2013). Diversified shade CAFS provides a range of ecosystem services such as crop production, climate adaptation, pest and disease suppression, pollination, soil fertility, water yield and carbon sequestration (Vaast and Somarriba, 2014). Schroth et al. (2016) estimated a loss of 24% of regional C stocks if intensification involving shade thinning is to be implemented over large scales. Other studies showed the negative impact of shade tree thinning on biodiversity. For instance, the shade tree thinning was related to a decrease in richness of forest-dwelling ants, (Bos et al., 2007) and greater species richness of shade trees was associated with higher species richness of frugivores and nectarivores birds (Clough et al., 2009). Beyond the local management, the decrease of native habitat in the landscape can impoverish native species assemblages in CAFS, and thus their conservation value (Faria et al., 2007).

CAFS have been identified as potential system to support medium to large-sized mammals, including species of conservation concern (Cassano et al., 2012; Estrada et al., 1994; Guiracocha et al., 2001). Large mammals play important roles on seed dispersal and predation (Terborgh et al., 2008; Wright, 2003), prey population control, and herbivory (Terborgh et al., 2001). However, land-use changes, human presence and contact with domestic dog population have been identified as negative impact for this group (Daily et al., 2003; Castilho et al., 2017; Doherty et al., 2017). Cassano et al. (2014) showed that local management intensification, including the indirect effect through an increase in domestic dog invasion, has a larger impact on large mammals’ distribution than the surrounding forest cover in a forested landscape. Here, we seek to understand if the direct (shade tree density and C stock) and indirect (dog invasion) consequences of local management intensification of CAFS affect medium to large-sized mammals equally in landscapes with contrasting amount of forest. We considered the domestic dog invasion as an output of agroforestry management because visits of dogs have been positively associated with human activity in CAFS and were more common in sites with simplified vegetation structure (Frigeri et al., 2014). Using camera-trap data collected in 40 CAFS sites and 25 forest (control) sites, we classified species as sensitive and non-sensitive to the conversion of forests into CAFS and tested 1) how management intensification affects richness and abundance of these groups, and overall assemblage structure in two contrasting landscapes; and 2) what are the assemblages’ similarity between CAFS and control areas. We expect greater assemblage homogenization among CAFS and between CAFS and forest sites in a landscape mainly covered by cacao agroforest than in a landscape predominantly covered by forest. This would be due to the lower number of forest-dwelling species sensible to changes in vegetation structure in landscapes lacking large forest remnants.

4.2 MATERIAL AND METHODS

Study area and sampling design

This study was carried out in southern Bahia, Brazil, where approximately 600,000 ha of land are occupied by cacao plantations (Landau, Hirsch, & Musinsky, 2008). We surveyed the medium-sized to large mammals within two large landscapes that are approximately 80 km apart: one largely covered by mature and late secondary forest in Una (66.822 ha with 50% old-growth and mid-successional forest cover, 15% cacao agroforestry; 15°03′–15°16′ S, 39°00′–39°17′ W), including the “Una Biological Reserve” (18.715 ha) and at least 14.216 ha of privately owned forest fragments contiguous to the reserve (Araujo et al., 1998); and another in Ilhéus, mainly occupied by cacao farms (29.264 ha with 5% old-growth and mid-successional forest cover, 60% cacao agroforestry; 14°35′–14º46′ S, 39°08′–39°17′ W) and with few and very small forestry patches ranging from 1 to 300 ha (Fig.1) . These landscapes, referred hereafter as high forest cover (HFC) and low forest cover (LFC), respectively, show similar aspects related to climate, original vegetation (Mori and Boom, 1983; Thomas, 2003) and mammal group (Prado et al. 2003), being the land use the main difference taken into account. The study was conducted at 40 sites in CAFS (20 in each landscape) and 25 sites in forests (15 at Una and 10 at Ilhéus). CAFS include *cabrucas* (30 sites), that are complex agroforestry stands where cacao trees (*Theobroma cacao*) are shaded by diverse canopy trees species (Rice and Greenberg, 2000), and intensified cacao agroforests (10 sites) that are structurally simpler systems, with cacao trees largely or entirely shaded by exotic species.

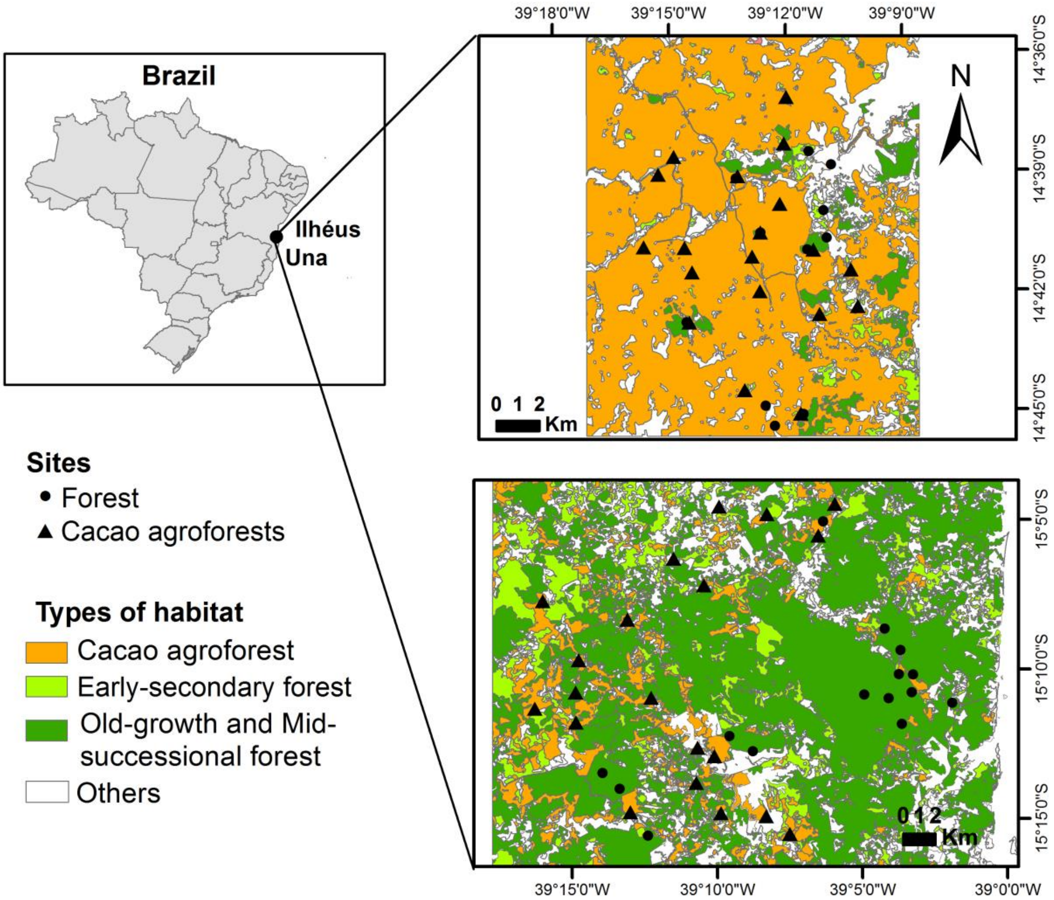

Fig. 1. Distribution of sampling sites along the Atlantic forest, including 40 cacao agroforests and 25 forest sites in Ilhéus (Low forest cover landscape, top panel) and Una (High forest cover landscape, bottom panel), southern Bahia, Brazil.

