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RESEARCH ARTICLE

Can secondary forests mitigate the negative effect of old-growth forest loss on biodiversity? A landscape-scale assessment of two endangered primates

Laura L. Saldívar-Burrola · Marisela Martínez-Ruíz · Víctor Arroyo-Rodríguez · Fabricio Villalobos · Pedro A. D. Dias · Fabiola López-Barrera · Ricard Arasa-Gisbert

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Abstract

Context Old-growth forest loss drives the global biodiversity crisis. Nevertheless, this impact could be buffered by the increasing expansion of secondary (regenerating) forests, which can provide supplementary habitat for wildlife.

Objectives We tested this hypothesis assessing the effect of old-growth and secondary forest cover on the abundance and immature-to-female ratio (proxy of reproductive success) of two endangered primates: Geoffroy' spider monkeys and black howler monkeys.

Methods We measured the response and predictor variables across 18 whole landscapes (landscape-scale approach) in the Lacandona rainforest, Mexico. As there could be tipping points of forest loss beyond which species extinction is accelerated (extinction thresholds), we separately tested the linear and non-linear effect of forest cover on each response, independently for three spatial scales.

Results We found stronger and larger-scale negative responses to forest loss in spider monkeys than in howler monkeys. However, the data were better predicted by linear models, giving no support to the extinction threshold hypothesis. In both species, forest loss had stronger negative impacts on monkey abundance when considering old-growth forest, than when considering secondary forest cover, or total (old-growth + secondary) forest cover. Yet, the immature-to-female ratio was weakly related to forest cover in both species.

Conclusion Secondary forests seem to have a weak buffering effect in both species, possibly because they are relatively young (< 30 years old) and do not have large trees. This implies that old-growth forests are irreplaceable for preventing primate extirpation, especially for species with specialized diet and large spatial requirements, such as spider monkeys.

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L. L. Saldívar-Burrola · F. Villalobos · F. López-Barrera
Instituto de Ecología, A.C., 91073 Xalapa, Veracruz, Mexico

M. Martínez-Ruíz · V. Arroyo-Rodríguez
Escuela Nacional de Estudios Superiores Unidad Mérida, Universidad Nacional Autónoma de México, 97357 Mérida, Yucatán, Mexico

V. Arroyo-Rodríguez (✉)
Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, 58190 Morelia, Michoacán, Mexico
e-mail: victorarroyo_rodriguez@hotmail.com

P. A. D. Dias
Primate Behavioral Ecology Lab, Instituto de Neuroetología, Universidad Veracruzana, 91190 Xalapa, Veracruz, Mexico

R. Arasa-Gisbert
Departamento de Ecología y Recursos Naturales, Universidad Nacional Autónoma de México, Coyoacán, 04510 Mexico, Mexico

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Introduction

The increasing demand for new agricultural lands is causing the loss of thousands of hectares of old-growth tropical forests every day, with 2020 being the third most devastating year of this century (Global Forest Watch 2021). This global pattern of forest loss has become the greatest threat to biodiversity (Fahrig 2003; Gibson et al. 2011; Watling et al. 2020), and affects key ecological processes for forest maintenance and recovery (e.g. herbivory: Morante-Filho et al. 2016; seed dispersal: San-José et al. 2020). In some regions, the abandonment of agriculturally unproductive lands has led to the expansion of secondary forests, bringing some hope that such forest gains through regrowth could buffer or mitigate the current biodiversity crisis (Wright and Muller-Landau 2006). This can be particularly plausible in landscapes with low to intermediate level of disturbance (Melo et al. 2013), especially for species that are able to use resources from secondary forests, which is the case of many vertebrates (e.g. mammalian carnivores: Asensio et al. 2009; Ferreira et al. 2018; primates: Galán-Acedo et al. 2019b; bats: Farneda et al. 2015; Rocha et al. 2018; amphibians and reptiles: Thompson and Donnelly 2018; birds: Martin and Blackburn 2014). However, the role of secondary forests in buffering the negative impact of old-growth forest loss on biodiversity patterns and processes remains poorly known and debated, especially at the landscape scale (Wright and Muller-Landau 2006; Melo et al. 2013; Smith et al. 2021).

While evaluating the response of forest species to landscape forest loss could seem unnecessary (i.e. anyone will predict the response to be negative), studies on this topic often show surprising results. For example, some species can persist in deforested landscapes, crowding in the remaining forest fragments (Ewers and Didham 2005). In fact, because of this “crowding effect”, the abundance of some forest-specialist species can increase in more deforested landscapes (e.g. Link et al. 2010; Arce-Peña et al. 2019; Vallejos et al. 2019; Gestich et al. 2021). Moreover, species responses to forest loss are not always linear, as expected if the magnitude of population changes is proportional to the magnitude of forest loss. Many species and communities show non-linear responses to old-growth forest loss because the loss of individuals and species can accelerate when forest loss exceeds a certain limit in the landscape (i.e. the so-called “extinction threshold”; Lande 1987; Fahrig 1997). The direction (positive or negative) and strength of these linear and non-linear effects can depend on species traits, such as their habitat spatial requirements (Swift and Hannon 2010). Therefore, additional studies on this topic are needed to better understand the impact of forest loss on biodiversity, and thus inform management and conservation strategies. This is particularly urgent in endangered taxa, such as most primate species (Estrada et al. 2017).

Primates play essential functional roles in their habitat, and some of which (e.g. seed dispersal) are critical for enhancing forest regeneration (Chapman et al. 2013; Arroyo-Rodríguez et al. 2015). As ~90% of primates are arboreal and undertake most of their activities on the forest canopy (Galán-Acedo et al. 2019c), they can be particularly susceptible to forest loss (Galán-Acedo et al. 2019b). In fact, forest loss is considered a major driver of primate population decline worldwide (Estrada et al. 2017; Chapman and Peres 2021). Paradoxically, most primate studies have assessed the impact of forest loss at the patch scale (i.e. forest patch size), not at the landscape scale (reviewed in Arroyo-Rodríguez et al. 2013a), and the few studies with a landscape approach are not conclusive (reviewed by Galán-Acedo et al. 2019b). For example, there is evidence that landscape forest loss can negatively affect the density and abundance of some primate species (Blanco and Waltert 2013; Piel et al. 2015; Supriatna et al. 2020), whereas other species seem to have larger populations in more deforested landscapes (e.g. Arroyo-Rodríguez et al. 2013b). Furthermore, primate studies usually assess the linear (proportional) effects of forest cover, overlooking potential extinction thresholds in the landscape. Finally, primate studies usually focus on the impacts of old-growth forest loss, overlooking the potential role of secondary forests in buffering the effects of old-growth forest loss on populations. Thus, additional studies are needed to assess the linear and non-linear effects of forest loss on primate populations, separately evaluating the influence of old-growth and secondary forest cover.

In this study, we assessed the impact of landscape forest loss on the abundance and immature-to-female ratio (a proxy of reproductive performance) of black howler monkeys (*Alouatta pigra*) and Geoffroy´s spider monkeys (*Ateles geoffroyi*) in the Lacandona rainforest, Mexico. We separately evaluated primate responses to old-growth forest cover, secondary forest cover, and total (old-growth + secondary) forest cover to assess whether secondary forests could buffer the effect of old-growth forest loss. As there could be tipping points of forest loss beyond which species extinction is accelerated (i.e. extinction thresholds), we tested both the linear and non-linear effect of forest cover on each response. We ran all models independently for forest cover values measured at three different (concentric) spatial scales. This allowed us to identify the scale at which each association was strongest, and thus increase the accuracy of inferred species-landscape relationships (Jackson and Fahrig 2015).

