PPG Ecologia da Conservação
Universidade Estadual de Santa Cruz

Respostas de primatas à degradação do habitat: Fatores determinantes para a ocupação do mico-leão-da-cara-dourada e de seus potenciais predadores em agroflorestas de cacau

Responses of primates to habitat disturbance: Factors determining the occupancy of the golden-headed lion tamarin and its potential predators in cocoa agroforests

Juliana Monteiro de Almeida Rocha

Ilhéus, Bahia
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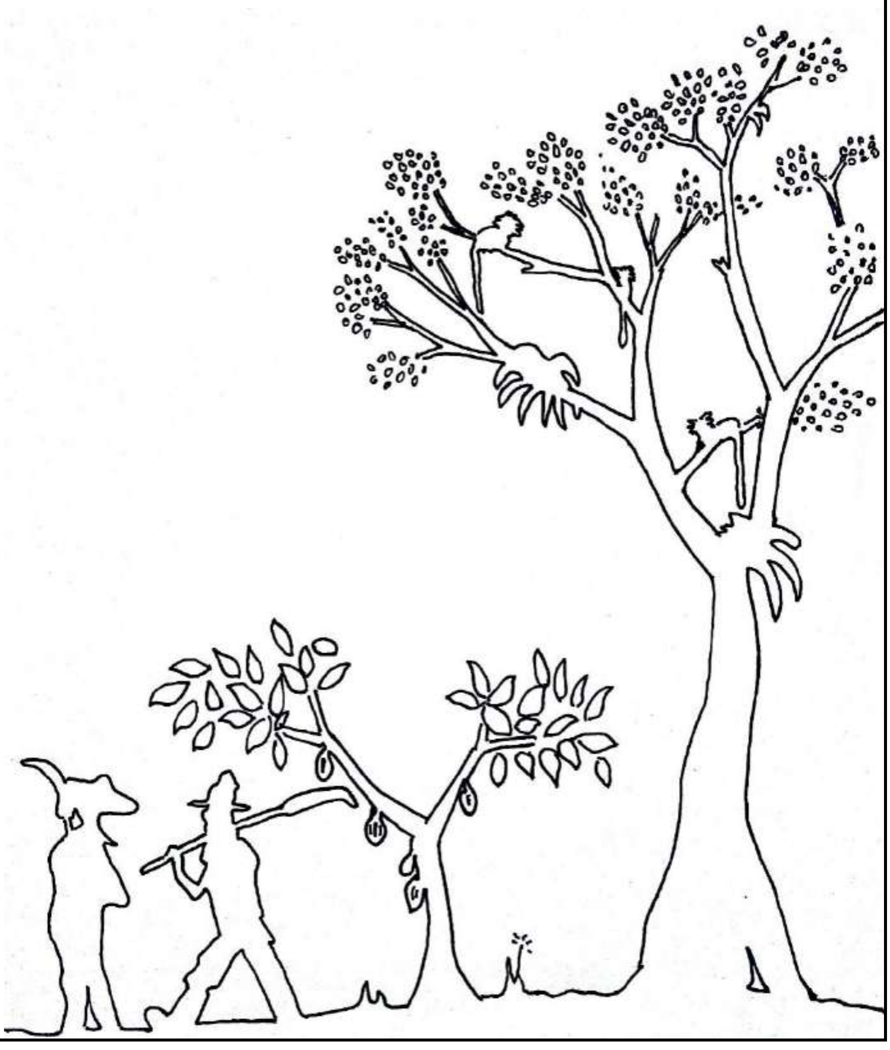

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ÍNDICE

RESUMO

Diferentes formas de intervenção humana têm levado à perda e alteração de habitats naturais, sendo estas as principais ameaças atuais à biodiversidade. Devido à alta dependência por florestas, primatas são muito afetados pela degradação do habitat, e cerca de 60% das espécies estão ameaçadas de extinção. O objetivo principal desta tese foi entender como espécies de primatas respondem à degradação estrutural do habitat induzida por diferentes atividades humanas. Foi realizada uma meta-análise global de estudos que compararam riqueza e/ou abundância de primatas em florestas tropicais degradadas e florestas controle, o que revelou um efeito geral negativo (capítulo 1). Tal efeito é mais deletério quando induzido por atividades agrícolas – embora agroflorestas e mosaicos agrícolas sejam capazes de subsidiar populações de primatas – e quando existe existe pressão de caça na região, sendo esta a principal fonte de heterogeneidade nos efeitos detectados por estudos primários. O mico-leão da cara dourada (MLCD), *Leontopithecus chrysomelas*, representa um excelente modelo para investigar a importância de um habitat modificado para a conservação de uma espécie de primata ameaçada de extinção. Grande parte de sua distribuição geográfica é representada por agroflorestas de cacau sombreado (cabrucas), onde os grupos sobrevivem e se reproduzem. Como nem todas as cabrucas parecem favoráveis à sua ocorrência, os fatores determinantes para a ocupação do MLCD neste sistema foram investigados nesta tese. Considerando o alto risco de predação nas cabrucas, principalmente por aves de rapina diurnas, a situação do MLCD foi investigada tanto do ponto de vista dos predadores (capítulo 2) quanto da própria espécie (capítulo 3). Uma alta riqueza de aves de rapina ocorre nas cabrucas, sendo estas aparentemente favorecidas pela simplificação estrutural das cabrucas. Já a ocupação do MLCD é maior em cabrucas mais heterogêneas e complexas, com alta abundância de cipós, árvores largas e composição arbórea diversificada. A intensificação do manejo das cabrucas, portanto, além de torná-las menos favoráveis à ocorrência do MLCD, pode desencadear um processo de cascata trófica, comprometendo a persistência da espécie neste sistema. A análise conjunta dos resultados dos três capítulos desta tese sugere que, embora habitats modificados devam de fato ser considerados em planos de conservação de primatas, estes sozinhos não asseguram a persistência das populações a longo prazo.

Palavras-chave: Accipitridae, agroecossistemas, Falconidae, Mata Atlântica, Primates, uso da terra

SUMMARY

Different forms of human intervention have led to the loss and alteration of natural habitats, representing the main threats to biodiversity. Due to a high dependence on forests, primates are greatly affected by habitat degradation, and about 60% of species are threatened with extinction. The main objective of this thesis was to understand how species of primates respond to the structural degradation of habitat induced by different types of human activities. It was conducted a global meta-analysis of studies comparing primate richness/abundance in degraded and control tropical forests, which revealed an overall negative effect (chapter 1). Such effect is even more deleterious when induced by agricultural activities - although agroforests and agricultural mosaics are able to subsidize primate populations – and when there is hunting pressure in the study region, being the main cause of heterogeneity in the effects detected by primary studies. The golden-headed lion tamarin (GHLT), *Leontopithecus chrysomelas*, is an excellent species model to investigate the importance of a modified habitat for the conservation of an endangered primate. Much of its geographical distribution is represented by shaded-cocoa agroforests (cabrucas), where groups can survive and reproduce. However, not all cabrucas seem favorable to its occurrence, thus the determinants of GHLT occupancy in cabrucas were investigated aiming to identify management practices more favorable to its occurrence. Considering the high predation risk mainly due to diurnal raptors in cabrucas, the situation of the GHLT was investigated here from both the point of view of predators (chapter 2) and of the species itself (chapter 3). A high richness of raptors inhabits cabrucas so that they seem to be favored by the structural simplification of the cabrucas. On the other hand, the occupancy of the GHLT is higher in more heterogeneous and structurally complex cabrucas with diverse shade-tree composition and high abundance of lianas. The management intensification of the cabrucas, therefore, besides making them less favorable to the occurrence of GHLT, can trigger a process of trophic cascade, compromising the persistence of the species in this system. These results suggest that modified habitats should be considered in primate conservation plans, but these systems alone do not ensure the long-term persistence of primate populations in altered landscapes.

Keywords: Accipitridae, agro-ecosystems, Falconidae, Atlantic Forest, Primates, land use

INTRODUÇÃO GERAL

Vários fatores interagem para determinar a distribuição geográfica das espécies e seus locais específicos de ocorrência (Brown, 1995; Gaston, 2003; Soberón & Peterson, 2005). O primeiro fator decisivo é a acessibilidade, e uma vez que os indivíduos de determinada espécie conseguem colonizar um local, o estabelecimento de uma população dependerá da existência de condições climáticas adequadas, bem como da existência de recursos fundamentais para a sobrevivência e reprodução dos indivíduos, tais como alimento e abrigo (Soberón & Peterson, 2005, Barve et al., 2011). As interações ecológicas como facilitação, mutualismo, competição e predação, desempenham um importante papel não só na regulação populacional, mas também nos padrões de co-ocorrência de espécies, podendo determinar a estrutura final das comunidades (Gotelli & McCabe, 2002; Kamilar & Ledogar, 2011; Almeida-Rocha et al, 2015a).

Diversas formas de interferência humana, incluindo atividades que afetam diretamente as espécies – ex.: caça, apanha e introdução de espécies – e atividades que atuam sobre os ecossistemas – ex.: exploração de recursos naturais, conversão de habitats naturais em sistemas de produção e centros urbanos, poluição e alterações climáticas – interferem com os fatores determinantes e regulatórios aqui mencionados. Atualmente, estamos vivenciando uma "crise da biodiversidade", caracterizada por taxas de perdas de espécies muito superiores às taxas de extinção que seriam esperadas naturalmente (Pimm et al., 1995; Laurance, 2006; Barnosky et al., 2011; Ceballos et al., 2015). Isto se deve muito às aceleradas taxas de perda e alteração dos habitats naturais, que atualmente resultam principalmente da expansão e intensificação agrícola (Maxwell et al., 2016).

A compreensão de como tais fatores determinantes e regulatórios estão sendo alterados em face à ação antrópica, bem como o entendimento de como as espécies respondem a tais mudanças, são aspectos cruciais para que possamos prever o futuro das espécies e delinear ações de conservação eficazes. Espera-se, por exemplo, que espécies com maior plasticidade ecológica possuam maior chance de sobrevivência em habitats e paisagens modificados (Isaac & Cowlishaw, 2004; Bonier et al., 2007). Por outro lado, espécies que possuem menor plasticidade ecológica devem ser mais sensíveis às alterações do habitat, de modo que suas respostas a tais alterações podem variar dependendo de diversos fatores, como por exemplo a sua capacidade de dispersão. Enquanto algumas espécies sensíveis podem migrar para locais mais favoráveis, experimentando mudanças no seu padrão de ocupação e possivelmente em sua extensão geográfica, outras espécies com capacidade de dispersão limitada - seja por restrições de mobilidade ou pela existência de barreiras geográficas - podem vir a ser extirpadas localmente ou até mesmo extintas da natureza (Thomas, 2000; Schloss et al., 2012).

Devido à sua elevada dependência por florestas, Primates é uma das ordens de vertebrados mais afetada pela perturbação antrópica do habitat (Isaac & Cowlishaw, 2004). Cerca de 60% de todas as espécies de primatas estão ameaçadas de extinção (Estrada et al., 2017) principalmente devido à perda de habitat (Mittermeier et al., 2013). Muitos estudos têm investigado como primatas respondem à diferentes formas de degradação do habitat, muitas vezes chegando a conclusões contraditórias (Johns, 1991; Ganzhorn, 1995; Chapman et al., 2000), o que dificulta a identificação de tendências claras de respostas a atividades antrópicas específicas. Por exemplo, sabe-se que diferentes espécies de primatas podem variar sua resposta à mesma ameaça, bem como as mesmas espécies podem responder à mesma ameaça de forma diferente, dependendo de onde ocorrem e da existência de múltiplas ameaças atuando simultaneamente (Isaac & Cowlishaw, 2004).

Entender os fatores que levam à variação nas respostas de primatas à degradação do habitat é essencial para viabilizar o planejamento de ações de conservação efetivas, buscando mitigar o impacto específico de diferentes atividades humanas sobre as diferentes espécies. Visando esclarecer esta questão, o **Capítulo 1** desta tese consiste em uma meta-análise global de estudos realizados em florestas tropicais dos Novo e Velho Mundo com o objetivo de investigar os efeitos da degradação antrópica do habitat sobre populações e/ou comunidades de primatas. Além da quantificação do efeito da degradação sobre os primatas, foram investigadas também as causas de heterogeneidade nos efeitos encontrados pelos estudos, considerando a atividade humana investigada, o delineamento amostral utilizado pelo estudo, a região biogeográfica onde o estudo foi realizado e o nível trófico da espécie investigada. Foram também investigada a existência de possíveis efeitos sinergísticos entre a degradação estrutural do habitat e a pressão da caça.

O mico-leão da cara dourada (MLCD), *Lentopithecus chrysomelas* (Kuhl, 1820; Fig. 1) é uma espécie de primata endêmica da Mata Atlântica brasileira que ilustra muito bem a importância de habitats modificados para a conservação de espécies ameaçadas de extinção. Com uma área de distribuição geográfica bastante restrita, o MLCD se encontra em perigo de extinção principalmente devido à perda de habitat (IUCN, 2016; MMA/ICMBio, 2016). A cobertura florestal dentro de sua área de ocorrência encontra-se bastante reduzida, fragmentada e imersa em uma matriz predominantemente composta por agroflorestas de cacau sombreado, localmente conhecidas como *cabrucas* (May & Rocha, 1996; Thomas et al., 1997; Fig. 2). Neste sistema, as árvores do sub-bosque são substituídas por cacaueiros, e algumas árvores predominantemente nativas são mantidas para o sombreamento do cacau (Johns, 1998). Apesar deste manejo resultar em uma simplificação do estrato vertical em comparação com florestas, as cabrucas ainda retêm certo grau de complexidade e heterogeneidade na vegetação que possibilita sua utilização por algumas espécies da fauna nativa (Argôlo, 2004; Delabie et al., 2007; Faria et al., 2007; Cassano et al., 2012).

Fig. 1. Mico-leão da cara dourada, *Leontopithecus chrysomelas*, adulto. (Foto: acervo pessoal)

A porção leste da distribuição geográfica do MLCD, onde se encontram os maiores e mais preservados fragmentos florestais bem como o maior número de populações atuais da espécie, é dominada por cabrucas (Zeigler et al., 2010), revelando a importância deste agrossistema para auxiliar na conservação deste primata. Dependendo das práticas de manejo utilizadas e da idade das plantações, as cabrucas podem ser bastante variáveis em termos de complexidade estrutural (Rice & Greenberg, 2000; Sambuichi et al., 2012), o que influencia na sua adequabilidade às espécies da fauna nativa (Cassano et al., 2014). Por isso, nem toda cabruca parece ser favorável à ocorrência do MLCD (Raboy et al., 2010), o que ressalta a necessidade de se identificar os fatores que favorecem a sua ocupação neste sistema, para que um manejo compatível com sua persistência possa ser incentivado.

Fig. 2. Fotografia de uma plantação de cacau sombreado (cabruca) no município de Ilhéus, BA, mostrando a estratificação vertical acima dos cacaueiros. (Foto: Leonardo de C. Oliveira)

Estudos têm demonstrado que grupos de MLCD são capazes de sobreviver e se reproduzir em áreas exclusivamente de cabruca (Oliveira et al., 2011), porém sob o custo de um alto risco de predação, principalmente por aves de rapina (Oliveira & Dietz, 2011). A taxa de encontro entre MLCDs e seus potenciais predadores em cabrucas é cerca de quatro vezes superior à observada em florestas (Oliveira & Dietz, 2011), e os grupos utilizam o estrato vertical arbóreo mais elevado com maior frequência nas cabrucas, aumentando ainda mais a sua exposição e vulnerabilidade a predadores aéreos (Almeida-Rocha et al., 2015b). Embora mudanças na estrutura trófica das comunidades como conseqüência da degradação do habitat ainda sejam pouco estudadas (Herrera & Doblas-miranda, 2013), há evidências de que alterações na estrutura vertical e tamanho de fragmentos florestais podem alterar as taxas de encontro entre predadores e presas, aumentando as taxas de predação e até mesmo levando à extinção local de espécies de primatas (Irwin et al., 2009). Deste modo, é possível que as relações predador-presa estejam desequilibradas nas cabrucas, e que a pressão de predação seja um fator determinante para a ocupação do MLCD neste sistema.

Nesta tese, foram adotadas duas abordagens para investigar a situação do MLCD nas cabrucas, sendo uma do ponto de vista da própria espécie e outra do ponto de vista dos seus principais predadores, as aves de rapina diurnas pertencentes às famílias Accipitridae e Falconidae. Entender o que afeta os predadores do MLCD pode ampliar o potencial de compreensão sobre a situação da espécie pois permite prever como as relações predador-presa podem estar sendo (ou vir a ser) alteradas diante das mudanças no habitat e que tipo de consequências (aumento, diminuição ou manutenção das taxas de mortalidade por predação) isto poderia acarretar para a espécie. Alem disso, tal entendimento possibilita a discussão sobre as possíveis consequências da intensificação do manejo das cabrucas, que vem sendo amplamente incentivada na região do estudo (ver artigo 19 do decreto estadual n° 15.180, publicado em 2014), sobre a estrutura das comunidades estabelecidas neste agrossistema. Sendo assim, o **Capítulo 2** teve como objetivo descrever pela primeira vez as comunidades de aves de rapina diurnas encontradas em cabrucas do sul da Bahia, e identificar os principais determinantes da sua ocupação neste habitat, considerando a influência específica de características relacionadas à estrutura da vegetação, intensidade de manejo e cobertura vegetal na paisagem.

Sabendo quais são as espécies de aves de rapina diurnas esperadas na região, bem como quais são os principais fatores que afetam a sua presença nas cabrucas, foi desenvolvido então o **Capítulo 3**, com o objetivo de identificar os fatores determinantes para a ocupação do MLCD neste sistema. Foram investigadas a influência de características relacionadas à complexidade e qualidade do habitat, intensidade de manejo, contexto da paisagem e abundância de predadores (terrestres e aéreos). Com base nos resultados deste capítulo, foram identificados alguns aspectos do manejo das cabrucas que podem favorecer a ocorrência do MLCD, seu potencial para contribuir com a conservação da espécie, e as possíveis consequências da intensificação do manejo das cabrucas sobre a persistência do MLCD neste sistema.

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CAPÍTULO 1

Primate responses to anthropogenic habitat disturbance: a pantropical meta-analysis*

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Abstract

Rapid human-induced conversion and degradation of natural habitats has severely altered patterns of species occupancy and population viability. Primates are highly vulnerable to tropical forest loss and degradation because they are highly arboreal, forest-dependent, and often highly sensitive to changes in forest structure. Here we quantify the effects of anthropogenic habitat modification on primate community structure using a global meta-analysis based on 72 studies to understand the variation in effect sizes between biogeographic regions, types of human disturbance, trophic levels of primate species, and sampling design protocols. We examined response ratios for 637 comparisons between disturbed forests and adjacent 'pseudo-control' forests with a history of little or no impact. This revealed an overall decrease of 30% (95% CI: 17-43%) in biodiversity metrics in response to habitat disturbance, which was particularly detrimental to primate assemblages in Madagascar and Southeast Asia. This effect was more severe in areas converted to agriculture (77%; 95% CI: 59-88%), while land use intensification led to far more detrimental effects than the initial degradation of forests, calling for the identification of habitat degradation thresholds. Negative effects of forest degradation were further exacerbated by ~30% under scenarios of persistent hunting pressure, emphasizing possible synergistic interactions between environmental stressors. Given that overall primate diversity was depressed in degraded habitats, our results emphasize the importance of retaining connectivity across remnants of undisturbed primary forest within human-modified landscapes to maintain full complements of primate species, and ensure their long-term persistence.

Keywords: agriculture; deforestation; habitat degradation; logging; threat; tropics

1. Introduction

Habitat loss and degradation, especially driven by agricultural expansion and intensification, are major threats to biodiversity (Maxwell et al., 2016). Over the last two decades, about one-tenth (~3.3 million km^2) of all wilderness areas worldwide were converted to anthropogenic land uses, with South America and Africa being the most affected regions (Watson et al., 2016). Given that the human footprint continues to expand relentlessly, particularly into the most species-rich biomes (Venter et al., 2016), the fate of biodiversity will increasingly rely primarily on human-modified habitats.

Anthropogenic habitat change, such as forest conversion to annual crops, cattle pastures, tree plantations, and mining, often results in forest loss, degradation and fragmentation, and these three outcomes usually interact with one another (Gardner et al., 2009). In addition to changes in forest structure and quality, including reduced canopy connectivity, availability and quality of food resources, land-use transitions are often associated with other types of interventions, such as road building, which facilitates non-structural threats to wildlife populations, such as overhunting (Wilkie et al., 2000). Furthermore, climate change exacerbated by human activities may contribute to habitat disturbance by altering patterns of fruit production that directly affect frugivores, thereby triggering cascading effects throughout the community (Morellato et al., 2015).

Human modification of natural habitats often leads to severe changes in species occurrence and population regulation mechanisms (Gardner et al., 2009). Several studies have sought to understand how different taxonomic groups cope with habitat alterations (Airoldi & Bulleri, 2011; Ribeiro-Neto et al., 2016), and to find overall patterns of species persistence following habitat disturbance (Sodhi et al., 2009; Gibson et al., 2011; Fontúrbel et al., 2014). Primates are among the vertebrate orders most affected by anthropogenic habitat disturbance, partly due to their high dependence on tropical forest ecosystems (Isaac & Cowlishaw, 2004). Anthropogenic disturbance can impact primate populations through a range of mechanisms, including reduced availability of structural resources (e.g. tall emergents, canopy continuity, and sleeping shelters); nutritional restrictions due to lower amount and/or quality of food resources; modified interspecific interactions due to species invasions/introductions, hunting and increased exposure to predators; and spread of diseases resulting from elevated contact with humans and domestic livestock (Irwin et al., 2010; Schwitzer et al., 2011). Local responses to these alterations can be expressed through changes in species occupancy, abundance, demography, use of space, activity budget, health status, and body condition.There is little consensus about how different primate species are affected by specific patterns of human habitat disturbance, such as those induced by agriculture and logging, and conclusions from previous studies remain largely contradictory (Johns, 1991; Ganzhorn, 1995; Chapman et al., 2000). Co-occurring species and conspecifics in different portions of their range can diverge in their responses to the same threat, particularly if multiple threats act synergistically (Isaac & Cowlishaw, 2004). Considering that nearly 60% of all primate species are currently threatened with extinction (Estrada et al., 2017), understanding what drives this variation in species responses to human-induced environmental stressors is crucial to enhance the effectiveness of conservation actions.

To our knowledge, there are no global analyses on the effects of human-induced habitat disturbance resulting from different forms of anthropogenic activities on primate populations and/or communities. Isaac & Cowlishaw (2004) attempted to synthesize the effects of agriculture, forestry and hunting on primates, but they focused on biological traits influencing species responses. Thus, the overall effects of different human-induced forms of habitat change within different biogeographic regions remain poorly understood. Here we present a global-scale meta-analysis of studies across the New and Old World tropics that compared primate species richness and/or abundance between undisturbed forests and neighbouring forest areas that had been affected by any given pattern of human activity leading to discernible habitat change. Since the twin effects of forest habitat loss and fragmentation have been relatively well documented for primates (Harcourt & Doherty, 2005; Benchimol & Peres, 2013), we focused entirely on studies that examined the effects of human disturbance on forest habitat structure, composition and/or quality. We also examine possible causes of variation in effect sizes between studies, such as the biogeographic region where the study was conducted, the main threat under investigation, study design, species trophic level, and whether hunting pressure operated in the study region. This analysis also enabled us to identify current knowledge gaps and suggest new research priorities.

2. Materials and Methods

2.1. Dataset

We systematically searched all research articles published until February 20th, 2016, that investigated the effects of human-induced habitat disturbance on primate populations and/or assemblages in tropical environments. This search was initially performed using three databases — *ISI Web of Knowledge* (www.isiwebofknowledge.com), *SciVerse SCOPUS* (www.scopus.com) and *Google Scholar* (https://scholar.google.com.br/) — using the query: [(primate*) AND ("habitat disturbance" OR "habitat degradation" OR "habitat conversion" OR "habitat alteration")]. Keywords were searched in all reference topics, except for *Web of Knowledge* searches, which were restricted to the title, abstract and keywords of the references. We then refined the searches by language (English, Spanish and Portuguese), and conducted additional searches in Google Scholar using keywords translated into both Portuguese and Spanish. As *Scopus* database is very broad, we refined our search by Subject Area (Agriculture and Biological Sciences; Environmental Sciences; and Earth and Planetary Sciences). In an attempt to include the "grey literature", we also searched for references in the *PrimateLit* (http://primatelit.library.wisc.edu/), a bibliographic primatology database that includes theses, dissertations, conference abstracts and reports, which was updated until 30 November 2010. Review articles returned by our search were used as additional bibliographic sources, and during the process of compiling, reading and sorting, we also identified new references that were assessed and added to our dataset.

We restricted our database to studies that performed any reported comparison between a degraded (or more degraded) site and a relatively intact (or less degraded) old growth forest within the same study landscape. Following a strict sorting procedure (Appendix A: Fig. A.1), the final database contained 81 studies that used biodiversity metrics at the population or community level, such as species richness (including number of species, rate of species loss, and diversity index; N = 5 studies) and abundance (including density, number of records per unit of sampling effort, encounter rate, population size or capture rate; N = 77 studies). These studies amounted to a total of 662 pairwise comparisons (mean ± SD = 8.2 ± 9.7 comparisons per study) including responses for 142 primate taxa across 17 countries and three provincial territories, spanning four biogeographic regions: Southeast Asia (25 studies and 139 comparisons), Neotropics (27 studies and 245 comparisons), mainland Africa (22 studies and 225 comparisons), and Madagascar (7 studies and 45 comparisons) (Fig. 1; Appendix B). More than 50% of all studies were concentrated in tropical forests of Brazil, Indonesia and Malaysia (Fig. 1).

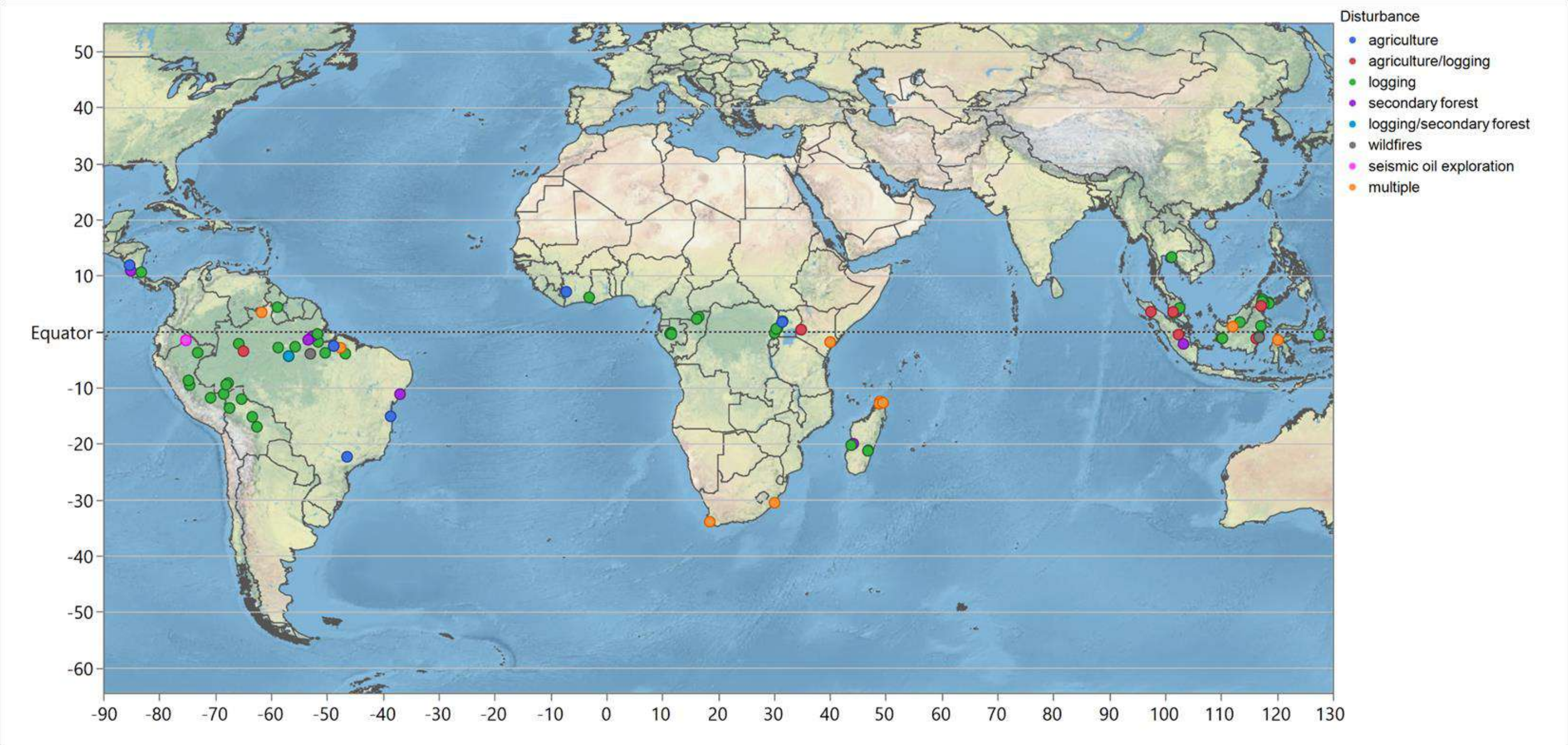

Fig. 1. Geographic distribution of study sites included in the dataset containing 81 studies. Solid circles are colour-coded according to the main patterns of land-use change reported in each study (see legend). Studies represented by two threat categories provided independent response ratios for more than one threat, while studies that did not specify a main activity, thus investigating the interaction among many stressors are represented by “multiple”.

2.2. Meta-analytical procedure

The meta-analysis approach combines quantitative results of primary studies to investigate a general pattern (Borenstein et al., 2009). About 60% of selected references (~75% of pairwise comparisons) neither presented any error estimates (and it was not possible to extract these values indirectly) nor made it clear which sample unit had been used to calculate error estimates, preventing us from calculating a standardized mean effect size (Borenstein et al., 2009). As an alternative to perform the meta-analysis without discarding valuable data, we used a Response Ratio (RR) as an index of effect size (Hedges et al., 1999). Thus, for 637 comparisons derived from 72 studies, we therefore calculated RR = $ln(\bar{X}_{\text{degraded}}/\bar{X}_{\text{control}})$, where $\bar{X}$ represents the mean biodiversity value in each treatment.

A negative RR indicates a detrimental effect of habitat disturbance and consequently a higher biodiversity value in the ‘control’ treatment. A median RR was calculated over all comparisons and a 95% confidence interval (CI) was estimated from 10 000 bootstrap samples (with replacement). To translate these values into percentage change, we used the equation: $(e^{RR} - 1) \bullet 100$. Since studies usually presented more than one comparison, we attempted to avoid pseudo-replication by resampling the dataset (with replacement) using only one comparison per study, and then we performed 10 000 bootstraps to generate a median effect size with a 95% CI. To support our findings, we repeated the meta-analysis for a data subset (30 studies and 155 comparisons) from which the Hedges’ g effect size - the difference between the mean biodiversity metric value in disturbed treatments and their control sites weighted by the within-group standard deviation - could be calculated, using a random-effect model. We used the same approach to account for pseudo-replication in this model.

To better understand what drives the variation in effect sizes among studies, we performed additional analyses using study sub-groups defined by four categorical variables: biogeographic region, main threat, species trophic level, and study design (Table A.1). Details about studies allocation into sub-groups and species classification into trophic levels are presented in Appendices A and B. Among threat types, Agriculture includes studies investigating the effects of different types of perennial plantations on primates (Table A.1). The degree to which agricultural lands can be used as primate habitat depends on the structural complexity of the converted land-use (Estrada et al., 2012), so combining different types of agriculture clearly adds heterogeneity to overall effect size estimates. Unfortunately, the limited number of studies addressing each type of agriculture prevented us from considering those effects separately, but this is revisited in the discussion. We also performed the meta-analysis for two-level factorial combinations of Main Threat and Study Design with Biogeographic Region and Trophic Level, to further examine the most important drivers of sensitivity to habitat disturbance. Finally, we performed another sub-group analysis considering primate species conservation status as defined by the IUCN (2016) to examine whether threatened species were more likely to be affected by habitat disturbance than least-concern species. We excluded species that were ‘*Data Deficient*’ and ‘*Not Evaluated*’, so we examined 592 comparisons from 67 studies, including responses for 116 species spanning five IUCN threat categories: *Least-Concern* (50 species), *Near-Threatened* (11), *Vulnerable* (25), *Endangered* (23) and *Critically Endangered* (7).

Excluding studies comparing the same site before and after a degradation event, there is always the possibility that intrinsic differences between any two sites will affect the final response ratio. We assume that authors investigated the most prevalent threats in their study areas, and since we restricted the dataset to studies comparing sites in the same region, it is unlikely that this represents a prohibitive problem in within-study estimates. However, this may add heterogeneity in between-study estimates, making it difficult to assign an overall effect. Primates are often targeted by subsistence and commercial hunters (Cowlishaw and Dunbar, 2000) and hunting can amplify effects of habitat degradation (Remis and Robinson, 2012). Thus, we compared the median effect size among studies at sites that were exposed to and without a history of hunting pressure to examine any possible synergistic effects between hunting and habitat disturbance. We classified study areas as *hunted* (253 comparisons from 26 studies) when authors declared that hunting on local primate assemblages was ubiquitous, even if they failed to test responses to hunting. Conversely, study areas were classified as *unhunted* (167 comparisons from 24 studies) if authors clearly stated that hunting was negligible, absent in the study area or if the study species was not usually hunted. We excluded from this analysis studies that failed to mention anything about hunting pressure (217 comparisons from 24 studies), and we used the same approach to account for pseudo-replication in all analyses.