Sampling sites were spaced apart by a minimum distance of 800 m, with exception of four forest sites at Ilhéus, which were spaced apart by 120 – 300 m from CAFS. Thirty sites in CAFS (*cabrucas*) were repeatedly sampled during four 1-month surveys, representing two seasons (warm season: January-March; and cold season: June-August) in different years. The ten other sites in CAFS (intensified agroforests) were surveyed only once in the warm season. Forest sites were surveyed up to four times. Sites at Una were surveyed in 2016 and 2017 and those at Ilhéus between 2013 and 2017.

Data acquisition

Mammal sampling

We deployed one camera-trap (Trapa Camera or Bushnell) at each sampling site, 30 cm above ground, baited with sardine and banana to surveying medium-sized to large terrestrial mammals. We also included *Didelphis aurita* (small mammal) and some arboreals, that were attracted by bait in the ground, because this method is efficient to record these species (Cassano et al., 2014, 2012) and they are game (Castilho et al., 2017), endemic and/or threatened species (i.e. *Callithrix kuhlii* and *Sapajus xanthosternos*) following IUCN red list. One record of *Lontra longicaudis* was excluded from analysis because the sample design used was not efficient to record semi-aquatic species. During each survey, cameras remained active for 30 days continuously, and were checked weekly for maintenance and rebaiting. We obtained a total of 2474 camera-trap*days for forests and 3672 for CAFS, respectively. Our analyses, however, explicitly account for differences in sampling effort.

Agroforestry management

We measured five vegetation variables likely to be affected by management in 10 plots of 10 x 10 m, randomly located up to 200 m from the camera in each site. Within each plot, we: (1) counted and measured diameter at breast height (DBH) of all native shade trees, (2) exotic shade trees and (3) bananas stems (including only those with DBH ≥ 10 cm), and (4) counted all cacao trees inside half of each plot (5 x 10 m). Further, we estimated the height of herbaceous vegetation, by measuring the height of the tallest herbaceous plant within a 0.5 x 0.5 m quadrate, at 6 points distributed at 2 m intervals in each plot. Dog invasion is represented by capture rate, calculated as the number of records in camera-traps (see Mammal sampling, independence of 24 hours) expected for a 30-day period (abundance/sampling effort *30), corresponding to one survey period (Table A.1.1).

Data analysis

Management intensification

We estimated the aboveground C stock of shade trees (both native and exotic) and banana stems of CAFS using published allometric equations based in DBH. For native trees, we used an equation for Atlantic forest in southern Brazil (Tiepolo et al., 2002) and for exotic trees, we computed C stocks using DBH, wood density and considering a bioclimatic stress variable (Chave et al., 2014) using the *BIOMASS* package (Rejou-Mechain et al., 2016).

We used a principal component analysis (PCA) in a correlation matrix to summarize the correlation among all vegetation variables and dog invasion, and to visualize how the synthesis of variables indicates the gradient of areas with differences in management intensification (Fig.A.1). After, we analyzed the Pearson correlation between these variables (Table A.1.2). From this analysis, we identified two vegetation measurements directly affected by shade tree management (native tree density and aboveground C stock of shade trees) and likely important to mammals as source of food, shelter and displacement structure (for arboreal and scansorial species). Further accessing the influence of these variables on mammal assemblages is important because: 1) native tree density is used as a criteria for authorization of tree thinning in southern Bahia CAFS; 2) C stock is an ecosystem service of regulation (Somarriba et al., 2013) and if there is a positive relationship between this service and mammals diversity, the same management strategies can be used to conserve both aspects. The analyses were developed in R using *vegan* package (Oksanen et al., 2018).

Modeling mammal distribution as a function of landscape and management intensification

We excluded images of the same species at each camera-trap station within a period of 24 h and calculated sampling effort (in trap-days) excluding days of camera-trap malfunction. We classified species as sensitive and non-sensitive to the conversion of forests into cacao agroforests using capture rates (abundance/sampling effort *30) that represented the number of records expected for one survey period. We log-transformed the average of record rate of each species in cacao agroforests and in forests at the HFC landscape (because this landscape harbors the most conserved forest remnants, so being considered as a control) and considered species sensitive when the ratio was equal or less than 0 and non-sensitive when it was higher than 0.

Estimates of species richness were generated using rarefaction or extrapolation, with Hill numbers ^{0}D (Chao et al., 2014) considering a standard effort of 40 photos, using the *iNEXT* package (Hsieh et al., 2016). We used this threshold because the average number of photos per site was of 38 photos. Mammal relative abundance (hereafter abundance) was calculated as the sum of independent records of all species at each site weighted by the sampling effort.

We modelled estimated species richness and abundance of sensitive and non-sensitive native species as a function of the independent variables: landscape (HFC and LFC), native tree density, C stock of shade trees and dog invasion. We used the Generalized Variance Inflation Factor to test for multicollinearity (GVIF > 3) between independent variables (Table A.2) using the *car* package (Fox and Weisberg, 2011) and examined the spatial autocorrelation in the residuals of the full model using a variogram (Fig. A.2) computed with the *gstat* package (Pebesma, 2004). We used GLMs to test the influence of the independent variables on estimated species richness and abundance. Dog invasion was log transformed ($\log_{10} + 1$) and C stock of shade trees was sqrt-transformed prior to analyses. We applied stepwise multivariate regression analysis with backward selection until all remaining covariates had *P* values < 0.1, based on the likelihood ratio test. We began selection with the full model and used the functions *drop1* and *anova* to select the final model for each dependent variable (Zuur et al., 2009). Models were validated using graphs to verify homogeneity, normality and independence (Zuur et al., 2009). Given our hypothesis that the effect of management intensification on mammal assemblages can change between landscapes with contrast amount of forest, we included interactions between each management variable and landscape. As survey effort varied among sampling sites, it was included as an offset term in models constructed to explain mammal abundance. The negative binomial distribution was used for the abundance models because of over-dispersion, but we used a Gaussian distribution for estimated species richness.

We fitted a multivariate GLM for abundance data using binomial distribution and effort as an offset term and we applied an analysis of deviance for this model in order to test the influence of independent variables on assemblage structure, using 999 resampling iterations in *mvabund* package (Wang et al. 2018).

Dissimilarities between cacao agroforests and forest remnants

We calculate the Bray-Curtis dissimilarity index on the basis of species capture rates using the function *vegdist* of the *vegan* package (Oksanen et al., 2018). Two sites with abundance zero and six species detected in less than five sites were excluded from this analysis. We obtained an average of dissimilarities between each of 18 CAFS sites and the 15 forest sites in HFC landscape; between 20 CAFS sites in LFC landscape and the 15 forest sites in HFC landscape; and between 20 CAFS sites and the 10 forests sites in LFC landscape. We compared the similarities between CAFS sites in LFC landscape and forest sites in HFC landscape in order to compare the structure with larger and more conserved forest fragments and consequently with a most original assembly (probably lost after intense habitat loss and fragmentation in LFC landscape). We tested if there are differences of dissimilarities between CAFS/forests groups (HFC/HFC; LFC/LFC and LFC/HFC) with an analysis of variance (ANOVA) and a Tukey's post hoc analysis. All analyses were performed in R 3.3.2 (R Core Team 2017).