As both species are strictly arboreal, and forest specialists (Galán-Acedo et al. 2019c), we predicted that both responses are positively related to old-growth forest cover in both species. However, we expect that such responses will be likely stronger in spider monkeys than in black howler monkeys because the former is mostly frugivorous (Wallace 2008; Mittermeier et al. 2013) and has a larger mean home range size (usually < 170 ha; Chaves et al. 2011a; Di Fiore et al. 2011) than the latter (< 30 ha; Fortes et al. 2015; Galán-Acedo et al. 2019a). Following this same rationale, if extinction thresholds cause non-linear responses to forest loss (Swift and Hannon 2010), we predict a relatively higher extinction threshold (i.e. lower tolerance to forest loss) in spider monkeys than in howler monkeys. Whatever the shape of the association (linear or non-linear), we could expect that, being a more mobile species, spider monkeys could interact with (and depend on) forest cover across larger scales than howler monkeys (Miguet et al. 2016). Finally, as secondary forests can provide supplementary food resources for spider monkeys (Ramos-Fernández and Ayala-Orozco 2003; Arroyo-Rodriguez et al. 2017) and howler monkeys (Dias et al. 2014), we also predicted a stronger effect of forest loss on both species when considering both old-growth and secondary forest cover, than when considering old-growth forest alone.

Methods

Study area

We conducted the study in the Lacandona region, located in the southern part of Chiapas, Mexico. The climate is hot and humid, with annual precipitation averaging 2500–3500 mm, and average monthly temperatures of 24–26 °C (Carabias et al. 2015). The Lacandona region (13,000 km^2) represents one of the largest areas of tropical rainforest in Mexico, and it is considered a priority area for the conservation of biodiversity in Mesoamerica (García del Valle et al. 2015). The Lacandona region is highly threatened by land-use change and other human related pressures (Arriaga et al. 2000; Carabias et al. 2015). In particular, land-use change started in the late 1970s, and nowadays the remaining old-growth forest cover (≈ 37%) is embedded in a matrix of secondary forests, agricultural lands and human settlements (Carabias et al. 2015; Lohbeck et al. 2022). We sampled primates in two adjacent areas of the Lacandona region: the continuous forest of the Montes Azules Biosphere Reserve and the fragmented forest of the Marqués de Comillas region, which are separated by the Lacantún River (Fig. 1). The agricultural dynamics in the Marqués de Comillas region have given place to relatively short-lived (range 2.7–25 years fallow age, mean 9.7 years) secondary forests, which in 2017 covered ≈ 11% of this region (Lohbeck et al. 2022).

Study landscapes and forest cover estimation

The protocol used to select the studied landscapes is detailed elsewhere (Wies et al. 2021), but a brief overview is given here. We generated a land cover map of the study region (Fig. 1) using Sentinel-2B satellite images (10-m resolution; 10% cloudiness; year 2019) and used QGIS v 2.18 (QGIS 2021) to generate raster layers and conduct an image interpretation using georeferenced points of in situ supervised land cover classes (old-growth forest, secondary forest, human settlement, agricultural land, and cattle pasture). In particular, we applied a combination of bands that highlight forest cover (8, 4, 3 combinations

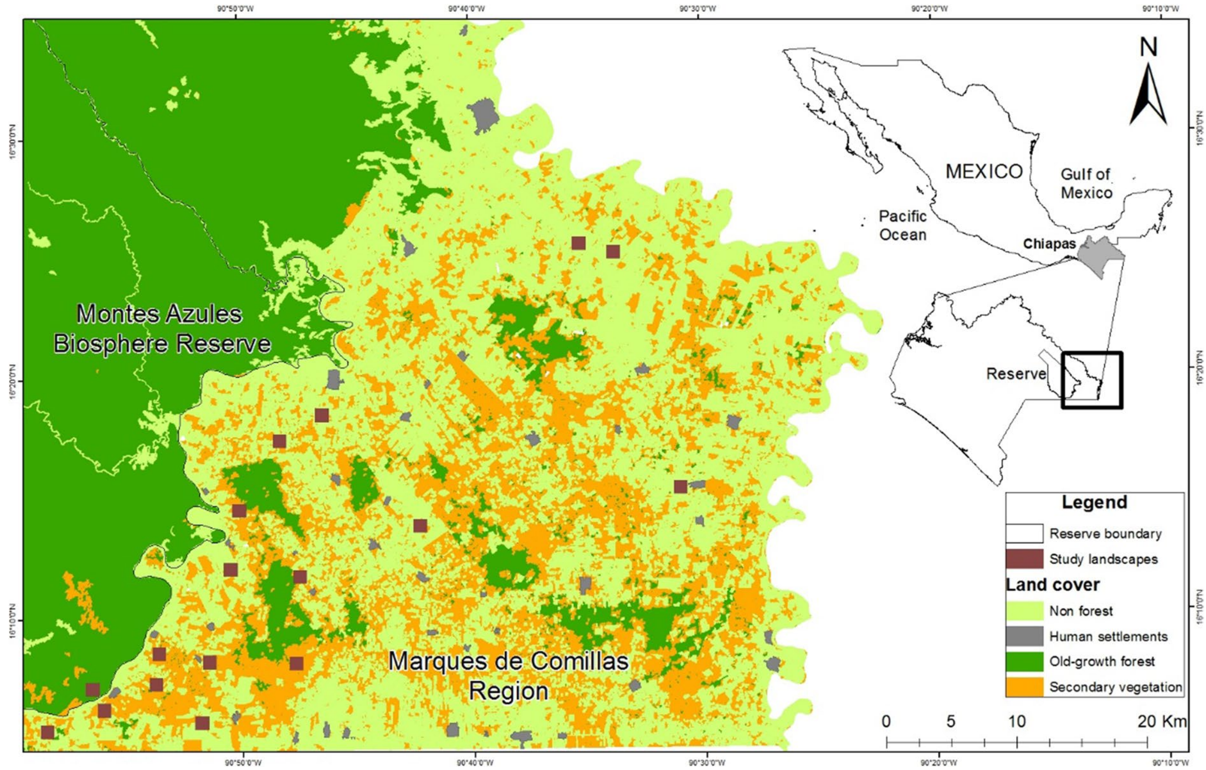

Fig. 1 Location of the 18 1-km^2 study landscapes in the Marqués de Comillas region and the Montes Azules Biosphere Reserve within the Lacandona region, Mexico

for Sentinel 2-B images). It is important to note that secondary forests in the region are forests regenerating after < 30 years of agricultural land abandonment (Wies et al. 2021; Brindis-Badillo et al. 2022; Lohbeck et al. 2022), so they are structurally different from old-growth forests; e.g. they have a higher abundance of thinner trees, and lower total tree biomass (Poorter et al. 2016). This makes it relatively easy to differentiate from old-growth forests both in the field and from satellite images. As 'landscape units' can be simply defined as heterogeneous land areas containing a mosaic of land cover types (e.g., old-growth forest, secondary forest, agricultural lands) (Arroyo-Rodríguez and Fahrig 2014), we selected 18 landscape units of 100 ha (1 × 1 km) each, maintaining a minimum distance of 4 km between them to avoid spatial overlap and autocorrelation (Holland et al. 2004). These landscape units encompassed the broadest range of deforestation in the region, with both the percentage of old-growth and secondary forest cover varying from 0 to 100% in 100 ha landscape units (Table S1 in Supplementary Information). Using this wide environmental gradient is critically needed to make accurate landscape-scale inferences (Eigenbrod et al. 2011). The percentage of old-growth forest cover and the percentage of secondary forest cover was estimated in each landscape unit with FRAGSTATS v4 (McGarigal et al. 2002). As we did not know a priori the spatial scale that best predicted primate responses to forest cover (i.e., the "scale of effect", sensu Jackson and Fahrig 2015), we measured forest cover at three different spatial scales, i.e. in concentric square landscapes of 1, 2, and 3 km^2. We selected this range of scales following the SoE values documented for the study species in the Lacandona rainforest (Ordóñez-Gómez et al. 2015; Galán-Acedo et al. 2018). We used square landscapes instead of circular landscapes to follow the shape of the sampling area (see below), and thus keep the distance (and related confounding factors) from sampling sites to landscape edges constant around the entire sampled area across all sampled landscapes.