Table 1. Sub-groups and categories used in this meta-analysis to investigate the variation in primate demographic or community-wide response ratios across studies.

Sub-group	Categories
1. Region	1. Africa
	1.2. Madagascar
	1. 3. Neotropics
	1.4. Southeast Asia
2. Study design	2.1. Primary (pristine/little impact) *versus* degraded forest
	2.2. Before *versus* after degradation
	2.3. Less-degraded *versus* more-degraded forest
	2.4. Long-degraded*versus*recently-degraded forest
3. Main threat	3.1. Timber extraction
	Selective logging; Extensive logging;Reduced-impact logging andConventional logging
	3.2. Agriculture
	Agroforestry (cocoa and teak);Agromosaics; Monoculture (sugar cane); Tree plantations including native and exotic species (e.g. acacia, cocoa, coffee, oil palm, rubber and eucalyptus); and Slash-and-burn swidden agriculture.
	3.3 Secondary forests
	Regenerating second-growth recovering fromman-made clear-cuts.
	3.4. Multiple threats
	Study sites were subject to more than one pattern of human disturbance, but authors failed to identify the main threat.
4. Trophic level	Trophic Levels ranging from 1 to 4[*]
	Levels were ordered from lower to higher energy content of major dietary classes (foliage<nectar/pollen/exudates/gum<fruits<seeds<arthropods<vertebrates)

[*] Classification was based on the proportion of each food item in species dietary profiles and energetic requirements. See Appendix A (Table A.1) for details.

2.3. Publication bias

We tested for publication bias using the dataset for which Hedges' g effect sizes could be calculated using two methods: (1) the Trim-and-Fill Method estimates the number of missing studies required to make a funnel plot (effect sizes plotted against standard errors) symmetric and recalculates an adjusted overall effect size including those missing studies (Duval & Tweedie, 2000); and (2) the Fail-Safe Number Rosenthal Approach estimates the number of unpublished studies with no effect (Hedges' $g = 0$) that would be required to render the overall effect size non-significant (Rosenthal, 1991). As for all previous analyses, we accounted for pseudo-replication biases (see details in section 4 of Appendix A).

2.4. Model selection approach

We fitted Generalized Linear Models (GLMs) using 518 comparisons from 64 studies to compare candidate models that could best predict the effect sizes. Since geographically restricted species are expected to be more vulnerable to extinction than widespread species (Payne & Finnegan, 2007), we included species range size as an additional explanatory variable, resulting in 23 plausible models encompassing all combinations of moderator variables (region, threat, trophic level, study design, hunting pressure and range size) plus a null model containing only the intercept and error parameters. We removed outliers (77 comparisons from 8 studies) and used the absolute response ratio ($\bar{X}_{\text{degraded}}/\bar{X}_{\text{control}}$) as the dependent variable, assuming a Gamma distribution. We accounted for pseudo-replication by using only one comparison per study to find the top-ranked models (the most selected within 10 000 sample fits) based on the Akaike Information Criterion corrected for small samples (AIC_c; Burnham and Anderson, 2002). For each candidate model, we calculated the percentage of simulations in which it was top-ranked (AICc-πi), the mean Akaike weight (w), and the mean goodness-of-fit (adjusted R^2).

All analyses were performed using R 3.3.1. (R Core Team, 2016). We used the *Metafor* package (Viechtbauer, 2010) to perform the meta-analysis with Hedges' g effect size and to check for publication bias.

3. Results

3.1. Overall effect of habitat disturbance

The overall RR effect size for 637 comparisons across all 72 primate studies was –0.19 [95%CI: –0.29, –0.08], and increased to –0.36 [–0.56, –0.19] when we considered only one comparison per study. Since pseudo-replication substantially affected the estimates, all results presented here are based on bootstrapped effect sizes (see Table A.3 for complete results). All forms of habitat disturbance led to a median decrease of 30% (17 - 43%) in biodiversity metrics across all primate assemblages. negative effect was corroborated by the meta-analysis performed with Hedges' g effect size (–0.47; 95%CI: –0.75, –0.20; T^2 = 0.42 +-0.09 SE; I^2 = 74%), and the results were robust to publication biases (see Section 4 of Appendix A).

3.2. Biogeographic regions

There was significant variation in effect sizes across biogeographic regions (Fig. 2a). Madagascar experienced the most severe effect size (48% decrease; 95%CI: 39-60%), followed by Southeast Asia (25% decrease; 10-54%), for which the negative effects were largely induced by logging and agriculture (Fig. 3a; Table A.4). Surprisingly, the median effect size for the Neotropics (44% decrease; 70% decrease to 1% increase) and Africa (15% decrease; 37% decrease to 30% increase) were not statistically significant (Fig. 2a). African primates were apparently the least sensitive to habitat disturbance, showing positive responses to logging, multiple threats, and secondary forests (Fig. 3a).

3.3. Anthropogenic activities

All forms of *agriculture* were by far the most detrimental patterns of habitat disturbance to primate communities (77% decrease; 59-88%), followed by *logging* (22% decrease; 8-37%) (Fig. 2b and 3). There was no overall effect for both *secondary forests* (30% decrease; 63% decrease to 42% increase) and *multiple threats* (27% decrease; 63% decrease to 15% increase). The effects of agriculture were consistently negative for Southeast Asia, where tree monocultures, such as rubber and oil palm plantations, accounted for a limited number of five studies, and for the Neotropics, for which degraded systems included agromosaics, agroforests and monocultures (Table A.4; Appendix B). A larger sample size would be required to investigate the specific impact of different agricultural production systems for each region. Also, Southeast Asian primates were apparently most sensitive to logging, compared to those in other regions (Table A.4).

3.4. Species trophic level

We found consistently negative effect sizes for the second trophic level (33% decrease; 20-54%), consisting primarily of frugivores and frugivore-folivores, and the third trophic level (23% decrease; 6-38%), consisting primarily of frugivore-faunivores (Fig. 2c). These species were particularly affected by agriculture and logging (Table A.4). We failed to find consistent effects of forest degradation for species in the lowest level (10% decrease; 27% decrease to 4% increase), comprised primarily of folivores, and the fourth level (35% decrease; 66% decrease to 3% increase), comprised mainly of insectivores. However, robust generalizations for this last category would require a larger sample size (Fig. 2c).

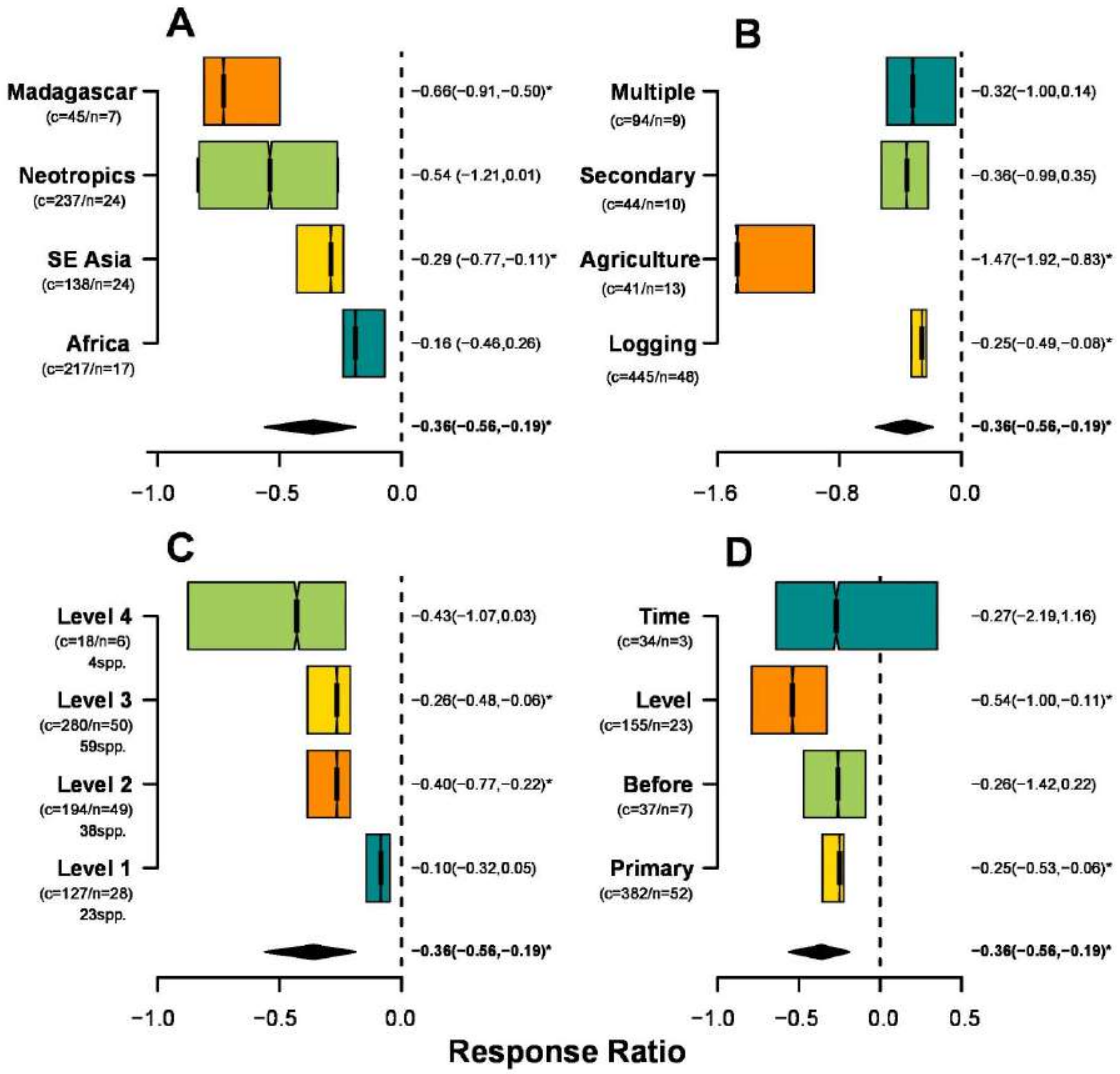

Fig. 2. Bootstrapped response ratios broken-down by (A) Biogeographic region, (B) Study design (names along the y-axis represent the control treatment; "time" and "level" represent comparisons between old- and recently-degraded sites, and less- and more-degraded sites, respectively), (C) Main threat, and (D) Trophic level. The black diamond represents the overall bootstrapped effect size obtained for the entire dataset without moderators, and the black dashed line indicates no effect of habitat disturbance. Box plots show the median values, and first and third quartiles of 10 000 resampled (with replacement) effect sizes for each category. Notches in boxes approximate 95% CIs. Values on the left of each panel show the total number of comparisons (c) and the number of studies (*N*; which represents the number of comparisons used in each bootstrap). Values on the right represent the median effect size and the 95% CI for the median effect size in each category (asterisks indicate statistically significant effect sizes).

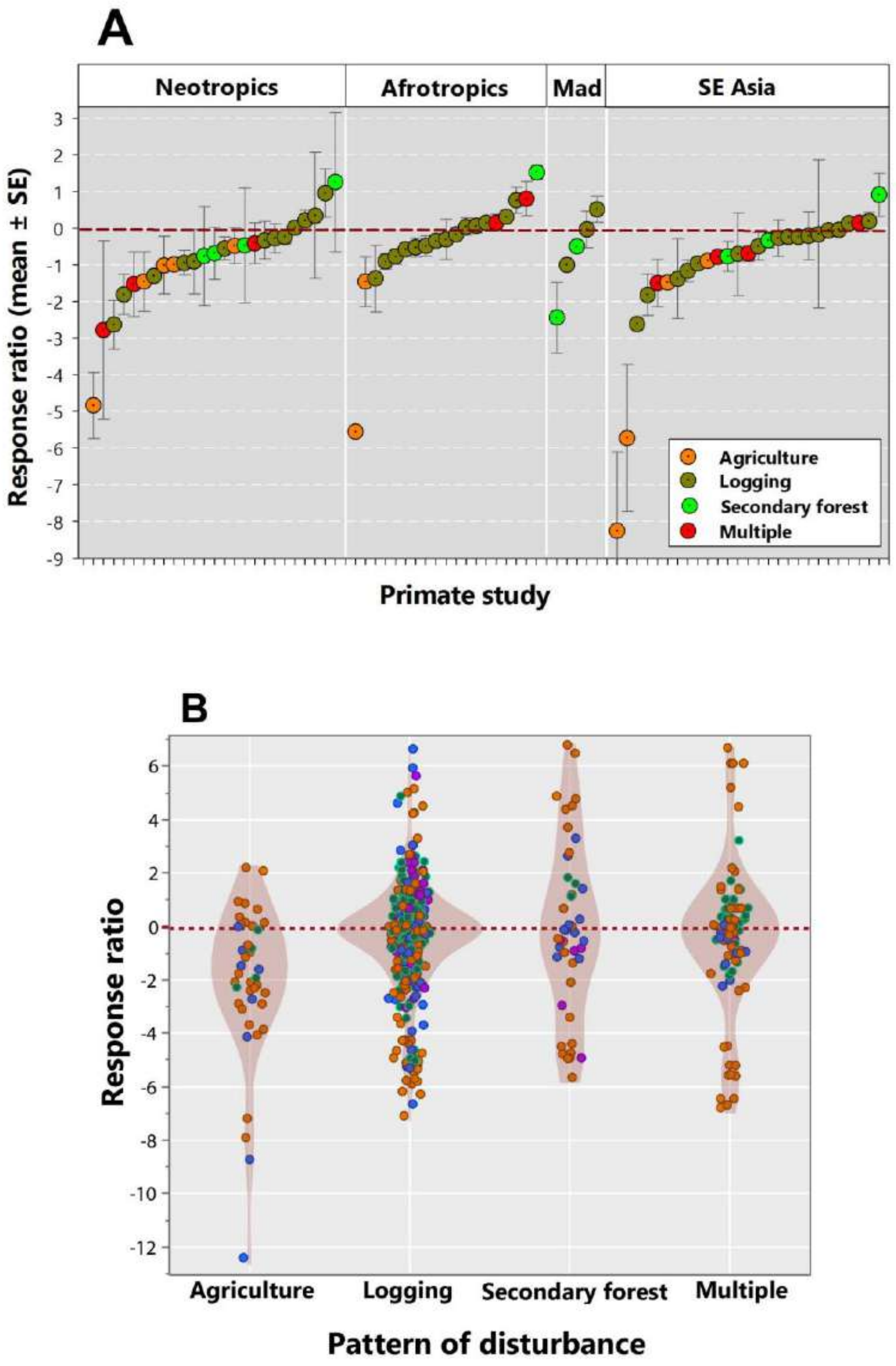

Fig.3. (A) Mean and standard errors of primate response ratios at the scale of individual studies broken-down by major biogeographic realm and type of threat; and (B) the overall distribution of response ratios at the scale of individual populations for major patterns of tropical forest habitat disturbance. Pink shading indicates violin plots. Dashed red lines indicate neutral response ratios.

3.5. Study design

When primary forests were compared to disturbed forests, there was an overall decrease of 23% [6-42%] in the biodiversity metrics (Fig. 2d). However, when areas that had already succumbed to some degree of disturbance were compared to more disturbed areas, the effect was more negative (42% decrease; 10-63%) (Fig. 2c), a pattern particularly evident in Southeast Asia (Table A.4). There was no overall effect for studies comparing the same sites before-and-after degradation (23% decrease; 76% decrease to 25% increase) or between long-degraded and recently-degraded forests (24% decrease; 89% decrease to 219% increase), but the latter category encompassed only one African and two Southeast Asian landscapes, so estimates are unreliable.

3.6. IUCN status

We detected overall negative effects for both near-threatened and threatened species, but not for *Least-Concern* species (14% decrease; 0-36%). The most negative effects were detected for *Vulnerable* species (55% decrease; 30-63%), followed by *CriticallyEndangered* species (37% decrease;7-95%), whereasthe overall effects for *Near-threatened* (23% decrease; 6-52%) and *Endangered* species (21% decrease; 13-39%) were similar (Fig. 4).

3.7. Hunting pressure

Primate assemblages at hunted sites experienced more negative effects of habitat disturbance (54% decrease; 19-70%) than those in unhunted sites (25%; 8-41%). Hunting therefore almost certainly aggravated the negative effects of habitat disturbance by further reducing biodiversity metrics by ~30% compared to habitat disturbance alone. However, it remains unclear whether these effects were induced by hunting *per se* or by an interaction between hunting and any co-occurring pattern of structural habitat disturbance.

3.8. Model selection

The best model predicting effect sizes was *hunting* (AICc=121.04; w=0.33; AICc-πi=29%), followed by the *null* model (AICc=127.56; w=0.26; AICc-πi=16%) and the *region+range* model (AICc=118.89; w=0.46; AICc-πi=11%) (Table 2). The *hunting* model explained 11-14% of the overall deviance, whereas the *region+range* model had a higher explanatory power of 23-27%. Regarding species range sizes, we failed to find an overall pattern of geographically restricted species experiencing more detrimental effects than widespread species, although this was apparently the caseof Malagasy primates (Fig. A.2).

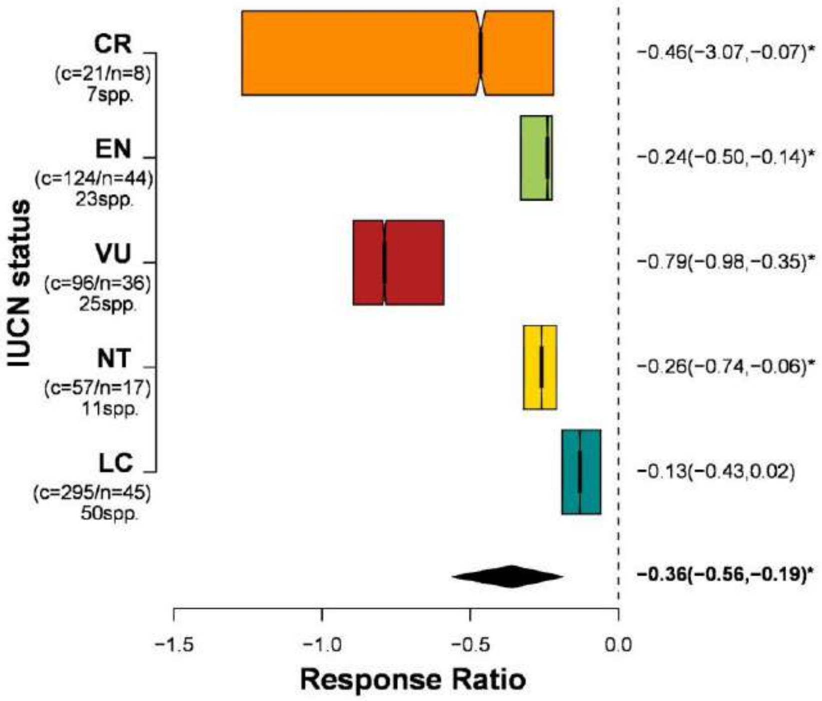

Fig. 4. Bootstrapped response ratios broken down by IUCN threat category: CR-*Critically Endangered*, EN- *Endangered*, VU-*Vulnerable*, NT – *Near-Threatened* and LC – *Least-Concern*. The black diamond represents the overall bootstrapped effect size obtained for the entire dataset without moderators, and the black dashed line indicates no effect of habitat disturbance. Box plots show median values, and first and third quartiles of 10,000 resampled (with replacements) effect sizes for each IUCN category. Notches in boxes approximate 95% CIs (significant effects are indicated by an asterisk). Values on the right of each panel show the median effect size and their 95% CIs. Values on the left show the total number of comparisons (c), the number of studies (*N*; which represents the number of comparisons used in each bootstrap), and the number of species (spp) in each category.

Table 2. Results of the generalized linear model (GLM) selection relating the absolute response ratio of each study (dependent variable) to six predictors — biogeographic region, study design, main threat, trophic level, hunting pressure and range size — which were modeled as fixed-effects in 23 possible combinations (including a null model containing only the intercept and error parameters). *K* is the number of parameters in the model (regression intercept, fixed-effects coefficients and residual variance), *logLik* is the log-likelihood of the model,*AICc* is the Akaike Information Criterion value corrected for small sample sizes, *AICc-πi* is the proportion of times each model was selected as the top-ranked model among all 10,000 sample fits, *w* is the Akaike weight, and R^2 is themean goodness of fit for each model with 95% CIs atthe 2.5 and 97.5 percentiles of all 10,000 sample fits.

ranking	variables	k	log.lik	AICc	w	AICc-πi	R^2 (95%CI)
1	hunting	3	-57.32	121.04	0.33	29.26	0.11 (0.10; 0.14)
2	null	2	-61.68	127.56	0.26	16.62	0 (0; 0)
3	region+range	6	-52.71	118.89	0.46	11.09	0.23 (0.23; 0.26)
4	trophic	5	-56.76	124.55	0.28	7.22	0.11 (0.10; 0.14)
5	design+hunting	6	-53.28	119.95	0.42	6.60	0.10 (0.10; 0.13)
6	region	5	-56.52	124.08	0.28	6.45	0.18 (0.18; 0.21)
7	trophic+hunting	6	-53.56	120.60	0.38	5.23	0.12 (0.12; 0.15)
8	region+hunting	6	-52.25	117.98	0.36	4.23	0.20 (0.20; 0.23)
9	hunting+range	4	-55.98	120.64	0.34	3.46	0.15 (0.15; 0.18)
10	design	5	-57.10	125.09	0.27	2.90	0.08 (0.08; 0.11)
11	range	3	-59.65	125.70	0.26	2.90	0.13 (0.13; 0.15)
12	region+design	8	-52.91	124.35	0.37	0.86	0.18 (0.17; 0.21)
13	region+trophic	8	-50.36	119.33	0.34	0.76	0.19 (0.20; 0.22)
14	trophic+range	6	-55.20	123.87	0.30	0.67	0.14 (0.14; 0.16)
15	design+trophic	8	-51.82	122.10	0.34	0.54	0.10 (0.10; 0.14)
16	design+range	6	-56.23	125.80	0.35	0.40	0.12 (0.12; 0.15)
17	threat+hunting	6	-56.86	127.20	0.30	0.38	0.10 (0.11; 0.13)
18	threat+trophic	8	-55.97	130.55	0.25	0.13	0.09 (0.09; 0.13)
19	region+threat	8	-49.78	118.18	0.42	0.08	0.19 (0.18; 0.24)
20	threat	5	-63.78	138.59	0.23	0.08	0.07 (0.07; 0.10)
21	all predictors	16	-39.09	121.25	0.26	0.07	0.17 (0.17; 0.19)
22	threat+design	8	-51.27	121.16	0.28	0.04	0.09 (0.09;0.10)
23	threat+range	6	-62.10	137.67	0.30	0.03	0.14 (-)

4. Discussion

4.1. Overall effect of habitat disturbance

Human-induced habitat change had an overall negative effect on primate assemblages, reducing population or community-wide metrics by 16-42%. These results extend those of previous global-scale meta-analyses on the effects of land-use on biodiversity considering multiple taxa (Gibson et al., 2011; Murphy & Romanuk, 2014; Newbold et al., 2015). We further shed light on apparent contradictions exposed by other studies. For example, Gibson et al. (2011) failed to find an overall effect of habitat change for tropical forest mammals but acknowledged that their results may have been masked by combining all mammalian orders, despite the wide variation in their sensitivity to habitat modification.

4.2. Biogeographic regions

Madagascar showed the most negative responses to habitat disturbance, despite the small number of studies in this land mass. Several studies have shown that Malagasy primate species persistence or local extinction in altered habitats is usually associated with behavioural, dietary and/or physiological plasticity (Irwin et al., 2010; Junge et al., 2011), but these were not included in our dataset because we focused on population or community-wide responses. Madagascar has succumbed to the highest deforestation rates over the last century (Harper et al., 2007) and the accelerated rate of forest loss of ~1,500 km^2 per year (Moat & Smith, 2007) poses a real threat to all forest-dwelling species. Although our effect size estimate for this region is imprecise, our result suggests high levels of sensitivity to habitat change, which is consistent with the fact that nearly 94% of all lemur species are currently threatened with extinction (Schwitzer et al., 2013).

Considering a wide range of taxa, Gibson et al (2011) identified Southeast Asia as the most sensitive region to tropical forest disturbance. Our overall 24% reduction in response metrics to disturbed forests in this region is comparable with the 22% detected in a previous meta-analysis that did not consider primate responses (Sodhi et al. 2009). Our effect size estimate for Southeast Asia was the most precise, suggesting little species flexibility in confronting habitat changes. Because of the recent disturbance history of Southeast Asian forests (Sodhi & Brook, 2006), this fauna may be less pre-adapted to habitat alterations than those elsewhere (Sodhi et al., 2009), which may explain the narrow variation in responses. Currently, Southeast Asia is under the highest anthropogenic pressure of all major tropical forest regions, and the human footprint is increasing mainly due to high human density and expansion of oil palm monoculture (Koh & Wilcove, 2008; Venter et al., 2016). Phillips et al. (2016) also identified the Asian fauna as the most affected by land-use effects, particularly in the case of tree monocultures. Oil palm plantations are largely incompatible with forest-dwelling species

(Danielsen & Heegaard, 1995; Fitzherbert et al., 2008) representing a major threat to primates, which is especially alarming in Southeast Asia, where ~80% of all primate species are threatened with extinction (Cotton et al., 2016).

Neotropical primate assemblages exhibited the widest variation in response ratios. The median effect size was high, which may reflect the dominance of studies addressing species from intermediate trophic levels that consume mostly fruits, which are highly sensitive to habitat changes. Also, ~60% of all Neotropical studies coincided with hunted areas, which aggravated the detrimental effects of habitat disturbance. However, there was no overall effect for this region, probably because this dataset included studies across different types of human-induced habitat disturbance, but only agricultural practices returned a consistently negative effect within this sub-group of studies.

African primates were apparently less affected by existing patterns of habitat disturbance, ranging from negative and neutral responses to logging (Chapman et al., 2000; Mammides et al., 2009), to positive responses to multiple threats (Lawes, 1992) and secondary forests (Decker, 1994). This apparent tolerance to habitat disturbance could be attributed to the higher ecological plasticity of Afrotropical primates in dealing with habitat changes. The paleoecological record shows that the overall drier African climate has predisposed the fragmentation of Afrotropical forests over millions of years (Hamilton & Taylor, 1991), exposing species to edge habitats typical of natural forest-savannah mosaics. This may have resulted in an evolutionary filter leading to pre-adaptations to contemporary forms of human-induced habitat alterations (Balmford, 1996). However, African primates are faring no better than those elsewhere: currently, 44% of all species are threatened, and great apes are the most endangered primate clade, with all species defined as threatened (Cotton et al., 2016). Deforestation has also drastically reduced forest areas, mainly in East and West Africa (Chapman et al., 1999), and hunting has been singled out as the main driver of extinction of some species (Struhsaker, 1999).

4.3. Anthropogenic activities

As observed for other taxa (Gibson et al., 2011), forest conversion into agricultural lands represents the most detrimental human activity for primates, leading to drastic population declines. Indeed, agricultural expansion and intensification impart the greatest current impact on species assessed by the IUCN Red List (Maxwell et al., 2016). Yet we found a limited number of studies comparing primate populations/communities in agricultural systems and primary forests. These studies indicate that agromosaics (Johns, 1991) and agroforests, such as shade-cocoa (Oliveira et al., 2011) and teak plantations (Oliveira, 2015), can support or subsidize some primate populations, but more structurally simplified systems, such as rubber and oil palm plantations retain a significantly lower biodiversity value than natural forests (Danielsen & Heegaard, 1995; van Schaik et al., 2001). This suggests that polyculture systems and intervening forest areas around agricultural patches can effectively maintain landscape heterogeneity to mitigate the negative effects of agriculture. Unfortunately, we failed to uncover studies comparing variable-aged agricultural systems to assess the time trajectory of persisting primate populations in the aftermath of initial habitat perturbation. Although some studies documented wholesale primate extinctions in cultivated areas such as oil palm and eucalyptus plantations (van Schaik et al., 2001; Dotta & Verdade, 2011), species richness is a weaker metric to evaluate the conservation value of modified habitats for primates because responses were more frequently related to abundance than occupancy. Also, while some systems such as agroforestry may function as primate habitat, other simplified systems such as monocultures can only be used as corridors between forest habitat patches (Estrada et al., 2012), thus using species richness as a response metric would return a similar biodiversity value for very different modified habitats.

Logging had an overall negative effect on primates, with variable responses across biogeographic regions, but selective logging had a less severe impact than agriculture (see also Edwards et al., 2010; Gibson et al., 2011; Sodhi et al., 2009). However, although logging is often seen as biodiversity-friendly, the degree to which population impacts are expressed depends on timber removal techniques, selectivity of timber species in conventional and reduced-impact logging (RIL) operations, length of the felling cycle, and design of skid trails and logging roads (Gullison & Hardner, 1993; Burivalova et al., 2014). Population impacts may be lower if target tree species are not key food resources for primate consumers, nor abundant emergent trees which would lead to profound changes in forest structure (Meijaard & Sheil, 2008). It is therefore largely possible to predict the effects of logging if the ecology of the local fauna is well documented and RIL techniques can be introduced (Sist, 2000). Moreover, the abundance of some primate species in logging concessions is often negatively correlated with distance from unlogged forests (Clark et al., 2009), emphasizing the critical landscape role of intact primary forests.

The biodiversity conservation role of tropical secondary forests has generated much debate (Chazdon et al., 2009). Previous analyses have shown that biodiversity retention of secondary forests is much lower than that in undisturbed forests, suggesting that primary forests are irreplaceable (Gibson et al., 2011; Newbold et al., 2015). Although vertebrate, invertebrate and plant species richness was not significantly different between primary and secondary forests, there was a tendency towards biotic homogenization (Phillips et al. 2016). Although we failed to uncover an overall effect of secondary forests, this does not necessarily mean that second-growth sites can support full complements of species typical of old-growth forests. Patterns of species richness and composition tend to converge with those of undisturbed old-growth as forest regeneration advances into late succession (Chazdon et al., 2009; Norden et al., 2009), so community effects in older secondary forests are expected to be less severe than those in early successional forests. Finally, different land uses may have arisen either independently or simultaneously, leading to highly variable vegetation structures, which can result in either stronger or weaker impacts on species. Age of secondary forests, previous land use history, and landscape context are therefore crucial considerations in better predicting the successional pathways and conservation role of tropical secondary forests (Melo et al., 2013; Arroyo-Rodríguez et al., 2017).

We failed to detect an overall effect of multiple threats. Although this may reflect a limited sample size, we expected a lack of consistency since multiple threats may interact in different ways. Nearly 80% of all currently threatened species are affected by more than a single major threat (Maxwell et al., 2016), so efficient conservation strategies must consider the synergistic effects among these threats (Brook et al., 2008). For example, hunting amplified the negative effects of structural habitat disturbance by ~30%, which is consistent with the synergistic effects between hunting and forest fragmentation on platyrrhine primates (Benchimol & Peres, 2013). Developing studies that dissect tropical forest wildlife responses to multiple threats is therefore a pressing research priority. Prospective meta-analyses, in which investigators develop independent primary studies sharing the same protocol with the common objective of integrating findings (Berlin & Ghersi, 2005), can be a good approach to achieve more conclusive evidence on how synergistic human activities erode tropical biodiversity.

4.4. Species trophic level

Part of the variance in response ratios can be attributed to species trophic level. Frugivores were most sensitive to forest degradation, corroborating previous findings (Purvis et al., 2000). Since ripe fruits are more patchily distributed in space and time than leaves, changes in habitat structure are expected to affect frugivores more than folivores (Isaac & Cowlishaw, 2004). Additionally, logging disturbance to the forest canopy tends to elevate young-leaf production but depress fruit availability in large canopy trees, particularly if those include commercially-valuable timber (Ganzhorn, 1995). Our results suggest that the impact of habitat disturbance on trophic levels can be non-linear, but a larger sample size is required to obtain more precise estimates for insectivores.

4.5. Study design

Only studies comparing primary *vs* degraded forests and less-degraded *vs* more-degraded forests returned consistently negative effect sizes. Interestingly, effects of disturbance were more negative in areas that had already been degraded to some degree. It is widely known that ecological systems are intrinsically resilient to some disturbance (Holling, 1973), so effects of disturbance could be cumulative and aggravated above a resiliency threshold whenever the extent or intensity of forest disturbance is elevated. For example, some primate species may thrive in some agricultural systems (Raboy et al., 2004; Merker et al., 2005), but are intolerant to others due to management intensification resulting in more severe changes in forest structure (Danielsen & Heegaard, 1995; van Schaik et al., 2001). Burivalova et al. (2014) found a higher species richness for some taxonomic groups in lightly-logged forests compared to unlogged forests, but as logging intensity increased, the richness of all taxa decreased linearly to values below those in primary forest until they reach a specific threshold. Mammals, for example, can tolerate a timber extraction rate of $10m^3\ ha^{-1}$, but an additional increase to $20m^3\ ha^{-1}$ resulted in a loss of ~35% in species richness (Burivalova et al., 2014). Land-use intensification may therefore pose an additional threat to wild primates, calling for additional research to identify operational thresholds above which net population growth rates become negative. Only studies comparing different levels of exploitation over time or across sites can derive tolerance thresholds, which could be used to design biodiversity-friendly management of production forests.