4.3 RESULTS

Species classification in sensitive and non-sensitive to the conversion of forests into cacao agroforests

We obtained records of 19 native species of mammals using CAFS (HFC: 17; LFC landscape: 12) and 20 using forests (HFC: 19; LFC landscape: 12) (Table A.3). Species only recorded in forest sites (*Cabassous tatouay* and *Sapajus xanthosternos* in both landscapes; *Potus flavus* and *Sciurus aestuans* at HFC landscape) or recorded once or twice in CAFS (*Euphractus sexcinctus* and *Mazama americana* at LFC and *Puma yagouaroundi* and *Sylvilagus brasiliensis* at HFC landscape) were excluded from this analysis.

Of 15 species analyzed, 5 species were recorded only in HFC landscapes (Fig. 2a) and 6 were classified as non-sensitive and 9 as sensitive (Fig. 2b). *Cerdocyon thous* and *Procyon cancrivorus* were the species less affected by conversion of forest in CAFS and were detected in most agroforest sites in both landscapes. On the other hand, *Pecari tajacu*, *Puma concolor*, *Dasyprocta leporina* and *Nasua nasua* were highly impacted by conversion of forests into agroforests and were recorded in few sites, only in HFC landscape.

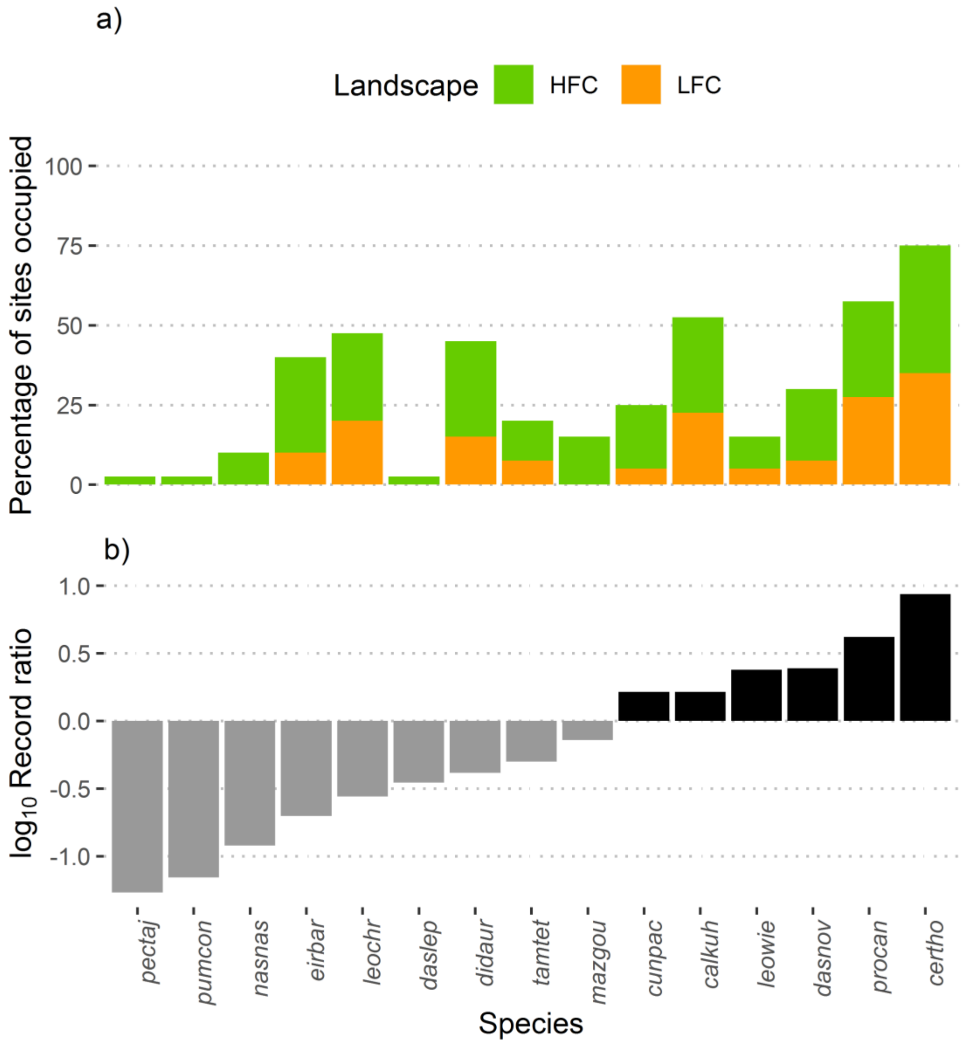

Fig. 2: a) Percentage of cacao agroforestry sites [total of 20 in each landscape – Ilhéus (Low forest cover landscape) and Una (High forest cover landscape), southern Bahia] that each mammal species was recorded. b) Log-transformed records ration (average between the record rates of each species in cacao agroforests and forests in Una). Sensitive species are identified in gray (ratio was less than 0) and non-sensitive in black (ratio higher than 0). Species latin binomial codes can be found in Table A.3.

Mammal distribution as a function of landscape and management intensification

The estimated richness of sensitive species was affected by the landscape, with an interaction between landscape and both aboveground C stock of shade trees (p = 0.05) and native tree density (p = 0.09) (Table 1). The richness of sensitive species was higher at HFC than at LFC landscape and the landscape had the strongest influence on mammal assemblages. The effect of management variables depended on the landscape. The increase of C stock of shade trees predicted higher richness of sensitive species in CAFS in LFC landscape, while the increase in the native tree density showed a tendency to increase records of sensitive species in CAFS in HFC landscape (Fig. 3). The estimated richness of non-sensitive species was not affected by any independent variable.