Study species

Two primate species occur in the study region: the black howler monkey and the Geoffroy´s spider monkey. Both species are diurnal and strictly arboreal. The black howler monkey has a folivore–frugivore diet, whereas spider monkeys are mostly frugivorous (Amato and Garber 2014; Dias and Rangel-Negrín 2015). Black howler monkeys weigh around 5.7–6 kg (Kelaita et al. 2011), hold home ranges of <30 ha (Fortes et al. 2015), and tend to be sedentary and relatively resilient to habitat changes (Arroyo-Rodríguez and Dias 2010). In contrast, spider monkeys are larger (weight = 7.5–8.2 kg; Garber et al. 2005) and relatively more sensitive to habitat disturbance (Boyle and Smith 2010; Galán-Acedo et al. 2021). Both species are classified as Endangered in the IUCN Red List, and their populations are declining (Cortés-Ortíz et al. 2020, 2021).

Primate surveys and response variables

Surveys were conducted during the dry season (February–June) of 2019, as it is easier to locate monkeys on sunny days (Galán-Acedo et al. 2018). Each landscape was surveyed by LLSB and a local guide, walking slowly (1 km/h) in a *zigzag* pattern to cover the whole landscape area (including all land cover types), totalling 312 km walked in the 18 landscapes. Walks were done during the morning (06:00–12:00) and in the afternoon (16:00–18:00), which coincides with the peak activity of primates (Galán-Acedo et al. 2018). We used cues as vocalizations and traces of excrement and urine to locate primates. Once a group was found, we counted the number of individuals and classified them following commonly used age–sex categories: adult males, adult females, and immatures (i.e., subadults, juveniles, and infants). We also took note of distinctive features of individuals (e.g., scars, facial features) to avoid double-counting groups or individuals. For each landscape, we estimated the total number of individuals of each species and the immature-to-female ratio as a proxy of reproductive performance (Arroyo-Rodríguez et al. 2013b; Galán-Acedo et al. 2018).

Data analyses

We assessed how the abundance of primates was related to forest cover assuming: (i) a linear association modeled with generalized linear models (GLM), and (ii) a non-linear association modeled with four-parameter logistic regressions, which follow an "s" shaped curve suitable for identifying critical thresholds (Ficetola and Denoel 2009; Morante-Filho et al. 2015). Following Morante-Filho et al. (2015), we used the Akaike Information Criterion corrected for small samples (AICc) to compare the linear and non-linear models with a null model (including only the intercept). We first fixed a Poisson distribution error to the abundance GLMs, but after failing to correct models for overdispersion, we used a negative binomial error (Zuur et al. 2009). Regarding the immature-to-female ratio, we tested only two possible models: (i) a null model (including only the intercept) to test the absence of effects, and (ii) a GLM with binomial distribution which contains a default logistic regression tendency given by "probit" link function (Prasetyo et al. 2019). We selected a binomial distribution for the immature-to-female ratio because the GLMs with a Gaussian error did not meet the normality assumption of residuals. We separately tested the models for old-growth forest cover and secondary forest cover. We adjusted one model per landscape scale (1, 2 and 3 km^2), for a total of 7 models for abundance (null model + 3 linear models + 3 non-linear models) and 4 models for immature-to-female ratio (null model + 3 binomial models) per primate species. We then ranked each set of models following a decreasing empirical support (i.e., lowest to highest AICc; Burnham and Anderson 2002) to identify which was the best predictive model of each response and at what scale. Finally, to assess whether secondary forests could buffer the impact of old-growth forest loss on each response, we evaluated whether the effect size (i.e., parameter estimate or slope) and explanatory power (goodness-of-fit) of these best models increased when including total (old-growth + secondary) forest cover instead of old-growth forest cover alone. All analyses were conducted using R version 4.0.4 (R Core Team 2020).

Results

We recorded monkeys in most (14 of 18, 78%) landscapes. Yet, spider monkeys occupied a lower percentage of landscapes (8 of 18, 44.4%) than howler monkeys (14 landscapes, 78% Fig. 2). Primate occurrence in the top 10 deforested landscapes (<40% remaining total forest cover) was 3.5 times lower in spider monkeys (n=2 landscapes) than in howler monkeys (n=7; Fig. 2). In total, we recorded 196 spider monkey individuals: 50 adult males, 87 adult females, and 50 immatures (we could not identify the age–sex

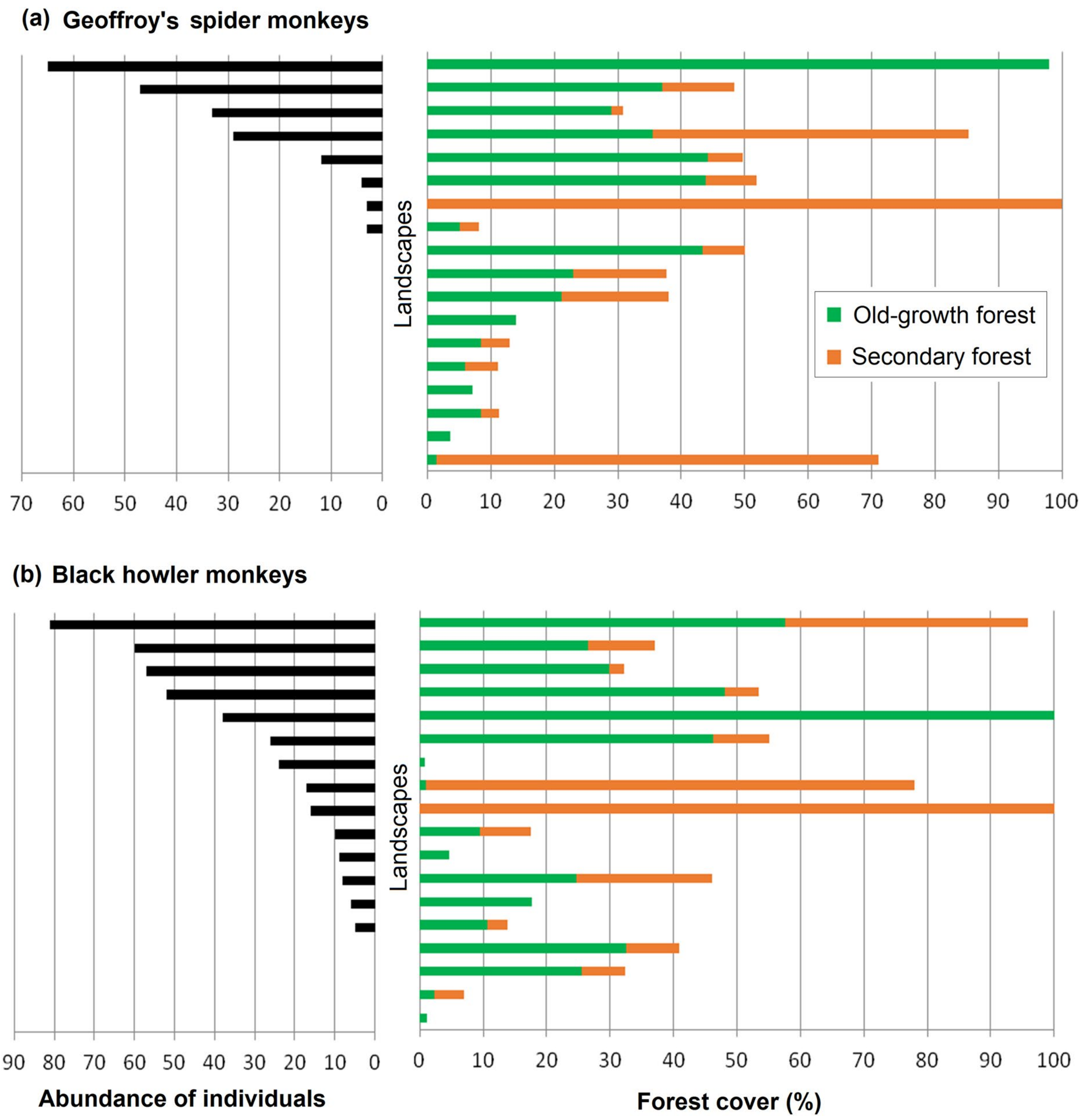

Fig. 2 Abundance of spider monkeys (**a**) and black howler monkeys (**b**) in each study landscape (panels on the left). In each species, the landscapes are ordered by decreasing abundance. The percentage of old-growth and secondary forest cover remaining in each landscape is also indicated (on the right), but at different scales considering the scale of forest cover effect (i.e. spider monkeys = 2 km^2, howler monkeys = 1 km^2; see Table 1)