Temporal comparisons of the same site before-and-after degradation are likely to return the most reliable signals since they preclude biases associated with intrinsic differences between sites. Unfortunately, only ~10% of all studies in our dataset adopted this design, so we failed to detect an overall effect. Likewise, studies monitoring responses to disturbance over time could throw further light into population recovery from degradation, but these represented only ~5% of our dataset, leading to inconclusive results. We strongly encourage longitudinal study designs, which can take advantage of research opportunities involving episodic disturbance events including wildfires, selective logging and mining operations.

4.6. IUCN status

The IUCN threat categories generally reflected species vulnerability to human disturbance: we detected an overall negative effect size for all threatened and near-threatened categories but not for *Least-Concern* species. However, the degree to which a species is sensitive to habitat disturbance could not be directly inferred through its IUCN status as the magnitude of the effect size was uncorrelated with threat categories. For instance, *Vulnerable* species apparently experienced the most detrimental effects. A greater research effort focused on *Critically Endangered* species would help clarify these findings.

4.7. Predicting effect sizes

Our model selection approach identified hunting pressure as the most important stressor influencing primate responses to habitat disturbance. The *null* model was the second best ranked, suggesting that habitat disturbance effects are essentially universal, as no single variable had a decisive impact on response ratios. Finally, a significant portion of sample fits returned *Region + Geographic range* as the top-ranked model, supporting the notion that species responses have a strong geographic context. However, the explanatory power of these models was weak (11-27%), suggesting that other important factors that were not investigated here may play a role. We did not consider the influence of landscape context and ‘spill-over’ effects from neighbouring undisturbed forest in our analysis, although it clearly played a role in most studies, calling for the inclusion of landscape variables into predictive models.

5. Conclusions and Recommendations

Human-induced habitat disturbance in tropical forests has a consistently negative effect on local primate faunas, leading to significant reductions in species richness and abundance. The biodiversity value of degraded habitats can be very low, underpinning the critical role of large tracts of primary forests in maintaining the full integrity of biotic assemblages through landscape supplementation, complementation and/or source-sink dynamics (Dunning et al., 1992). Differences in species responses are associated with the four major biogeographic realms, likely reflecting the interaction between historical and ecological context, particularly resilience to disturbance conferred over evolutionary time scales and contemporary trophic requirements. Among all threats examined here, forest conversion to agricultural practices induced the most detrimental effects on primates, often leading to population extirpations, even if some species can adjust to agroforests and agro-mosaics. Although some studies suggest a role of selective logging in contributing for biodiversity conservation (Edwards et al., 2010), we found logging to be the second most severe threat for primates. It is possible, however, to mitigate the effects of selective logging by combining ecological knowledge about local faunas with reduced-impact logging (RIL) techniques.

Increasingly intensified land-use systems gradually reduced the baseline character of primate faunas typical of undisturbed primary forests, thereby calling for the identification of acceptable forest degradation thresholds. We also recommend a greater research focus on multiple co-occurring threats, which remain poorly understood in terms of at local scales how they affect different species. Hunting pressure, for example, exacerbated the negative effects of habitat structural degradation, so it should be considered, for example, when granting environmental licenses for forest management plans. Finally, since some degraded habitats could still retain populations of several primate species, we suggest the adoption of a ‘countryside biogeography framework’, which recognizes the importance of human-modified habitats for the fate of wildlife (Mendenhall et al., 2014). However, because of the overall low biodiversity value of degraded forests, retaining primary forest patches remains critical in safeguarding more resilient populations through individual fluxes among neighbouring patches.

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Appendix A

Table A.1. Checklist of 81 selected studies, biogeographic region and main threat investigated in both disturbed and 'pseudo-control' forest sites.

Table A.2. Checklist of primate species included in the dataset and their trophic classification.

Table A.3. Results of the meta-analysis using response ratios within sub-groups: biogeographic region, study design, main threat, and trophic level.

Table A.4. Results of the meta-analysis using response ratios for two-level combinations of Main Threat/Study Design and Biogeographic Region/Trophic Level.

Fig. A.1. Steps followed during the scientific reference sorting.

Fig. A.2. Linear relationship between species range sizes and response ratios to habitat disturbance within each biogeographic realm.

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APPENDIX A

1. Dataset: sorting of papers

As we selected studies that investigated the effect of anthropogenic habitat degradation upon primate communities in tropical forests, we excluded: studies on natural phenomena, paleontology, captivity (including studies that compared field data with captive data), computer modelling (unless it makes available the real value on the metric analyzed) and studies performed in temperate forests. Since the twin effects of forest habitat loss and fragmentation *per se* (area and isolation effects) have been relatively well documented for primates (Harcourt & Doherty, 2005; Benchimol & Peres, 2013), we focused entirely on studies that examined the effects of human disturbance on forest habitat structure, composition and/or quality.

We restricted our database to studies that performed any reported comparison between a degraded (or more degraded) site and a relatively intact (or less degraded) old growth forest within the same study landscape. However, we included studies that used correlative analyses to investigate spatial or temporal effects of land-use intensification, such as levels of disturbance intensity and recovery time since timber exploitation. When studies performed comparisons between field-sampled and published data, we only included them if authors ensured that all data had been collected using exactly the same methodology, in the same geographic region, within roughly the same study period, and if all required data to perform the analysis had been presented. After a strict sorting procedure (Fig. A1), we finished with 259 references that were classified into one of the six following categories depending on the research focus, and selected only those that investigated population or community-wide responses: (1) Behaviour: studies that investigated changes in specific behaviours, activity patterns or use of space (home range, daily distance traveled and vertical strata use); (2) Population/Community: studies that investigated changes in species richness (number of species, rate of species loss or diversity index) and/or abundance (density, encounter rates, population size or capture rates); (3) Demography: studies that investigated changes in demographic parameters such as group size, group composition, sex ratio, infant survival and fecundity; (4) Diet: studies that investigated changes in food quality, dietary diversity and dietary specialization; (5) Genetic: studies that investigated gene flow between populations and genetic diversity; and (6) Health: studies that investigated changes in parasite infection rates, stress level, diseases incidence and body condition. Finnaly, we finished with 81 studies with a population/community focus that were used in the meta-analysis (Table A.1).

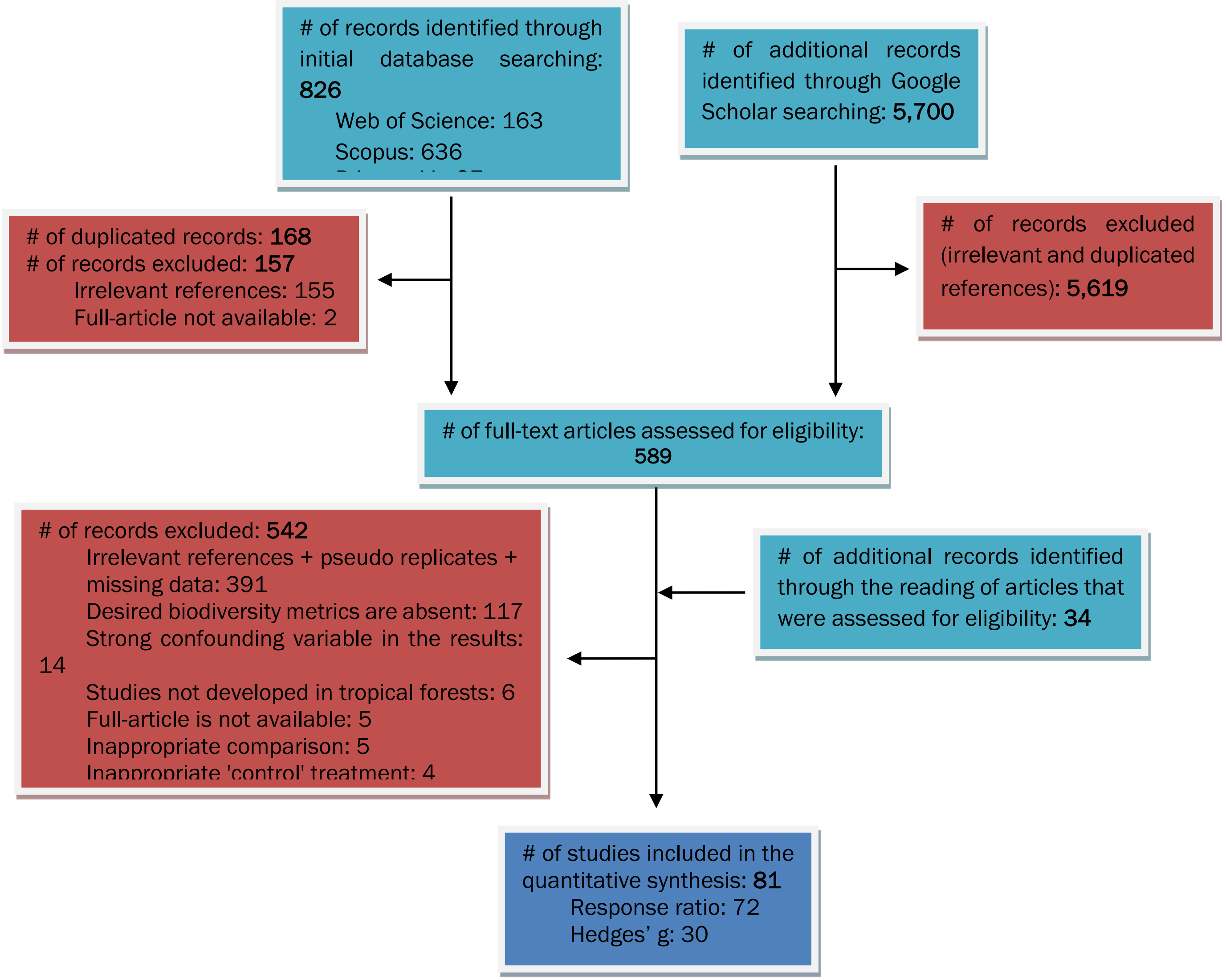

Fig. A.1. Flow of information through the systematic review and references' sorting.

Table A1. Checklist of 81 selected studies grouped by main investigated threat,and biogeographical region.

Main Threat	References	Region
Agriculture	Bernard et al, 2014	Africa
	Bitty et al, 2015	Africa
	Blanco & Waltert, 2013	Africa
	Fashing et al, 2012	Africa
	Cassano et al, 2012	Neotropics
	Dotta & Verdade, 2011	Neotropics
	Johns, 1991	Neotropics
	McCann et al, 2003	Neotropics
	Mineiro, 2016	Neotropics
	Oliveira et al, 2011	Neotropics
	Oliveira, 2015	Neotropics
	Danielsen & Heegaard, 1995	Southeast Asia
	Laidlaw, 2000	Southeast Asia
	Merker & Mühlenberg, 2000	Southeast Asia
	van Schaik et al, 2001	Southeast Asia
	Wilson & Johns, 1982	Southeast Asia
Timber extraction	Chapman & Chapman, 1999	Africa
	Chapman et al, 2000	Africa
	Clarketal, 2009	Africa
	Hashimoto, 1995	Africa
	Mammides et al, 2009	Africa
	Martin & Asibey, 1979	Africa
	Oates, 1977	Africa
	Phoonjampa et al, 2011	Africa
	Plumptre & Reynolds, 1994	Africa
	Remis & Robinson, 2012	Africa
	Remis, 2000	Africa
	Skorupa, 1986	Africa
	Weisenseel et al, 1993	Africa
	White, 1994	Africa
	Ganzhorn, 1995	Madagascar
	Ganzhorn, 1997	Madagascar
	Grassi, 2006	Madagascar
	Herrera et al, 2011	Madagascar
	Ayres & Johns, 1987	Neotropics
	Bicknell & Peres, 2010	Neotropics
	Bobadilla & Ferrari, 2000	Neotropics
	Branch, 1983	Neotropics
	Calouro, 2005	Neotropics
	Carvalho Jr., 2003	Neotropics
	Flescher, 2015	Neotropics
	Freese et al., 1982	Neotropics
	Freitas, 2008	Neotropics
	Goffard et al, 2008	Neotropics

Table A.1. continuation

Main Threat	References	Region
Timber extraction	Johns, 1986	Neotropics
	Laufer et al, 2015	Neotropics
	Lindshield, 2006	Neotropics
	Brugiere, 1998	Southeast Asia
	Dahaban et al, 1996	Southeast Asia
	Davies & Payne, 1982	Southeast Asia
	Felton et al, 2003	Southeast Asia
	Johns & Johns, 1995	Southeast Asia
	Johns, 1983	Southeast Asia
	Johns, 1992	Southeast Asia
	Marsh & Wilson, 1981	Southeast Asia
	Marshall et al, 2006	Southeast Asia
	Onoguchi & Matsubayashi, 2008	Southeast Asia
	Rosenbaum et al, 1998	Southeast Asia
	Samejima et al, 2012	Southeast Asia
	Wilson & Wilson, 1975	Southeast Asia
Secondary forest	Decker, 1994	Africa
	Ganzhorn & Schmid, 1998	Madagascar
	Smith et al, 1997	Madagascar
	Chagas & Ferrari, 2010	Neotropics
	Parry et al, 2007	Neotropics
	Sorensen & Fedigan, 2000	Neotropics
	Tardio & Silveira, 2015	Neotropics
	Lee et al, 2015	Southeast Asia
	Pliosungnoen et al, 2010	Southeast Asia
	Southwick & Cadigan, 1972	Southeast Asia
Multiple threats	Hoffman & O'Riain, 2012	Africa
	Lawes, 1992	Africa
	Muoria et al, 2003	Africa
	Rodrigues, 2014	Neotropics
	Merker et al, 2005	Southeast Asia
	Russon et al, 2000	Southeast Asia
Fire	Barlow & Peres, 2006	Neotropics
	Gilhooly et al, 2015	Southeast Asia
Seismic oil exploitation	Kolowski & Alonso, 2012	Neotropics
Non-specified main threat	Schaeffler & Kappeler, 2014	Madagascar
	Johnson et al, 2005	Southeast Asia

2. Species Trophic Levels

We compiled dietary information for each species from the literature (Wilman et al., 2014; Hawes & Peres, 2014) to achieve the percentage of each food item in species dietary. All information was then revised and supplemented by CAP. We ranked the food items across trophic levels based on their energetic value, from least to most energy-rich: (1)leaves, (2)nectar/pollen/exudates/gum/fruits, (3)fruits, (4) invertebrates and (5) vertebrates. The trophic level was then determined as the sum of the percentages of each food item, weighted by its energetic rank and divided by 100 (Table S.2).

Table A.2. Mean percentage of each food item in species dietary and species classification into trophic levels.

Family	**Species**	**leaves**	**nectar/polen/ exudates/gum**	**fruits**	**seeds**	**invertebrates**	**vertebrates**	**Trophic level**
Aotidae	*Aotus nigriceps*	5	5	50	15	20	5	3
Atelidae	*Alouatta belzebul*	55	0	40	5	0	0	2
Atelidae	*Alouatta caraya*	65	0	30	5	0	0	1
Atelidae	*Alouatta macconnelli*	45	0	50	5	0	0	2
Atelidae	*Alouatta palliatta*	45	0	50	5	0	0	2
Atelidae	*Alouatta sara*	45	0	50	5	0	0	2
Atelidae	*Alouatta seniculus*	45	0	50	5	0	0	2
Atelidae	*Ateles belzebuth*	10	0	60	10	10	10	3
Atelidae	*Ateles chamek*	10	0	60	10	10	10	3
Atelidae	*Ateles geoffroyi*	10	0	60	10	10	10	3
Atelidae	*Ateles paniscus*	10	0	60	10	10	10	3
Atelidae	*Lagothrix cana*	28	2	65	5	0	0	2
Atelidae	*Lagothrix lagotricha*	28	2	65	5	0	0	2
Atelidae	*Lagothrix poeppigii*	28	2	65	5	0	0	2
Callithrichidae	*Callithrix kuhlii*	0	40	30	0	20	10	3
Callithrichidae	*Leontopithecus chrysomelas*	0	5	60	0	30	5	3
Callithrichidae	*Mico argentatus*	0	10	65	0	20	5	3
Callithrichidae	*Mico humeralifer*	0	10	65	0	20	5	3
Callithrichidae	*Saguinus fuscicollis*	0	15	53	0	30	2	3
Callithrichidae	*Saguinus avilapiresi*	0	15	53	0	30	2	3
Callithrichidae	*Saguinus imperator*	0	15	53	0	30	2	3
Callithrichidae	*Saguinus midas*	0	15	53	0	30	2	3
Callithrichidae	*Saguinus mystax*	0	15	53	0	30	2	3
Callithrichidae	*Saguinus niger*	0	15	53	0	30	2	3

Table A.2. continuation

Family	***Species***	**leaves**	**nectar/polen/ exsudates/gum**	**fruits**	**seeds**	**invertebrates**	**vertebrates**	**Trophic level**
Callithrichidae	*Saguinus nigricollis*	0	15	53	0	30	2	3
Callithrichidae	*Saguinus ursulus*	0	15	53	0	30	2	3
Cebidae	*Saimiri boliviensis*	5	0	50	10	25	10	3
Cebidae	*Saimiri collinsi*	5	0	50	10	25	10	3
Cebidae	*Saimiri sciureus*	5	0	50	10	25	10	3
Cebidae	*Saimiri ustus*	5	0	50	10	25	10	3
Cebidae	*Saimiri vanzolinii*	5	0	50	10	25	10	3
Cebidae	*Sapajus apela*	10	5	45	15	20	5	3
Cebidae	*Sapajus xanthosternos*	10	5	45	15	20	5	3
Cebidae	*Callimico goeldii*	0	0	50	0	40	10	3
Cebidae	*Cebus albifrons*	10	10	35	20	20	5	3
Cebidae	*Cebus capucinus*	10	10	35	20	20	5	3
Cebidae	*Cebus kaapori*	10	10	35	20	20	5	3
Cebidae	*Cebus olivaceus*	10	10	35	20	20	5	3
Cebidae	*Cebus unicolor*	10	10	35	20	20	5	3
Cercopithecidae	*Cercocebus atys*	0	0	40	50	10	0	3
Cercopithecidae	*Cercocebus galeritus*	0	0	70	0	20	10	3
Cercopithecidae	*Cercopithecus ascanius*	10	0	50	10	20	10	3
Cercopithecidae	*C. ascanius schmidti*	10	0	50	10	20	10	3
Cercopithecidae	*Cercopithecus diana*	10	0	50	0	30	10	3
Cercopithecidae	*Cercopithecus lhoesti*	10	0	50	30	0	10	3
Cercopithecidae	*Cercopithecus mitis*	10	0	50	30	0	10	3
Cercopithecidae	*C. mitis albotorquatus*	10	0	50	30	0	10	3
Cercopithecidae	*C. mitis stuhlmanni*	10	0	50	30	0	10	3
Cercopithecidae	*Cercopithecus mona*	10	0	50	10	20	10	3
Cercopithecidae	*Cercopithecus nictitans*	10	0	50	10	20	10	3
Cercopithecidae	*Chlorocebus pygerythrus*	20	0	40	0	20	20	3
Cercopithecidae	*Colobus guereza*	70	0	30	0	0	0	1
Cercopithecidae	*Colobus guereza matschiei*	70	0	30	0	0	0	1
Cercopithecidae	*Colobus polykomos*	70	0	30	0	0	0	1
Cercopithecidae	*Colobus satanás*	70	0	30	0	0	0	1
Cercopithecidae	*Lophocebus albigena*	50	0	50	0	0	0	2
Cercopithecidae	*Lophocebus aterrimus*	0	20	40	40	0	0	2
Cercopithecidae	*Macaca fascicularis*	10	0	40	0	50	0	3
Cercopithecidae	*Macaca nemestrina*	10	0	70	10	10	0	2
Cercopithecidae	*Macaca nigra*	10	0	70	10	10	0	2
Cercopithecidae	*Nasalis larvatus*	80	0	20	0	0	0	1

Table A.2. continuation

Family	**Species**	**leaves**	**nectar/polen/ exsudates/gum**	**fruits**	**seeds**	**invertebrates**	**vertebrates**	**Trophic level**
Cercopithecidae	*Papio cynocephalus*	60	0	20	0	10	10	2
Cercopithecidae	*Presbytis comata*	40	0	20	40	0	0	2
Cercopithecidae	*Presbytis frontata*	40	0	20	40	0	0	2
Cercopithecidae	*Presbytis hosei*	40	0	20	40	0	0	2
Cercopithecidae	*Presbytis melalophos*	20	0	40	40	0	0	2
Cercopithecidae	*Presbytis rubicunda*	20	0	40	40	0	0	2
Cercopithecidae	*Procolobus badius*	80	0	20	0	0	0	1
Cercopithecidae	*Procolobus rufomitratus*	70	0	20	10	0	0	1
Cercopithecidae	*Procolobus tephrosceles*	80	0	20	0	0	0	1
Cercopithecidae	*Procolobus verus*	80	0	10	10	0	0	1
Cercopithecidae	*Trachypithecus cristatus*	70	0	30	0	0	0	1
Cercopithecidae	*Trachypithecus obscurus*	70	0	30	0	0	0	1
Cheirogaleidae	*Cheirogaleus medius*	30	20	30	0	20	0	2
Cheirogaleidae	*Microcebus berthae*	20	10	30	0	20	20	3
Cheirogaleidae	*Microcebus murinus*	20	10	30	0	20	20	3
Cheirogaleidae	*Microcebus rufus*	20	10	30	0	20	20	3
Cheirogaleidae	*Mirza coquereli*	10	0	10	10	60	10	4
Cheirogaleidae	*Phaner furcifer*	0	100	0	0	0	0	2
Hominidae	*Gorilla gorila*	90	0	10	0	0	0	1
Hylobatidae	*Hylobates agilis*	20	0	70	0	10	0	2
Hylobatidae	*Hylobates lar*	20	0	70	0	10	0	2
Hylobatidae	*Hylobates muelleri*	20	0	70	0	10	0	2
Hylobatidae	*Hylobates pileatus*	20	0	70	0	10	0	2
Hominidae	*Pan troglodytes*	30	0	60	0	10	0	2
Hominidae	*Pongo pygmaeus*	0	0	80	0	10	10	3
Hominidae	*Pongo pygmaeus wurmbii*	0	0	80	0	10	10	3
Hylobatidae	*Symphalangus syndactylus*	10	0	80	0	10	0	2
Indriidae	*Avahi peyrierasi*	100	0	0	0	0	0	1
Indriidae	*Propithecus edwardsi*	50	0	40	10	0	0	2
Indriidae	*Propithecus verreauxi*	70	0	30	0	0	0	1
Lemuridae	*Eulemur fulvus*	20	10	70	0	0	0	2
Lemuridae	*Eulemur rubriventer*	14	6	80	0	0	0	2
Lemuridae	*Eulemur rufifrons*	20	10	70	0	0	0	2
Lemuridae	*Hapalemur aureus*	100	0	0	0	0	0	1
Lemuridae	*Hapalemur griséus*	100	0	0	0	0	0	1
Lemuridae	*Varecia variegata*	0	0	100	0	0	0	2
Lepilemuridae	*Lepilemur mustelinus*	100	0	0	0	0	0	1
Lepilemuridae	*Lepilemur ruficaudatus*	100	0	0	0	0	0	1
Lorisidae	*Nycticebus bengalensis*	0	0	20	0	40	40	4

Table A.2. continuation

Family	Species	leaves	nectar/polen/ exsudates/gum	fruits	seeds	invertebrates	vertebrates	Trophic level
Lorisidae	*Nycticebus menagensis*	0	0	20	0	40	40	4
Lorisidae	*Perodicticus potto*	0	10	80	0	10	0	2
Pitheciidae	*Cacajao calvus*	5	0	30	50	10	5	3
Pitheciidae	*Callicebus coimbrai*	20	0	65	5	10	0	2
Pitheciidae	*Callicebus cupreus*	20	0	65	5	10	0	2
Pitheciidae	*Callicebus discolor*	20	0	65	5	10	0	2
Pitheciidae	*Callicebus hoffmannsi*	20	0	65	5	10	0	2
Pitheciidae	*Callicebus melanochir*	20	0	65	5	10	0	2
Pitheciidae	*Callicebus moloch*	20	0	65	5	10	0	2
Pitheciidae	*Callicebus nigrifrons*	20	0	65	5	10	0	2
Pitheciidae	*Callicebus torquatus*	10	0	60	5	25	0	2
Pitheciidae	*Chiropotes albinasus*	10	0	40	45	5	0	2
Pitheciidae	*Chiropotes chiropotes*	5	0	55	35	5	0	2
Pitheciidae	*Chiropotes satanás*	10	0	40	45	5	0	2
Pitheciidae	*Chiropotes utahickae*	10	0	35	50	5	0	3
Pitheciidae	*Pithecia aequatorialis*	30	10	30	0	0	30	3
Pitheciidae	*Pithecia albicans*	30	10	30	0	0	30	3
Pitheciidae	*Pithecia irrorata*	30	10	30	0	0	30	3
Pitheciidae	*Pithecia monachus*	30	10	30	0	0	30	3
Pitheciidae	*Pithecia pithecia*	30	10	30	0	0	30	3
Tarsiidae	*Tarsius bancanus*	0	0	0	0	100	0	4
Tarsiidae	*Tarsius dentatus*	0	0	0	0	100	0	4

3. Results

Table A.3. Results of the meta-analysis using response ratios as effect index within sub-groups (Biogeographic region, Main threat, Trophic level, Study design and IUCN status). The table shows the total number of pairwise comparisons (C) and the number of studies (S) in each sub-group category that was used for the analysis, the median response ratios and a 95% confidence intervals generated with 10,000 permutations (with replacement) considering all comparisons, and only one comparison per study (to avoid the problem of pseudo-replications). Confidence intervals that did not include "zero" represent overall effect sizes.

			all comparisons		1 comparison/study	
Sub-group	**C**	**S**	**median**	**95%CI**	**median**	**95%CI**
Region						
Africa	217	17	-0.06	-0.19; -0.08	-0.16	-0.46; 0.26
Neotropics	237	24	-0.45	-0.77; -0.14	-0.58	-1.22; 0.01
Southeast Asia	138	24	-0.27	-0.46; -0.08	-0.29	-0.77; -0.11
Madagascar	45	7	-0.08	-0.54; 0.69	-0.66	-0.91; -0.50
Main Threat						
Logging	445	48	-0.15	-0.26; -0.04	-0.25	-0.49; -0.08
Agriculture	41	13	-1.92	-2.39;-0.89	-1.47	-2.08; -0.89
Secondary Forests	44	10	-0.48	-0.91; 0.48	-0.36	-0.99; 0.35
Multiple Threats	94	9	-0.02	-0.47; 0. 14	-0.32	-1.00; 0.14
Trophic Level						
Level 1	127	28	-0.07	-0.20;0.09	-0.10	-0.32;0.05
Level 2	194	49	-0.38	-0.66;-0.21	-0.41	-0.77;-0.22
Level 3	280	50	-0.14	-0.32;0.00	-0.30	-0.52;-0.08
Level 4	18	6	-0.66	-1.07;0.05	-0.43	-1.07;0.03
Study Design						
Control	382	52	-0.22	-0.40; -0.06	-0.26	-0.54; -0.06
Before	37	7	-0.10	-0.43; 0.21	-0.26	-1.42; 0.22
Levels	155	23	-0.08	-0.28; 0.02	-0.54	-1.00; -0.11
Time	34	3	-0.38	-0.76; 0.19	-0.27	-2.19; 1.16
IUCN Status						
LC	296	45	-0.07	-0.22; 0.00	-0.15	-0.45; 0.00
NT	57	17	-0.14	-0.26; 0.08	-0.26	-0.74; -0.06
VU	96	36	-0.67	-0.97; -0.39	-0.79	-0.98; -0.35
EN	124	44	-0.26	-0.58; -0.07	-0.24	-0.50; -0.14
CR	21	8	-1.92	-3.01; -0.16	-0.46	-3.07; -0.07

LC=Least Concern; NT=Near Threatened; VU=Vulnerable; EN=Endangered; CR=Critically Endangered.

Table A.4. Results of the meta-analysis using response ratios as effect size index for two-level combinations of the Main Threat/Study Design and Biogeographic Region/Trophic Level. The table shows the total number of pairwise comparisons (C) and the number of studies (S) used for the analysis in each combination, the median response ratios and a 95% confidence intervals generated with 10,000 permutations (with replacement) considering all comparisons and only one comparison per study (to avoid the problem of pseudo-replications).Confidence intervals that do not includes "zero" represent overall effect sizes. “NA” indicates that no data is available or sample size is too small (N≤ 2 studies) for effect size or confidence interval calculations.

				all comparisons		1 comparison/study	
category	**region**	**C**	**S**	**median**	**95%CI**	**median**	**95%CI**
THREAT							
Timber extraction	Africa	177	14	-0.08	-0.22; 0.00	-0.24	-0.50; 0.05
	Southeast Asia	105	17	-0.24	-0.44; 0.00	-0.24	-0.75; -0.04
	Neotropics	125	13	-0.38	-0.77; -0.02	-0.29	-1.25; 0.04
	Madagascar	38	4	0.31	-0.36; 1.01	-0.16	-1.26; 0.90
	Level1	112	24	-0.08	-0.29; 0.06	-0.09	-0.46; 0.00
	Level2	144	35	-0.27	-0.54; -0.11	-0.24	-0.46; -0.15
	Level3	169	31	-0.14	-0.34; 0.00	-0.26	-0.45; 0.00
	Level4	6	3	1.15	-2.80; 2.65	0.00	-2.61; 0.00
Agriculture	Africa	4	2	-2.12	-5.55;-0.12	NA	NA
	Southeast Asia	8	5	-2.16	-8.72; -0.89	-1.61	-1.61; -1.48
	Neotropics	29	6	-2.08	-2.48; -0.69	-1.51	-2.54; -0.10
	Madagascar	0	0	NA	NA	NA	NA
	Level1	1	1	NA	NA	NA	NA
	Level2	9	4	-2.30	-3.85; -1.76	-2.58	-2.99; -2.19
	Level3	22	7	-1.06	-2.68; 0.11	-1.15	-2.39; -0.83
	Level4	1	1	NA	NA	NA	NA
Secondary Forest	Africa	3	1	NA	NA	NA	NA
	Southeast Asia	12	3	-0.13	-0.66; 0.85	-0.15	-0.78; 0.06
	Neotropics	24	4	-0.51	-3.37; 2.77	-0.35	-4.16; 4.03
	Madagascar	5	2	-0.93	-4.91; -0.50	NA	NA
	Level1	5	3	0.28	-4.91; 3.26	0.28	-0.15; 1.13
	Level2	5	2	-0.22	-0.78; 2.56	NA	NA
	Level3	7	21	0.69	-0.93;1.83	0.69	-0.93; 1.60
	Level4	3	1	-1.15	-1.21; 0.06	NA	NA
Multiple Threats	Africa	33	2	0.43	0.02; 0.70	NA	NA
	Southeast Asia	10	3	-0.70	-1.51;- 0.18	-0.41	-1.40; 0.05
	Neotropics	50	3	-0. 22	-1.00; 0.00	-1.00	-5.56; 4.47
	Madagascar	1	1	NA	NA	NA	NA
	Level1	6	1	0.75	0.08;1.29	NA	NA
	Level2	24	4	-0.63	-1.74; 0.00	-1.01	-3.46; 0.28
	Level3	55	6	0.00	-0.47; 0.34	-0.27	-3.06; 1.22
	Level4	9	5	0.00	-1.14; 2.40	0.00	-0.81; 0.06

TableA.4. continuation

				all comparisons		1 comparison/study	
category	**region**	**C**	**S**	**median**	**95%CI**	**median**	**95%CI**
STUDY DESIGN							
Primary	Africa	113	14	-0.1	-0.22;0.00	-0.14	-0.45; 0.25
x	Southeast Asia	88	19	-0.16	-0.35;0.00	-0.24	-0.53;-0.04
Disturbed	Neotropics	164	18	-0.54	-0.96;-0.01	-0.56	-1.25;0.02
	Madagascar	30	6	-0.49	-0.83;0.10	-0.62	-1.06;-0.04
	Level1	75	24	-0.08	-0.33;0.09	-0.09	-0.37;0.04
	Level2	122	40	-0.51	-0.98;-0.25	-0.36	-0.85;-0.23
	Level3	189	43	-0.13	-0.39;0.00	-0.23	-0.42;-0.06
	Level4	9	5	0.00	-1.15;2.30	0.00	-0.86;0.06
Before	Africa	8	2	-0.22	-0.54;-0.07	NA	NA
x	Southeast Asia	5	2	-1.42	-12.40;1.28	NA	NA
After degradation	Neotropics	17	2	-0.14	-0.51;0.10	NA	NA
	Madagascar	7	1	1.01	0.59;2.30	NA	NA
	Level1	7	4	0.21	-0.09;1.28	0.46	-0.08;1.14
	Level2	9	5	-0.19	-2.27;0.69	-0.26	-1.52;-0.19
	Level3	20	6	-0.31	-0.52;0.06	-0.34	-0.54;-0.02
	Level4	1	1	NA	NA	NA	NA
Less-degraded	Africa	80	6	0.11	-0.12;0.47	-0.27	-1.22;0.80
x	Southeast Asia	27	9	-0.46	-1.00;-0.11	-0.46	-1.02;-0.22
More-degraded	Neotropics	40	6	-0.19	-1.26;0.00	-0.66	-1.79;0.35
	Madagascar	8	2	0.43	-1.89;2.13	NA	NA
	Level1	29	10	0.00	-0.24;0.70	0.04	-0.09;0.52
	Level2	52	17	-0.09	-0.62;0.06	-0.11	-0.75;0.04
	Level3	64	14	0.00	-0.34;0.32	-0.43	-1.14;-0.07
	Level4	8	3	-0.97	-1.40;-0.41	-1.21	-1.40;-1.21
Old-degraded	Africa	10	1	0.08	-0.64;0.96	NA	NA
x	Southeast Asia	24	2	-0.51	-2.16;0.15	NA	NA
Early-degraded	Neotropics	0	0	NA	NA	NA	NA
	Madagascar	0	0	NA	NA	NA	NA
	Level1	16	3	-0.19	-1.07;0.37	-0.12	-2.19;1.38
	Level2	11	3	-0.39	-3.79;0.59	0.15	-0.76;0.91
	Level3	7	2	-0.64	-2.77;1.16	NA	NA
	Level4	0	0	NA	NA	NA	NA

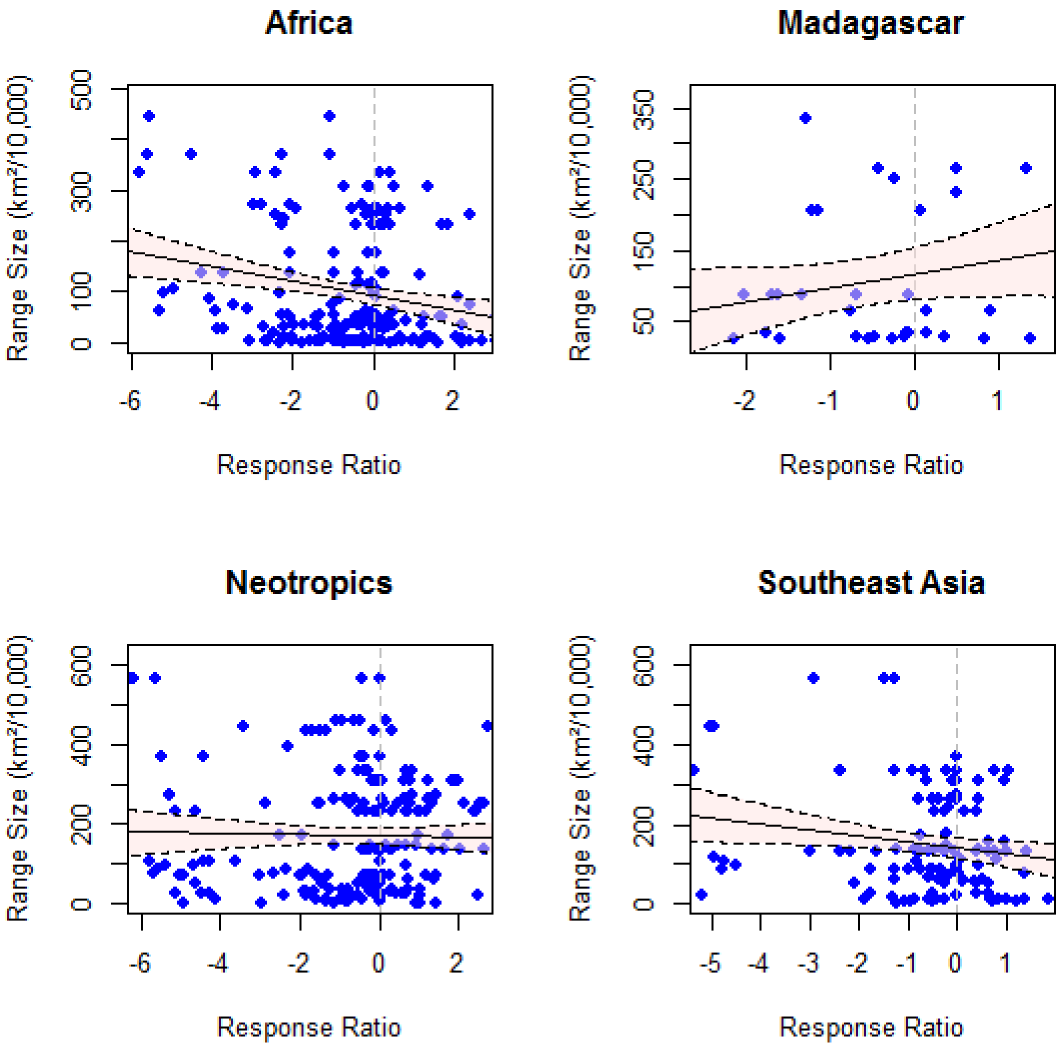

Fig. A.2. Linear relationships between species geographic range size and response ratio to habitat disturbance obtained for each pairwise comparison broken-down by biogeographic region. The linear regression trend and confidence intervalsare represented by the solid black line and the pink area, respectively. Vertical grey dashed lines indicate no effect of habitat disturbance.