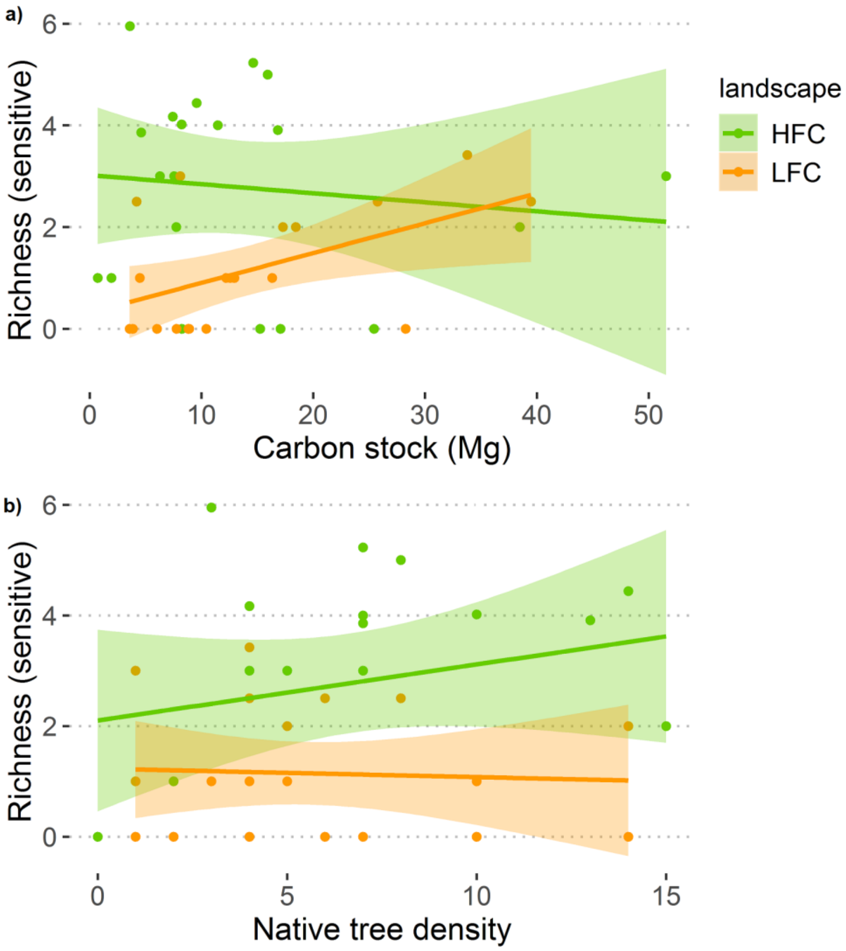

Fig. 3: Relationship between estimated species richness of sensitive species to the conversion of forest in cacao agroforest and management intensification variables: (a) Carbon stock of shade trees and b) native tree density, in 40 sites surveyed at two landscapes in southern Bahia, Brazil: Low forest cover landscape (LFC; Ilhéus) and High forest cover landscape (HFC; Una).

The landscape was the only variable affecting the abundance of sensitive ($p < 0.001$) and non-sensitive species ($p < 0.001$), being both higher in HFC than in LFC landscape (Table 1). Mammal assemblage structure was affected by the landscape too ($p = 0.001$, Table A.4.1) with the abundance of *Cuniculus paca*, *Didelphis aurita*, *Eira barbara* and *Mazama gouazoubira* increasing in cacao agroforests in HFC landscape (Table A.4.2).

Table 1: Coefficients and *p*-values of selected models based on 40 survey sites explaining estimated species richness and abundance of medium to large-sized mammals (species sensitive and non-sensitive to the conversion of forest in cacao agroforests), which were generated by backward selection. McFadden's pseudo-R^2 values are indicated for final models. HFC: high forest cover landscape and NA: not included in selected models

	Richness (sensitive)		**Abundance (sensitive)**		**Abundance (non-sensitive)**	
	coef.	*p*-value	coef.	*p*-value	coef.	*p*-value
Intercept	-0.41	0.69	-3.74	< 0.01	-2.26	< 0.01
Landscape (HFC)	3.03	0.04	1.67	< 0.01	1.12	< 0.01
Carbon stock	0.61	0.06	NA	NA	NA	NA
Native tree density	-0.01	0.28	NA	NA	NA	NA
Landscape (HFC): C stock	-0.79	0.05	NA	NA	NA	NA
Landscape (HFC): Native tree density	0.02	0.09	NA	NA	NA	NA
McFadden's pseudo-R^2	0.11		0.13		0.07	

Dissimilarities between cacao agroforests and forestry remnants

The structure of medium to large-sized mammal assemblages between CAFS and forest remnants showed different dissimilarities depending on the landscape (F = 23.74; p < 0.001; Fig. 4; Table A.5). CAFS in LFC landscape harbor mammal assemblages relatively similar to forest sites in the same landscapes, but very distinct to forest sites in HFC landscapes (i.e. control assemblages). Mammal asemblages in CAFS in HFC landscape retain intermediary levels of dissimilarity with forest remnants inside in this landscape.

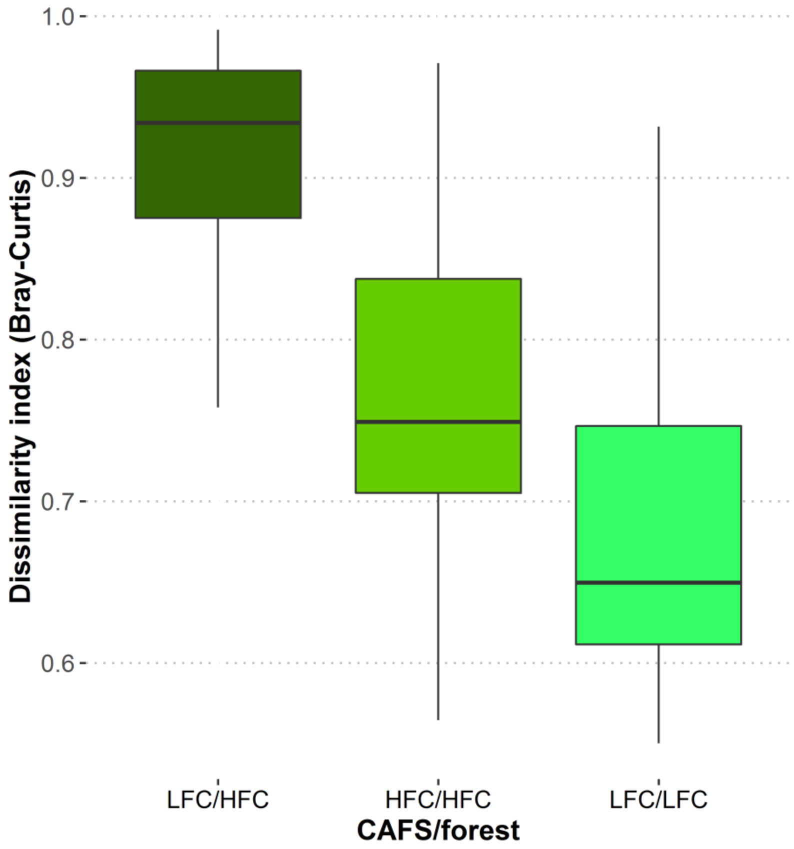

Fig. 4 Bray-Curtis dissimilarity index on the basis of species capture rates between cacao agroforests and forest remnants (CAFS/forest) located in Low forest cover landscape (LFC; Ilhéus) and High forest cover landscape (HFC; Una), southern Bahia, Brazil. Forest sites in Ilhéus are used as local control for CAFS in the same landscape. Forest sites in Una represent the most pristine habitats and, for this reason, are used as control for CAFS in both landscapes.

4.4 DISCUSSION

Agroforestry systems have been identified as an alternative farming that reduces the loss of biodiversity in agricultural lands (Santos et al., 2019). In Brazil, agroforestry systems can recompose native vegetation even in protected areas or inside private lands, as they are allowed in Legal Reserves (a percentage of rural property that needs to be preserved) and in Permanent Preserved Areas (e.g. river banks, spring and lake surrounds, slopes, hills, and mountain tops) conditioned by factors such as previous land use and property size (Native Vegetation Protection Law of Brazil – 12651/2012). CAFS are an efficient wildlife friendly system, harboring a substantial part of the flora (Sambuichi, 2002) and fauna in southern Bahia

(Cassano et al., 2009; Pardini et al., 2009). However, there is no information about the consequences of CAFS' implementation inside protected areas simultaneously in several properties, what can result in landscapes dominated by wildlife-friendly systems but with a little amount of native habitat.