class of 9 individuals). The mean (± SD) abundance of spider monkeys per landscape was 10.8 (± 19.6) individuals (range = 0–65 individuals), and the mean subgroup size was 4 (± 2.3) individuals. On the other hand, we recorded 409 howler monkey individuals (128 adult males, 168 adult females, and 133 immatures), averaging 22.7 (± 24.7) individuals per landscape, and 5 (± 5.2) individuals per group. In general, most monkeys (543 of 605 individuals, 89.7%) were recorded in old-growth forest, but most (87%) of the 62 sightings in the anthropogenic matrix occurred in secondary forests (51 howler monkeys and 3 spider monkeys). We also recorded seven howler monkeys in live fences, and one spider monkey was observed crossing a cattle pasture on the ground near an old-growth forest.

Linear vs. non-linear effects of forest loss on each primate species

We found that the effect of old-growth forest cover on the abundance of spider monkeys and howler monkeys was better predicted by linear models (Table 1). In particular, the abundance of both species increased with increasing old-growth forest cover in the landscape (panels a and c in Fig. 3), but spider monkeys were susceptible to forest spatial changes across larger scales (2 km^2) than howler monkeys (1 km^2; Table 1). In contrast, the abundance of both species was weakly related to secondary forest cover (Table 2), and the immature-to-female ratio of both species was also weakly related to forest cover, irrespective of forest type (Tables 1, 2).

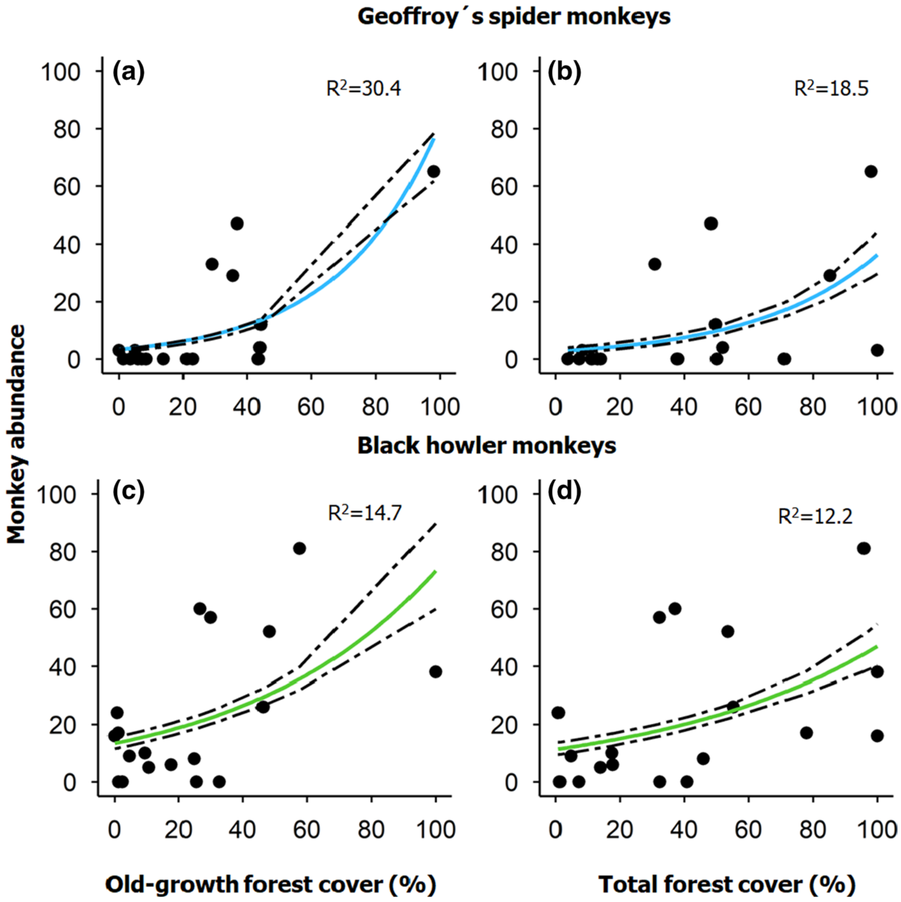

Fig. 3 The best statistical models (i.e. generalized linear models) describing how the abundance of monkeys related to landscape forest cover. We separately show the models for Geoffroy's spider monkeys (**a**, **b**) and black howler monkeys (**c**, **d**), with panels on the left (**a**, **c**) showing responses to old-growth forest alone, and panels on the right (**b**, **d**) showing responses to total (old-growth + secondary) forest cover. Note that in the case of spider monkeys, we measured forest cover in 2-km^2 landscapes, whereas in howler monkeys forest cover was measured in 1-km^2 landscapes

Table 1 Effect of old-growth forest cover on the relative abundance (Abu) and immature-to-female ratio (IFR) of two primate species in the Lacandona rainforest, Mexico

Species	Response	Model	AICc	ΔAICc	w_i	Pseudo-R^2
Spider monkeys						
	Abu	GLM (2 km^2)	96.02	0.00	0.77	0.3
		GLM (3 km^2)	96.33	0.31	0.31	0.29
		GLM (1 km^2)	97.11	1.09	0.21	0.25
		Null	98.39	2.37	0.23	0
		Logistic (1 km^2)	163.19	67.17	<0.001	0.42
		Logistic (2 km^2)	166.20	70.18	0.00	0.41
		Logistic (3 km^2)	170.22	74.20	0.00	0.40
	IFR	Null	21.47	0.00	0.80	0
		GLM (3 km^2)	24.26	2.79	0.20	0.14
		GLM (2 km^2)	24.733	3.267	0.122	0.13
		GLM (1 km^2)	25.182	3.717	0.098	0.11
Black howler monkeys						
	Abu	GLM (1 km^2)	149.66	0.00	0.56	0.15
		Null	150.10	0.44	0.44	0
		GLM (2 km^2)	150.35	0.70	0.23	0.12
		GLM (3 km^2)	150.97	1.31	0.17	0.09
		Logistic (2 km^2)	220.88	71.22	0.00	0.34
		Logistic (3 km^2)	223.61	73.95	0.00	0.33
		Logistic (1 km^2)	245.22	95.56	0.00	0.26
	IFR	Null	26.09	0.00	0.73	0
		GLM (1 km^2)	28.06	1.97	0.27	0.07
		GLM (2 km^2)	28.453	2.365	0.158	0.1
		GLM (3 km^2)	28.781	2.693	0.134	0.1

The changes in abundance were assessed with a linear (generalized linear model, GLM) and a non-linear (logistic) model, whereas the immature-to-female ratio was assessed with a GLM with binomial distribution which follows a default logistic regression tendency. We measured forest cover at three different scales (1, 2, and 3 km^2, indicated in parenthesis) to identify the scale that yields the strongest species-landscape association. All models were compared with a null model, which included only the intercept. Models are ordered following a decreasing order of support (i.e. increasing Akaike Information Criterion corrected for small samples, AICc)

w_i Akaike weight

Effect of total forest cover on the abundance of primates

The negative impact of forest loss on the abundance of both species was stronger when considering old-growth forest cover alone, than when considering the sum of old-growth and secondary forest cover (Table 3; Fig. 3). For spider monkeys, the inclusion of total (old-growth + secondary) forest cover instead of old-growth forest cover decreased the effect size of forest cover (i.e., parameter estimate) by 42% and the explanatory power of the model (i.e., pseudo-R^2) by 37%. The same pattern emerged in howler monkeys, with the effect size decreasing by 29% and the explanatory power by 20% (Table 3).