4. Publication bias

Meta-analyses may suffer from publication bias since studies with non-significant results are less likely to be published (Iyengar & Greenhouse, 1988). We attempted to reduce this bias by including unpublished studies from the 'grey literature' in our bibliographic compilation but this may not have solved the problem. Some methods have been proposed to identify publication biases in meta-analyses but these cannot be performed without error estimates (Borenstein et al., 2009), so we searched for such biases only in the dataset for which Hedges' g effect sizes could be calculated. The funnel plot approach allows a visual examination of how studies (=comparisons) are distributed around the overall effect size. We used the Trim-and-Fill Method (Duval & Tweedie, 2000) to estimate the number of missing studies that would be required to make the funnel plot symmetric and to recalculate an adjusted overall effect size including those missing studies. We also used the Fail-Safe Number Rosenthal Approach (Rosenthal, 1991) to estimate the number of unpublished studies with no effect (Hedges' g = 0) that would be necessary to render the overall effect size non-significant (target significance value = 0.05). Following Rosenthal's approach, a meta-analysis can be defined as free from publication bias if the fail-safe number is ≥ 5N + 10, where N is the total number of studies (Rosenthal, 1991). As for all previous analyses, we accounted for pseudo-replication using 10,000 permutations.

The trim-and-fill analysis indicated that between 0 to 4 missing studies from our dataset would be required to render funnel plots symmetric, and returned an overall adjusted mean effect size that did not differ from that observed (–0.47; 95%CI –0.76, –0.21). A fail-safe number of 118 unpublished studies with no effect (RR=0) would therefore be required to cancel out the overall significant effect of this meta-analysis. According to Rosenthal (1991), a number ≥160 would provide sufficient evidence that this meta-analysis is not skewed by publication bias. Although our estimate is slightly lower than this, we highlight that we subset this analysis including only part of our full dataset. Including studies that did not provide error estimates (which can be interpreted here as missing data) would have added only 10 studies (36 comparisons) with no effect to the dataset. Therefore, considering that we performed an exhaustive bibliographic search, we remain confident about the robustness of this meta-analysis.

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CAPÍTULO 2

Occupancy of diurnal raptors in cocoa agroforests of Southern Bahia, Brazil*

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Abstract

Habitat loss and fragmentation, especially resultant of agriculture expansion, poses the main threats to biodiversity conservation. While some species are able to survive and even proliferate in human-modified habitats (winner species), others are highly dependent on well-preserved habitats, being more vulnerable to extinction (losers). Most raptors can be considered loser species due to their high trophic position, large home ranges, and low reproductive rates. Consequently, this group is frequently used to reflect the environmental quality of habitats and the biodiversity status of communities. Here we described the diurnal raptors assemblages found in shaded-cocoa agroforests (*cabrucas*) of Southern Bahia, Brazil, and tried to identify the determinants of raptors occupancy in this system. For this, we modeled species occupancy using covariates related to vegetation structure, management intensity, vegetation cover as well as some biological traits (body mass, trophic level and dietary specialization). We used complementary sampling methods – active search, playback, and point-count – to systematically survey diurnal raptors in 16 cabruca sites, which resulted in the recording of 22 species. The features that most affected raptors occupancy in cabrucas were shade-trees density and management intensification, both suggesting a high incidence of raptors in more managed cabrucas. Shade-trees diameter also affects raptors occupancy positively. Regarding the biological characters, we found more specialized and large-bodied species as less likely to occur in cabrucas. Our results reveal a high potential of cabrucas to mitigate the effects of forest loss and fragmentation on diurnal raptors but also indicates that cabrucas alone cannot support complete assemblages of diurnal raptors, calling for the maintenance of forest remnants in the landscapes to assure the regional conservation of this group.

Keywords: agriculture; birds of prey; sensitivity; disturbance; Neotropics; Atlantic forest

Introduction

Habitat conversion to attend human demand for natural resources is rapidly expanding worldwide (Steffen et al., 2015; Venter et al., 2016; Watson et al., 2016). As a consequence, many forest species are experiencing habitat loss and fragmentation, threatening biodiversity conservation (Maxwell et al., 2016). Species that are flexible to deal with habitat changes, such alterations in microclimate conditions and vegetation structure, are expected to have a higher chance of surviving in human-modified habitats than more sensitive species which may not be able to occupy or persist in such habitats, increasing their chance of local extinction (Purvis et al., 2000; Gardner et al., 2009; Cowlishaw et al., 2009; Tabarelli et al., 2012).

Many studies have investigated species' tolerance to habitat changes, focusing on different taxonomic groups (Airoldi & Bulleri, 2011; Schwitzer et al., 2011; Fontúrbel et al., 2014; Ribeiro-neto et al., 2016). Among birds, there is a high variation in species responses to habitat modification, ranging from species that seems to be highly dependent on pristine environments to species that are well-adapted to urban environments (Jullien & Thiollay, 1996; Abrahamczyk et al., 2008; Rullman & Marzluff, 2014). Raptors are expected to be very sensitive to habitat disturbance due to their large home ranges, low reproductive rates and high trophic position in food webs (Bierregaard Jr., 1995; Carrete et al., 2009) becoming an interesting group to investigate issues related habitat disturbance. Due to their trophic position as top predators, raptors are frequently used to reflect the biodiversity status of biological communities (Sergio et al., 2006, 2008), as well as to indicate the habitat quality (Rodríguez-Estrella et al., 1998). For example, raptors are not expected to occur in agricultural lands that receive high inputs of pesticides, since bioaccumulation and biomagnification of such substances potentiate its detrimental effects on top predators (Espín et al., 2016).

Three orders of diurnal raptors – Cathartiformes, Accipitriformes, and Falconiformes – encompassing 102 species are found in the Neotropics (Remsen et al., 2017), and ~22% of them are globally threatened (IUCN, 2016). Seventy-five species of diurnal raptors occur in the Brazilian territory (Piacentini et al., 2015), and a large portion of them inhabits the Atlantic forest (~76%; Ferguson-Lees & Christie, 2006), a world biodiversity hotspot (Myers et al., 2000). The Brazilian Atlantic forest is one of the most threatened biomes in the world, currently reduced to about 12% of its original extent (Ribeiro et al., 2009). The "Central Corridor of the Atlantic Forest" is a region of particular conservation interest inside this biome due to the large extent of forest remnants combined with a high degree of floristic and faunistic diversity (Galindo-Leal & Câmara, 2003). Within this corridor, there are some Important Bird Areas (IBA) such as southern Bahia (Bencke et al., 2006), where three of the six species of Accipitriformes that are threatened in the Brazilian territory can be found – *Morphnus guianensis, Harpia harpyja* and *Buteogallus lacernulatus* (MMA/ICMBio, 2016) – being thus a very important region for raptors' conservation.

In Southern Bahia, less than 5% of the Atlantic forest remains (~ 3500 km²; Thomas et al., 1997) in a landscape that is highly dominated by cocoa (*Theobroma cacao*) plantations (~5,500 km²; May & Rocha, 1996). Due to the high degree of forest fragmentation, researchers have been investigating the role of cocoa plantations to help in the conservation of the regional fauna (Delabie et al., 2007; Faria et al., 2007; Schroth et al., 2011; Cassano et al., 2012). The predominant cocoa production system in this region is locally called *cabruca* (Araujo et al., 1998), and consists of an agroforestry system where the understory is replaced by cocoa trees that grow under the canopy of predominantly native forest trees, partly retained when cocoa is planted plus trees that regenerated or have been planted later (Alves, 1990). Despite the vertical structural simplification, cabrucas are much more complex than other agriculture systems such as annual crops (Alves, 1990), and holds a significant portion of the native fauna (Argôlo, 2004; Delabie et al., 2007; Faria et al., 2007; Cassano et al., 2012) being therefore considered a wildlife-friendly system (Schroth et al., 2011). However, management intensification of cabrucas may compromise this status since cocoa yields are usually improved through reducing the density of shade trees, which can negatively influence the ability of the native fauna to use this system (Cassano et al., 2014).

Although the use of cabrucas has already been investigated for many taxonomic groups, to our knowledge there is no study specifically developed to survey raptors' communities in cabrucas of Southern Bahia. Such investigation is particularly important since agricultural expansion and intensification is pointed out as the major threat to Brazilian biodiversity (MMA/ICMBio, 2016), and Brazil's National Action Plan for the Conservation of Birds of Prey (Soares et al., 2008) highlights the importance of understanding how raptors are being affected in agricultural lands, especially by the use of pesticides. The response of each raptor species to environmental degradation gradients is also poorly understood in the Neotropics (Carrete et al., 2009), and new field data are needed to clarify these issues. Additionally, since communities of this region are very depauperated in mammalian carnivores (Alves, 1990; Cassano et al., 2012), raptors end up being the major (and perhaps the only) predators regulating populations of many taxa, including some endangered species such as the golden-headed lion tamarin, *Leontopithecus chrysomelas* (Oliveira & Dietz, 2011). Thus, identifying which raptors are using cabrucas can also help us to evaluate the predation pressure this group is exerting on their preys. Such knowledge is particularly important in human-modified habitats where predator-prey relationships can be unbalanced and sometimes lead to the local extinction of preys (Irwin et al., 2009).

The aim of this study was to describe the raptor assemblages in cabrucas of Southern Bahia, as well as to understand the determinants for raptors' occupancy in this human-modified habitat. For this, we performed occupancy modeling to identify cabruca' features, such as those related to vegetation complexity and management intensity, which can drive cabruca occupancy by raptors. We expected to find a positive correlation between raptors occupancy and habitat structural complexity (Thiollay, 1985; Jullien & Thiollay, 1996), in particular, cabrucas with a higher density of shade-trees, taller and large-diameter shade-trees, better-connected canopy, as well as a lower density of cocoa trees and a low management intensity. The percentage of vegetation cover in the landscape has proved to positively affect raptors richness and abundance (Jullien & Thiollay, 1996), so we also expected it to positively affect the raptors occupancy in cabrucas. As species may be more or less prone to survive in agricultural lands, we added some biological characteristics such as body mass, dietary requirements, and use of vertical strata, to predict raptors' occupancy in cabruca sites. We expected to find a lower occupancy of: species with higher dependence on intermediate strata for foraging, since these strata are replaced by cocoa trees in cabrucas (Johns, 1998); larger species, since they usually occur at low population densities and have large home ranges, being thus more sensitive to habitat disturbances (Gaston & Blackburn, 1995; Bregman et al., 2014); and species with higher energetic requirements and dietary specialization, since they are expected to be less tolerant to changes in food resources' availability (Terraube et al., 2011).

Methods

Study area

From August 2014 to May 2015, 16 cabrucas located in private farms and rural settlements were surveyed, covering 12 municipalities (encompassing an area of ~700,000 ha) in the cocoa-growing region of Southern Bahia, Brazil (Fig. 1). Previous studies suggest that our survey period was appropriate since it included the breeding season for most raptor species in Atlantic forest (Mañosa et al., 2003; Zorzin, 2011). In addition, previous field surveys in the same region yielded good results in detecting diurnal raptors at this time of the year (JABM, unpubl. data).

The dominant vegetation in this region is tropical lowland rainforest (Oliveira-Filho & Fontes, 2000), the mean annual temperature is 24 °C and rainfall averages 2,500 mm/yr, with no marked seasonality (Mori et al., 1983). The surveyed cabrucas were at least 11 km (52-114 km) apart to assure their spatial independence (Fig. 1).

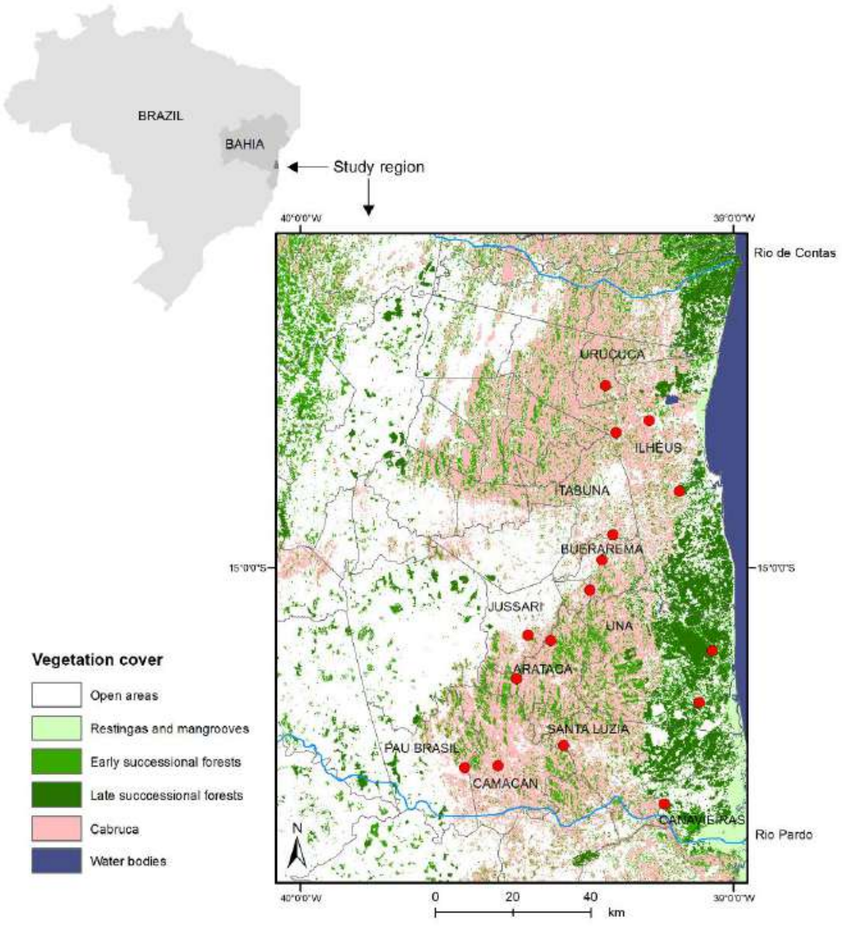

Fig. 1. Vegetation cover in the study region and the location of the 16 cabrucas surveyed in this study (red circles). Vegetation classification followed Landau et al. (2008).

Data collection

1. Species dataset

Prior to sampling, a set of diurnal raptor species expected to occur in the study region was determined through the compilation of occurrence records and geographic distribution maps (http://www.wikiaves.com/; http://www.avesderapinabrasil.com/; Sigrist, 2014; IUCN, 2016; Del Hoyo et al., 2017). It resulted in a list of 46 species for which we compiled information about diet preferences, body mass, foraging strata, sensitivity to habitat disturbance, relative abundance, and conservation status (all data and its respective literature source are presented in the supplementary information: Tables S1 and S2). Taxonomy follows Remsen et al. (2017), and classification of species' sensitivity to habitat disturbance and abundance patterns follows Parker III et al. (1996).

2. Raptors' survey

All methodology was based on Granzinolli & Motta-junior (2008), with small adjustments based on researchers' experience. A combination of active search, playback and point-count were applied in each area during two visits, always performed by the same observer with the help of a field assistant. All sampling was carried out between 6:00 and 12:00, a period of greater activity of most species of diurnal raptors (Thiollay, 1989; Mañosa et al., 2003), avoiding days with rain and strong wind due to a possible decrease in species detectability (Jones, 2000; Granzinolli & Motta-Junior, 2008).

Between 6:00 and 9:00, the sampling was carried out within the cabruca sites, focusing on species with forest habit that only occasionally fly above the canopy - such as the two largest eagles, *Harpia harpyja* and *Morphnus guianensis*, and the forest-falcons, *Micrastur* spp. (Thiollay, 1989). We also looked for soaring species that have not started their flight activities yet, such as *Leptodon cayanensis* and *Spizaetus* hawk-eagles. Using Landsat images with 30 m resolution obtained from Google Earth (Google Inc., 2016), we designed two parallel linear transects of 800 m separated by 400 m in each cabruca site (Fig. 2). The active search was performed by walking through these transects at a constant velocity while identifying species using 10x50 binoculars and a digital voice recorder to record vocalizations whenever possible.

We performed playbacks at two opposite points of the sampling grid (Fig. 2), separated by a mean linear distance of 665±160 m, a placement that is consistent with those used by previous studies (Carvalho Filho et al., 2008/2009; Vázquez-Pérez et al., 2009). The playback methodology consists in playing a recording of the species vocalization to attract individuals and stimulate intra-specific responses, although it is also common to elucidate interspecific responses. Aiming to enhance the sampling efforts, playbacks were performed only to a set of diurnal raptors that are known to respond well to this technique, such as *Leptodon cayanensis, Micrastur ruficollis, M. semitorquatus, Accipiter bicolor* and *Spizaetus tyrannus* (Zorzin, 2011; JABM, pers. obs.).

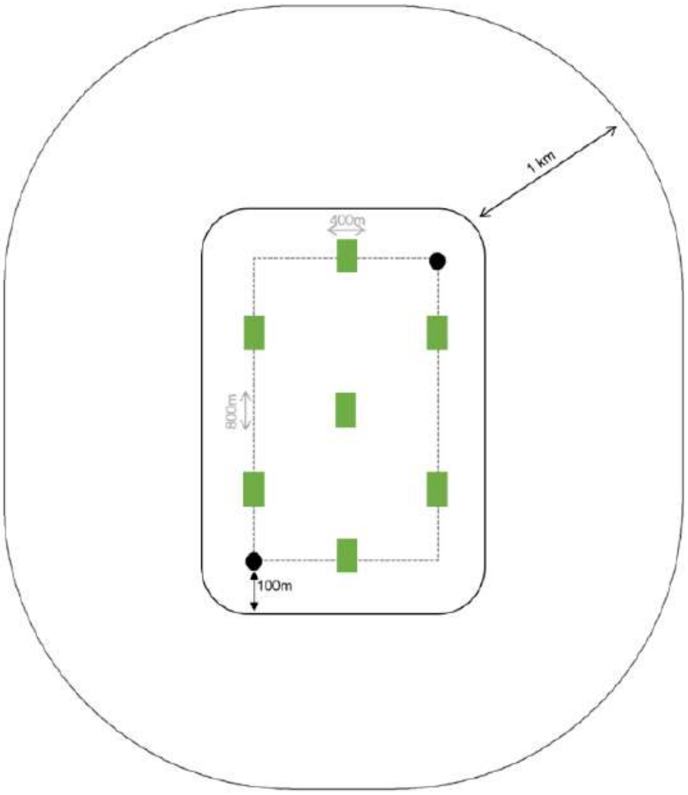

Fig. 2. Scheme of the sampling grid designed in each cabruca site showing the linear transects (dashed gray line) where an active search was performed, assuring at least 100m distance from fragment's edge, the playback points (black circles), and the location of vegetation plots (green rectangles). Vegetation cover was estimated within the area delimited by the 1km-radius.

We used recordings available on Wiki Aves (http://www.wikiaves.com/), selecting preferentially those recordings made in the study region, avoiding aggressive vocalizations and pair duets. Using the aforementioned recorder coupled with a portable speaker, the recordings of all focal species were played in a pre-established order that taken into account both body size and aggressive behavior, considering that large and fierce species could repel smaller ones. Each vocalization was played continuously for 3 min, holding the speaker at approximately 2 meters above the ground and rotating it 360° at a constant speed, followed by a 3-min on-site wait.

Most raptors - such as *Buteogallus* spp. and *Pseudastur polionotus* - often start soaring when thermals are well-formed, so the best period to perform the point-count methodology is between 9:00 and 12:00 (Thiollay, 1989; Mañosa et al., 2003). During this period, we recorded all individuals visually or through their vocalizations from a fixed location. Point-counts for raptors are typically located in high places that offer a wide view of the canopy, such as tops of hills adjacent to the study area (Thiollay, 1989; Whitacre et al., 1990; Mañosa et al., 2003). Such approach was done for almost all cabruca sites but in six of them the relief was very flat, so we located two complementary point-counts at the edge of the cabruca (approximately 100 m from the edge and separated by 690±170 m from each other) and remained 1 h 30 min at each point.

Except for single point-counts, the starting sampling point was always alternated in the second visit to ensure that species with different peaks of activity could be detected at all points (Jones, 2000). Most Atlantic Forest fragments are smaller than the mean territory sizes of Neotropical raptors (Thiollay, 1989; Zorzin, 2011), thus repeated detections of the same species at the same site were attributed to the same individual unless more than one individual was observed simultaneously.

3. Habitat characterization

In each cabruca site, seven 200-m² plots were placed in interspersed points of the sampling grid (Fig. 2), where features of habitat structure and cabrucas' management were collected (Table 1), resulting in seven explanatory variables: (1) shade-trees density; (2) shade-trees diameter; (3) canopy height; (3) canopy connectivity; (4) heterogeneity of the vertical strata; (5) cocoa trees density; (6) shading level and (8) management intensity. The values obtained for each variable in each plot were summed to obtain a unique value per area, representing an index of abundance to be used in the analyses. Any signal of hunting (e.g. waiting stations) and selective logging (e.g. stumps) was recorded to describe the degree of human disturbance in each area.

Based on the Landsat images, we estimated the percentage of vegetation cover inside an area defined by a 1-km radius from the extreme points of the sampling grid (Fig. 2). This distance was based on Zorzin (2011), which have analyzed the response of diurnal raptors to forest fragmentation at different scales and identified major responses occurring between 500 m and 1-km radius. We estimated the vegetation cover inside this buffer by visually identifying clearings and subtracting their extension (in square meters) from the total area of the buffer. The vegetation cover estimate includes both cabruca and forest due to the difficulty of accurately differentiating it using the images. Spatial analyses were performed on Quantum Gis 2.18.2 (www.qgis.org) using its interface with Google Earth (Google Inc., 2016). The distance measurements were made with the Raster Package (Hijmans et al., 2016) in R 3.3.1 (R Core Team, 2016).

Data Analysis

Occupancy modeling was used to identify the determinants for raptors' occurrence in cabrucas, in the software Mark version 8.x (White & Burnham, 1999). Occupancy estimates represent the proportion of sample units that is occupied by a species (Mackenzie et al., 2002). We used a single-season multi-species approach to model the occupancy (Ψ) and detectability (p) of all species simultaneously, assuming that detection is imperfect (<1) since some species may be present in the area but may not be detected (Mackenzie et al., 2002). In this approach, 'species' and 'visits' represent the sample units and occasions, respectively [see chapter 9 of Mackenzie et al. (2006) for more details]. Thus, for each species, a detection history was determined based on the two independent visits per sampling method - considering that methods are independent in relation to species detectability - which resulted in six occasions per species per each area. This analysis included only the subset of species detected at least once at one of the sampling areas.

One assumption of single-season modeling is that population is closed to changes in occupancy during the season, but given that raptors home ranges are probably larger than all of our sampling areas (Thiollay, 1989), such assumption may not have been achieved. In order to deal with this problem, we interpreted the occupancy estimate as the proportion of the area 'used' by the species rather than the true occupancy, as proposed by Mackenzie et al. (2006). The detectability was interpreted as the probability of detecting the species when it is present in the area *and* using the sampling unit during the survey, assuming that movement of species through their home range is random (see similar interpretations in Keane et al., 2012, and Kalan et al., 2015).

Variables collected in the field and extracted from satellite images were used as covariates to model Ψ and p using a series of competing models. We also included some biological traits as covariates to investigate the influence of species characteristics in their responses to habitat change. We derived two indexes based on the proportional consumption of each food category in species dietary: trophic level – the sum of the proportional consumption of each food category weighted by its energetic value, assuming a decreasing energy content from vertebrates to invertebrates to fruits; and dietary specialization – the number of different food categories in species dietary (for details about indexes calculation see Table S1). We also included the species average body mass (gr) and the percentage of foraging in each strata level (ground, understory, midhigh, canopy, and air; Table S1).

Prior to analyses, we assessed the pairwise correlations through a Spearman correlation test, using the R Stats package (R Core Team, 2016), and excluded highly correlated variables ($r \geq 0.6$): percentage of foraging in intermediate strata [negatively correlated with body mass; $r = -0.63$]; percentage of foraging in air [positively correlated with percentage of foraging in the canopy ($r = 0.67$)]; percentage of shadow [positively correlated with canopy connectivity ($r = 0.60$), and with vertical stratification ($r = 0.66$)]; and canopy height [positively correlated with canopy connectivity ($r = 0.84$), and with diameter of shade-trees ($r = 0.64$)]. We assessed the multi-collinearity among the remaining variables through the Variance Inflation Factor (VIF), using the CAR package of R (R Core Team, 2016), and since none variable had VIF > 4, we kept all of them for the analyses. Thus, we finished with six covariates to model p: (1) sampling method; (2) body mass; (3) percentage of foraging in the canopy; (4) vertical strata heterogeneity; (5) shade-trees density; and (6) cocoa trees density. We expected that: sampling methods would result in different species detectability (Thiollay, 1989); larger species would be more easily detected; species could be more or less easily detected depending on its preferred foraging strata; canopy height, vertical heterogeneity, shade-tree density and cocoa density could interfere with visual obstruction and sound propagation, thus affecting species detectability. We modeled Ψ as a function of 10 covariates: (1) shade-trees density; (2) shade-trees diameter; (3) canopy connectivity; (4) vertical strata heterogeneity; (5) management intensity; (6) cacao density; (7) vegetation cover; (8) body mass; (9) trophic level; and (10) specialization degree. We also included two constant models where p and Ψ were held constant.

Table 1. Habitat variables collected in seven plots of 200m² in sixteen cabrucas, applied methodology and the derived co-variables to be used in the occupancy-detection modeling.

Variable measured	**Methodology**	**Index calculation (per plot)**	**Final variables**
1. Number of shade-trees	Visual couting of all shade-trees with diameter above the breast (DBH) ≥ 10 cm inside each plot.	Number of shade-trees per m²	1- Shade-trees density 2- Shade-trees diamater
2. Canopy height	While a field assistant remained beside each shade-tree holding a 2m stick perpendicular to the ground, the observer estimated tree's height using the stick as scale. Cabrucas' vertical struture prevented the use of a rangefinder, but a observer calibration with such equipment revealed an error of approximately 2m.	Median canopy height and standard deviation of trees' height	3- Canopy height 4- Vertical stratification
3. Canopy connectivity	Visual counting of all trees connecting to each shade-tree through the canopy.	Median number of connections per tree	5- Canopy connectivity
4. Management activity	Categorical classification of the plot from less to most managed depending on the level of current activity: 1) old abandoned plot in process of forest regeneration with no (or very few and old) cocoa trees; 2) recently abandoned plot that is still dominated by cocoa trees and presents signs of forest regeneration; 3) active plot that is not being managed at the moment, characterized by the presence of seedlings and shrubs; and 4) active and managed plot, with absence of seedlings and shrubs.	Categorical classification: 1-4	7- Management intensity
5. Number of cocoa trees	Quantification of cocoa trees inside each plot.	Number of cocoa trees per m²	8- Density of cocoa trees
6. Percentage of shadow	A photograph was taken in the center of each plot using a digital camera equipped with a 55 mm hemispheric "fish-eye" lens (180°) supported by a tripod at a height of 1.5 meters from the ground and focused up. The pictures were analyzed in Gap Light Analyzer software (Frazer et al., 1999).	Percentage of leaf cover (shade)	9- Percentage of shadow

We applied the *ad hoc* method of model selection, which consists of first modeling *p* with one variable at a time while keeping Ψ with maximum covariates possible. After fixing the most important covariates to *p,* it was repeated the process of modeling Ψ with a covariate at a time until we find the best overall model. The competing models were ranked according to the Akaike Information Criterion corrected for small sample sizes (AICc) so that models with ΔAIC ≤ 2 were considered equally plausible, models with ΔAIC >2 and ≤ 7 were considered to have less but still significant support, and models with ΔAIC > 10 were considered to have no support (Burnham & Anderson, 2002; Bromaghin et al., 2013). In the case of too much uncertainty about the best model, the final estimates of parameters *p* and Ψ were model-averaged by taking the weighted mean among all competing models' estimates (Burnham & Anderson, 2002). We accessed the fit of the most general model (namely the model with the greatest number of parameters) through the estimation of the overdispersion parameter *c-hat* with 10,000 bootstrap samples (Mackenzie & Bailey, 2004) in the software PRESENCE 11.7 (http://www.mbr-pwrc.usgs.gov/software/presence.shtml).

Results

Raptor assemblages in cabrucas

A total sampling effort of 64 playback points (four per area), 91 h 11 min of active search (mean effort: 5 h 40 min per area; range: 4 h 48 min to 06 h 45 min) and 96 h of point-count (6 h per area) resulted in the record of 22 species of diurnal raptors (three to 16 per site; Table 2), including three occasionally recorded owls: *Megascops* cfr. *atricapilla*, *Pulsatrix koeniswaldiana* and *Glaucidium brasilianum*. We did not systematically survey for the smaller New World vultures – *Cathartes aura*, *C. burrovianus* and *Coragyps atratus* – but they were recorded in all cabruca sites. Some species for which we did not perform playbacks, as *Buteo* hawks, responded to the vocalizations of other species, therefore increasing their detectability (Table S3). We fail to detect 20 species from our potential species pool and did not made secure records of other four species: *Accipiter bicolor* (four sites), *Falco* sp. (two sites), *Harpagus diodon* (two sites), and *Rostrhamus sociabilis* (one site).