Our study indicates that CAFS retain some conservation value for medium to large-sized mammals; however, the assemblages are more impoverished in a landscape with less than 5% of native remnants than in a landscape majorly composed by forest. We identified that some species are not affected by the conversion of forest in CAFS over large areas (non-sensitive species), while others were highly impacted (sensitive species). Species with high tolerance to this conversion are more opportunistic and omnivorous, as *Cerdocyon thous* and *Procyon cancrivorus* (Aguiar et al., 2011; Faria-Corrêa et al., 2009; Ferraz et al., 2010). On the other hand, *Pecari tajacu*, *Puma concolor*, *Dasyprocta leporina*, *Nasua nasua* and *Mazama gouazoubira*, classified as sensitive in our study and identified as forest specialists in other studies (e.g. Beca et al., 2017; Umetsu and Pardini, 2007; Zimbres et al., 2016), may use CAFS as corridors between the patches. Further, the presence of humans in CAFS can lead to low abundances of some of these species in agroforests sites due to overhunting (Castilho et al., 2017).

Although studies have also demonstrated the contribution of CAFS for the maintenance of biodiversity and environmental services, local management, and the amount and configuration of native forest in the landscape are vital to understand the conservation value of the agroecosystems (Clough et al., 2009; Tscharntke et al., 2005). We found that forest amount at landscape is the main factor predicting the richness of sensitive species and abundance of medium to large-sized mammals (sensitive and non-sensitive species). A similar pattern was observed for different groups of vertebrates in the same landscapes, where CAFS located in the LFC landscape with few and small forest patches supported impoverished assemblages compared with CAFS in the HFC landscape (Faria et al., 2007). The distance from forest remnants is another factor that negatively affected richness in agroecosystems (Bali et al., 2007; Tscharntke et al., 2011), and can explain the higher species diversity in HFC landscape. This shows the paramount importance of integrating native forests with agroforestry systems to increase biodiversity within agricultural landscapes (Santos et al., 2019).

The traditional farming practice of keeping forest trees to shade the cacao (Rice and Greenberg, 2000; Bhagwat et al., 2008), and consequent maintenance of characteristics that resemble the forest (Sambuichi and Haridasan, 2007), allowed the support of biodiversity in cacao agroforests. However, there is a wide variation in shade tree management among CAFS, resulting in different vegetation structure and composition (Sambuichi et al., 2012). In HFC landscape, we found a tendency of higher richness of sensitive species with increasing numbers of native trees, and greater dissimilarities of mammal assemblage structure between CAFS and forests from the same landscape. We suggest that it happens because some forest-dwelling species were restrict to forest fragments and probably depend on resources available in native trees found more commonly in forests and in CAFS with high tree density. In LFC landscape, the CAFS and forest fragments harbor highly similar mammal assemblages and the increase of C stock of shade trees predicted higher richness of sensitive species. This supports the idea that species remaining in landscape with few forest remnants survive in very small patches because they can also utilize resources in the matrix (Andrén, 1994). With the increase of C stock of shade trees (native and exotic), probably there are more tree resources as fruit, shelter, substrate, and refuge (Raboy et al., 2004; McNeely and Schroth, 2006; Tisovec et al., 2014) and consequently this habitat can support more species. Although we did not consider the shade species in analysis, we observed that in Ilhéus the largest trees usually produce fleshy fruits (*Artocarpus heterophyllus*, *Schefflera morototoni*, *Spondias monbin* and *Tapirira guianensis*). Contrary to our expectation, the management intensification affected assemblages in both landscapes, and regional peculiarities (mammalian and tree species pool) seem to influence management effects.

Animal diversity is typically higher in CAFS that present high plant diversity, structurally complex vegetation, and abundant surrounding forest cover, but different groups respond differently to local management practices and landscape contexts (Schroth and Harvey, 2007). We detected different effects of management variables on the richness of sensitive species in CAFS inserted in contrasting landscapes. These landscapes have different forest amount and configuration of fragments (connectivity and size), and consequently different species composition with more forest-dwelling occurring at HFC landscape and habitat generalists being recorded at LFC landscape. Although previous studies showed that invasive species negatively affects the occurrence of mammalian species in agroforests (Cassano et al., 2014; Santos et al., 2018) and in forests (Lessa et al., 2016), we did not find the influence of domestic dog invasion on mammal assemblages in CAFS.

Despite the fact that legislation considered the number of native trees as a management strategy to ensure increased cacao yield and conservation of biodiversity in *cabrucas*, our study showed that preserving sufficient areas of natural forest within the landscape is the most important strategy for mammals' conservation. Although, we found a weak influence of shade management intensification on mammals in CAFS, we must take into account the idea that if the management intensification occurs in all farms in a landscape, the management influence can enhance high impacts on fauna. We reinforce the ideas presented by Cassano et al. (2009): 1) forest remnants in cacao landscapes mainly composed by forest should be conserved to ensure the permanence of sensitive species while CAFS should be maintained to provide connection between patches; 2) In landscapes dominated by CAFS, it is essential to restore forest to ensure the conservation of sensitive species and CAFS should be conserved for their essential role as habitat for native species and as corridor between patches. And we suggest that the shade tree thinning in CAFs should be restricted (avoiding the remotion of a high number of native trees and individuals that store high values of carbon) and punctual to avoid the formation of landscapes dominated by high intensive management CAFS and consequently with poor value for biodiversity.

Recent studies have shown that is possible to reach higher yields when balance cacao tree density and associated shade tree density in complex agroforestry system (Jagoret et al., 2017). Although the shade is needed only for young cacao trees, shade tree species in CAFS can provide supporting and regulation services likely to improve cacao resistance to extreme climate conditions, pests and diseases (Mortimer et al., 2018 ; Santhyami et al., 2018). Further, the native trees can provide food and non-food resources such as wood, fruits, medicines (provision services) that can implement the income of local communities (Schroth and Harvey, 2007; Tscharntke et al., 2011). What shows that the maintenance of shade trees in CAFS can provide benefits for both biodiversity and farmers. Future studies may focus on understanding how the shade management of cacao agroforests can support yield and conservation of biodiversity and ecosystem services, attending the challenge of increasing yield with low impact on biodiversity (Waldron et al., 2015).

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SUPPORTING INFORMATION

APPENDIX A1

TABLE A.1.1 Minimum, mean and maximum values of vegetation variables in 0.1 ha and domestic dog capture rate among the 40 cacao agroforest sites. Variables in bold were used in models to explain medium to large-sized mammal distribution among agroforests in two landscape of southern Bahia.