Discussion

This study is the first in using a landscape-scale approach to evaluate the linear and non-linear effects of forest loss on two endangered primates. To our knowledge, it is also the first to separately assess the effect of old-growth, secondary, and total (old-growth + secondary) forest cover on primates—a novel contribution to assessing whether, as suggested in previous studies (Wright and Muller-Landau 2006;

Table 2 Effect of secondary forest cover on the relative abundance (Abu) and immature-to-female ratio (IFR) of two primate species in the Lacandona rainforest, Mexico

Species	Response	Model	AICc	ΔAICc	w_i	Pseudo-R^2
Spider monkeys						
	Abu	Null	98.39	0	1	0
		Logistic (3 km^2)	269.65	171.26	6E-38	0.02
		Logistic (1 km^2)	269.65	171.26	6E-38	0.02
		Logistic (2 km^2)	273.36	174.97	1E-38	0
		GLM (1 km^2)	512.24	413.85	1E-90	0.02
		GLM (2 km^2)	513.93	415.54	6E-91	0.01
		GLM (3 km^2)	518.85	420.46	5E-92	0.07
	IFR	Null	21.47	0	0.42	0
		GLM (1 km^2)	22.66	1.20	0.23	0.06
		GLM (2 km^2)	23.07	1.61	0.19	0.04
		GLM (3 km^2)	23.24	1.77	0.17	0.03
Black howler monkeys						
	Abu	Null	150.10	0	0.56	0
		GLM (3 km^2)	152.64	2.53	0.16	0.18
		GLM (2 km^2)	152.79	2.69	0.15	0.01
		GLM (1 km^2)	152.95	2.85	0.14	0.00
		Logistic (3 km^2)	298.28	148.18	0	0.10
		Logistic (2 km^2)	312.24	162.14	0	0.05
		Logistic (1 km^2)	312.37	162.27	0	0.05
	IFR	Null	26.09	0	0.46	0
		GLM (3 km^2)	27.79	1.70	0.20	0.01
		GLM (1 km^2)	28.07	1.99	0.17	0.07
		GLM (2 km^2)	28.14	2.05	0.17	0.05

The changes in abundance were assessed with a linear (generalized linear model, GLM) and a non-linear (logistic) model, whereas the immature-to-female ratio was assessed with a GLM with binomial distribution which follows a default logistic regression tendency. We measured forest cover at three different scales (1, 2, and 3 km^2, indicated in parenthesis) to identify the scale that yields the strongest species-landscape association. All models were compared with a null model, which included only the intercept. Models are ordered following a decreasing order of support (i.e., increasing Akaike Information Criterion corrected for small samples, AICc)

w_i Akaike weight

Melo et al. 2013), secondary forests can buffer the negative impact of old-growth forest loss on biodiversity. Importantly, our findings do not support this hypothesis in Geoffroy´s spider monkeys and black howler monkeys of the Lacandona rainforest, as the impact of forest loss on monkey abundance was weaker when considering old-growth and secondary forest cover than when considering old-growth forest alone. In fact, the abundance of individuals was independent of the percentage of secondary forest cover in the landscape, irrespective of the spatial scale. Interestingly, old-growth forest loss caused a proportional (linear) population decline in both species, thus giving no support to the extinction threshold hypothesis (Swift and Hannon 2010). However, as predicted, we found stronger (and larger-scale) negative responses to old-growth forest loss in spider monkeys than in black howler monkeys, adding to an increasing body of literature demonstrating the high sensitivity of spider monkeys and other large-bodied and specialized mammals to habitat loss (Palmeirim et al. 2018; Laurindo et al. 2019; Rios et al. 2022). Finally, the fact that the immature-to-female ratio of both species was weakly related to forest cover could be considered good news, as it suggests that forest loss does not impact the reproductive performance of these species. Below, we discuss how these findings can be applied to design optimal landscape scenarios for the

Table 3 Effect of forest cover on the abundance of spider monkeys and black howler monkeys separately assessing the effect of old-growth forest (OGF) alone, and total (old-growth + secondary) forest cover (OGF + SF)

Species	Model	Estimate	2.5% CI	97.5% CI	p	Pseudo-R^2
Spider monkeys						
	OGF 2-km^2	0.071	0.014	0.136	0.001	0.30
	OGF + SF 2-km^2	0.041	−0.002	0.102	0.020	0.19
Black howler monkeys						
	OGF 1-km^2	0.024	0.000	0.053	0.039	0.15
	OGF + SF 1-km^2	0.017	−0.002	0.039	0.066	0.12

We show the parameter estimates of the models with 95% confidence intervals (and associated p-values), along with the pseudo-R^2 as a measure of goodness-of-fit of the models

conservation of these, and potentially other, endangered forest taxa.

Contrary to our expectations, secondary forests do not appear to mitigate the negative impact of old-growth forest loss on the primate species studied here. As both species are known to be able to use food resources from secondary forests (Ramos-Fernández and Ayala-Orozco 2003; Arroyo-Rodríguez et al. 2017; Galán-Acedo et al. 2019b), we expected that this forest type could provide supplementary habitat for them. Our findings partially support this, as most (87%) of the individuals observed outside old-growth forests, i.e. in the anthropogenic matrix (sensu Galán-Acedo et al. 2019b), occurred in secondary forests. However, we found no support to the idea that such temporary use of secondary forests is important enough to have a significant impact on primate populations. In particular, the abundance of both species decreased principally with the loss of old-growth forests, and the addition of secondary forests to the models (i.e., considering total forest cover) decreased the effect size and explanatory power of the models by 20–42%. Such a lack of buffering effect can be related to the fact that in this recently deforested region, secondary forests are relatively young (< 30 years old) and of small stature (Brindis-Badillo et al. 2022; Lohbeck et al. 2022). This limits the occurrence of top food tree species (reviewed by González-Zamora et al. 2009), such as *Dialium guianense* (Fabaceae), *Brosimum alicastrum* (Moraceae), *Ampelocera hottlei* (Ulmaceae), and *Guarea glabra* (Meliaceae), which are among the 10 most abundant and widely distributed species in old-growth forests of the study region (Navarrete-Segueda et al. 2017) but are rarely present in secondary forests (Brindis-Badillo et al. 2022). Therefore, although monkeys may supplement their diet in secondary forests, especially with some light-demanding trees (e.g., *Bursera simaruba*, *Cecropia* spp.; Cristóbal-Azkarate and Arroyo-Rodríguez 2007), the populations of both species are mainly shaped by the amount of old-growth forest in the landscape.

In contrast to what could be expected from the extinction threshold hypothesis (Swift and Hannon 2010), the abundance of primates was better predicted by linear models. Extinction thresholds are usually caused by exponential changes in habitat configuration (e.g., increased interpatch isolation distance) in landscapes with < 10–30% habitat amount (Andren 1994; Swift and Hannon 2010). Thus, the lack of an extinction threshold would be related to the fact that, as demonstrated in previous studies with primates (Arce-Peña et al. 2019) and other vertebrates (arboreal mammals: Cudney-Valenzuela et al. 2022; birds: Carrara et al. 2015; amphibians and reptiles: Russildi et al. 2016), habitat configuration changes in this region has weak effects on biodiversity. However, we found some evidence that population decline could be accelerating in the top most deforested landscapes (< 30–40% of remaining total forest cover), as these landscapes were almost empty of spider monkeys. This is consistent with previous studies on the population collapse of different species in landscapes with < 30% of natural habitats (e.g. Rybicki and Hanski 2013; reviewed by Arroyo-Rodríguez et al. 2020, 2021). Therefore, our findings add some preliminary support to the idea that we must preserve at least 40% of forest cover in the landscape to prevent the extinction of forest-specialist species (Arroyo-Rodríguez et al. 2020, 2021). Such extirpation of spider monkey populations could be related to the fact that, in the Lacandona region, there is a sharp decline in the population of top food trees in landscapes with < 40% forest cover (Brindis-Badillo et al. 2022). However, additional studies are needed to better understand the minimum habitat amount required for the persistence of this and other primate species, especially because the long life spans of primates can promote time-delayed responses to habitat modifications (extinction debts) (Jackson and Sax 2010).