Table 2. Records of diurnal raptors made between August 2014 and May 2015 in 16 cabruca sites (S1-S16). Total species richness per site is presented as a range, considering some uncertainty in species identification. Unconfirmed identifications are indicated with “?”, and doubts between two species in the same area are indicated with “*”.

Species	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**	**S13**	**S14**	**S15**	**S16**
Accipiter bicolor		X$^{?}$	X$^{?}$			X$^{?}$										X$^{?}$
Buteo albonotatus	X	X	X	X	X	X$^{?}$	X	X	X	X	X$^{?}$	X$^{?}$	X$^{?}$		X	X
Buteo brachyurus	X		X													
Buteo nitidus	X*	X*	X		X											
Buteogallus meridionalis				X											X	
Buteogallus urubitinga	X*	X	X								X*			X		
Caracara plancus	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
Chondrohierax uncinatus			X							X						
Falco femoralis			X*		X*											
Falco rufigularis			X*		X*											
Geranospiza caerulescens	X$^{?}$		X		X	X				X						X
Harpagus diodon					X$^{?}$	X$^{?}$										
Herpetotheres cachinnans	X	X	X	X	X	X		X		X		X	X	X	X	X
Leptodon cayanensis	X	X	X	X$^{?}$		X		X$^{?}$		X		X			X$^{?}$	
Micrastur semitorquatus		X	X$^{?}$			X										
Milvago chimachima	X	X		X	X			X				X	X	X	X	X
Pseudastur polionotus		X		X	X	X	X		X		X		X	X		X
Rostrhamus sociabilis											X*					
Rupornis magnirostris	X		X	X		X	X	X$^{?}$	X$^{?}$			X	X	X	X	X
Sarcoramphus papa					X								X			
Spizaetus melanoleucus			X	X	X				X							
Spizaetus tyrannus	X		X		X	X				X			X	X	X	
unidentified raptors	X		X	X	X	X	X	X	X	X	X	X		X	X	X
total species richness	8-12	9	12-16	7-10	12-13	8-12	3-4	4-7	4-6	7-9	3-5	5-7	6-7	8-10	7-10	6-8

Regarding the species' sensitivity to habitat disturbance, 44% (11 spp.) of all recorded species are considered low sensitive, 48% (12 spp.) are moderately sensitive and 8% (2 spp.) are highly sensitive. The most common species in the cabruca sites, ordered from the most to the less abundant, were *Caracara plancus*, *Buteo albonotatus*, *Herpetotheres cachinnans* and *Rupornis magnirostris*. With the exception of *B. albonotatus*, which is classified as an uncommon and patchily distributed and moderately sensitive to habitat disturbances, the aforementioned species are all considered to be common and weakly related to habitat disturbance. The highly sensitive species detected in this study were the Black-and-White Hawk-Eagle, *Spizaetus melanoleucus* (four sites), and the Mantled Hawk, *Pseudastur polionotus* (10 sites).

The raptor species detected in cabruca sites vary a lot in their degree of dependence on forested habitats. For example, the Collared Forest-Falcon, *Micrastur semitorquatus*, a forest-dependent species that uses mainly the low forest strata to forage, was recorded in two cabruca sites using the playback technique, wherein in one of these sites we obtained the response of two individuals from opposite directions. In both cabruca sites, the species vocalized continuously during some minutes but the visual contact was never possible, which highlights the importance of playback to detect cryptic species. Such records were made in cabruca plots with a high density of shade-trees and near regenerating forest plots. In the opposite extreme, we recorded individuals of savanna hawk, *Buteogallus meridionalis*, a species that is typical of open areas, on pastures near cabruca sites in two different occasions.

Regarding the reproductive activity of the diurnal raptors in the study region, we observed breeding pairs of *Buteo albonotatus* (three sites), *Buteogallus urubitinga* (one site), *Caracara plancus* (six sites), *Pseudastur polionotus* (foursites), *Spizaetus melanoleucus* (one site), and *Spizaetus tyrannus* (two sites). Breeding pairs of the latter species were even observed performing courtship displays. A juvenile of *Buteo nitidus* was recorded alone in the edge of a cabruca site, close to a stream, and a family group of *B. albonotatus* (two adults and one juvenile) was observed foraging and interacting in the canopy near the edge of another cabruca site. We also observed immature birds of other species, such as *Sarcoramphus papa* and *Rupornis magnirostris*.

Habitat characterization

We found significant variation in structural features among the surveyed cabrucas (Table S4). Cabruca sites have a mean density of 623 ± 182 cacao trees/ha and 182 ± 60 shade-trees/ha. Mean diameter of shade-trees is 37.2 ± 30.7 cm, mean canopy height is 15.6 ± 2.6m and shading level averages 73 ± 10%. Hunting signs (traps, hunters and/or firearm blows) and logging signs (chainsaw noises and stumps) were recorded in 10 and nine of the 16 areas, respectively. We estimated vegetation cover to range between 73% and 96%.

Occupancy modeling

Diurnal raptor's detectability seemed to be primarily influenced by the sampling method (Table 3) so that point-count was the most efficient method to detect cabruca raptors ($p_{\text{search}}= 0.14 \pm 0.02$; $p_{\text{playback}}= 0.17 \pm 0.03$; $p_{\text{point-count}} = 0.29 \pm 0.03$). The most important covariates to explain Ψ were dietary specialization (negative effect) and shade-tree density (negative effect). To a lesser extent, we also found significant effects of management intensity (positive), body size (negative), and diameter of shade-trees (positive) on Ψ (Table 3; Fig. 3). As the 'Ψ constant model' was best ranked than the models including canopy connectivity, vertical stratification, species trophic level, and vegetation cover (Table 3), we considered these covariates to have an insignificant influence on Ψ. The model-averaged estimate of Ψ is 0.56 (95% CI: 0.45; 0.66), with no evidence of lack of fit ($\chi^2 = 78.20$; P = 0.47; *c-hat* =0.77).

Table 3. Results of the *ad hoc* occupancy (Ψ) and detection (*p*) model selection for diurnal raptors in 16 cabrucas of Southern Bahia in which 'QAICc' is the quasi-likelihood Akaike information criterion corrected for small samples, 'ΔQAICc'isthe difference between the QAICc value of each model and the top-ranked model, and 'AICcW' is the Akaike weight, which represents the conditional probabilities for each model. Constant models are indicated with '.'.

Model	**QAICc**	**ΔQAICc**	**AICcW**
Detection models			
{Ψ(all)*p*(Method)}	1030.70	0.00	1.00
{Ψ(all)*p*(Shade-tree density)}	1045.91	15.21	0.00
{Ψ(all)*p*(.)}	1046.18	15.48	0.00
{Ψ(all)*p*(Body mass)}	1046.77	16.07	0.00
{Ψ(all)*p*(Vertical stratification)}	1047.99	17.30	0.00
{Ψ(all)*p*(Canopy foraging)}	1048.20	17.50	0.00
{Ψ(all)*p*(Cocoa tree density)}	1048.25	17.55	0.00
Occupancy-detection models			
{Ψ(Dietary specialization)*p*(Method)}	1028.88	0.00	0.41
{Ψ(Shade-tree density)*p*(Method)}	1030.56	1.68	0.18
{Ψ(Management intensity)*p*(Method)}	1030.89	2.01	0.15
{Ψ(Body mass)*p*(Method)}	1031.56	2.68	0.11
{Ψ(Diameter of shade-trees)*p*(Method)}	1033.46	4.57	0.04
{Ψ(.)*p*(Method)}	1033.50	4.62	0.04
{Ψ(Canopy connectivity)*p*(Method)}	1034.79	5.90	0.02
{Ψ(Vertical stratification)*p*(Method)}	1035.36	6.47	0.02
{Ψ(Trophic level)*p*(Method)}	1035.50	6.62	0.02
{Ψ(Vegetation cover)*p*(Method)}	1035.58	6.69	0.01

all=shade-tree density + shade-tree diameter + canopy connectivity + vertical stratification + cocoa tree density + management intensity + vegetation cover + body mass + dietary specialization + trophic level

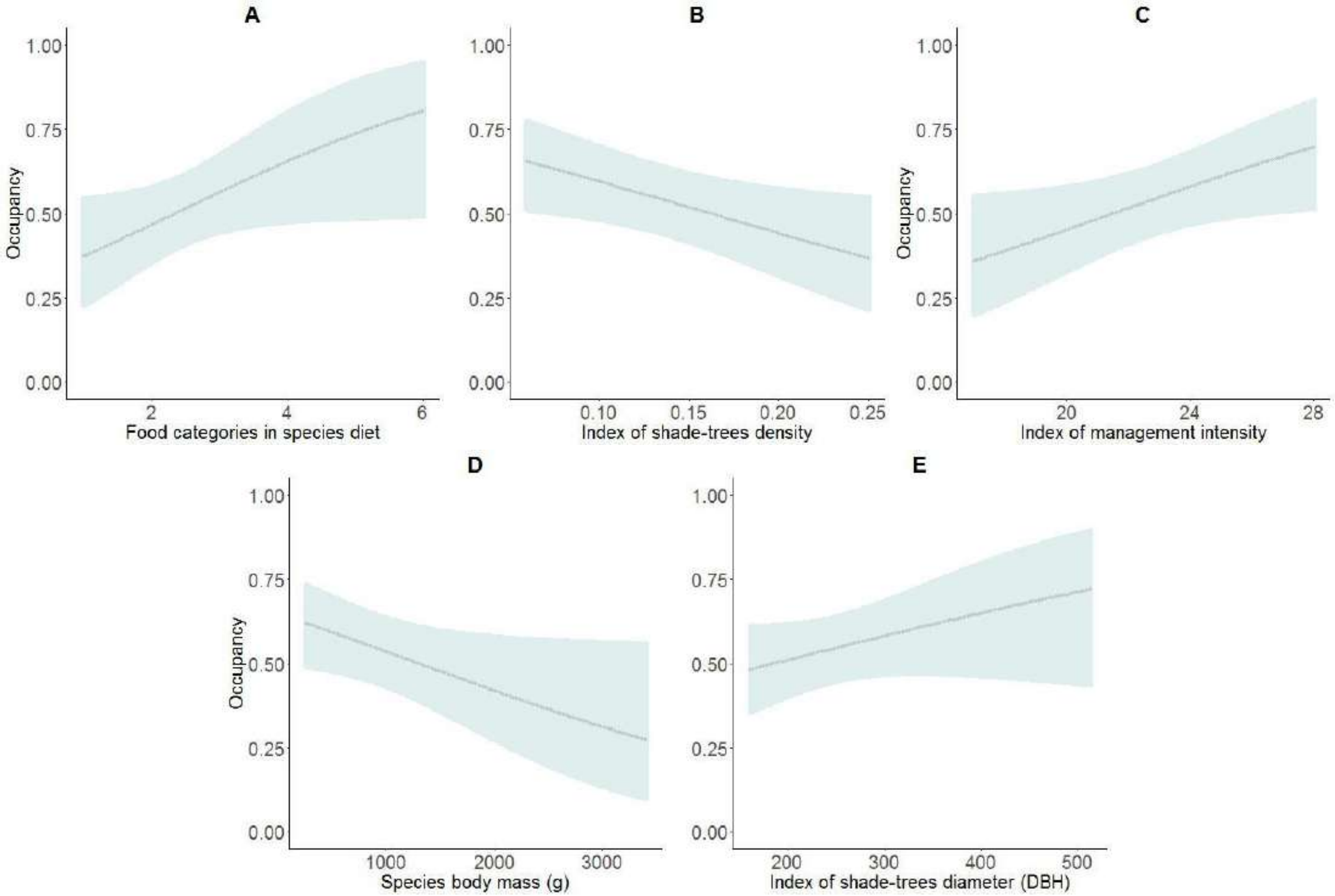

Fig. 3. Diurnal raptors' occupancy probability in cabrucas as a function of: dietary specialization (A), shade-trees density (B), management intensity (C), body mass (D), and shade-trees diameter (E). Colorful areas represent the 95% confidence intervals.

Discussion

To our knowledge, this is the first study designed to systematically survey diurnal raptor assemblages in Southern Bahia. We present the first occupancy modeling used to investigate the determinants for diurnal raptors' occupancy in cabrucas of this region, focusing on the role of vegetation structure, management intensity, and landscape context. A significant number of diurnal raptors species is able to forage in cabruca sites, with a high occupancy in more structurally simplified cabrucas such as those with lower shade-trees density and higher management intensity, but with large-diameter shade-trees. We identified a lower occupancy of dietary specialists and large-bodied species, which suggests that cabruca raptor assemblages may be simplified compared to forest assemblages.

Raptors assemblages in cabrucas

Our survey revealed a significant number of raptor species as able to forage in cabrucas. The majority of recorded species are considered to be naturally 'common' or 'very common', but species such as *Leptodon cayanensis*, *Pseudastur polionotus,* and *Buteo albonotatus*, that are considered to be 'uncommon' according to Parker III et al. (1996), were very frequent in the surveyed cabruca sites. We could not find published studies designed to specifically survey raptors in forests of Southern Bahia to compare with our data, and previous records come from bird surveys that did not use specific techniques to survey this group (Silveira et al., 2005) and occasional records (Sánchez-Lalinde et al., 2011; Araújo et al., 2015; Suscke et al., 2016). The lack of such studies prevents us from concluding if these species are benefiting from cabrucas' environment or if they are actually common in the region as a whole.

More than half of species recorded in cabruca sites are considered moderately or highly sensitive to habitat disturbance. Our recordings of *S. melanoleucus* and *P. polionotus*, for example, contradicts their previous classification as highly sensitive species (Parker III et al., 1996). In fact, although cabrucas are structurally simplified in comparison to forests, this agroecosystem is much more complex than other agricultural systems such as annual crops (Alves, 1990). The sensitivity classification proposed by Parker III et al. (1996) did not specify the type of habitat disturbance they considered, so it is possible that the authors have based their conclusions on modified-habitats with more intense disturbance degree than cabrucas. In any case, some authors have questioned this sensitivity classification of raptors claiming that species-specific responses to habitat alterations can change depending on the disturbance context (Sergio et al., 2008; Alexandrino et al., 2016). For example, *S. melanoleucus* and *L. cayanensis* have been repeatedly recorded foraging in urban areas (Carvalho & Marini, 2007; Carvalho Filho et al., 2008; Meyer, 2016). In the specific context of Southern Bahia, cabrucas have been proved to be a sub-optimal habitat for many species (Argôlo, 2004; Delabie et al., 2007; Faria et al., 2007; Oliveira & Dietz, 2011; Cassano et al., 2012), and our results indicates that it is also true for a subset of diurnal raptors.

An interesting finding was the recording of breeding pairs from six species, including *S. melanoleucus* and *P. polionotus*, and juveniles from four species. Although juveniles of *Sarcoramphus papa* and *Rupornis magnirostris* were somewhat older individuals that could be away from their actual nest sites (Bodrati et al., 2010), all these records suggest that many raptor species may be reproducing in cabruca sites. Specific studies on this topic should be developed to confirm if these species are actually nesting in cabrucas, since it would contradict the high-quality requirements proposed for raptors' breeding sites, like the existence of tall trees required for *Spizaetus* spp. to nest (Joenck et al., 2011; Canuto et al., 2012). In fact, there are some nesting records of Neotropical accipitrids, such as *Buteo brachyurus* and *Harpya harpija*, in areas that do not match such high-quality demands (Silva, 2007; Monsalvo, 2012), suggesting that a re-evaluation of this topic is needed, at least for some hawks and eagles. Understanding the extent to which cabrucas are being used as habitat by such species would enhance our knowledge about the role of cabrucas in contributing to raptors' conservation in Southern Bahia.

Among the seven globally threatened species expected to be found in the study region, only *P. polionotus* (Near-Threatened; IUCN, 2016) was confirmed to occur in cabrucas. The commonness of this species in cabrucas sites is supported by unpublished reports from the Serra Bonita reserves complex, Camacan, within the study region (JABM, pers. obs.). An earlier study have found *P. polionotus* to be extremely affected by Atlantic forest fragmentation (Zorzin, 2011), thus its high tolerance to cabrucas may reveal an important role of this agroecosystem on mitigating the detrimental effects of forest fragment isolation.

The failure to detect some species from the potential dataset may be explained by their high dependence on specific habitat types, such as the Snail Kite, *Rostrhamus sociabilis*, that is most commonly associated with wetlands, and the Long-winged Harrier, *Circus buffoni,* that prefer open areas (Thiollay, 2007). An adult pale-morph male of the latter species was occasionally observed while flying above a *restinga* (vegetation on the sandbanks), during the team displacement between study areas, confirming their presence in the region despite the absence of records in cabruca sites. During the phase of sites selection for this study, we occasionally recorded a group of Swallow-tailed Kites, *Elanoides forficatus*, foraging under a pasture in the proximities of a cabruca site. This is a migratory species that reproduces in the Atlantic Forest and that is traditionally considered 'uncommon' (Parker III et al., 1996). To our knowledge, this is the first published record of this species in the study region and, although we did not detect any individual in our surveys in cabruca sites, such record suggests an ability to forage in landscapes totally dominated by this agroecosystem. The same conclusion applies for the savanna hawk, *Buteogallus meridionalis*, a common species that preferentially uses open habitats (Parker III et al., 1996; Thiollay, 2007).

Determinants for raptors' occupancy in cabrucas

We found diurnal raptors as most likely to occur in cabruca sites with low shade-tree density and high management intensity, that is more managed and structurally simplified cabrucas. Previous studies have already shown that some raptors may occupy (and sometimes prefer) areas with moderate to high levels of anthropogenic alteration (Carvalho & Marini, 2007; Carrete et al., 2009; Piana & Marsden, 2014), even species previously considered restricted to preserved forests (Blendinger et al., 2004; Monsalvo, 2012). The high incidence of raptors in more open cabrucas may be related to an increased foraging efficiency, since preys can be more exposed (Alves, 1990; Silva, 2007; Piana, 2015). Despite this apparent benefit from cabrucas simplification, we found raptors as more likely to occur in cabrucas that retain large-diameter trees. It may be related to the need for large trees to nest (Canuto et al., 2012), but since we don't know if these species indeed nest in cabruca sites, further studies are needed to better understand this relationship.

Regarding the biological traits, we found raptors occupancy to decrease with the degree of dietary specialization. Despite the increased exposition of preys in cabrucas compared to forests (Alves, 1990; Silva, 2007; Piana, 2015), the overall availability of preys is expected to decrease in simplified habitats (August, 1983) such as cabrucas. Thus, species that depend on specific food resources and that are consequently less flexible to deal with food changes, may be less likely to occur in cabrucas than species with more varied diet. Another biological trait with a significant effect on raptors occupancy is the body size. Although we recorded species with a wide range of body sizes (e.g. *Rupornis magnirostris* ~270 g; *Sarcoramphus papa* ~3400 g; Dunning, 1993), raptors occupancy in cabrucas decreases as body size increases, corroborating the hypothesis that large-bodied species are more affected by habitat disturbance (Gaston & Blackburn, 1995; Thiollay, 1995; Carvalho & Marini, 2007). We did not detect the largest species from our potential species pool, *Morphnus guianensis* and *Harpia harpya*, which are among the rarest Neotropical raptors (Thiollay, 2007), but recent records of both species were made in Southern Bahia sites including our study region (Sánchez-Lalinde et al., 2011; Araújo et al., 2015; Suscke et al., 2016). Unpublished records from a survey on raptors conducted between 2012-2013 in the Serra Bonita reserves complex includes the observation of a Harpy Eagle foraging in cabrucas (JABM, unpubl. data). Considering the difficulty in detecting such species, an increased survey effort would be necessary to best estimate their occupancy in the surveyed cabruca sites.

Conservation implications and recommendations

The present study revealed a significant number of diurnal raptor species as able to use cabrucas of Southern Bahia, emphasizing the potential of this agroecosystem to mitigate the effects of forest loss and fragmentation on this group. However, there is a tendency of simplification of raptor assemblages, with the decrease of dietary specialists and large-bodied species. It proves that cabrucas alone cannot assure the regional conservation of all raptor species, calling for the maintenance of forest remnants in the landscape.

Although many species recorded in cabruca sites are considered to be environmental quality indicators (Espín et al., 2016), the ability of many raptors to adapt and benefit from habitat disturbance has leading researchers to question such indicator role (Rodríguez-Estrella et al., 1998). In fact, a greater occupancy of diurnal raptors in more structurally simplified cabrucas suggests a positive effect of habitat disturbance on these species, but our findings should be interpreted considering the context of habitat disturbance in the study region. All cabruca sites surveyed in the present study present high density of shade-trees, as is typical of traditional cabrucas of this region (Schroth et al., 2013). Despite the lower structural complexity compared to forests, this system still maintains some degree of habitat complexity and heterogeneity (Rice & Greenberg, 2000), which may be a sub-optimal alternative for species in a highly fragmented landscape. Due to this apparent compatibility with biodiversity conservation, cabrucas have been considered a wildlife friendly system (Schroth et al., 2011). However, a state decree (N° 15.180; article 19) published by the Bahia Government in 2014 sanctioned the management intensification of cabrucas by reducing the density of shade-trees. An immediate consequence of such reduction may be an increase in raptors occupancy in intensified cabrucas, which can initiate a trophic cascade (Sergio et al., 2008). After that, raptors assemblages will probably not be sustainable in very intensified cabrucas since a minimum level of habitat complexity and heterogeneity is necessary to support species-rich bird communities in altered habitats (Thiollay, 1995; Abrahamczyk et al., 2008; Philpott et al., 2008).

Any conclusions about the role of cabrucas for diurnal raptors conservation depends on the knowledge about raptors assemblage’s status in the forests of this region. Thus, studies designed to specifically survey raptors with the appropriate sampling methods in forests of Southern Bahia, as well as ecological and behavioral studies in both forest and cabruca sites, are crucial to understanding how raptors are dealing with habitat changes. Such knowledge would clarify the extent to which cabrucas are important to assure raptors conservation at a regional scale, and also about how these species can be affected by cabrucas’ intensification. Ultimately, understanding such issues would add insights about the stability of food webs already established in this human-modified habitat.

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Supplementary Material

Table S1 – Description of biological traits and ecological information compiled for each species in the potential dataset

Table S2 – List of diurnal raptors with potential occurrence in the study area, description of dietary and foraging strata preferences, body size, sensitivity to habitat disturbance, abundance pattern and conservation status.

Table S3 – List of species detected per method.

Table S4 – Characterization of cabruca sites regarding the vegetation structure, habitat quality and vegetation cover in the landscape.

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SUPPLEMENTARY MATERIAL

Table S1. Description of biological traits and ecological information compiled for each species in the potential dataset.

Category	Description	Source
Diet (%)	*Inv*: Percent consumption of invertebrates *End*: Percent consumption of endothermic vertebrates (mammals and birds) *Ect*: Percent consumption of ecthotermic vertebrates (reptiles, snakes, amphibians, salamanders) *Fish*: Percent consumption of fish *Fruit*: Percent consumption of fruit, drupes *Dead*: Percent consumption of carcasses, carrion, and garbage	Categories and values proposed by Wilman et al. (2014)were adapted based on recent literature and researcher's experience
Specialization (Sp)	Index of specialization calculated as the number of different food categories present in species dietary	this study
Trophic Level (Tr)	Index of trophic level based on energy requirements, assuming different energetic weights depending on the food category: (3) vertebrates (includingcarcasses and carrion); (2) invertebrates; and (1) fruits	this study
Foraging	*ground*: Prevalence of prey capture on ground *und*: Prevalence of prey capture below 2m in understory in forest *mid*: Prevalence of prey capture in mid to high levels in trees, but below canopy *can*: Prevalence of capture in or just above tree canopy *aer*: Prevalence of capture well above vegetation or any structures	Categories and values proposed by Wilman et al. (2014) were adapted based on recent literature and researcher's experience
Sensitivity (Se)	Degree of species sensitivity to habitat disturbance: L-low; M-medium; H-high	Parker III et al., 1996
Abundance (Ab)	Species abundance pattern:R-rare; U-uncommon; F-fairly common; C-common; P-patchily distributed	Parker III et al., 1996
BodyMass (g)	Average body mass in grams	Dunning, 2007
IUCN conservation status	VU= Vulnerable; NT=Near threatened; EN= Endangered; CR=Critically Endangered	IUCN, 2016

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Table S2. List of diurnal raptors with potential occurrence in the study region, description of dietary and foraging strata preferences, body size, sensitivity to habitat disturbance, abundance pattern and conservation status. See Table S1 for categories' legends and descriptions.

Species	**record**	**Diet (%)**						**Sp**	**Tr**	**Foraging Strata (%)**					**Se**	**Ab**	**Weight**	**IUCN**
		Inv	End	Ect	Fish	Dead	Fruit			G	U	M	C	A			**(g)**	**Status**
Accipiter bicolor	CF	0	100	0	0	0	0	1	3.0	10	25	35	25	5	M	U	287.54	LC
Accipiter poliogaster	n	0	100	0	0	0	0	1	3.0	10	27	27	27	10	H	R	300.00*	NT
Accipiter striatus	n	5	90	5	0	0	0	3	3.0	15	25	25	25	10	L	F	130.59	LC
Accipiter superciliosus	n	0	100	0	0	0	0	1	3.0	0	50	50	0	0	H	U	99.51	LC
Busarellus nigricollis	n	15	5	10	70	0	0	4	2.9	100	0	0	0	0	L	F	766.14	LC
Buteo albonotatus	y	0	70	30	0	0	0	2	3.0	30	30	0	30	10	M	U/P	745.92	LC
Buteo brachyurus	y	10	80	10	0	0	0	3	2.9	7	7	0	66	20	M	F	496.01	LC
Buteo nitidus	y	20	60	20	0	0	0	3	2.8	20	20	20	20	20	M	F	519.04	LC
Buteogallus aequinoctialis	n	100	0	0	0	0	0	1	2.0	100	0	0	0	0	M	U	657.63	NT
Buteogallus lacernulatus	n	40	30	30	0	0	0	3	2.6	80	10	10	0	0	H	U	595.50	VU
Buteogallus meridionalis	y	28	28	28	8	8	0	5	2.7	50	20	0	20	10	L	F	807.99	LC
Buteogallus urubitinga	y	10	20	40	10	15	5	6	2.8	40	20	20	20	0	M	F	1152.87	LC
Caracara plancus	y	30	15	15	0	35	5	5	2.6	50	15	15	15	5	L	C	1078.62	LC
Cathartes aura	y	0	5	0	0	90	5	3	2.9	100	0	0	0	0	L	C	1518.24	LC
Cathartes burrovianus	y	5	0	5	5	80	5	5	2.9	100	0	0	0	0	M	F/P	935.00	LC
Chondrohierax uncinatus	y	90	0	10	0	0	0	2	2.1	25	25	25	25	0	L	U/P	286.07	LC
Circus buffoni	n	0	80	20	0	0	0	2	3.0	80	20	0	0	0	M	U/P	507.40	LC
Coragyps atratus	y	5	10	5	0	75	5	5	2.9	85	5	5	5	0	L	C	1881.69	LC
Elanoides forficatus	n	70	10	10	0	0	10	4	2.1	0	0	0	70	30	M	U	416.24	LC
Elanus leucurus	n	5	90	5	0	0	0	3	3.0	90	0	0	0	10	L	U/P	850.28	LC
Falco femoralis	CF	50	40	10	0	0	0	3	2.5	20	20	20	20	20	L	U	2950.00	LC
Falco peregrinus	n	10	80	10	0	0	0	3	2.9	40	10	5	5	40	M	R	759.95	LC
Falco rufigularis	CF	30	70	0	0	0	0	2	2.7	7	11	11	11	60	L	F	163.64	LC
Falco sparverius	n	60	20	20	0	0	0	3	2.4	50	25	5	5	15	L	F	496.01	LC
Falco sparverius	n	60	20	20	0	0	0	3	2.4	50	25	5	5	15	L	F	496.01	LC
Gampsonyx swainsonii	n	15	10	75	0	0	0	3	2.9	85	5	0	0	10	L	U/P	92.90	LC
Geranoaetus albicaudatus	n	35	35	20	0	10	0	4	2.7	85	5	0	0	10	L	F	885.00	LC

Table S2. Continuation

Species	**record**	**Diet (%)**						**Sp**	**Tr**	**Foraging Strata (%)**					**Se**	**Ab**	**Weight**	**IUCN**
		Inv	End	Ect	Fish	Dead	Fruit			G	U	M	C	A			**(g)**	**Status**
Geranospiza caerulescens	y	20	40	40	0	0	0	3	2.8	10	30	40	20	0	M	U	302.50	LC
Harpagus bidentatus	n	65	5	30	0	0	0	3	2.4	5	0	30	50	15	M	F	215.25	LC
Harpagus diodon	CF	65	5	30	0	0	0	3	2.4	5	5	40	45	5	M	F	200.00	LC
Harpia harpyja	n	0	80	20	0	0	0	2	3.0	15	15	20	40	10	H	R	4800.00	NT
Herpetotheres cachinnans	y	10	10	80	0	0	0	3	2.9	50	20	20	5	5	L	F	623.58	LC
Ictinia plumbea	n	90	5	5	0	0	0	3	2.1	10	5	10	35	40	M	C	249.90	LC
Leptodon cayanensis	y	50	20	30	0	0	0	3	2.5	0	33	33	33	0	M	U	474.00	LC
Micrastur ruficollis	n	10	40	50	0	0	0	3	2.9	34	28	28	0	10	M	F	315.21	LC
Micrastur semitorquatus	y	0	80	20	0	0	0	2	3.0	40	30	20	5	5	M	F/P	621.68	LC
Milvago chimachima	y	40	15	15	5	20	5	6	2.5	25	25	25	25	0	L	C	315.21	LC
Morphnus guianensis	n	0	60	40	0	0	0	2	3.0	10	35	35	10	10	H	R	1750.00	NT
Parabuteo unicinctus	n	0	90	10	0	0	0	2	3.0	35	30.0	5.0	15.0	15.0	L	U	850.28	LC
Pandion haliaetus	n	0	0	0	100	0	0	1	3.0	100	0.0	0.0	0.0	0.0	M	U	1483.20	LC
Pseudastur polionotus	y	5	70	25	0	0	0	3	3.0	50	30	20	0	0	H	U	595.5	NT
Rostrhamus sociabilis	CF	100	0	0	0	0	0	1	2.0	100	0	0	0	0	L	C	366.94	LC
Rupornis magnirostris	y	40	25	35	0	0	0	3	2.6	50	15	15	15	5	L	C	269.00	LC
Sarcoramphus papa	y	0	0	0	0	100	0	1	3.0	100	0	0	0	0	M	F	3400.00	LC
Spizaetus melanoleucus	y	0	90	10	0	0	0	2	3.0	10	0	0	70	20	H	U/P	1518.24	LC
Spizaetus ornatus	n	0	90	10	0	0	0	2	3.0	15	15	40	15	15	M	U	1197.40	NT
Spizaetus tyrannus	y	0	75	25	0	0	0	2	3.0	5	20	30	35	10	M	U	1007.11	LC

Table S3. Species recorded using each sampling method. Uncertain identifications are indicated with (?).

species	playback	point count	active search	occasional record
Acciper bicolor (?)	1	0	1	0
Buteo albonotatus	1	1	1	1
Buteo brachyurus	0	1	0	1
Buteo nitidus	1	0	1	1
Caracara plancus	1	1	1	1
Chondrohierax uncinatus	1	0	1	1
Falco sp. (?)	0	1	0	0
Geranospiza caerulescens	1	1	1	1
Herpetotheres cachinnans	1	1	1	1
Heterospizias meridionalis	0	1	0	1
Leptodon cayanensis	1	1	1	0
Micrastur semitorquatus	1	0	1	0
Milvago chimachima	1	1	1	1
Pseudastur polionotus	1	1	1	1
Rostrhamus sociabilis	0	1	0	0
Rupornis magnirostris	1	1	1	1
Sarcoramphus papa	0	1	0	0
Spizaetus melanoleucus	1	1	0	0
Spizaetus tyrannus	1	1	1	1
Urubitinga urubitinga	0	1	1	0
Total species detected	14	16	14	12

Table S4. Characterization of surveyed cabrucas (S1-S16) according to vegetation structure, habitat quality and vegetation cover in the landscape.