Variable identification	**Variable description**	**Min.**	**Mean ± SD**	**Max.**
cocoa	Number of cacao trees	8.0	56.5 ± 25.9	134.0
cstock	**C stock of shade trees (native and exotic, Mg)**	**0.7**	**13.9 ±11.3**	**51.6**
dog	**Domestic dog invasion (records*30 trap-days^{-1})**	**0.8**	**7.1 ± 6.0**	**19.1**
herb	Average herbaceous vegetation height (cm)	0.4	49.0 ± 29.9	114.0
nat	**Native tree density**	**0**	**6.1 ± 4.2**	**15.0**
nat_BA	Sum of basal area of native trees (m^2)	0	1.2±1.2	5.6
total_BA	Sum of basal area of native and exotic trees (m^2)	0.1	1.8±1.3	5.9

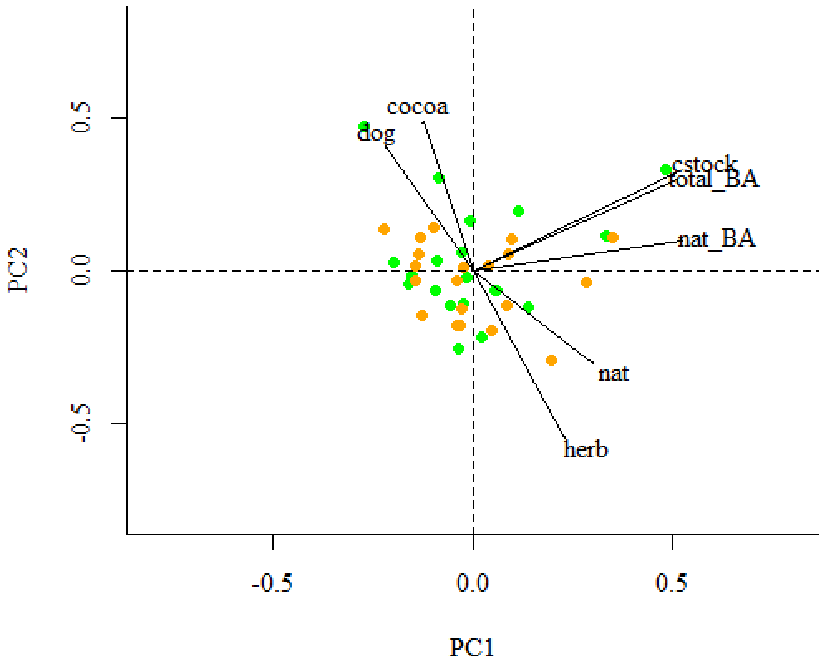

Fig. A.1 Ordination of cacao agroforests (orange dots identified sites in Ilhéus (Low forest cover landscape) and green in Una (High forest cover landscape) in a PCA bi-plot according to vegetation measurements and domestic dog invasion. Variable names as in Table A.1.1. The first PCA axis explained 44% of the variation in vegetation structure and domestic dog invasion among sites. This axis represents low management intensification associated with higher values of herbaceous vegetation height, native tree density, basal area of native trees and total trees, C stock of shade trees and lower values in cacao tree density and domestic dog invasion. The second PCA axis explained 24% of the variation in dataset with values of native tree density, and herbaceous vegetation height negatively correlated with this axis.

TABLE A.1.2 Pearson's correlation coefficients between management intensification variables and p value in italic, showing the significant correlations in bold. Variable names as in Table A.1.1.

	cocoa	**cstock**	**dog**	**herb**	**nat**	**nat_BA**	**total_BA**
cocoa	1.00	*0.90*	*0.31*	< *0.01*	*0.30*	*0.40*	*0.99*
cstock	-0.02	1.00	*0.31*	*0.56*	*0.13*	**< *0.001***	**< *0.001***
dog	0.17	-0.16	1.00	< *0.05*	< *0.05*	*0.19*	*0.46*
herb	-0.40	0.09	-0.36	1.00	< *0.05*	< *0.05*	*0.67*
nat	-0.17	0.24	-0.33	0.33	1.00	< *0.05*	*0.11*
nat_ba	-0.14	**0.83**	-0.21	0.31	0.39	1.00	**< *0.001***
total_ba	0.00	**0.99**	-0.12	0.07	0.26	**0.82**	1.00

APPENDIX A2

TABLE A.2 Generalized Variance Inflation Factor (GVIF) showing if there is multicollinearity (GVIF > 3) between the independent variables [landscape (Una and Ilhéus), native tree density, C stock of shade trees and domestic dog invasion] in full models with richness and abundance of sensitive and non-sensitive species of medium to large-sized mammals as dependent variables at 40 survey sites. This was developed using the *car* package (Fox and Weisberg, 2011) in the R platform 3.3.2 (R Core Team 2017).

	GVIF (richness and abundance)
C stock of shade trees	1.12
Domestic dog invasion	1.09
Landscape	1.04
Native tree density	1.20

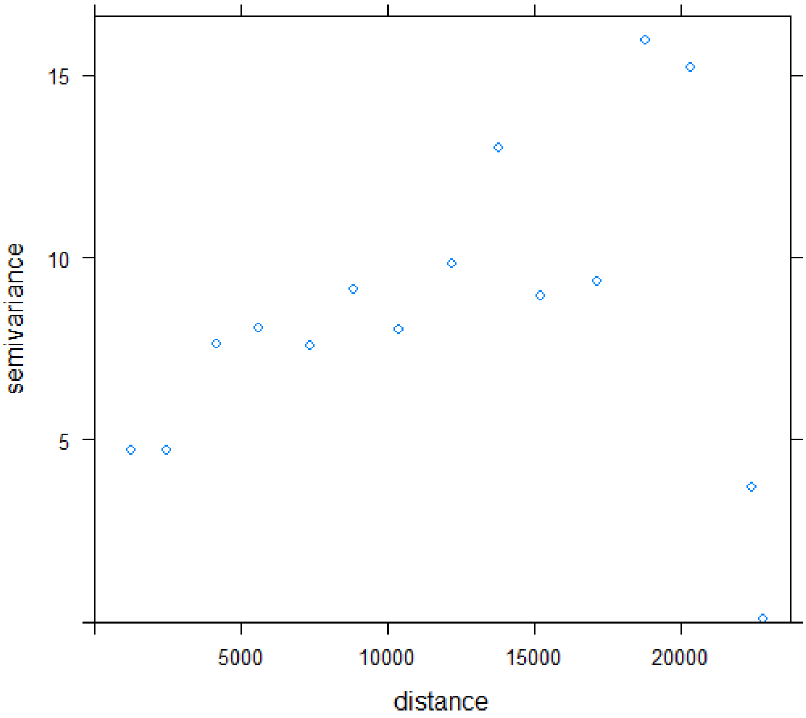

Fig. A.2 Experimental spatial variogram of full model residuals showing lack of spatial autocorrelation among survey sites.

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APPENDIX A3.

TABLE A.3 Average of species capture rates over a 30-day period (abundance/sampling effort *30) at 25 forest sites (15 in Una and 10 in Ilhéus) and 40 cacao agroforest sites (20 in each landscape) in southern Bahia, Brazil.