Importantly, multiple lines of evidence support the hypothesis that howler monkeys are relatively more resistant to old-growth forest loss than spider monkeys. First, forest loss showed weaker effects (i.e., lower regression slope and explanatory power in the models) on howler monkeys than spider monkeys. Second, howler monkeys were present in all occupied landscapes, and landscape occupancy in the top 10 most deforested landscapes (< 40% of remaining total forest cover) was 3.5 times higher in howler monkeys (n = 7 landscapes) than in spider monkeys (n = 2). Finally, although most monkeys were recorded in old-growth forests, most individuals (58 of 62, 94%) observed in the anthropogenic matrix were howler monkeys. This is not surprising, as howler monkeys are known to be relatively tolerant to habitat disturbance (reviewed by Arroyo-Rodríguez and Dias 2010), being usually present in forest fragments where other primate species (e.g. *Ateles* spp.) have disappeared (Estrada and Coates-Estrada 1996; Gilbert 2003). Such a relatively high tolerance to forest loss has been associated with several ecological aspects, including high dietary flexibility, the use of energy-saving activity budgets, small home range sizes, and a high ability to move among forest fragments in fragmented landscapes (Arroyo-Rodríguez and Dias 2010). Together, these ecological traits can help to explain why in moderately deforested regions, such as the Lacandona rainforest, howler monkeys appear to cope with forest loss more successfully than spider monkeys.

The fact that forest loss impacted spider monkeys across larger spatial scales than howler monkeys also supports our expectations. Theory predicts that the scale of landscape effect on biodiversity is driven by species mobility, with the more mobile species interacting with (and depending on) environmental variables across larger scales (reviewed by Jackson and Fahrig 2015; Miguet et al. 2015). As home range size is positively related to dispersal distance in mammals (Bowman et al. 2002), it is usually used as a good proxy of species mobility (Jackson and Fahrig 2015). In this sense, as the home range of spider monkeys is notably larger than that of howler monkeys (see above), it is not surprising that spider monkeys are more strongly affected by forest cover across larger scales than howler monkeys. In fact, the scales of effect observed in howler monkeys (1-km^2 landscape, or landscapes of 564-m radius) and spider monkeys (2 km^2, or 798-m radius) are similar to those reported in previous studies (howler monkeys: 500-m radius, Carretero-Pinzon et al. 2017; 710–711 m, Galán-Acedo et al. 2018; spider monkeys: 633 m, Ordóñez-Gómez et al. 2015; 558 m, Galán-Acedo et al. 2018). This implies that conservation strategies for these two endangered species will be likely more effective if planned and implemented at these scales.

Finally, but contrary to our expectations, the immature-to-female ratio of both species seems to be weakly related to forest cover. This finding could be considered good news, as it suggests that forest loss does not impact the reproductive performance of these species. However, care should be taken with this interpretation since the observed immature-to-female ratio in all landscapes (mean and range values: howler monkeys = 0.74, 0.40–1.50; spider monkeys = 0.67, 0.33–1.00) was lower than expected from their life-history parameters. In particular, interbirth intervals are approximately 15 months in black howler monkeys (Dias et al. 2015) and 32 months in Geoffroy's spider monkeys (Shimooka et al. 2008). As the individuals of both species usually disperse from their natal groups at 4–5 years (Di Fiore et al. 2011; Dias et al. 2015), on any particular year, each howler monkey female could co-reside with up to four offspring (i.e., a newborn, two juveniles, and one subadult) and a spider monkey female with two (i.e., a newborn and a juvenile). Immature-to-female ratios would then reach up to 4 in howler monkeys and 2 in spider monkeys. These are obviously theoretical (potential) values, as they do not take into account that infant mortality by natural causes (e.g. predation, accidental injuries, and aggression from conspecifics; see Shimooka et al. 2008; Van Belle et al. 2010) can lead to the loss of ≈ 25% of immature in howler monkeys (Dias et al. 2015) and ≈ 17% in spider monkeys (Shimooka et al. 2008). Anthropogenic disturbances can also affect these numbers because if females do not meet their energetic requirements (e.g., because of food scarcity; Rangel-Negrín et al. 2018a), conceptions are less likely, and interbirth intervals increase (Rangel-Negrín et al. 2018b). Therefore, additional long-term monitoring of these populations is needed to better understand if the relatively low values of immature-to-female ratio in the entire region are caused by natural or anthropogenic factors, and why this population parameter is independent of the remaining forest cover in the landscape.

In summary, our findings indicate that secondary forests cannot mitigate the negative impact of old-growth forest loss on two Mexican primates in the Lacandona rainforest. Therefore, in agreement with Gibson et al. (2011), old-growth forests appear to be irreplaceable for preserving tropical biodiversity. This is particularly true in species with specialized diets and high habitat spatial requirements, such as spider monkeys. In fact, the extirpation of spider monkeys in most of the landscapes with $<40\%$ forest cover supports the idea that at least 40% old-growth forest cover should be maintained in the landscape to prevent the extinction of this forest species (Arroyo-Rodríguez et al. 2020, 2021). In this sense, it is worth highlighting that the remaining old-growth forest in the Lacandona region is within this threshold, so stopping deforestation is a top priority for conserving these endangered primates in the region. As both spider monkeys (Chaves et al. 2011b; González-Zamora et al. 2014) and howler monkeys (Arroyo-Rodríguez et al. 2015) are important seed dispersers and play a key role for forest recovery in preserved and degraded forests, preserving old-growth forests is not only paramount for preventing primate extirpation, but for maintaining their important functional role in the ecosystem.

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Author contributions VAR and LLSB developed the idea of the study, with support from FV, PADD and FLB. LLSB collected and analyzed the data with guidance from MMR, RAG, PADD and VAR. All authors made substantial contributions to the intellectual content, interpretation and editing of the manuscript.

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Declarations

Conflict of interest The authors declare no competing interests.

References

Amato KR, Garber PA (2014) Nutrition and foraging strategies of the black howler monkey (*Alouatta pigra*) in Palenque National Park, Mexico. Am J Primatol 76:774–787

Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat, a review. Oikos 71(3):355–366

Arce-Peña NP, Arroyo-Rodríguez V, Dias PAD, Franch-Pardo I, Andrensen E (2019) Linking changes in landscape structure to population changes of an endangered primate. Landsc Ecol 34:2687–2701

Arriaga L, Espinoza JM, Aguilar C, Martínez E, Gómez L et al (2000) Regiones terrestres prioritarias de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico City

Arroyo-Rodríguez V, Dias PAD (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. Am J Primatol 72:1–16

Arroyo-Rodríguez V, Fahrig L (2014) Why is a landscape perspective important in studies of primates? Am J Primatol 76:901–909

Arroyo-Rodríguez V, Cuesta-del Moral E, Mandujano S, Chapman CA, Reyna-Hurtado R, Fahrig L (2013a) Assessing habitat fragmentation effects for primates: the importance of evaluating questions at the correct scale. In: Marsh LK, Chapman CA (eds) Primates in fragments: complexity and resilience. Developments in primatology: progress and prospects. Springer, New York, pp 13–28

Arroyo-Rodríguez V, Gonzalez-Perez IM, Garmendia A, Sola M, Estrada A (2013b) The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico. Landsc Ecol 9:1717–1727