Variables	S1	S2	S3	S4	S5	S6	S7	S8
Index of human disturbance	1	0	3	1	4	2	5	0
Shade-tree density (trees/ha)	121 ± 115	186 ± 99	93 ± 53	107 ± 98	81 ± 46	307 ± 172	257 ± 213	236 ± 131
Diameter of shade-trees (cm)	19.5 ± 22.2	33.4 ± 20.2	31.0 ± 29.4	65.0 ± 79.7	22.3 ± 27.7	25.2 ± 22.4	30.4 ± 35.6	33.9 ± 35.8
Canopy height (m)	14 ± 8	18 ± 4	13 ± 7	16 ± 8	13 ± 7	15 ± 2	13 ± 7	15 ± 4
Trees connectivity per plot	2 ± 2	3 ± 1	1 ± 1	2 ± 1	1 ± 1	3 ± 1	2 ± 2	3 ± 2
Vertical stratification (SD height)	2.4 ± 3.1	3.2 ± 1.3	2.9 ± 3.3	4.1 ± 6.6	3.0 ± 4.7	4.3 ± 3.4	2.1 ± 2.4	3.5 ± 2.3
Mean shading level (%)	76 ± 10	77 ± 7	45 ± 16	72 ± 5	71 ± 18	80 ± 8	75 ± 16	75 ± 16
Cocoa density (cocoa/ha)	286 ± 173	643 ± 93	600 ± 135	414 ± 144	719 ± 333	707 ± 217	664 ± 630	693 ± 406
Manegement (index of intensity)	2.8 ± 0.8	4.0 ± 0.0	3.5 ± 1.0	3.4 ± 0.7	3.4 ± 0.8	3.2 ± 0.8	2.9 ± 0.9	3.8 ± 0.6
Vegetation cover (%)	82	78	96	87	84	75	94	74

	S9	S10	S11	S12	S13	S14	S15	S16
Index of human disturbance	0	1	1	7	5	4	2	4
Shade-tree density (trees/ha)	129 ± 144	179 ± 99	314 ± 308	157 ± 89	357 ± 281	143 ± 53	86 ± 24	164 ± 107
Diameter of shade-trees (cm)	23.5 ± 32.7	34.8 ± 25.3	27.5 ± 22.2	26.5 ± 30.4	24.1 ± 15.1	64.2 ± 49.3	40.6 ± 35.2	42.6 ± 44.9
Canopy height (m)	10 ± 6	16 ± 5	17 ± 5	15 ± 5	15 ± 4	20 ± 3	18 ± 4	13 ± 6
Trees connectivity per plot	2 ± 1	4 ± 1	2 ± 2	3 ± 1	4 ± 1	3 ± 2	2 ± 1	1 ± 1
Vertical stratification (SD height)	5.6 ± 3.7	4.4 ± 2.3	4.0 ± 2.7	3.8 ± 1.9	4.4 ± 3.2	2.6 ± 2.5	3.7 ± 2.9	1.7 ± 2.5
Mean shading level (%)	67 ± 17	68 ± 32	89 ± 4	76 ± 12	74 ± 14	86 ± 3	84 ± 10	63 ± 14
Cocoa density (cocoa/ha)	371 ± 168	879 ± 202	536 ± 537	471 ± 200	557 ± 412	643 ± 388	907 ± 207	836 ± 238
Manegement (index of intensity)	3.4 ± 0.8	3.4 ± 0.7	2.4 ± 0.8	2.8 ± 0.7	3.2 ± 1.0	3.6 ± 0.6	3.9 ± 0.4	3.5 ± 0.9
Vegetation cover (%)	84	82	93	90	73	82	74	88

CAPÍTULO 3

Determinants of patch occupancy by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in cocoa agroforests*

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Abstract

The distribution of species in human-modified landscapes largely depends on their capacity to adapt to changes in habitat structure and quality. The golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*) is an endangered primate from the Brazilian Atlantic forest whose remaining populations inhabit heterogeneous landscapes mainly composed of shade cocoa (*Theobroma cacao*) plantations, locally known as *cabrucas*. Such biodiversity-friendly crops maintain high numbers of native species, but they are increasingly threatened by a new legislation that promotes management intensification. Although this situation can threaten the distribution of GHLTs, the main drivers of cabruca occupancy are unknown, thus limiting our ability to design and implement adequate conservation practices. We surveyed 16 patches of cabruca in southern Bahia, Brazil, and used occupancy modeling to identify the best predictors of patch occupancy. We considered explanatory variables related to vegetation structure, key resources (food and sleeping sites), landscape context, human disturbance and predation pressure, all of which could affect GHLT occurrence in cabrucas. We observed GHLTs in 10 out of 16 cabrucas, with densities ranging from 0.01 to 0.08 groups/ha. The equitability of shade-tree species and abundance of lianas were the most important predictors of cabruca occupancy. Therefore, maintaining a higher diversity and evenness of native shade tree species, and retaining high-climbing lianas in the canopy is of paramount importance to increase the conservation value of cabrucas. This would benefit not only GHLTs, but other native animals that use cabrucas as supplementary habitat, including many arboreal and scansorial vertebrates that move through the (sub)canopy forest strata. Our novel findings highlight that the biodiversity-friendly status of cabrucas should be reevaluated, particularly under scenarios of management intensification through canopy tree thinning.

Keywords: agriculture, raptors, camera-trap, playback, point-count, primates, tamarins

Introduction

Given burgeoning human demands on Earth's natural resources (Steffen et al., 2015), human-modified landscapes have expanded relentlessly, particularly in species-rich biomes (Venter et al., 2016; Watson et al., 2016). The long-term persistence of many taxa is therefore strongly contingent on species survival in these "novel" habitat mosaics (Tabarelli et al., 2012). Species flexibility to deal with habitat changes, such as those related to microclimate, vertical stratification, and availability and quality of food resources, will determine their ability to occupy and persist in many anthropogenic habitats (Balmford, 1996; Purvis et al., 2000; Cowlishaw et al., 2009).

Several studies have addressed how different taxonomic groups are affected by habitat disturbance (Carrete et al., 2009; Airoldi & Bulleri, 2011; Hoffman & O'Riain, 2012; Ribeiro-Neto et al., 2016). For example, a global meta-analysis revealed an overall negative effect of habitat disturbance on primate populations, so that perturbations caused by different human activities can result in declines of 17-43% in biodiversity values (Chapter 1 of this thesis). Although this effect is more detrimental when habitat is converted to agriculture, agromosaics and agroforests can support or subsidize some primate populations due to a higher degree of habitat heterogeneity (Chapter 1 of this thesis; Estrada et al., 2012). Indeed, many authors extol agroforestry as a viable solution in reconciling human economic demands with biodiversity conservation (Rice & Greenberg, 2000; Perfecto & Vandermeer, 2008). However, the capacity of these agro-systems to retain native forest biodiversity relies heavily on the residual amount of forest cover in the landscape and the type and intensity of management practices (Steffan-Dewenter et al., 2007; Faria et al., 2007; Tscharntke et al., 2012; Cassano et al., 2014).

The Atlantic forest of southern Bahia, Brazil, has sufered a severe deforestation process, and less than 5% of the original forest (~ 3500 km²) remains (Thomas et al., 1997). The landscape is nowadays dominated by cocoa (*Theobroma cacao*) plantations (~5500 km²; May & Rocha, 1996). The main cash crop in this region is shade-cocoa agroforestry, locally known as "*cabruca*". Traditional cabrucas of this region consist of replacing the understory by cocoa trees that grow underneath the canopy of predominantly native forest trees that are retained when cocoa is planted, in addition to trees that regenerated or have been planted subsequently (Alves, 1990). Consequently, the vertical structure of cabrucas is very simplified compared with intact forests, but much more complex than other agricultural systems, such as annual or perennial conventional crops (Alves, 1990). The official recommendation is to retain between 25 and 30 shade trees per hectare (Alvim & Pereira, 1970), but traditional cabrucas of southern Bahia typically hold a much higher density (mean = 197, range = 70-480 shade-trees/ha), in which ~63% (18-100%) of these tree species are native (Schroth et al., 2013). Consequently, cabrucas retain a high degree of vegetation complexity that enables a significant proportion of native fauna to use it as habitat, supplementary resources, and/or dispersal corridors between forest patches (Argôlo, 2004; Delabie et al., 2007; Faria et al., 2007; Cassano et al., 2012).

Due to their compatibility with both biodiversity conservation and forest carbon storage (Schroth et al., 2011, 2013), cabrucas are considered a wildlife-friendly productive system. Unfortunately, this status is now threatened by land-use intensification (Schroth et al., 2011). Former Brazilian environmental legislation banned felling forest trees within cabrucas, but a state decree (N° 15.180; article 19) published by the Bahia Government in 2014 (hereafter, *management decree*) sanctioned the legal removal of shade trees in high-density cabrucas to increase cocoa yields, encouraging landowners to retain at least 40 native shade-trees/ha. Residual timber trees can further be legally sold, as authorized by a state-level environmental agency (Instituto do Meio Ambiente e Recursos Hídricos, INEMA). This proposed tree density threshold is far below that observed in traditional cabrucas of Southern Bahia (Schroth et al., 2013), which will undoubtedly render this system far more structurally simplified (Fig. 1), thereby degrading their wildlife-friendly status (Schroth et al., 2013; Cassano et al., 2014).

The golden-headed lion tamarin (*Leontopithecus chrysomelas*, hereafter GHLT) is an endemic endangered primate of the Brazilian Atlantic forest whose remaining geographic range is currently dominated by cabrucas (Raboy et al., 2004; IUCN, 2016). Viable breeding groups of GHLTs can occupy areas entirely covered by cabrucas, where they usually occur at higher densities than in forests (Oliveira et al., 2011). The former geographic range of this species has been severely reduced by deforestation, and despite its ability to use cabrucas, GHLTs do not occupy all patches of cabruca (Raboy et al., 2010). Vertical structural complexity of cabrucas can be highly variable depending on the density and diversity of residual shade trees coupled with local management practices (Rice & Greenberg, 2000; Sambuichi et al., 2012), which directly interfere with the ability of native species to colonize and survive in this system (Cassano et al., 2014). Identifying cabruca features that favour native species occupancy is therefore critical to stimulate best management practices and maintain the wildlife-friendly status of cabrucas, particularly given the current policy context inducing management intensification.

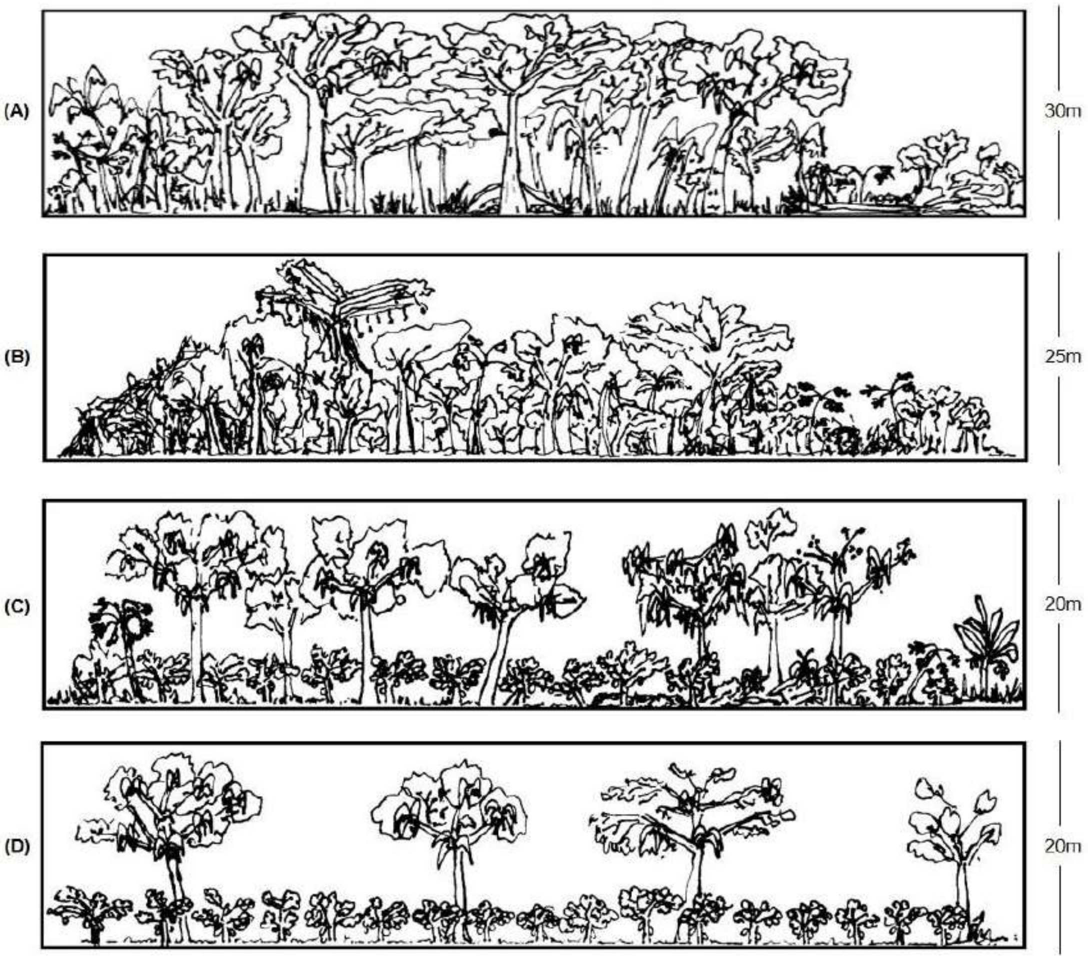

Fig. 1. Profiles of vertical structure and diversity of trees in (A) mature forests, (B) secondary forests, (C) traditional cabrucas, and (D) intensified cabrucas. Bars on the right of the panels indicate the mean canopy height. Ilustration's autorship: Gastón Giné.

Several studies have sought to understand how GHLTs have adapted to cabrucas (Raboy et al., 2004; Oliveira et al., 2010, 2011; Oliveira & Dietz, 2011; Almeida-Rocha et al., 2014, 2015). A key finding is that GHLTs experience a higher predation risk, mainly from raptors, compared to relatively undisturbed forests (Oliveira & Dietz, 2011). In addition, domestic dogs (*Canis familiaris*) elicit intense alarm calls and bouts of mobbing from GHLTs (JMAR and LCO pers. obs.), with local residents reporting that dogs chase GHLTs, suggesting that dogs are potential GHLT predators within cabrucas, particularly given their high abundance in this habitat (Cassano et al., 2012). Dogs are associated with proximity to human settlements, and cabruca workers are typically accompanied by dogs, which often assist in opportunistic hunting. Moreover, synergistic effects between habitat alteration and predation may lead to unbalanced trophic interactions resulting in more detrimental effects to prey species (Irwin et al., 2009). It is therefore possible that predation pressure exerts a strong influence on GHLT occupancy of cabrucas.

Here, we investigated the habitat and landscape features of cabrucas that favor patch occupancy by GHLTs. We also examined the role of natural and domesticated predators on GHLT occupancy. For this, we surveyed cabrucas within the range of GHLTs and used occupancy modeling to evaluate the influence of vegetation structure, key resources, vegetation cover, predation pressure, and some aspects of management intensity on GHLT distribution (presence/absence) in this habitat. We expected to find that patch occupancy is positively related to (1) vegetation structural complexity (e.g. density and height of shade trees, vertical stratification, canopy connectivity and abundance of lianas); (2) availability of key trophic resources, such as key native food species, jackfruits, banana trees, and bromeliads; and (3) total amount of vegetation cover at the local and landscape scales. In contrast, predation risk (i.e. abundance of potential aerial and terrestrial predators) and management intensity of cocoa plantations (i.e. frequency of weeding, density of cocoa trees, and amount of shade) will be negatively related to patch occupancy.

Methods

1. Study species

The GHLT is a small-bodied callithrichid primate with an average body weight of 620 g, and whose diet consists mainly of ripe fruits, arthropods and small vertebrates (Rylands, 1989). Bromeliads represent a key resource for GHLTs since is the main microhabitat for arthropod foraging (Rylands, 1989). The GHLT diet in cabrucas is mainly comprised of exotic jackfruit, *Artocarpus heterophylus*, which is very abundant almost all year-round (Oliveira et al., 2011). GHLT’s home ranges average 83 ha and the species typically occur at a mean density in cabrucas of 0.12 (0.04-0.21) ind/ha (Oliveira et al., 2011), living in groups of 2 to 15 individuals with usually one breeding female (Baker et al., 2002). All group members sleep together preferentially in large tree cavities so they rely on sufficiently large canopy trees to provide shelter (Rylands, 1989).

2. Study area

From May 2014 to May 2015, we surveyed 16 cabruca sites located within private farms and rural settlements within the GHLT geographic range, covering 11 municipal counties (encompassing an area of ~700,000 ha) in the cocoa-growing region of southern Bahia, Brazil (Figure 2). This region is characterized by a high degree of deforestation and fragmentation mainly in the western portion of species' range, where the dominant vegetation is tropical seasonal semi-deciduous forest (Zeigler et al., 2010). The eastern portion has the largest and most intact fragments, and the dominant vegetation is coastal evergreen tropical rainforest (Zeigler et al., 2010). The mean annual temperature is 24 °C and rainfall averages 2,500 mm/yr, with no marked seasonality (Mori et al., 1983). All cabruca sites surveyed were at least 11 km (52-114 km) apart, ensuring a high degree of spatial independence (Fig. 2).

3. GHLT survey

All sampling was performed by the same researcher with the help of a field assistant. Active search and playback technique were used to systematically search for GHLTs in each study area over three non-consecutive days. The number of visits was defined a priori based on the GHLT detection history within cabrucas of a previous project carried out in the same region and using the same field techniques (L.G. Neves, pers. comm.). Using satellite images obtained from Google Earth (Google Inc., 2016), we deployed a pre-selected sampling grid within each study cabruca so that playbacks could be deployed in the intersection points of this grid, whereas the active searches were performed during travel on foot between playback points (Fig. 3).

The playback methodology consisted of playing GHLT long-calls, which in this genus typically attract neighbouring groups prior to territorial encounters (Peres, 1989), to attract individuals and stimulate intra-specific responses. We used a digital voice recorder and a directional microphone to record long-calls of a GHLT adult male which had been in captivity as part of another study (Cabruca Project). This recording was subsequently edited using the free Audacity® software (http://www.audacityteam.org/). The playback was carried out using the same recorder and a portable speaker. At each playback point, a complete long-call was directed towards the four cardinal point sholding the recorder at ~2 m above ground, followed by a 5-min on-site wait.

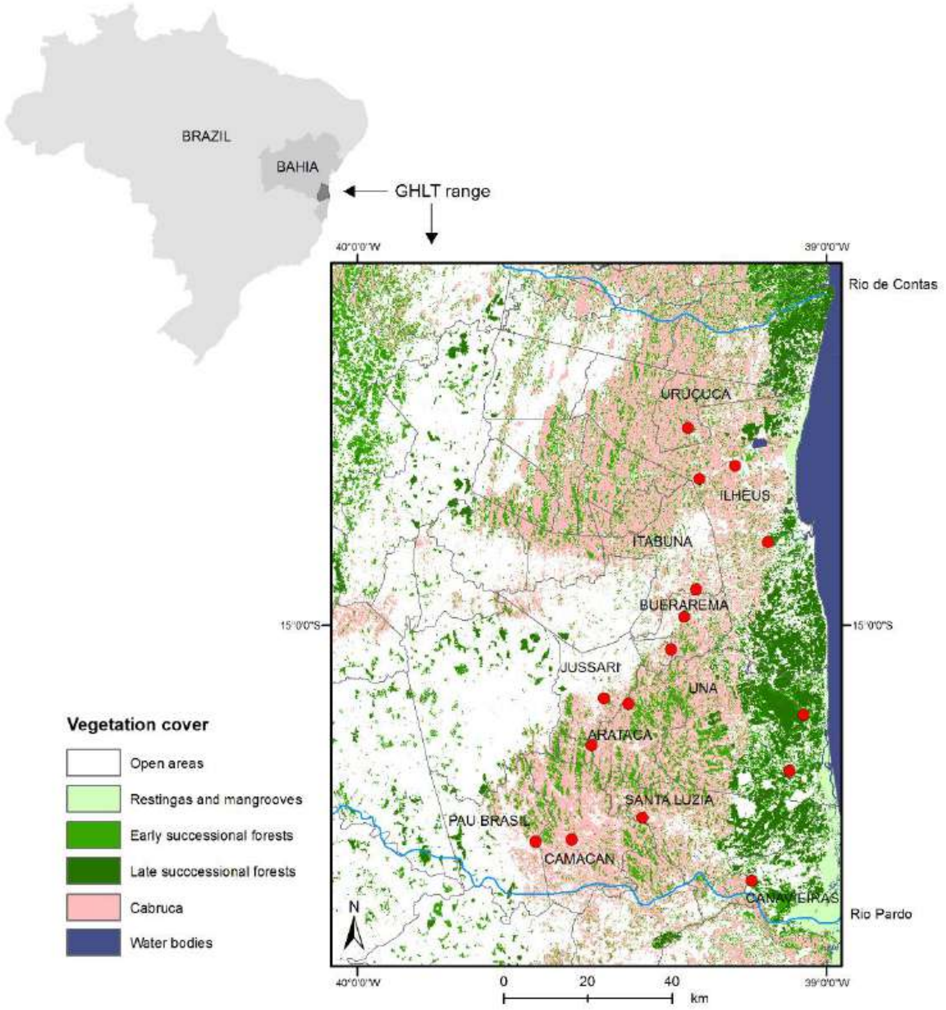

Fig. 2. Vegetation cover within the geographical range of the golden-headed lion tamarin (GHLT) and the location of the sixteen cabrucas surveyed in this study (red circles). Vegetation cover classification was based on Landau et al. (2008).

When responses were detected, we recorded the location, time, direction of the response and number of vocalizations. The two last parameters helped us to assess whether more than one group responded to the playbacks. To reduce the chance of detecting the same group more than once on the same day, playback points were spaced 200 m apart as their range radius (100 m) did not overlap, which had been previously tested experimentally using a radio collared GHLT group (a field assistant remained with the group while the researcher pulled away and played the recording at different distances, which revealed 100m as ideal for the tamarins to respond and also for the observer to listen). Visits to the same cabruca site were spaced by at least one week to avoid habituation to playbacks (Dong & Clayton, 2009), but all surveys within the same site were completed within 30 days.

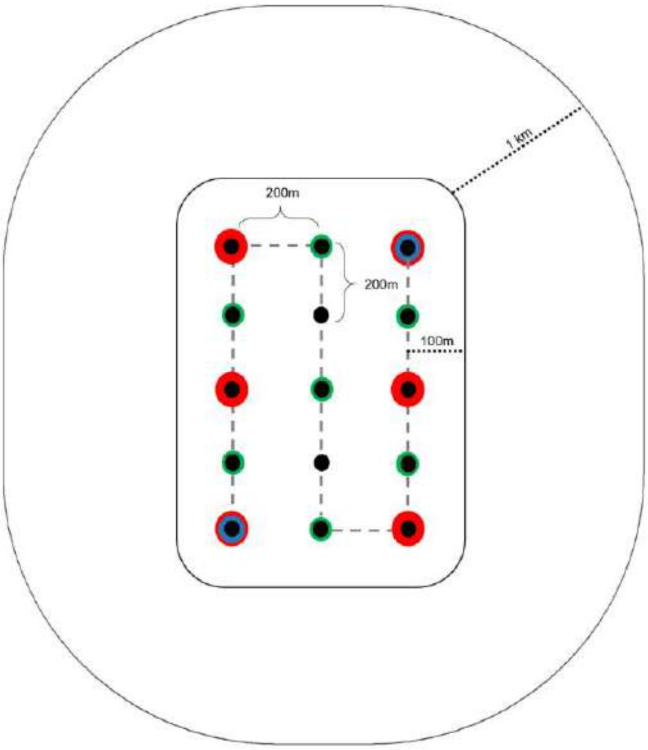

Fig. 3. Scheme of the sampling grid used in this study, where an active search for both golden-headed lion tamarins (GHLT) and diurnal raptors was performed in linear transects (dashed gray line), playback points for the GHLTs (black circles) and raptors (blue circles) were performed every 200m, and camera traps stations (red circles) as well as vegetation plots (green circles) were allocated in interspersed points. The survey area is delimited by the playback range radius of 100m, and the area where landscape metrics were measured is delimited by the 1km-radius calculated from the survey area limits.

Each sampling grid had at most 15 playback points (equivalent to a sampling area of 60 ha, considering the playback range) to enable sampling of all points in the morning day between 06:00 h and 11:00 h, when GHLTs are most active in cabrucas (Reis, 2012). At each visit, the starting point was alternated to increase detection probability due to any variation in the use of space by the groups throughout the day. Detectability can also be affected by climatic conditions that can interfere with both species activity and sound propagation (Waser & Waser, 1977), so we used a thermo-hygrometer (Instrutemp Model ITHT-2200) to record mean air temperature and humidity levels during each visit. Playback surveys were not performed under rainy weather or strong winds.

4. Predators survey

Based on published records and geographic distribution maps (IUCN, 2016; http://www.mma.gov.br/) we listed 16 mammalian species potentially occurring in the study region (Table S2), and a previous study (Chapter 2 of this thesis) have listed 46 diurnal raptors species (Table S3). These species were classified according to their potential as a GHLT predator based on the following criteria: (1) record of predation on primates, (2) record of attack on primates, (3) body size, (4) typical prey size, (5) record of mammals in the diet, (6) degree of dietary specialization, and (7) foraging strategy. To make the classification more systematic, each criterion received a categorical value (based on published information and researcher experience), with high values attributed to characters that favor GHLT predation. These values were then summed to create an index of predation potential that was used to rank all species according to their probability of preying on GHLTs, giving greater weights to categories (1), (2) and (7), which were considered most important (details in Supplementary Information: Tables S1-S3).

We also included in this list the yellow-breasted capuchin monkey, *Sapajus xanthosternos*, and domestic dogs as potential predators of GHLTs, considering published records of predation on primates (Lawrance, 2003; Sampaio & Ferrari, 2004; Galetti & Sazima, 2006; Oliveira et al., 2008) and regional-scale unpublished observations. Our final checklist included 30 potential predator species in the study region (Table 1), but this is not complete since venomous and constricting non-venomous serpents are not considered. Unffortunatly, some logistic limitations prevented us from surveying serpents, even though some species that inhabit cabrucas in southern Bahia (Argôlo, 2004) are known to predate on small primates (e.g. *Bothrops jararaca*: Corrêa & Coutinho, 1997; *Bothrops leucurus*:Ferrari & Beltrão-Mendes, 2011; *Boa constrictor*: Teixeira et al., 2016).

4.1. Terrestrial predators

We sampled terrestrial predators (considered species with primarily terrestrial, arboreal or scansorial habits) using four to six digital camera traps (Tigrinus®6.0D), depending on the size of the sampling grid. The cameras operated simultaneously for 24 hours during approximately 20 days in each site (or more, in the sites where we used less cameras), aiming for total sampling effort of 120 camera-days (following Espartosa et al., 2011). Camera-trap stations were spaced by at least 300 m positioned near playback points (Fig. 2), where one camera was fixed to a tree at approximately 50 cm above ground.

Table 1. List of potential predators of golden-headed lion tamarins in the study region. Taxonomy nomenclature follows Paglia et al. (2012) and Remsen et al. (2017).

Order	**Family**	**Species**	**Common name**
Carnivora	Canidae	*Canis familiaris*	Domestic dog
Carnivora	Felidae	*Leopardus guttulus*	Southern Tiger Cat
Carnivora	Felidae	*Leopardus pardalis*	Ocelot
Carnivora	Felidae	*Leopardus wiedii*	Margay
Carnivora	Felidae	*Puma concolor*	Puma
Carnivora	Felidae	*Puma yagouaroundi*	Jaguarundi
Carnivora	Mustelidae	*Eira barbara*	Tayra
Carnivora	Procyonidae	*Nasua nasua*	South American Coati
Primates	Cebidae	*Sapajus xanthosternos*	Yellow-breasted capuchin monkey
Accipitriformes	Accipitridae	*Accipiter bicolor*	Bicolored Hawk
Accipitriformes	Accipitridae	*Accipiter striatus*	Sharp-shinned Hawk
Accipitriformes	Accipitridae	*Accipiter poliogaster*	Gray-bellied Hawk
Accipitriformes	Accipitridae	*Buteo albonotatus*	Zone-tailed Hawk
Accipitriformes	Accipitridae	*Buteo brachyurus*	Short-tailed Hawk
Accipitriformes	Accipitridae	*Buteo nitidus*	Gray-lined Hawk
Accipitriformes	Accipitridae	*Buteogallus meridionalis*	Savanna Hawk
Accipitriformes	Accipitridae	*Buteogallus urubitinga*	Great Black Hawk
Accipitriformes	Accipitridae	*Geranospiza caerulescens*	Crane Hawk
Accipitriformes	Accipitridae	*Harpia harpyja*	Harpy Eagle
Accipitriformes	Accipitridae	*Leptodon cayanensis*	Gray-headed Kite
Accipitriformes	Accipitridae	*Morphnus guianensis*	Crested Eagle
Accipitriformes	Accipitridae	*Parabuteo unicinctus*	Harris's Hawk
Accipitriformes	Accipitridae	*Pseudastur polionotus*	Mantled Hawk
Accipitriformes	Accipitridae	*Rupornis magnirostris*	Roadside Hawk
Accipitriformes	Accipitridae	*Spizaetus melanoleucus*	Black-and-white Hawk-eagle
Accipitriformes	Accipitridae	*Spizaetus ornatus*	Ornate Hawk-eagle
Accipitriformes	Accipitridae	*Spizaetus tyrannus*	Black Hawk-eagle
Falconiformes	Falconidae	*Caracara plancus*	Southern Caracara
Falconiformes	Falconidae	*Micrastur ruficollis*	Barred Forest-falcon
Falconiformes	Falconidae	*Micrastur semitorquatus*	Collared Forest-falcon

Cameras were baited with a balanced combination of banana lure, carnivore essence (Bobcat urine) and sardine oil (10 ml of each), which were placed separately into pots with holes (protected from rain and animal consumption) that were attached to wooden sticks at ~50 cm from the ground and at a distance of 2 m perpendicular to the camera. Baits and lures were specifically selected to attract potential GHLT predators, such as felids and tayras (Schlexer, 2008). Camera-trap stations were checked weekly to replace baits, lures, batteries, memory cards or the cameras them selves due to occasional malfunction. Malfunctioning cameras were replaced and then exposed for a longer period to compensate for any losses in sampling effort. Photographs of conspecifics recorded within a 24-h period were considered as a single record, unless individual identification was possible through natural marks, as in the case of domestic dogs. In the case of social species, such as coatis (*Nasua nasua*), we used ‘group’ rather than ‘individual’ records.

4.2. Aerial predators

A combination of active searches, playbacks and point-counts were used to survey diurnal raptors within each site, which were sampled twice. These surveys were always subsequent to GHLT surveys to avoid interference with its behavior and detectability. All sampling was carried out between 06:00h and 12:00h — the peak period of activity for most diurnal raptors (Thiollay, 1989; Mañosa et al., 2003) — but always avoiding rainy and windy days due to possible reductions in detectability (Jones, 2000; Granzinolli & Motta-Junior, 2008).

Between 06:00h and 09:00h, sampling was carried out within the cabruca, focusing on forest species that only occasionally fly above the canopy (Thiollay, 1989), but also searching for soaring species that start flight activity later. An active search was carried out throughout the sampling grid using 10x50 binoculars and a recorder to record vocalizations whenever possible. Additionally, we performed playbacks at two points located at the beginning and at the end of the sampling grid (Fig. 2), separated by a mean linear distance of 665±160 m (which is consistent with previous studies: Carvalho Filho et al., 2008/2009; Vázquez-Pérez et al., 2009).

We adjusted our methodology following Granzinolli & Motta-Junior (2008) plus our own field experience. We performed playbacks only to a set of diurnal raptors that are known to respond well to this technique (Zorzin, 2011; JABM, pers. obs.): *Leptodon cayanensis*, *Micrastur ruficollis*, *Micrastur semitorquatus*, *Accipiter bicolor* and *Spizaetus tyrannus*. We used recordings available on Wiki Aves (http://www.wikiaves.com/), preferentially selecting recordings from the study region, and avoiding aggressive vocalizations and pair duets. At each playback point, recordings of all focal species were played in a pre-established ordertaking into account both body size and aggressive behavior, considering that larger-bodied species could shun smaller raptors. Each vocalization was played continuously for 3 min, holding the speaker at ~2 m above ground and rotating it 360° at a constant rate, followed by a 3-min on-site wait.

Most raptors often start soaring when thermals are well-formed, so the best period to perform point-count techniques is between 9:00h and 12:00h (Thiollay, 1989; Mañosa et al., 2003). During this period, we recorded all individuals using visual or vocal cues from a fixed location. In the case of raptors, point-counts are typically deployed at high sites that offer a wide canopy view, such as hilltops adjacent to the study area (Thiollay, 1989; Whitacre et al., 1990; Mañosa et al., 2003). Whenever possible point-counts were located at hill tops, but in six areas where the relief was very flat we located two complementary point-counts at ~100 m from the edge of the cabruca, spaced apart by mean distances of 690 ± 170 m, and remained at each point for 1h 30min.

Except for single point-counts, the initial sampling point was always alternated in the second visit to ensure detection of species with different activity peaks at all points (Jones, 2000). Given that even small raptors use home ranges of up to 100 ha (Thiollay, 1989), most Atlantic Forest fragments are smaller than the mean territory size of Neotropical raptors (Zorzin, 2011). Repeated detections of the same species in the same area were thus attributed to the same individual, unless more than one individual was observed simultaneously. Finally, we estimated the total relative abundance of each aerial predator species per site, which also took into account occasional records.

5. Habitat structure and quality

At each site, several habitat structure and cabruca management features were sampled at seven 200-m² plots placed at interspersed points across the sampling grid (Fig. 2; Table 2). in particular, we assessed 14 explanatory variables: (1) relative density of shade-trees; (2) mean canopy height; (3) mean canopy connectivity; (4) heterogeneity of vertical strata; (5) shade-tree species richness; (6) equitability of shade-tree species; (7) importance value index (IVI; Curtis & McIntosh, 1951) of key resource trees (food and/or shelter); (8) IVI of jack fruit; (9) mean diameter at breast height (DBH) of shade-trees; (10) abundance of woody lianas; (11) abundance of bromeliads; (12) abundance of banana trees; (13) management intensity of cabruca plots; (14) relative density of cacao trees; and (15) average canopy shade. Except for variables 5-8, which were measured for the entire area as a single value, we summed the values obtained for each variable per plot to obtain an overall value for each site, which represented an abundance index to be used in the analyses.

Table 2. Variables collected in seven plots of 200 m² in sixteen cabrucas, ecological meaning, applied methodology and the derived co-variables to be used in the GHT occupancy modeling.