Species / Latin binomial codes	**Common name**	**Forest**		**Cacao agroforests**	
		Ilhéus	**Una**	**Ilhéus**	**Una**
Order Arctiodactyla					
Mazama americana (mazame)	South American Red Brocket	0.00	0.00	0.03	0.00
Mazama gouazoubira (mazgou)	South American Brown Brocket	0.00	0.20	0.00	0.20
Pecari tajacu (pectaj)	Collared Peccary	0.00	0.67	0.00	0.66
Order Carnivora					
Cerdocyon thous (certho)	Crab-eating Fox	1.49	0.69	1.74	4.57
Eira barbara (eirbar)	Tayra	1.53	4.05	0.10	0.89
Leopardus wiedii (leowie)	Margay	0.00	0.03	0.03	0.08
Nasua nasua (nasnas)	South American Coati	0.03	1.25	0.00	0.17
Potos flavus (potfla)	Kinkajou	0.00	0.81	0.00	0.00
Procyon cancrivorus (procan)	Crab-eating Raccoon	0.14	0.00	0.27	0.54
Puma concolor (pumcon)	Cougar	0.00	0.07	0.00	0.01
Puma yagouaroundi (pumyag)	Jaguarundi	0.00	0.00	0.00	0.01
Order Cingulata					
Cabassous tatouay (cabtat)	Greater Naked-tailed Armadillo	0.09	0.14	0.00	0.00
Dasypus novemcinctus (dasnov)	Nine-banded Armadillo	0.47	0.14	0.07	0.37
Euphractus sexcinctus (eupsex)	Six-banded Armadillo	0.00	0.03	0.13	0.00
Order Didelphimorphia					
Didelphis aurita (didaur)	Big-eared Opossum	1.22	3.14	0.19	1.32
Order Lagomorpha					
Sylvilagus brasiliensis (sylbra)	Tapeti rabbit	0.00	0.00	0.00	0.01
Order Pilosa					

Tamandua tetradactyla (tamtet)	Southern tamandua	0.12	0.25	0.11	0.13
Order Primates					
Callithrix kuhlii (calkuh)	Wied's Marmoset	6.27	0.83	1.13	3.24
Sapajus xanthosternos (sapxan)	Golden-bellied Capuchin	1.14	0.24	0.00	0.00
Leontopithecus chrysomelas (leochr)	Golden-headed Lion Tamarin	0.85	1.95	0.28	0.84
Order Rodentia					
Cuniculus paca (cunpac)	Lowland Paca	0.14	0.47	0.03	0.56
Dasyprocta leporina (daslep)	Red-rumped Agouti	0.00	0.56	0.00	0.21
Sciurus aestuans (sciaes)	Guianan Squirrel	0.00	0.13	0.00	0.00

APPENDIX A4.

TABLE A.4.1 Results of multivariate GLM (binomial distribution and effort as an offset term) for mammalian abundance data in function of independent variables (Landscape: Una and Ilhéus, native tree density, C stock of shade trees and dog invasion) in cacao agroforests, using an analysis of deviance for this model with 999 resampling iterations in *mvabund* package (Wang et al. 2018) in R 3.3.2 software (R Core Team 2017).

Model: Community ~ landscape + native tree density + C stock of shade trees + dog invasion + offset(log(effort))

Mammalian data	**DF**	**Deviance**	**Pr(>Dev)**
landscape	1	63.39	P < 0.01
native tree density	1	13.84	0.34
C stock of shade trees	1	6.34	0.91
dog invasion	1	15.32	0.29

TABLE A.4.2 Results of multivariate GLM (binomial distribution and effort as an offset term) for mammalian species in function of variables measured (Landscape: Una and Ilhéus, native tree density, C stock of shade trees and dog invasion) in cacao agroforests, using an analysis of deviance for this model with 999 resampling iterations in *mvabund* package (Wang et al. 2018) in R 3.3.2 software.

	Callithrix kuhlii		***Cunicus paca***	
	Deviance	**Pr(>Dev)**	**Deviance**	**Pr(>Dev)**
Landscape	2.59	0.36	8.36	**P < 0.05**
native tree density	0.71	0.96	0.00	0.97
C stock of shade trees	0.05	0.99	0.76	0.98
dog invasion	0.92	0.94	3.48	0.60
	Cerdocyon thous		***Dasypus novemcinctus***	
	Deviance	**Pr(>Dev)**	**Deviance**	**Pr(>Dev)**
Landscape	6.15	0.15	5.19	0.17
native tree density	5.25	0.30	0.07	0.99
C stock of shade trees	0.19	0.99	1.12	0.98
dog invasion	0.40	0.94	2.38	0.74
	Didelphis aurita		***Eira barbara***	
	Deviance	**Pr(>Dev)**	**Deviance**	**Pr(>Dev)**
Landscape	9.06	**P < 0.05**	10.09	**P < 0.05**
native tree density	1.51	0.88	2.11	0.81

C stock of shade trees	0.11	0.98	0.6	0.98
dog invasion	2.59	0.73	2.16	0.76
	Leontopithecus chrysomelas		***Leopardus wiedii***	
	Deviance	**Pr(>Dev)**	**Deviance**	**Pr(>Dev)**
Landscape	3.14	0.36	1.58	0.38
native tree density	1.44	0.88	0.03	0.99
C stock of shade trees	0.81	0.99	0.00	0.99
dog invasion	0.64	0.94	0.71	0.94
	Mazama gouazoubira		***Procyon cancrivorus***	
	Deviance	**Pr(>Dev)**	**Deviance**	**Pr(>Dev)**
Landscape	10.32	**$P < 0.05$**	5.44	0.17
native tree density	0.36	0.98	2.26	0.81
C stock of shade trees	0.18	0.99	1.54	0.96
dog invasion	0.01	0.94	0.79	0.94
	Tamandua tetradactyla			
	Deviance	**Pr(>Dev)**		
Landscape	1.48	**0.37**		
native tree density	0.10	0.99		
C stock of shade trees	0.98	0.95		
dog invasion	1.24	0.91		

References

Wang, Y., Naumann, U., Eddelbuettel, D., Warton, D., 2018. mvabund: Statistical Methods for Analysing Multivariate Abundance Data. R package version 3.13.1.https://CRAN.R-project.org/package=mvabun

APPENDIX A5.

TABLE A.5 Results of a Tukey's post hoc analysis, showing the comparison dissimilarities between groups (represent cacao agroforests landscape/forests landscape), the difference between groups, the 95% confidence intervals and the p-value adjusted.

Groups	Difference	Lower 95% confidence bound	Upper 95% confidence bound	P
LFC/HFC – LFC/LFC	0.22	0.14	0.30	<0.0001
HFC/HFC– LFC/LFC	0.08	0.00	0.16	<0.05
HFC/HFC– LFC/HFC	-0.14	-0.22	-0.06	<0.001

5 CONSIDERAÇÕES FINAIS

Os resultados obtidos nessa tese demonstram o uso da matriz agrícola por mamíferos, um grupo com inúmeras espécies ameaçadas de extinção e que apresenta diversas funções ecossistêmicas. A revisão desenvolvida no primeiro capítulo é a primeira a sistematizar o conhecimento sobre o uso de agroecossistemas por mamíferos da ordem Carnivora em todo o mundo. Nós acessamos a relação entre os traços biológicos e o estado de conservação com a ocorrência das espécies em diferentes tipos de agroecossistema. As principais conclusões obtidas nesse capítulo foram:

- Existe um crescente número de trabalhos reportando a presença de carnívoros em matrizes agrícolas, sendo a maior parte dos estudos desenvolvida nas América e Ásia. Espécies de carnívoros foram registradas nos quatro tipos de agroecossistemas analisados (plantações florestais, agroflorestas, monocultivos perenes e anuais), apresentando as plantações anuais o menor registro de espécies.