Arroyo-Rodríguez V, Andresen E, Bravo SP, Stevenson PR (2015) Seed dispersal by howler monkeys: current knowledge, conservation implications and future directions. In: Kowalewski M, Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D (eds) Howler monkeys: behavior, ecology and conservation. Springer developments in primatology, progress and prospects book series. Springer, New York, pp 111–139

Arroyo-Rodríguez V, Pérez-Elissetche GK, Ordóñez-Gómez JD, González-Zamora A, Chaves OM, Sánchez-López S, Chapman CA, Morales-Hernández K, Pablo-Rodríguez M, Ramos-Fernández G (2017) Spider monkeys in human-modified landscapes: the importance of the matrix. Trop Conserv Sci. https://doi.org/10.1177/1940082917719788

Arroyo-Rodríguez V, Fahrig L, Tabarelli M, Watling JI, Tischendorf L, Benchimol M, Cazetta E, Faria D, Leal IR, Melo FPL, Morante-Filho JC, Santos BA, Arasa-Gisbert R, Arce-Peña N, Cervantes-López MJ, Cudney-Valenzuela S, Galán-Acedo C, San-José M, Vieira ICG, Slik JWF, Nowakowski J, Tscharntke T (2020) Designing optimal human-modified landscapes for forest biodiversity conservation. Ecol Lett 23:1404–1420

Arroyo-Rodríguez V, Fahrig L, Watling JI, Nowakowski J, Tabarelli M, Tischendorf L, Melo FPL, Santos BA, Benchimol M, Morante-Filho JC, Slik JWF, Vieira IDG, Tscharntke T (2021) Preserving 40% forest cover is a valuable and well-supported conservation guideline: reply to Banks-Leite et al. Ecol Lett 24:1114–1116

Asensio N, Arroyo-Rodríguez V, Dunn JC, Cristobal-Azkarate J (2009) Conservation value of landscape supplementation for howler monkeys living in forest patches. Biotropica 41:768–773

Blanco V, Waltert M (2013) Does the tropical agricultural matrix bear potential for primate conservation? A baseline study from Western Uganda. J Nat Conserv 21:383–393

Bowman J, Jaeger JA, Fahrig L (2002) Dispersal distance of mammals is proportional to home range size. Ecology 83:2049–2055

Boyle SA, Smith AT (2010) Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? Biol Conserv 143:1134–1143

Brindis-Badillo D, Arroyo-Rodríguez V, Mendoza E, Wies G, Martínez-Ramos M (2022) Conserving dominant trees in human-modified landscapes at the Lacandon tropical rainforest. Biol Conserv 270:109548

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Carabias J, De la Maza J, Cadena R (2015) Conservación y desarrollo sustentable en la Selva Lacandona. Natura y Ecosistemas Mexicanos A.C., Mexico City

Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, Schondube JE, de Freitas SM, Fahrig L (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biol Conserv 184:117–126

Carretero-Pinzon X, Defler TR, McAlpine CA, Rhodes JR (2017) The influence of landscape relative to site and patch variables on primate distributions in the Colombian Llanos. Landsc Ecol 32:883–896

Chapman CA, Peres CA (2021) Primate conservation: lessons learned in the last 20 years can guide future efforts. Evol Anthropol 30:345–361

Chapman CA, Bonnell TR, Gogarten JF, Lambert JE, Omeja PA, Twinomugisha D, Wasserman MD, Rothman JM (2013) Are primates ecosystem engineers? Int J Primatol 34:1–14

Chaves OM, Stoner KE, Arroyo-Rodríguez V (2011a) Seasonal differences in activity patterns of Geoffroyi's spider monkeys (Ateles geoffroyi) living in continuous and fragmented forests in southern Mexico. Int J Primatol 32:960–973

Chaves OM, Stoner KE, Arroyo-Rodríguez V, Estrada A (2011b) Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rainforests in southern Mexico. Int J Primatol 32:177–192

Cortés-Ortíz L, Rosales-Meda M, Marsh LK, Mittermeier RA (2020) Alouatta pigra. The IUCN Red List of Threat Species 2020: e.T914A17926000. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T914A17926000.en. Accessed Oct 2021

Cortés-Ortíz L, Solano-Rojas D, Rosales-Meda M, Williams-Guillen K et al (2021) Ateles geoffroyi (amended version of 2020 assessment). The IUCN Red List of Threat Species 2021: e.T2279A191688782. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T2279A191688782.en. Accessed Oct 2021

Cristóbal-Azkarate J, Arroyo-Rodríguez V (2007) Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. Am J Primatol 69:1013–1029

Cudney-Valenzuela S, Arroyo-Rodríguez V, Andrensen E, Toledo-Aceves T (2022) What determines the scale of landscape effect on tropical arboreal mammals? Landsc Ecol 37:1497–1507

Di Fiore A, Link A, Campbell CJ (2011) The Atelines: behavioural and socioecological diversity in a New World monkey radiation. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) Primates in perspective, 2nd edn. Oxford University Press, New York, pp 155–188

Dias PAD, Rangel-Negrín A (2015) Diets of howler monkeys. In: Howler monkeys. Springer, New York, pp 21–56

Dias PAD, Rangel-Negrín A, Coyohua-Fuentes A, Canales-Espinosa D (2014) Variation in dietary breadth among groups of black howler monkeys is not associated with the vegetation attributes of forest fragments. Am J Primatol 76:1151–1162

Dias PAD, Coyohua-Fuentes A, Canales-Espinosa D, Rangel-Negrín A (2015) Group structure and dynamics in black howler monkeys: a 7-year perspective. Int J Primatol 36:311–331

Eigenbrod F, Hecnar SJ, Fahrig L (2011) Sub-optimal study design has major impacts on landscape-scale inference. Biol Conserv 144:298–305

Estrada A, Coates-Estrada R (1996) Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. Int J Primatol 17:759–783

Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, Nekaris KA, Nijman V, Heymann EW, Lambert JE, Rovero F, Barelli C, Setchell JM, Gillespie TR, Mittermeier RA, Arregoitia LV, de Guinea M, Gouveia S, Dobrovolski R, Shanee S, Shanee N, Boyle SA, Fuentes A, MacKinnon KC, Amato KR, Meyer ALS, Wich S, Sussman RW, Pan R, Kone I, Li B (2017) Impending extinction crisis of the world's primates: why primates matter. Sci Adv 3:e1600946

Ewers RM, Didham RK (2005) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142

Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. J Wildl Manag 61(3):603–610

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Farneda FZ, Rocha R, López-Baucells A, Groenenberg M, Silva I et al (2015) Trait-related responses to habitat fragmentation in Amazonian bats. J Appl Ecol 52:1381–1391

Ferreira AS, Peres CA, Bogoni JA, Cassano CR (2018) Use of agroecosystem matrix habitats by mammalian carnivores (Carnivora): a global-scale analysis. Mamm Rev 48:312–327

Ficetola FG, Denoel M (2009) Ecological thresholds: an assessment of methods to identify abrupt changes in species–habitat relationships. Ecography 32:1075–1084

Fortes VB, Bicca-Marques JC, Urbani B, Fernández VA, Pereira TS (2015) Ranging behavior and spatial cognition of howler monkeys. In: Kowalewski M, Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D (eds) Howler monkeys: behavior, ecology and conservation. Springer developments in primatology, progress and prospects book series. Springer, New York, pp 219–255

Galán-Acedo C, Arroyo-Rodríguez V, Estrada A, Ramos-Fernandez G (2018) Drivers of the spatial scale that best predict primate responses to landscape structure. Ecography 41:2027–2037

Galán-Acedo C, Arroyo-Rodríguez V, Estrada A, Ramos-Fernandez G (2019a) Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests. Landsc Ecol 34:147–158

Galán-Acedo C, Arroyo-Rodríguez V, Cudney-Valenzuela SJ, Fahrig L (2019b) A global assessment of primate responses to landscape structure. Biol Rev 94:1605–1618