Variable measured	**Meaning**	**Methodology**	**Final variables**
1. Number of shading trees	Complexity of vertical strata; Key resources (food and shelter)	All shading trees with diameter above the breast (DBH) ≥ 10cm that occurred inside the plots were quantified and identified preferably to the species level. Density was calculated as the number of shading trees per m²; species richness as the total number of tree species recorded in each area; and the Hill's Equitability index ranges from 0 to 1 and illustrates how species abundance is distributed inside each area so that it increases towards 1 when species abundance is more balanced in the area. The Importance Value Index (IVI) was calculated jointly for key species (used by the GHLT for food and/or shelter) and separately for jackfruits, *Artocarpus heterophyllus*, the food item most consumed by GHLTs in cabrucas (for details about the index calculation, please see Curtis & McIntosh, 1951).	1- Density of shading trees 2- Species richness of shade trees 3- Equitability of shading trees 4- IVI of key species 5- IVI of jackfruits 6- Mean DBH of shading trees
2. Canopy height	Complexity of vertical strata	A field assistant remained beside each shade tree recorded inside the plot holding a 2m stick perpendicular to the ground while the observer estimated the tree's height using the stick as scale. The vertical struture prevented the use of a rangefinder, but observer calibration with such equipment revealed an approximate error of 2m. Canopy height was estimated as the sum of median heights inside each plot per area, and strata heterogeneity was calculated as the standard deviation of trees' height inside each plot.	7- Canopy height 8- Vertical stratification
3.Canopy connectivity	Travel routes	Visual counting of all trees that connects to each shading tree through the canopy and calculation of the median number of connections per tree in each plot.	9- Canopy connectivity

Table 2. Continuation

Variable measured	Meaning	Methodology	Final variables
4. Lianas	Travel routes	Visual quantification of shading trees in the plot that support lianas. Abundance of lianas in each area was represented by the sum of the plot's percentages.	10- Abundance of lianas
5. Bromeliads	Foraging place	Categorical visual counting of all bromeliads inside the plot, ranging from 0 to 3, where: 0= no bromeliads; 1= 1-10 bromeliads; 2= 11-20 bromeliads; and 3 >20 bromeliads. Abundance of bromeliads was calculated as the sum of plot values per area.	11- Abundance of bromeliads
6. Banana trees	Food resource	Quantification of all banana trees inside each plot and sum of such values per area.	12- Abundance of banana trees
7. Activity status of the cabruca plot	Intensity of management	Categorical classification of the plot from less to most managed depending on the level of current activity: 1) old abandoned plot in process of forest regeneration with no (or very few and old) cocoa trees; 2) recently abandoned plot that is still dominated by cocoa trees and presents signs of forest regeneration; 3) active plot that is not being managed at the moment, characterized by the presence of seedlings and shrubs; and 4) active and managed plot, with absence of seedlings and shrubs.	13- Management intensity
8. Cocoa trees	Intensity of management	Quantification of cocoa trees inside each plot. Density was calculated as the number of cocoa trees per m².	14- Density of cocoa trees
9. Shadow	Intensity of management	A photograph was taken in the center of each plot using a digital camera equipped with a 55 mm hemispheric “fish-eye” lens (180°) supported by a tripod at a height of 1.5 meters from the ground and focused up. The pictures were analyzed in Gap Light Analyzer software (Frazer et al., 1999) to estimate the percentage of leaf cover (shade) in each plot.	15- Percentage of shadow

Shade-trees were identified in situ to the species level whenever possible with the help of an experienced local field assistant. When necessary, voucher specimens were collected for further identification in the herbarium of the State University of Santa Cruz. To calculate resource IVI values (see details in Table 2), the checklist of tree species recorded in this study was compared with published lists of species used by GHLTs (Cardoso, 2008; Catenacci et al., 2009, 2016, Oliveira et al., 2010, 2011). Throughout the sampling, any signs of hunting (e.g. waiting stations) and selective logging (e.g. stumps) werealso recorded to describe the degree of human disturbance at each site.

6. Landscape context

Based on Landsat 8 images of 2016 (30 m resolution) provided by Google Earth (Google Inc., 2016) and using the Raster Package (Hijmans et al., 2016) in R 3.3.1 (R Core Team, 2016), we measured the minimum linear distance between each playback point to the nearest household and fragment edge. In Quantum GIS 2.18.2 (http://www.qgis.org/), we calculated the percentage of vegetation cover in the surroundings of each cabruca site by extracting all visually identified clear-cut areas from an area defined by a 1-km radius buffer from the extreme points of the sample grid (Fig. 3). The difficulty of accurately distinguishing cabruca from forest areas on satellite images does not pose a problem for our analysis, since we are interested in the total amount of available habitat for GHLTs.

7. Occupancy modeling

Occupancy modeling, performed in the Mark software, version 8.x (White & Burnham, 1999), was used to identify the determinants of GHLT occurrence within cabrucas. In this approach, occupancy (Ψ) is interpreted as the proportion of an area that is occupied by a species (Mackenzie et al., 2002). As our survey was completed within a single unique season for each cabruca site, we fitted *single-season* models, which assumes that the population is closed to changes in occupancy inside each sampling unit during the survey season. We modelled the detection probability (p) as imperfect, considering that GHLTs may be present in an area but may not always be detected (Mackenzie et al., 2002).

A GHLT detection history (1 = detected and 0 = undetected) was created for each playback point in each cabruca site based on the three independent visits so that playback points served as independent sampling units for the analysis. In doing so, the assumption of population closure may not have been achieved, since GHLTs have can move >200 m (distance between neighbouring playback points) thus leaving or entering the sampling units many times during the season. As proposed by Mackenzie et al. (2006), we deal with this problem by interpreting the occupancy estimate as the proportion of the area 'used' by the species, rather than as true occupancy, and detectability as the probability of detecting the species when it is present in the area *and* using the sampling unit during the survey, assuming that GHLT movements through their home range is random (see similar interpretations in Keane et al., 2012; Kalan et al., 2015).

Variables collected in the field and extracted from satellite images were used as covariates to model Ψ and p using a series of competing models. Prior to analyses, we assessed the pairwise correlations through a Spearman correlation test, using the R Stats package (R Core Team, 2016), and excluded highly correlated variables ($r \geq 0.6$): shade-tree species richness, bromeliads, canopy height and connectivity. Then, we accounted for multi-collinearity among the remaining variables through the Variance Inflation Factor (VIF), using the CAR package of R (R Core Team, 2016). We excluded variables with VIF>4: percentage of shadow, IVI of key species, shade-tree density and vertical stratification. Thus, we finished with twelve covariates to model Ψ: (1) management intensity, (2) density of cacao, (3) equitability of shade-trees, (4) DAP of shade-trees, (5) abundance of lianas, (6) IVI of jackfruits, (7) abundance of banana trees, (8) distance to houses, (9) distance to fragment's edge, (10) vegetation cover, (11) abundance of diurnal raptors, and (12) abundance of carnivores. We used five covariates to model p: (1) survey method, (2) density of cacao, (3) hour of playback execution, (4) temperature and (3) air humidity during playback execution.

Model selection followed the *ad hoc* method, which consists in first modelling p with only one variable at a time while keeping Ψ with maximum number of possible covariates. After fixing the most important covariates to p, we repeated the process of modeling Ψ with one covariate at a time until we found the best overall model. We also included a constant model considering no covariates affecting Ψ. The candidate models were ranked according to the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002): models with $\Delta AIC \leq 2$ were considered equally plausible; those with $\Delta AIC > 2$ and ≤ 7 were considered to yiled lower but still significant support; and those with $\Delta AIC > 10$ were considered to be unsupported

(Burnham & Anderson, 2002; Bromaghin et al., 2013). In case of excessive uncertainty about the best model, the final estimates of parameters *p* and Ψ were model averaged by taking the weighted mean among all competing models (Burnham & Anderson, 2002). We accessed the fit of the most general model (the model with the greatest number of parameters) by estimating the overdispersion parameter *c-hat* using 10,000 bootstrap samples (Mackenzie & Bailey, 2004) using the PRESENCE 11.7 software (http://www.mbr-pwrc.usgs.gov/software/presence.shtml).

Results

1. GHLT surveys

Total sampling effort amounted 612 playbacks (24-48 per cabruca site) and 173 h 14 min of active searches (range = 6 h 15 min to 16 h 4 min per cabruca site). GHLTs were detected at 10 of the 16 surveyed cabrucas, with a mean density of 0.03 groups/ha (0.01-0.08 groups/ha). Detections were made possible primarily through playbacks, totaling 31 responses at eight sites, while at two areas GHLTs were detected only through active searches. A frequent event (67 occasions in 14 cabruca sites) was Wied's marmosets (*Callithrix kuhlii*) responding to GHLT playbacks. In eight occasions, we obtained responses from both species, and GHLTs usually responded first (six occasions). Playbacks also elucidated responses from raptors, including some potential predators such as *Caracara plancus*, *Geranospiza caerulescens*, *Pseudastur polionotus*, *Rupornis magnirostris*, and *Spizaetus tyrannus*. We also heard domestic dogs barking but we cannot be sure if they were responding to the playbacks.

2. Predator surveys

The overall sampling effort of 128 ± 28 camera-trap/days per site recorded 10 native mammals, domestic dogs, domesticated livestock, and humans. Such records include three potential predators: domestic dogs (14 sites); coatis, *Nasua nasua* (three sites); and tayras, *Eira barbara* (two sites; Table 3). Yellow-breasted capuchin monkeys were recorded during active GHLT search at one site (Table 3). Excepting domestic dogs, all predators were recorded in low-activity cabruca plots near regenerating forest patches. Due to such low detectability of terrestrial predators, we summed the abundances of the detected species and used this as a unique covariate for data analysis.

Table 3. Camera trap's records (X) of mammalian species - including those with (y) and without (n) potential to predate on GHLTs - in each sampling area (1-16) during the study period, and its respective index of predation potential (IPP). The estimates of species richness and abundance are presented as a range, considering the records losses and uncertainties in some species identification.

Species	**Predator**	**IPP**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Eira barbara	y	11					X		X									
Canis familiaris	y	11	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X
Sapajus xanthosternos	y	11											X					
Nasua nasua	y	9								X			X		X			
Cerdocyon thous	n	6	X	X	X	X			X		X							X
Procyon cancrivorous	n	3				X	X		X									
Cuniculus paca	n	0	X						X		X							
Dasypus novencinctus	n	0	X					X										
Didelphis aurita	n	0	X		X													
Mazama sp.	n	0	X	X		X					X			X				X
Pecari tajacu	n	0												X				
Livestock	n	0		X							X			X			X	
non-identified mammal	-	-										X					X	
records-loss	-	-	X	X	X				X			X	X				X	X
Species richness (total)			5	4-5	3-4	4	3	2	5	2	5	2	1	4-5	2	1	3	3
Species richness (predators)			1	1	1	1	2	1	2	2	1	1	1	1	2	1	1	1
Abundance (predators)			4	3	2	1	9	3	4	2	5	2	1	4	2	2	3	2

Zero values were atributted to non-carnivores IPP (except for *S. xanthosternos*) because they were not classified in relation to this index.

Sampling effort for diurnal raptors amounted to 64 playback points (4 per site), 91 h 11 min of active searches (4 h 48 min – 06 h 45 min per site), and 96 h of point-counts (6 h per site). We confirmed the occurrence of 22 diurnal raptor species in cabruca sites (Table 4), including three occasionally recorded owls – *Glaucidium brasilianum*, *Megascops* sp. and *Pulsatrix koeniswaldiana* – and 14 GHLT potential predators, with abundances ranging between twoand 14 individuals per site (Table 4). Some potential predators that were not expected to respond to playbacks, such as *Buteo* hawks, in fact responded to vocalizations of other raptor species for which we carried out playbacks, thereby increasing detectability. We fail to confirm the identification of *Accipiter bicolor* (4 sites), *Falco* sp. (2 sites), *Harpagus diodon* (2 sites) and *Rostrhamus sociabilis* (1 site).

Table 4. Records of diurnal raptors in each sampling area (1-16), and species classification regarding to their ability to prey on GHLTs (P; y=yes, n=no). Species are ordered by their index of potential predation (IPP). The estimates of species richness and abundance are presented as a range, considering the uncertainties in the identification of some species and the number of individuals observed. X = species detected at the area, X$^?$ = unconfirmed identification, and X* = doubt between two species in the same area.

species	**P**	**IPP**	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Spizaetus tyrannus	y	31	X		X		X	X	
Accipiter bicolor	y	25		X$^?$	X$^?$			X$^?$	
Rupornis magnirostris	y	25	X		X	X		X	X
Micrastur semitorquatus	y	20		X	X$^?$			X	
Buteogallus urubitinga	y	20	X*	X	X				
Caracara plancus	y	19	X	X	X	X	X	X	
Buteo brachyurus	y	18	X		X				
Buteo nitidus	y	18	X*	X*	X		X		
Leptodon cayanensis	y	17	X	X	X	X$^?$		X	
Spizaetus melanoleucus	y	17			X	X	X		
Buteo albonotatus	y	13	X	X	X	X	X	X$^?$	X
Buteogallus meridionalis	y	13				X			
Pseudastur polionotus	y	12		X		X	X	X	X
Milvago chimachima	n	12	X	X		X	X		
Herpetotheres cachinnans	n	9	X	X	X	X	X	X	
Geranospiza caerulescens	n	8	X$^?$		X		X	X	
Sarcoramphus papa	n	7					X		
Chondrohierax uncinatus	n	5			X				
Harpagus diodon	n	5					X$^?$	X$^?$	
Falco rufigularis	n	3			X*		X*		
Falco femoralis	n	3			X*		X*		
Rostrhamus sociabilis	n	3							
Unidentified individuals	-		X		X	X	X	X	X
Species richness (total)			8-12	9	12-16	7-10	12-13	8-12	3-4
Species richness (predators)			7-8	6-7	10-12	5-6	7	7-9	2
Abundance (predators)			9-10	12-13	13-14	8-9	9	8-10	3

Table 4. Continuation

Species	**P**	**IPP**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Spizaetus tyrannus	y	31			X			X	X	X	
Accipiter bicolor	y	25									X$^?$
Rupornis magnirostris	y	25	X$^?$	X$^?$			X	X	X	X	X
Micrastur semitorquatus	y	20									
Buteogallus urubitinga	y	20				X*			X		
Caracara plancus	y	19	X	X	X	X	X	X	X	X	X
Buteo brachyurus	y	18									
Buteo nitidus	y	18									
Leptodon cayanensis	y	17	X$^?$		X		X			X$^?$	
Spizaetus melanoleucus	y	17		X							
Buteo albonotatus	y	13	X	X	X	X$^?$	X$^?$	X$^?$		X	X
Buteogallus meridionalis	y	13								X	
Pseudastur polionotus	y	12		X		X		X	X		X
Milvago chimachima	n	12	X				X	X	X	X	X
Herpetotheres cachinnans	n	9	X		X		X	X	X	X	X
Geranospiza caerulescens	n	8			X						X
Sarcoramphus papa	n	7						X			
Chondrohierax uncinatus	n	5			X						
Harpagus diodon	n	5									
Falco rufigularis	n	3									
Falco femoralis	n	3									
Rostrhamus sociabilis	n	3				X*					
Unidentified individuals	-		X	X	X	X	X		X	X	X
Species richness (total)			4-7	4-6	7-9	3-5	5-7	6-7	8-10	7-10	6-8
Species richness (predators)			2-4	4-5	5	2-4	3-4	4-5	5	6	5-6
Abundance (predators)			3-6	5-6	7	2-4	4-5	5-6	8	8	7-8

3. Habitat structure and landscape metrics

There was significant variation in structural features between cabruca sites (Table S3). Cabrucas had a mean density of 623 ± 182 cacao trees/ha and 182 ± 60 shade-trees/ha, with a mean diameter of shade-trees of 37.2 ± 30.7 cm, mean canopy height of 15.6 ± 2.6m and mean shade levels of 73 ± 10%. We identified 79 shade-tree species (15 ± 5 species/site), 46 of which were used by GHLTs for either food or shelter (Table S4). The IVI of key resource tree species and jackfruits ranged between 15-78% and 0-19%, respectively. Signs of hunting (traps, hunters and/or firearm blows) were recorded at 10 of the 16 sites, and logging signs (chainsaw noise and stumps) at nine of the 16 sites (Table S3). Vegetation cover ranged from 73% to 96% between sites (Table S3).

4. Occupancy modelling

The detectability of GHLTs varied with the survey method so that playbacks yielded higher detectability compared to active searches [$p_{\text{playback}} =$ 0.05, 95% CI (0.02, 0.10); p_{search} = 0.02, 95% CI (0.01, 0.06)], especially under higher air humidity levels and later hours of the morning (Fig. 4). We found low but substantial support for models that included mean survey temperature and density of cocoa trees, both affecting p positively (Table 5; Fig. 4). The covariates with greatest influence on Ψ were abundance of liana and DBH of shade-trees (Table 5), which were equally important in positively affecting Ψ (Fig. 5). To a lesser degree, the equitability of shade-trees also affected Ψ positively, and there is a tendency of decreasing Ψ when the IVI of jackfruits increases (Fig 5). Although the ΔAICc of the 'distance to edge' model was lesser than 7, we did not discuss the effect of this variable because this model was worse ranked than the constant model. Model averaged Ψ was 0.61 (95% CI: 0.19; 0.91), with no evidence of a lack of fit (χ^2=92.65; P-value = 0.55; *c-hat* = 0.34).

Table 5. Results of *ad hoc* occupancy (Ψ) and detection (*p*) modeling for the golden-headed lion tamarin in cabrucas. Constant models are indicated with ".".

Model	AICc	ΔAICc	AICw
Detection models			
Ψ(all)*p*(Air humidity)	304.96	0.00	0.43
Ψ(all)*p*(Method)	305.86	0.89	0.28
Ψ(all)*p*(Hour)	306.59	1.63	0.19
Ψ(all)*p*(Temperature)	308.75	3.78	0.07
Ψ(all)*p*(Cacao density)	310.26	5.30	0.03
Ψ(all)*p*(.)	312.95	7.99	0.01
Occupancy-detection models			
Ψ(Lianas)*p*(Hu+Me+Ho+Ca+Te)	304.20	0.00	0.52
Ψ(DBH)*p*(Hu+Me+Ho+Ca+Te)	305.73	1.53	0.24
Ψ(Equitability)p(Hu+Me+Ho+Ca+Te)	308.26	4.06	0.07
Ψ(Jackfruit IVI)*p*(Hu+Me+Ho+Ca+Te)	308.78	4.58	0.05
Ψ(.)*p*(Hu+Me+Ho+Ca+Te)	310.09	5.89	0.03
Ψ(Distance to edge)*p*(Hu+Me+Ho+Ca+Te)	310.53	6.33	0.02
Ψ(Carnivores)p(Hu+Me+Ho+Ca+Te)	311.88	7.68	0.01
Ψ(Management)p(Hu+Me+Ho+Ca+Te)	312.05	7.85	0.01
Ψ(Distance to houses)*p*(Hu+Me+Ho+Ca+Te)	312.06	7.86	0.01
Ψ(Vegetation cover)*p*(Hu+Me+Ho+Ca+Te)	312.21	8.01	0.01
Ψ(Raptors)*p*(Hu+Me+Ho+Ca+Te)	312.25	8.05	0.01
Ψ(Cacao density)*p*(Hu+Me+Ho+Ca+Te)	312.26	8.06	0.01
Ψ(Banana)*p*(Hu+Me+Ho+Ca+Te)	312.53	8.33	0.01

Model selection was based on Akaike Information Criterion corrected for small samples (AICc), where models with $\Delta\text{AICc} \leq 2$ were considered as top-ranked and equally plausible, while models with $\Delta\text{AICc} > 2$ and ≤ 7 were considered to be less important but still have significant support. AICw=models weight (probability that the model is the best among all competing models; Burnham & Anderson, 2002).
Hu=humidity; Me=Method; Ho=Hour; Te=Temperature; and Ca=Cacao density.

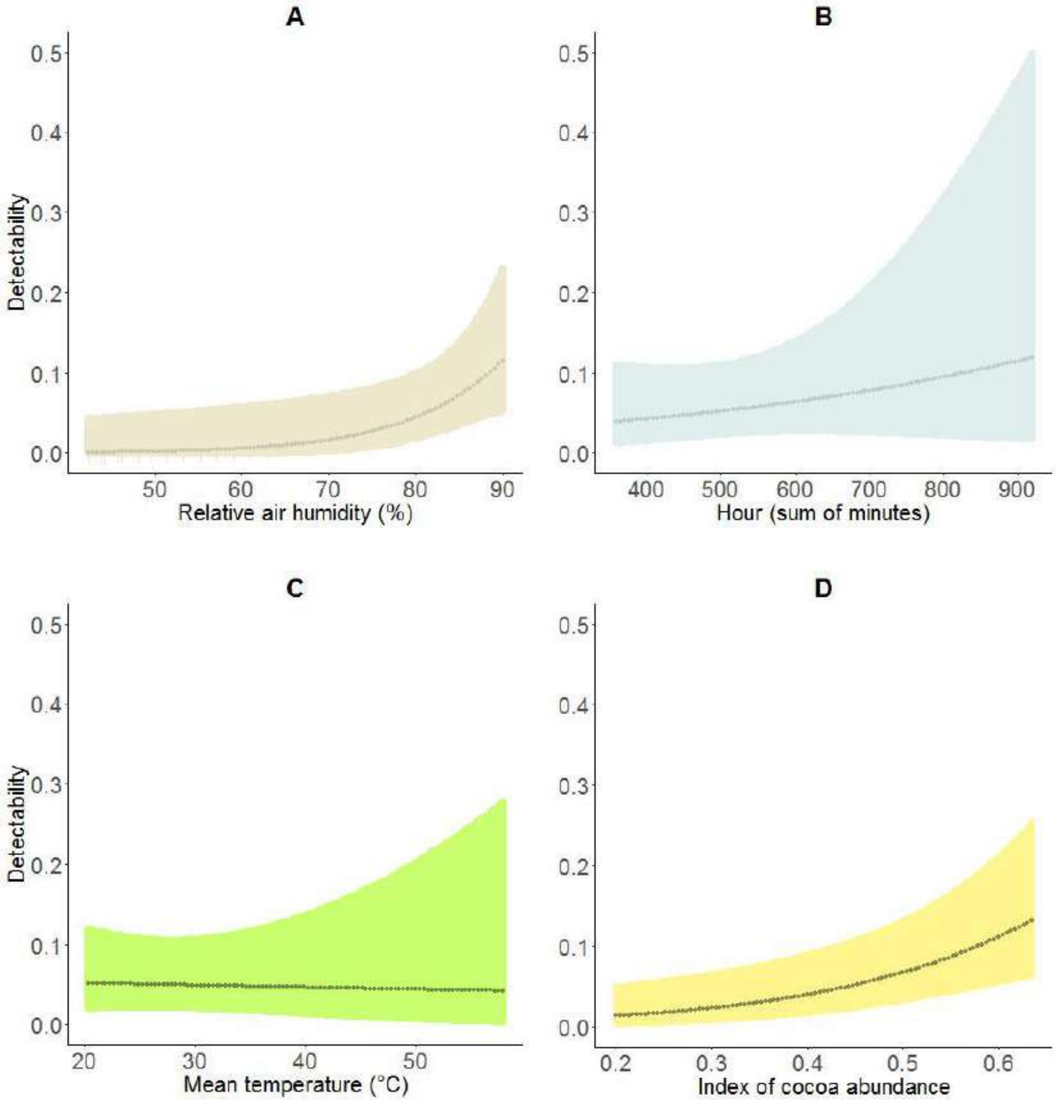

Fig. 4. Golden-headed lion tamarin's detection probability in cabruca sites as a function of: relative air humidity (A), hour of playback execution (B), mean temperature during the survey (C) and cocoa density (D). The dashed line represent the estimates and colorful areas represent the 95% confidence intervals.

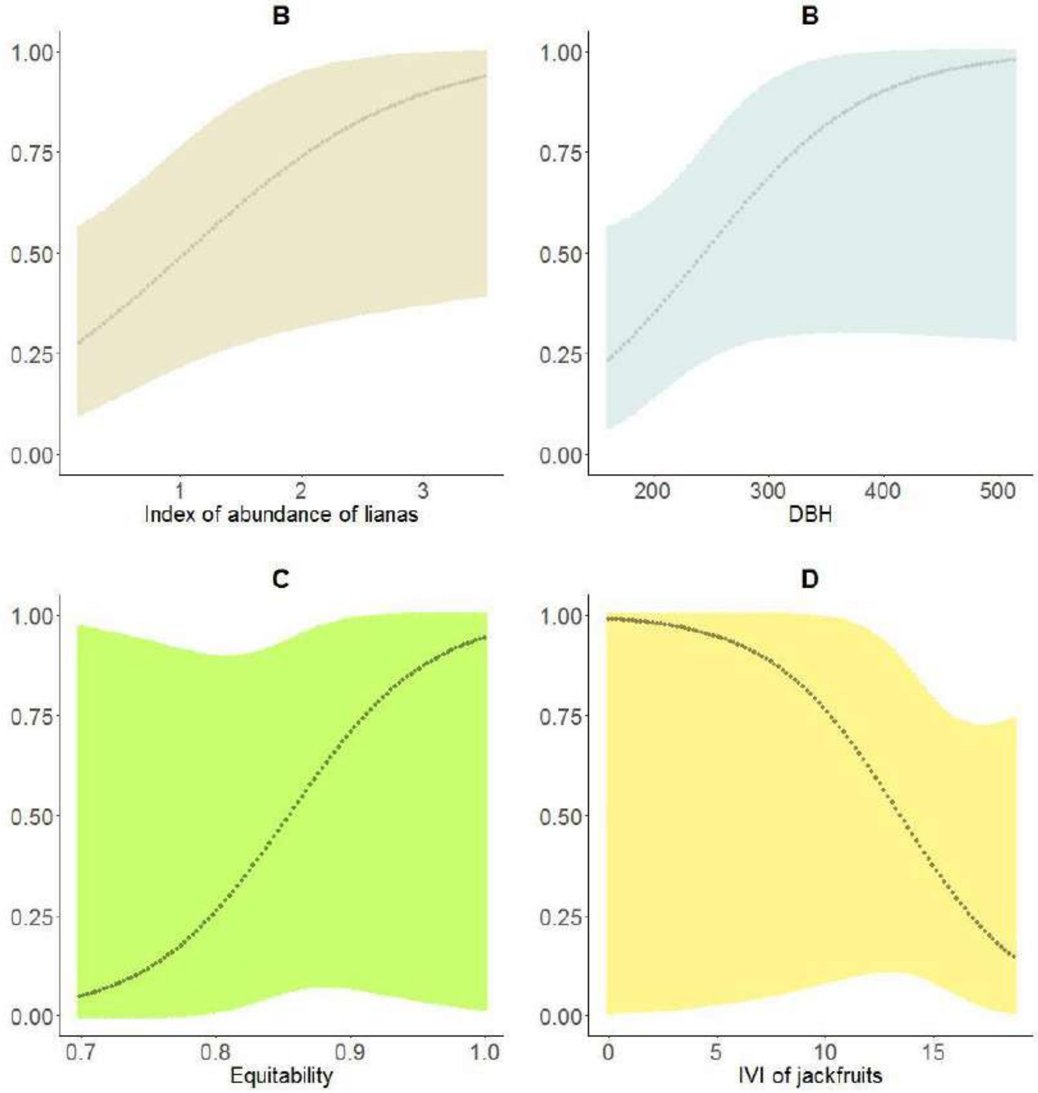

Fig. 5. Golden-headed lion tamarin's occupancy probability in cabrucas as a function of: abundance of lianas (A), diameter at breast height (DBH) of shade-trees (B), equitability of shade-trees (C), and index of importance value (IVI) of jackfruits (D). DBH is shown as an index (=sum of median values recorded per plot in each cabruca site). The dashed line represent the estimates and colorful areas represent the 95% confidence intervals.

Discussion

We investigated the determinants for the golden-headed lion tamarin (GHLT) occupancy in cabrucas of Southern Bahia, Brazil focusing on the specific influence of vegetation structure, habitat quality, management intensity, and predation pressure on GHLTs. Our results suggest that GHLTs occupancy in cabruca sites is mainly determined by vegetation heterogeneity and complexity, and we will discuss here some aspects of cabruca's management that can favour species occurrence.

GHLTs occupancy in cabruca sites revealed to be most influenced by the abundance of lianas and the diameter of shade-trees, features that are directly impacted by the management practices adopted in the plantations. One of the most striking features that differentiate cabrucas from forests is the canopy discontinuity (Johns, 1998), thus lianas end up playing a key role in connecting shade-trees thus providing alternative travel routes for arboreal and scansorial animals. Also, lianas provide shelter and protection against predators (Boinski et al., 2003; Frechette, 2007), which can be particularly important in open habitats such as cabrucas. Since these structures are almost completely removed from cabrucas during management practices (Alves, 1990), lianas are commonly restrict to less-managed or abandoned cabruca plots. Lianas are also a limitant for the endangered thin-spined porcupine, *C. subspinosus,* to use cabrucas in the same region (Giné et al., 2015), which increases the importance of our findings. We argue that lianas should be retained as much as possible to facilitate the movement of the arboreal fauna, otherwise the value of this system for the conservation of native endangered species may be compromised.

Although is known that lianas may increase trees mortality in forests (Clark & Clark, 1990), we did not find any study that clearly demonstrates if lianas affect cabruca's productivity, which limits our reccomendations. Also, the current management decree also does not directly state anything about this step of cabruca's management, but it exempts the need for authorization to collect non-timber forest products in forests of this region, contrary to previous researchers recommendations (Cassano et al., 2009). We then recognize that estabilish a number of trees to not remove lianas can be difficult to put in practice, so we suggest that lianas should be kept at least in isolated shade-trees to favor the movement of all arboreal species with occurrence in cabrucas.

Another important aspect of cabruca's management is the choice of shade-trees to be retained for cacao shading. We found cabrucas with larger diameter shade-trees as more likely to be occupied by GHLTs. It may be related to the availability of sleeping sites, since lion tamarins typically sleep inside holes of larger diameter trees within their territories (Hankerson et al., 2007). Retaining larger trees in cabrucas would not only favour the occupancy of the GHLT but also contributes for climate change mitigation, since the larger portion of Carbon storage in cabrucas concentrates in shade-trees with DBH>35cm (Schroth et al., 2013). Thus, the DBH profile of cabrucas largely determines its status as wildlife friendly or not.

Another two aspects of cabrucas' structure seem to influence GHLT occupancy to some degree: equitability of shade-trees and IVI of jackfruits. However, the occupancy estimates derived directly from these features are very imprecise, so we should interpret these results with cautious. Cabrucas with more diversified composition of shade-trees seem more likely to be occupied by the GHLT, which probable reflects a higher variety of key resources necessary to fill all species requirements. Tree species composition can largely vary between cabrucas depending on which species are preferentially kept for cocoa shading, besides the age of cabrucas (Sambuichi & Haridasan, 2007). A low equitability may result from the farmer's choice to favor some fast-growing species for cocoa shading, such as the exotic *Erythrina* spp. (Rolim & Chiarello, 2004). Some authors have advocated for the planting/maintenance of key tree species for the regional fauna in order to keep the cabruca's suitability for such species (Cassano et al., 2009; Oliveira et al., 2010; Schroth et al., 2011), but at the moment there are no official ways to effectively incentive the use of such species. For example, Oliveira et al. (2010) listed tree species that are both important for the GHLT to provide food and/or shelter, and suitable for cocoa shading. Such recommendation could be incorporated as one of the criteria necessary to achieve the biodiversity cocoa certification, which has been discussed for years in the region (Schroth et al., 2011), as well as the concession of tax incentives for the farmers who agree to adopt it.

We found a negative relationship between the IVI of jackfruits and GHLTs occupancy. At first results we very surprising, considering that jackfruits represent an important food resource for the GHLT in cabrucas (Oliveira et al., 2011). But actually, it is in accordance with the equitability findings. As the IVI of jackfruits increases, the IVI of the other key-species decreases, which results in a lower availability of complementary resources. Thus, this result reinforces the idea that more heterogeneous cabrucas have a higher chance of supporting GHLTs.

Contrary to our expectations, predators do not seem to play a decisive role for GHLT occupancy. The detectability of wild terrestrial predators consisted of few records that were restricted to low-activity cabruca plots near forest patches, suggesting that these species may be transient in cabrucas, as already suggested (Alves, 1990). The yellow-breasted capuchin monkey, for example, was detected in only one cabruca site that was recently incorporated into the Una Biological Reserve territory. The low human activity plus the forest regeneration in many abandoned cabruca plots and a large amount of forest in the surroundings may have favored the occurrence of the capuchin monkeys in this site. Thus, we believe this species is not common in cabrucas, as already suggested by previous studies (Alves, 1990; Flesher, 2015), and do not exerts a relevant predation pressure on GHLTs in this habitat. Another possible explanation for the low detectability of wild terrestrial predators may be the high hunting pressure in the region (Cassano et al., 2012), as we found hunting signs in 62% of the studied cabrucas.

Still regarding terrestrial predators, a negative relationship between GHLTs occupancy and domestic dogs in cabruca sites was previously suggested by Cassano et al. (2014). Although we indeed identified such tendency, the model including this covariate was poorly ranked, suggesting that it is not really determinant for GHLTs occupancy. However, our results should be interpreted with cautious because even if dogs did not directly affect GHLTs occupancy in cabrucas at the moment, they can induce changes in space use, foraging behavior and also disseminate diseases (Galetti & Sazima, 2006; Vanak & Gompper, 2009; Farris et al., 2014), leading to future changes in occupancy patterns. These issues still need to be investigated by future studies.