- Tanto os traços biológicos quanto o estado de conservação predisseram a ocorrência de carnívoros em agroecossistemas, dominando nesses sistemas antrópicos as espécies terrestres, com pesos intermediários e classificadas como “pouco preocupantes”, segundo a IUCN (International Union for Conservation of Nature). A ausência de carnívoros ameaçados e posicionados em níveis tróficos superiores (i.e. essencialmente consumidores de vertebrados) sugere que manter habitat nativo é essencial para a conservação de alguns carnívoros dentro das matrizes agrícolas.

- Por fim, apesar do grande número de estudos reportando o uso de paisagens agrícolas por carnívoros, existe uma gama de assuntos pouco compreendidos. Nós identificamos lacunas que podem ser investigadas futuramente: 1) identificar a função e quais os recursos são utilizados por carnívoros nos agroecossistemas; 2) analisar como o uso dos agroecossistemas pelas espécies pode impactar a viabilidade populacional em longo prazo; 3) avaliar a importância da intensificação do manejo e o impacto dos humanos e de espécies exóticas nas populações de carnívoros; 4) identificar qual a quantidade mínima de habitat nativo necessário e a importância da heterogeneidade na paisagem para carnívoros; 5) analisar os efeitos diretos e indiretos de humanos nas cadeias alimentares que incluem carnívoros; 6) identificar se há benefícios do controle de pragas por carnívoros para a produção agrícola e 7) como atitudes humanas e suas tolerâncias podem influenciar na persistência dos carnívoros em agroecossistemas.

No segundo capítulo, ao abordar os efeitos em multiescalas que influenciam os mamíferos de médio e grande porte nas paisagens cacaueiras do Sul da Bahia, concluímos que:

- Na escala local, os tipos de habitat diferem em seu potencial para abrigar mamíferos. Os remanescentes florestais e as agroflorestas de cacau tradicionais apresentam alto poder de conservação, enquanto as agroflorestas de cacau intensificadas abrigam menor diversidade de espécies tanto na paisagem florestada quanto na paisagem dominada por agroflorestas.

- Na escala intermediária (buffers de 2 ou 3 km - delimitados ao redor dos sítios, áreas de 12,56 ou 28,26 km^2), os fragmentos florestais e as agroflorestas de cacau intensificadas apresentam maior riqueza quando há maior porcentagem de floresta na paisagem. E a densidade humana populacional afeta a estrutura da assembleia de mamíferos, estando algumas espécies ausentes das áreas com alta densidade humana.

- Em escala ampla, identificamos que a paisagem dominada por floresta suporta uma assembleia mais rica e é importante na manutenção de espécies especialistas florestais não encontradas na paisagem dominada por agroflorestas. A cobertura florestal nessa escala foi a variável de maior influência sobre a diversidade de mamíferos, enquanto as variáveis em outras escalas adicionam efeito às assembleias de espécies.

Por fim, no terceiro capítulo, investigamos como o manejo das agroflorestas de cacau afeta as assembleias de mamíferos, considerando um grupo de espécies sensíveis e um grupo de espécies não sensíveis à conversão de CAFS em florestas, e se este efeito difere em paisagens com diferentes usos da terra, concluindo que:

- A quantidade de floresta na paisagem ampla foi o principal fator a afetar a distribuição das espécies sensíveis à conversão de floresta em agroflorestas, sendo a influencia do manejo diferente de acordo a paisagem. Na paisagem florestal, encontramos uma tendência ao aumento da riqueza de espécie em agroflorestas sombreadas por maior número de nativas, enquanto na paisagem dominada por agroflorestas, o aumento do estoque de carbono nas árvores de sombra predisse maior riqueza desse grupo de espécies.

Juntos, os capítulos dois e três reforçam a importância das agroflorestas de cacau para a diversidade de mamíferos de médio e grande porte. Mas em paisagens dominadas por agroflorestas, esses sítios abrigam apenas uma parcela da diversidade de espécies ainda encontradas nos maiores remanescentes florestais da região cacaueira. O manejo das agroflorestas, a presença de humanos e, principalmente, a quantidade de floresta na paisagem são relevantes para predizer o valor dessas agroflorestas para a conservação de mamíferos. Enfatizamos nessa tese a importância dos grandes remanescentes florestais para garantir a manutenção de espécies florestais especialistas, principalmente espécies de alto valor conservacionista e que são diretamente impactadas pela presença humana através da caça. Logo, nós sugerimos que as agroflorestas não devem substituir as florestas em Áreas de Preservação Permanente (APPs) e nas Reservas Legais (RLs) a ponto de formar paisagens com baixo percentual de habitat nativo (5% no caso estudado). Segundo o Código Florestal Brasileiro (Lei 12.727, 2012), as agroflorestas podem recompor até 50 % da área total a ser recomposta em APPs de pequenas propriedades rurais ou posse rural familiar e recompor RLs em propriedades. Agroflorestas também podem ser mantidas para o cumprimento das RLs em pequenas propriedades ou posse rural familiar. Porém não há distinção ou menção de quais os tipos de agroflorestas podem ser implantadas nessas condições. Essa tese traz críticas à legislação ao mostrar que as agroflorestas não substituem as florestas para todos os mamíferos de médio a grande porte, e que, a depender do manejo das agroflorestas e das características da paisagem ao redor, o valor de conservação desta fauna nesse agroecossistema é baixo.

Por outro lado, as agroflorestas de cacau devem ser mantidas para garantir habitat alternativo e conectividade da paisagem para algumas espécies de mamíferos. Diante da intensificação do manejo nas agroflorestas de cacau e da possibilidade de autorização do raleamento das *cabrucas* (desde que sejam mantidos 40 indivíduos de árvores nativas por hectare), visando à manutenção da produtividade, conservação e uso sustentável desse agroecossistema (Decreto 03/2017; Lei 15.180 de 2014), nós enfatizamos a importância de manter as árvores nativas e árvores com grande capacidade de estoque de carbono que sombreiam o cacau para se conservar os mamíferos de médio e grande porte na região do Sul da

Bahia. Apesar do potencial de conservação e da provisão de serviços ecossistêmicos como o estoque de carbono encontrado nas agroflorestas de cacau, é necessário que futuros estudos encontrem um equilíbrio para garantir a sustentabilidade nesse sistema agrícola, considerando também aspectos econômicos e sociais.

Por fim, essa tese traz contribuições teóricas ao reforçar que é essencial entender não só o papel das machas de habitat nativo para a conservação da fauna, mas também como a matriz influencia na distribuição das comunidades nas paisagens fragmentadas. Além disso, ao acessar efeitos em diferentes escalas e mostrar que a importância local do habitat para os mamíferos é alterada a depender das condições circundantes (escala intermediária e ampla), essa tese também enfatiza a necessidade de se acessar múltiplas escalas para o melhor entendimento das questões ecológicas.