Despite the high richness of diurnal raptors in cabruca sites, they also do not seem to drive GHLTs occupancy in this habitat. Interestingly, there is a greater probability of diurnal raptors occupancy in more intensely managed cabrucas that present lower density of shade-trees (chapter 2 of this thesis), which may be related to an increased foraging efficience. Although more preys are expected to be found in more complex habitats (August, 1983; Pinto et al., 1993), preys can be more exposed in simplified habitats such as cabrucas, thus favoring their capture by some raptors (Alves, 1990; Silva, 2007; Piana, 2015). The higher encounter rate between GHLTs and raptors in cabrucas when compared to forests (Oliveira & Dietz, 2011) corroborates this hypothesis. This apparent preference of raptors for simplified cabrucas raises a question: If cabrucas became even more simplified due to land-use intensification, how it will affect predator-prey relationships? It is reasonable to suppose an immediate increase in raptors’ occupancy and a consequent rise in predation pressure on GHLTs. Also, GHLTs as well as many other species will certainly be much more exposed to predators due to an even more reduced canopy connectivity and lower availability of shelter, besides a probable decrease in the availability of food resources that could lead groups to increase foraging travel distances thus exposing themselves even more to predators (Garber & Bicca-Marques, 2002). These issues still need to be investigated by future studies.

Conservation Considerations

A significant portion of GHLT's geographic range is covered by cabrucas, an agroecosystem that has been proved able to support or subsidize GHLT's populations (Oliveira et al., 2011). Consequently, a conservation plan for the GHLT that do not include cabrucas seems doomed to failure. Unffortunately, the role of cabrucas to assist in GHLT's conservation can be threatened by the management intensification. The most defended way to increase cocoa yields is by reducing shade-trees density but it has already proved possible to combine high yields with high biodiversity levels in cocoa agroforests (Clough et al., 2011). In the specific case of southern Bahian cabrucas, it has proved possible to double yields (compared to the regional productivity levels) just using the right levels of mineral fertilizers and maintaining a shading level up to 55%, without necessarily reducing shade-trees density (Schroth et al., 2014). If such intensification is unavoidable despite all alternatives, we strongly defend the monitoring of cabruca plots before and after it to understand how it will impact the GHLTs, allowing the proposal of ways for mitigating the negative effects caused to this species.

Some good management practices can be adopted to minimize the negative impacts of cabrucas' intensification on the native fauna. a wildlife-friendly management should consider the presence of lianas, which despite other functions such as providing protection against predators and food for many species, are crucial to maintain shade-trees connectivity and facilitate the movement of arboreal animals in cabrucas, especially under management intensification. It is important to highlight that all cabruca sites investigated by the present study retain a high density of shade-trees, as typical of traditional cabrucas in this region, and this is probable the reason why we did not detect an important role of shade-trees density. Even in this high-density context, lianas played a very important role, so it is reasonable to expect an increased importance of this feature if management intensification is implemented.

Another way to improve the conservation value of cabrucas under intensification is to favor the maintenance of large diameter trees from species already identified as important for the regional fauna (Oliveira et al., 2010), assuring a diversified and balanced species composition to provide complementary key resources. Since cabruca is an unstable system because regrowth of dead shade-trees is prevented with weeding (Rolim & Chiarello, 2004), the long-term persistence of GHLTs and other native species in this habitat depends heavily on key-species replanting. Schroth et al. (2014) recommends farmers to favor the removal of exotic species such as *Erythrina* spp. and jackfruits, as these species are expected to have a lower ecological value than native species. According to the management decree, exotic vegetable products (timber or others) are not subject to control, except for charcoal production, so there is no official mechanism to regulate the extraction of exotic species in both cabrucas and forests, which can strongly affect the adapted fauna (Gosper & Vivian-Smith, 2009). We recommend that such removal have to be done with cautious since exotic species has proved to be key resources for the GHLTs, as well as many frugivorous species in human modified-habitats (Cunha et al., 2006; Oliveira et al., 2011; Canale et al., 2016). In the specific case of jackfruits, our data suggests a threshold level above which GHLTs occupancy starts to decrease, so it could help to guide this practice.

Finnaly, the reasons why farmers should manage their properties to favor GHLTs' occurrence are not limited to species conservation purposes, but it also can bring some benefits to them. GHLTs play an important role as seed dispersers without causing damages to cocoa trees, thus contributing to the regeneration and maintainance of cabrucas (Catenacci et al., 2009). Also, the GHLT is a flagship species of southern Bahia, which also adds touristic value to cabrucas where it occurs. Although this touristic potential is still unexplored, some producers are already using GHLT's image in their logos or exploring species' presence for ecotourism purposes. Primate watching has proved to be a profitable economic activity and a successful conservation strategy when good tourism practices are adopted (Macfie & Williamson, 2010; Russon & Wallis, 2014). For example, the Lion Tamarin Association (http://www.micoleao.org.br/) has been achieved positive results from sustainable tourism activities developed with the endangeredgolden lion tamarin, *Leontopithecus rosalia*, proving that this activity can be further explored in Brazil. The promotion of sustainable rural and ecological tourism as an alternative income combined with biodiversity conservation is already proposed by the management decree so that it may be a good solution to ally regional economic development with biodiversity conservation, maintaining the status of cabrucas as a wildlife-friendly system.

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Supplementary Material

Table S1. Criteria and categories used to calculate to classificate species according to their potential to prey on golden-headed lion tamarins (GHLT).

Table S2. List of carnivore species with potential occurrence in Southern Bahia region and its classification as potential predators of golden-headed lion tamarins.

Table S3. List of raptors species with potential occurrence in Southern Bahia region and its classification as potential predators of golden-headed lion tamarins.

Table S4. Characterization of surveyed cabrucas according to vegetation structure, habitat quality and vegetation cover in the landscape.

Table S5. List of tree species identified in the sixteen cabrucas and their use by golden-headed lion tamarins as food source or sleeping site.

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SUPPLEMENTARY MATERIAL

Appendix SI. Predators classification and index of predation potential (IPP)

Carnivores and diurnal raptors with potential occurrence in the study areas were classified according to their potential to prey on golden-headed lion tamarins. This classification was based on the following criteria: (1) record of predation on primates, (2) record of attack on primates, (3) body size, (4) typical prey size, (5) record of mammals in the diet, (6) dietary specialization in mammals, and (7) foraging strategy. To make the classification more systematic, each criterion received a categorical value (based on published information and researchers experience), with high values attributed to characters that favor a GHLT predation (Table S1). These values were then summed to create an index of predation potential that was used to rank all species according to their probability of preying on GHLTs, giving greater weights to categories (1), (2) and (7), which were considered most important.

Table S1. Criteria and categories used to calculate to classificate species according to their potential to prey on golden-headed lion tamarins (GHLT). 'Values' represents the importance attributed to each criteria to determine the species' potential to prey on GHLTs.

Criteria	**value**	**category**		
		0	1	2
Body size	1	Lower than a young GHLT	Between the size of a young and an adult GHLT	Similar or larger than an adult GHLT
Mammal consumption	2	no record	feeds on mammals	x
Diet specialization	3	mammals represent < 50% of species diet	mammals represent ≥ 50% of species diet	x
Foraging behavior	4	It is unlikely to prey on GHLTs due to habitat/strata preferences	It is possible to prey on GHLTs due to habitat/strata preferences	x
Prey size	5	Lower than a young GHLT	Between the size of a young and an adult GHLT	Similar or larger than an adult GHLT
Attack on primates	6	no record	there are records	x
Predation on primates	7	no record	there are records	x

GHLT body size was considered as ~60g for youngs and ~620g for adults.

Table S2. List of carnivore species with potential occurrence in Southern Bahia region, classification as potential predators of golden-headed lion tamarins(y=predator, n=non-predator, and y^{EX}=locally extinct predator) and index of predation potential (IPP).

Family	**Species**	**Commoon name**	**1-predation/attack**	**2-body size**	**3-prey size**	**4-mammal consumption**	**5-diet specialization**	**6-foraging behavior**	**Predator**	**IPP**
Mustelidae	*Eira barbara*	Tayra	1	2	2	1	2	1	y	11
Felidae	*Leopardus guttulus*	Oncilla	1	2	2	1	2	1	y	11
Felidae	*Leopardus pardalis*	Ocelot	1	2	2	1	2	1	y	11
Felidae	*Leopardus wiedii*	Margay	1	2	2	1	2	1	y	11
Felidae	*Puma concolor*	Puma	1	2	2	1	2	1	y	11
Felidae	*Puma yagouaroundi*	Jaguarundi	1	2	2	1	2	1	y	11
Felidae	*Panthera onca*	Jaguar	1	2	2	1	2	1	y^{Ex}	11
Cebidae	*Sapajus xanthosternos*	Yellow-breasted capuchin monkey	1	2	2	1	2	1	y	11
Canidae	*Speothos venaticus*	Bush Dog	0	2	2	1	2	1	y^{Ex}	9
Procyonidae	*Nasua nasua*	South American Coati	0	2	2	1	2	1	y	9
Canidae	*Cerdocyon thous*	Crab-eating Fox	0	2	1	1	2	0	n	6
Mustelidae	*Galictis cuja*	Lesser Grison	0	2	1	1	2	0	n	6
Mustelidae	*Lontra longicaudis*	Neotropical Otter	0	2	1	1	2	0	n	6
Mephitidae	*Conepatus semistriatus*	Striped Hog-nosed Skunk	0	2	0	0	2	0	n	4
Procyonidae	*Potos flavus*	Kinkajou	0	2	0	0	1	0	n	3
Procyonidae	*Procyon cancrivorus*	Crab-eating Raccoon	0	2	0	0	1	0	n	3

Table S3. List of diurnal raptor species with potential occurrence in Southern Bahia region, classification as potential predators of golden-headed lion tamarins (y = predator and n = non-predator) and index of predation potential (IPP).

Family	**Species**	**Comoon name**	**1-predation**	**2-attack**	**3-body size**	**4-prey size**	**5-mammal consumption**	**6-diet specialization**	**7- foraging behavior**	**Predator**	**IPP**
Accipitridae	*Harpia harpyja*	Harpy Eagle	1	1	2	2	1	1	1	y	34
Accipitridae	*Morphnus guianensis*	Crested Eagle	1	1	2	2	1	1	1	y	34
Accipitridae	*Spizaetus tyrannus*	Black Hawk eagle	1	1	2	2	1	1	1	y	34
Accipitridae	*Spizaetus ornatus*	Ornate Hawk eagle	1	1	2	2	1	0	1	y	31
Accipitridae	*Accipiter bicolor*	Bicolored Hawk	1	1	1	1	1	0	1	y	25
Accipitridae	*Rupornis magnirostris*	Roadside Hawk	1	1	1	1	1	0	1	y	25
Accipitridae	*Buteogallus urubitinga*	Great Black Hawk	1	0	2	1	1	0	1	y	20
Falconidae	*Micrastur semitorquatus*	Collared Forest-Falcon	1	0	2	1	1	0	1	y	20
Falconidae	*Caracara plancus*	Southern Caracara	0	1	2	1	1	0	1	y	19
Falconidae	*Micrastur ruficollis*	Barred Forest-Falcon	1	0	1	1	1	0	1	y	19
Accipitridae	*Buteo brachyurus*	Short-tailed Hawk	0	1	1	1	1	0	1	y	18
Accipitridae	*Buteo nitidus*	Gray-lined Hawk	0	1	1	1	1	0	1	y	18
Accipitridae	*Spizaetus melanoleucus*	Black-and-white Hawk eagle	0	0	2	2	1	0	1	y	18
Accipitridae	*Geranospiza caerulescens*	Crane Hawk	0	0	1	2	1	0	1	y	17
Accipitridae	*Leptodon cayanensis*	Gray-headed Kite	1[?]	0	1	1	0	0	1	y	17
Accipitridae	*Accipiter striatus*	Sharp-shinned Hawk	0	0	1	2	0	0	1	y	15
Accipitridae	*Parabuteo unicinctus*	Harris's Hawk	0	0	2	2	1	0[1]	0	y	14
Accipitridae	*Buteo albonotatus*	Zone-tailed Hawk	0	0	2	1	1	0	1	y	13
Accipitridae	*Buteogallus meridionalis*	Savanna Hawk	0	0	2	1	1	0	1	y	13
Accipitridae	*Accipiter poliogaster*	Gray-bellied Hawk	0	0	1	1	1	0	1	y	12

Table S3. Continuation

Family	Species	Comoon name	1-predation	2-attack	3-body size	4-prey size	5-mammal consumption	6-diet specialization	7- foraging behavior	Predator	IPP
Accipitridae	*Pseudastur polionotus*	Mantled Hawk	0	0	1	1	1	0	1	y	12
Accipitridae	*Cathartes aura*	Turkey Vulture	0	0	2	2	0	0	0	n[2]	12
Accipitridae	*Cathartes burrovianus*	Lesser Yellow-headed Vulture	0	0	2	2	0	0	0	n[2]	12
Accipitridae	*Coragyps atratus*	Black Vulture	0	0	2	2	0	0	0	n[2]	12
Accipitridae	*Milvago chimachima*	Yellow-headed Caracara	0	0	1	1	1	0	1	n[3]	12
Accipitridae	*Elanus leucurus*	White-tailed Kite	0	0	1	1	1	1	0	n	11
Accipitridae	*Busarellus nigricollis*	Black-collared Hawk	0	0	2	1	1	0	0	n	9
Accipitridae	*Geranoaetus albicaudatus*	White-tailed Hawk	0	0	2	1	1	0	0	n	9
Accipitridae	*Herpetotheres cachinnans*	Laughing Falcon	0	0	2	1	1	0	0	n	9
Falconidae	*Falco peregrinus*	Peregrine Falcon	0	0	2	1	1	0	0	n	9
Accipitridae	*Amadonastur lacernulatus*	White-necked Hawk	0	0	1	1	1	0	0	n	8
Accipitridae	*Circus buffoni*	Long-winged Harrier	0	0	1	1	1	0	0	n	8
Falconidae	*Falco femoralis*	Aplomado Falcon	0	0	1	1	1	0	0	n	8
Accipitridae	*Accipiter superciliosus*	Tiny Hawk	0	0	1	0	1	0	1	n	7
Accipitridae	*Harpagus bidentatus*	Double-toothed Kite	0	0	1	0	1	0	1	n	7
Accipitridae	*Sarcoramphus papa*	King Vulture	0	0	2	1	0	0	0	n	7
Accipitridae	*Elanoides forficatus*	Swallow-tailed Kite	0	0	2	0	0	0	1	n	6
Accipitridae	*Chondrohierax uncinatus*	Hook-billed Kite	0	0	1	0	0	0	1	n	5
Accipitridae	*Harpagus diodon*	Rufous-thighed Kite	0	0	1	0	0	0	1	n	5
Accipitridae	*Ictinia plumbea*	Plumbeous Kite	0	0	1	0	0	0	1	n	5

Table S3. Continuation

Family	**Species**	**Comoon name**	**1-predation**	**2-attack**	**3-body size**	**4-prey size**	**5-mammal consumption**	**6-diet specialization**	**7- foraging behavior**	**Predator**	**IPP**
Accipitridae	*Gampsonyx swainsonii*	Pearl Kite	0	0	1	0	1	0	0	n	3
Accipitridae	*Rostrhamus sociabilis*	Snail Kite	0	0	1	0	1	0	0	n	3
Falconidae	*Falco rufigularis*	Bat Falcon	0	0	1	0	1	0	0	n	3
Falconidae	*Falco sparverius*	American Kestrel	0	0	1	0	1	0	0	n	3
Pandionidae	*Pandion haliaetus*	Osprey	0	0	2	1	0	0	0	n	3
Accipitridae	*Buteogallus aequinoctialis*	Rufous Crab Hawk	0	0	2	0	0	0	0	n	2

[?] Printes et al. (1996) raises the possibility of a predation on two infant muriquis, *Brachyteles arachnoides*, by a gray-headed kite, but it was not confirmed.

[1] Although the species' diet includes a large proportion of mammals, studies suggest a specialization on preying birds in Brazil(Silva & Olmos, 1997; Godoy et al., 2012).

[2] We considered these species as improbable predators of GHLTs since prefer to eat dead animals.

[3] This species uses to capture larger preys on the ground (GRIN, 2010; Bierregaard et al., 2017), a stratum that is less used by GHLTs in cabrucas (Almeida-Rocha et al., 2015), thus we considered itas an improbable predator of GHLTs.

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Table S4. Characterization of surveyed cabrucas (S1-S16) regarding the presence of the golden-headed lion tamarin (GHLT), vegetation structure, habitat quality and vegetation cover in the landscape. Variables values that were averaged among all plots within each cabruca site are shown as means and standard deviations.

Variables	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**
GHLT detection	yes	no	yes	no	yes	no	no	no
GHLT density (groups/ha)	0.02	0.00	0.02	0.00	0.02	0.00	0.00	0.00
Index of human disturbance	1	0	3	1	4	2	5	0
IVI of key tree species	14.69	22.70	73.96	63.01	62.52	60.94	15.79	43.55
IVI of jackfruit	5.29	8.01	8.26	5.29	0.00	14.69	14.89	18.73
Shade-trees richness (S)	10	9	10	13	13	20	18	13
Shade-trees equitability (E)	0.94	0.70	1.00	0.97	1.00	0.93	0.89	0.87
Shade-trees density (trees/ha)	121 ± 115	186 ± 99	93 ± 53	107 ± 98	81 ± 46	307 ± 172	257 ± 213	236 ± 131
Shade-trees diameter (cm)	19.5 ± 22.2	33.4 ± 20.2	31.0 ± 29.4	65.0 ± 79.7	22.3 ± 27.7	25.2 ± 22.4	30.4 ± 35.6	33.9 ± 35.8
Canopy height (m)	14 ± 8	18 ± 4	13 ± 7	16 ± 8	13 ± 7	15 ± 2	13 ± 7	15 ± 4
Canopy connectivity	2 ± 2	3 ± 1	1 ± 1	2 ± 1	1 ± 1	3 ± 1	2 ± 2	3 ± 2
Vertical stratification (SD height)	2.4 ± 3.1	3.2 ± 1.3	2.9 ± 3.3	4.1 ± 6.6	3.0 ± 4.7	4.3 ± 3.4	2.1 ± 2.4	3.5 ± 2.3
Mean shading level (%)	76 ± 10	77 ± 7	45 ± 16	72 ± 5	71 ± 18	80 ± 8	75 ± 16	75 ± 16
Cocoa trees density (cocoa/ha)	286 ± 173	643 ± 93	600 ± 135	414 ± 144	719 ± 333	707 ± 217	664 ± 630	693 ± 406
Banana density (banana/ha)	29 ± 76	79 ± 208	429 ± 910	100 ± 224	200 ± 433	114 ± 239	36 ± 94	357 ± 323
Bromeliads (index of abundance)	1.3 ± 1.4	1.1 ± 1.2	0.6 ± 0.8	1.9 ± 1.5	1.3 ± 1.4	1.0 ± 1.4	0.4 ± 0.5	2.4 ± 1.1
Lianas (% of trees with lianas/plot)	20 ± 40	10 ± 20	30 ± 40	10 ± 20	10 ± 20	0 ± 10	20 ± 40	0 ± 10
Index of management intensity	2.8 ± 0.8	4.0 ± 0.0	3.5 ± 1.0	3.4 ± 0.7	3.4 ± 0.8	3.2 ± 0.8	2.9 ± 0.9	3.8 ± 0.6
Vegetation cover (%)	82	78	96	87	84	75	94	74

Table S4. Continuation.

Variables	**S9**	**S10**	**S11**	**S12**	**S13**	**S14**	**S15**	**S16**
GHLT detection	no	yes	yes	yes	yes	yes	yes	yes
GHLT density (groups/ha)	0.00	0.03	0.02	0.01	0.01	0.03	0.08	0.02
Index of human disturbance	0	1	1	7	5	4	2	4
IVI of key tree species	40.40	73.41	78.15	64.99	69.54	53.60	17.93	42.74
IVI of jackfruit	8.10	4.22	0.00	12.64	7.54	14.43	6.66	9.50
Shade-trees richness (S)	16	20	26	14	22	14	7	18
Shade-trees equitability (E)	0.99	0.96	0.94	0.95	0.92	0.97	0.91	0.95
Shade-trees density (trees/ha)	129 ± 144	179 ± 99	314 ± 308	157 ± 89	357 ± 281	143 ± 53	86 ± 24	164 ± 107
Shade-trees diameter (cm)	23.5 ± 32.7	34.8 ± 25.3	27.5 ± 22.2	26.5 ± 30.4	24.1 ± 15.1	64.2 ± 49.3	40.6 ± 35.2	42.6 ± 44.9
Canopy height (m)	10 ± 6	16 ± 5	17 ± 5	15 ± 5	15 ± 4	20 ± 3	18 ± 4	13 ± 6
Canopy connectivity	2 ± 1	4 ± 1	2 ± 2	3 ± 1	4 ± 1	3 ± 2	2 ± 1	1 ± 1
Vertical stratification (SD height)	5.6 ± 3.7	4.4 ± 2.3	4.0 ± 2.7	3.8 ± 1.9	4.4 ± 3.2	2.6 ± 2.5	3.7 ± 2.9	1.7 ± 2.5
Mean shading level (%)	67 ± 17	68 ± 32	89 ± 4	76 ± 12	74 ± 14	86 ± 3	84 ± 10	63 ± 14
Cocoa trees density (cocoa/ha)	371 ± 168	879 ± 202	536 ± 537	471 ± 200	557 ± 412	643 ± 388	907 ± 207	836 ± 238
Banana density (banana/ha)	0	0	0	179 ± 251	157 ± 159	164 ± 263	0	107 ± 201
Bromeliads (index of abundance)	0.1 ± 0.4	0.9 ± 1.1	0.6 ± 1.1	1.6 ± 1.3	1.0 ± 0.8	2.0 ± 1.3	2.0 ± 1.3	1.6 ± 1.5
Lianas (% of trees with lianas/plot)	10 ± 10	20 ± 20	10 ± 20	10 ± 20	30 ± 30	50 ± 50	20 ± 20	20 ± 20
Index of management intensity	3.4 ± 0.8	3.4 ± 0.7	2.4 ± 0.8	2.8 ± 0.7	3.2 ± 1.0	3.6 ± 0.6	3.9 ± 0.4	3.5 ± 0.9
Vegetation cover (%)	84	82	93	90	73	82	74	88

Table S5. List of shade-tree species recorded in the sixteen cabruca sites and their potential use by the golden-headed lion tamarins (GHLT) as food source (F) and sleeping site (S). Species with no record of use by the GHLT are indicated with (N).

Family	**Species**	**Common name**	**Use**	**Reference**
Anacardiaceae	*Anacardium occidentale*	cajueiro	F	5
Anacardiaceae	*Spondias mombin*	cajazeira	N	
Anacardiaceae	*Tapirira guianensis*	pau-pombo	F; S	1,3,4
Annonaceae	*Guatteria* sp.	pindaíba-preta	S$^{?}$	3
Annonaceae	Non-identified 1	pinha-da-mata	F	1,2,3
Apocynaceae	*Aspidosperma polyneuron*	peroba-rosa	S	3
Apocynaceae	*Aspidosperma* sp.	Peroba	S$^{?}$	3
Apocynaceae	*Himatanthus* sp.	janaúba	N	
Araliaceae	*Schefflera morototoni*	matataúba	N	
Areacaceae	*Polyandrococus caudescens*	côco-de-buri	N	
Bombacaceae	*Eriotheca* sp.	imbiruçu	S	3
Boraginaceae	*Cordia magnoliaefolia*	baba-de-boi	F	3,5
Burseraceae	*Protium* sp.	unkown	F$^{?}$; S$^{?}$	3,4
Caesalpiniaceae	*Bauhinia longifolia*	pata de vaca	N	
Caricaceae	*Carica* sp.	Mamão	F	4
Caricaceae	*Jacaratia heptaphylla*	mamão-de-veado	N	
Cecropiaceae	*Cecropia* sp.	embaúba	F	3
Chrysobalanaceae	Non-identified 2	Oiti	F$^{?}$; S	3
Clusiaceae	*Symphonia globulifera*	guanandi	F; S	1,3,4,5
Combretaceae	*Terminalia dichotoma*	pequi-amarelo	S	3
Dichapetalaceae	*Stephanopodium blanchetianum*	borboleta	N	
Elaeocarpaceae	*Sloanea* sp.	Gindiba	F; S	3
Euphorbiaceae	*Cnidoscolus marcgravii*	Penão	N	
Euphorbiaceae	*Croton macrobotrys*	lava-prato	F	3
Euphorbiaceae	*Croton* sp.	Velame	F$^{?}$	3
Euphorbiaceae	*Hevea brasiliensis*	seringueira	N	
Euphorbiaceae	Non-identified 3	lava-prato-branco	N	
Euphorbiaceae	Non-identified 4	lava-prato-vermelho	N	
Euphorbiaceae	*Senefeldera multiflora*	pau-osso	S	3
Euphorbiaceae	*Urera* sp.	cansanção	N	
Euphorbiaceae	*Pogonophora schomburgkiana*	Cocão	S	3
Fabaceae	*Erythrina poeppigiana*	Eritrina	N	
Fabaceae	*Erythrina* sp.	Eritrina	N	

Table S4. Continuation.

Family	**Species**	**Common name**	**Use**	**Reference**
Fabaceae	*Inga edulis*	ingá-cipó	F	3,4
Fabaceae	*Inga* sp.	Ingá	F	1,2,3,4,5
Fabaceae	*Inga thibaudiana*	ingá-tábua	F	2,3
Fabaceae	Non-identified 5	Sucupira	S$^{?}$	3
Fabaceae	Non-identified 6	Jacarandá	N	
Fabaceae	*Plathymenia foliolosa*	Vinhático	N	
Fabaceae	*Pterocarpus rhorii*	pau-sangue	F; S	3
Fabaceae	*Sclerolobium densiflora*	Ingauçú	S	3
Fabaceae	*Senna multijuga*	Cobi	N	
Fabaceae	*Dialium guianense*	Jitaí	F; S	3
Lauraceae	*Nectandra membranacea*	louro-sabão	F$^{?}$; S$^{?}$	3
Lauraceae	*Persea americana*	Abacateiro	F	4
Lauraceae	Non-identified 9	Louro	F; S	3
Lecythidaceae	*Cariniana* sp.	Jequitibá	N	
Lecythidaceae	*Eschweilera ovata*	Biriba	S	3
Melastomataceae	Non-identified 10	Mundururu	F	1,2,3,5
Meliaceae	*Cedrela odorata* CF	cedro-rosa	N	
Meliaceae	*Trichilia pleena*	rosa-branca-verdadeira	S	3
Meliaceae	Non-identified 11	Cedro	S$^{?}$	3
Moraceae	*Artocarpus heterophyllus*	Jaqueira	F; S	3,5
Moraceae	*Helicostylis tomentosa* CF	amora-preta	F	2,5
Moraceae	Non-identified 7	gameleira branca	F$^{?}$; S$^{?}$	1,2,3,4
Moraceae	Non-identified 8	gameleira preta	F$^{?}$; S$^{?}$	1,2,3,4
Moraceae	*Pourouma* sp.	Tararanga	F	1,2,3,4,5
Myristicaceae	*Virola gardneri*	Bicuíba	S	3
Myrtaceae	Non-identified 12	Araçá	F; S	3,4,5
Myrtaceae	Non-identified 13	araçá-branco	F; S	3,4,5
Myrtaceae	Non-identified 14	Murta	F; S	2,3
Non-identified	Non-identified 15	rama-de-bezerra	N	
Non-identified	Non-identified 16	peito-de-porca	N	
Nyctaginaceae	Non-identified 17	farinha-seca	F; S	3
Peraceae	*Pera glabrata*	Óleo	N	
Rubiaceae	*Genipa americana*	Jenipapeiro	N	
Rutaceae	*Citrus* sp.	Laranjeira	N	

Table S4. Continuation.

Family	Species	Common name	Use	Reference
Sapotaceae	*Manilkara maxima*	Paraju	F; S	1,3
Sapotaceae	Non-identified 18	Bapeba	F; S	1,2,3,4,5
Sapotaceae CF	*Pradosia lactenses* CF	cacau-de-macaco	F	3,5
Simaroubaceae	*Simarouba amara*	pau-paraíba	F	3
Solanaceae	*Cestrum* sp.	Coarana	N	
Tiliaceae	*Apeiba* sp.	pau-de-jangada	N	
Ulmaceae	*Trema micrantha* CF	Corindiba	N	
Verbenaceae CF	*Aegiphila sellowiana* CF	Fidalgo	S	3
Violaceae	*Rinorea guianensis*	Cinzeiro	F; S	1,3

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CONCLUSÕES GERAIS

Os resultados deste tese contribuem para o avanço do conhecimento acerca das respostas de primatas à degradação estrutural do habitat resultante de diferentes atividades humanas. A meta-análise desenvolvida no capítulo 1 foi a primeira a quantificar o efeito de tal degradação em termos de decréscimos percentuais nas métricas de biodiversidade obtidas em habitats degradados e não-degradados (ou menos degradados) na mesma região. Esta análise também ajudou a esclarecer reconhecidas contradições nos resultados encontrados por estudos primários, as quais dificultavam a conclusão sobre o efeito de determinadas atividades, como por exemplo o corte seletivo. As principais conclusões obtidas neste capítulo foram:

- Existe um efeito consistentemente negativo da degradação antrópica do habitat sobre populações/comunidades de primatas;
- O grau de sensibilidade das espécies à degradação do habitat varia de acordo com a região biogeográfica na qual ocorrem, indicando que a forma como respondem à ameaças específicas está intimamente relacionada com o seu contexto histórico-evolutivo, o qual determina diferentes graus de resiliência aos distúrbios atuais;
- Atividades agrícolas são as mais prejudiciais para os primatas mas algumas formas de cultivo, como agroflorestas e agromosaicos, demonstraram compatibilidade com a conservação de algumas espécies;
- Mesmo diante de toda inconsistência existente na literatura acerca do efeito do corte madeireiro sobre primatas, foi encontrado um efeito consistentemente negativo;
- A intensificação no uso da terra leva a efeitos ainda mais negativos do que a degradação inicial das florestas, o que torna urgente a identificação de limiares de exploração que sejam compatíveis com a manutenção das populações;
- E por fim, a identificação de um efeito sinérgico entre a degradação do habitat e a pressão de caça enfatiza a importância de considerar as múltiplas ameaças que atuam sobre as espécies ao elaborar planos de conservação.

Esta tese apresentou uma abordagem inovadora ao investigar a situação de uma espécie de primata ameaçada de extinção também sob o ponto de vista dos seus predadores. Isso permitiu uma discussão mais ampla sobre o futuro do MLCD em um cenário de intensificação do uso da terra. As principais conclusões do capítulo 2 foram:

- A alta diversidade de aves de rapina diurnas detectada nas cabrucas confirma o alto valor de conservação deste sistema, o qual pode mitigar os efeitos da fragmentação e perda de habitat para este grupo;
- Aves de rapina possuem maior probabilidade de ocupar cabrucas mais simplificadas estruturalmente (com menor densidade de árvores de sombreamento e maior intensidade de manejo), porém que retêm árvores de sombreamento mais largas;
- Cabrucas sozinhas não garantem a integridade das comunidades de rapinantes, pois há uma tendência de simplificação das assembléias, com diminuição de especialistas e de espécies de grande porte.

Com relação aos fatores que afetam de forma direta a ocupação do MLCD nas cabrucas, as principais conclusões foram:

- A probabilidade de ocupação do MLCD aumenta em cabrucas mais complexas e heterogêneas, onde existe maior abundância de cipós, árvores de sombreamento mais largas e mais diversas;
- Apesar da jaca, *Artocarpus heterophyllus*, ser um recurso-chave na dieta do MLCD em cabrucas, os resultados sugerem uma diminuição na probabilidade de ocupação da espécie quando este recurso se torna muito dominante, ressaltando a importância da heterogeneidade na composição arbórea e complementaridade de recursos para o MLCD.

Analisando conjuntamente os resultados dos capítulos 2 e 3, e considerando o cenário atual de incentivo à intensificação das cabrucas através da redução na densidade das árvores de sombreamento, pode-se concluir que:

- Cabrucas tradicionais de fato possuem um alto potencial de contribuição para a conservação do MLCD e de aves de rapina diurnas no sul da Bahia, mas tal potencial pode estar comprometido pela intensificação do manejo deste sistema;
- A intensificação do manejo poderá desencadear um processo de cascata trófica nas cabrucas, com o aumento da ocupação por predadores de topo

– aves de rapina – alterando toda a estrutura trófica estabelecida nestas comunidades;

- Tal desequilíbrio poderá acarretar em efeitos extremamente deletérios para as populações de MLCD, cuja conservação depende em grande parte das áreas de cabruca;
- A adoção de algumas práticas de manejo, como a manutenção e o plantio de árvores de sombra de grande porte que são reconhecidamente utilizadas como alimento ou abrigo por espécies da fauna nativa, bem como a manutenção de lianas, pode mitigar os efeitos deletérios da simplificação estrutural de cabrucas e favorecer a persistência do MLCD neste habitat;
- Ainda, o uso da modelagem de ocupação se revelou uma abordagem eficiente que pode ser adotada para o monitoramento de mudanças na ocupação do MLCD (e de outras espécies) em cabrucas ao longo do tempo, ajudando a entender os efeitos de uma possível intensificação do manejo.

Finalmente, todos estes resultados demonstram que os habitats modificados devem ser considerados no planejamento de conservação de espécies de primatas, mas que o valor de biodiversidade desses habitats é muito inferior ao de florestas preservadas, não sendo estes, portanto, suficientes para garantir a persistência das populações a longo prazo em paisagens alteradas.