Galán-Acedo C, Arroyo-Rodríguez V, Andresen E, Arasa-Gisbert R (2019c) Ecological traits of the world's primates. Sci Data 6:1–5

Galán-Acedo C, Arroyo-Rodríguez V, Chapman CA (2021) Beyond patch size: the impact of regional context and habitat quality on three endangered primates. Perspect Ecol Conserv 19:207–215

Garber PA, Estrada A, Pavelka MSM, Luecke L (2005) New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. Springer, New York, pp 563–584

García del Valle Y, Caballero EJ, Martorell C, Ruan-Soto F, Enriquez PL (2015) Cultural significance of wild mammals in Mayan and Mestizo communities of the Lacandon Rainforest, Chiapas, Mexico. J Ethnobiol Ethnomed 11:1–14

Gestich CC, Arroyo-Rodríguez V, Saranholi BH, Cunha RGT, Setz LZF, Ribeiro MC (2021) Forest loss and fragmentation can promote the crowding effect in a forest-specialist primate. Landsc Ecol 37:147–157

Gibson L, Lee TM, Koh LP, Brook BW, Gardner, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhiet NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:378–383

Gilbert KA (2003) Primates and fragmentation of the Amazon forest. In: Marsh LK (ed) Primates in fragments: ecology and conservation. Kluwer Academic/Plenum Press, New York, pp 145–157

Global Forest Watch (2021) World Resources Institute. http://www.globalforestwatch.org.. Accessed 1 June 2022

González-Zamora A, Arroyo-Rodríguez V, Chavez O, Sanchez-Lopez S, Stoner KE, Riba-Hernández P (2009) Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. Am J Primatol 71:8–20

González-Zamora A, Arroyo-Rodríguez V, Escobar F, Rös M, Oyama K, Ibarra-Manríquez G, Stoner KE, Chapman CA (2014) Contagious deposition of seeds in spider monkeys' sleeping trees limits effective seed dispersal in fragmented landscapes. PLoS ONE 9(2):e89346

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. Bioscience 54:227–233

Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr 24:52–63

Jackson ST, Sax DF (2010) Balancing biodiversity in a changing environment: extinction debt, migration credit and species turnover. Trends Ecol Evol 25:153–160

Kelaita M, Dias PAD, Aguilar-Cucurachi MS, Canales-Espinosa D, Cortes-Ortiz L (2011) Impact of intrasexual selection on sexual dimorphism and testes size in the Mexican howler monkeys *Alouatta palliata* and *A. pigra*. Am J Phys Anthropol 146:179–187

Lande R (1987) Extinction thresholds in demographic models of territorial populations. Am Nat 130:624–635

Laurindo RS, Novaes RLM, Vizentin-Bugoni J, Gregorin R (2019) The effects of habitat loss on bat–fruit networks. Biodivers Conserv 28:589–601

Link A, de Luna AG, Alfonso F, Giraldo-Beltran P, Ramirez F (2010) Initial effects of fragmentation on the density of three neotropical primate species in two lowland forests of Colombia. Endanger Species Res 13:41–50

Lohbeck M, DeVries B, Bongers F, Martinez-Ramos M, Navarrete-Segueda A, Nicasio-Arzeta S, Siebe C, Pingarroni A, Wies G, Decuyper M (2022) Mexican agricultural frontier communities differ in forest dynamics with consequences for conservation and restoration. Remote Sens Ecol Conserv. https://doi.org/10.1002/rse2.262

Martin TE, Blackburn GA (2014) Conservation value of secondary forest habitats for endemic birds, a perspective from two widely separated tropical ecosystems. Ecography 37:250–260

McGarigal K, Cushman S, Ene E(2012) FRAGSTAT v4 (WWW Document) spatial pattern analysis program for categorical continuous maps, computer software program. Authors University of Massachusetts, Amherst. Available follow web site. www.umass.edu/landeco/research/fragstats/frags. Accessed Nov 2020

Melo FPL, Arroyo-Rodríguez V, Fahrig L, Martínez-Ramos M, Tabarelli M (2013) On the hope for biodiversity-friendly tropical landscapes. Trends Ecol Evol 28:461–468

Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L (2016) What determines the spatial extent of landscape effects on species? Landsc Ecol 31:1177–1194

Mittermeier RA, Wilson DE, Rylands AB (2013) Handbook of the mammals of the world: primates, vol 3. Lynx Edicions, Barcelona

Morante-Filho JC, Faria D, Mariano-Neto E, Rhodes J (2015) Birds in anthropogenic landscapes: the responses of ecological groups to forest loss in the Brazilian Atlantic forest. PLoS ONE 10:e0128923

Morante-Filho JC, Arroyo-Rodríguez V, Lohbeck M, Tscharntke T, Faria D (2016) Tropical forest loss and its multitrophic effects on insect herbivory. Ecology 97:3315–3325

Navarrete-Segueda A, Martínez-Ramos M, Ibarra-Manríquez G, Cortés-Flores J, Vázquez-Selem L, Siebe C (2017) Availability and species diversity of forest products in a Neotropical rainforest landscape. For Ecol Manag 406:242–250

Ordóñez-Gómez JD, Arroyo-Rodríguez V, Nicasio-Arzeta S, Cristóbal-Azkarate J (2015) Which is the appropriate scale to assess the impact of landscape spatial configuration on the diet and behavior of spider monkeys? Am J Primatol 77:56–65

Palmeirim AF, Benchimol M, Morante-Filho JC, Vieira MV, Peres CA (2018) Ecological correlates of mammal β-diversity in Amazonian land-bridge islands: from small-to large-bodied species. Divers Distrib 24:1109–1120

Piel AK, Cohen N, Kamenya S, Ndimuligo SA, Pintea L (2015) Population status of chimpanzees in the Masito-Ugalla Ecosystem, Tanzania. Am J Primatol 77:1027–1035

Poorter L, Bongers F, Aide TM, Almeyda AM, Balvanera P, Becknell JM, Boukili V, Brancalion PHS, Broadbent EN, Chazdon RL, Craven D, de Almeida-Cortez JS, Cabral GAL, de Jong BHJ, Denslow JS, Dent DH, DeWalt SJ, Dupuy JM, Durán SM, Espírito-Santo MM, Fandino MC, César RG, Hall JS, Hernandez-Stefanoni JL, Jakovac CC, Junqueira AB, Kennard D, Letcher SG, Licona JC, Lohbeck M, Marín-Spiotta E, Martínez-Ramos M, Massoca P, Meave JA, Mesquita R, Mora F, Muñoz R, Muscarella R, Nunes YRF, Ochoa-Gaona S, de Oliveira AA, Orihuela-Belmonte E, Peña-Claros M, Pérez-García EA, Piotto D, Powers JS, Rodríguez-Velázquez J, Romero-Pérez IE, Ruíz J, Saldarriaga JG, Sanchez-Azofeifa A, Schwartz NB, Steininger MK, Swenson NG, Toledo M, Uriarte M, van Breugel M, van der Wal H, Veloso MDM, F M Vester H, Vicentini A, Vieira ICG, Vizcarra Bentos T, Williamson GB, Rozendaal DMA (2016) Biomass resilience of Neotropical secondary forests. Nature 530:211–214

Prasetyo RB, Kuswanto H, Iriawan N, Ulama BSS (2019) A comparison of some link functions for binomial regression models with application to school drop-out rates in East Java. AIP Conf Proc 2194:020083

QGIS Development Team (2021) QGIS geographic information system. Open Source Geospatial Foundation. http://qgis.org

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.uage. Accessed June 2022

Ramos-Fernández G, Ayala-Orozco B (2003) Population size and habitat use of spider monkeys at Punta Laguna, Mexico. In: Marsh LK (ed) Primates in fragments. Springer, Boston, pp 191–209

Rangel-Negrín A, Coyohua-Fuentes A, Canales-Espinosa D, Dias PAD (2018a) The influence of leaf consumption on time allocation in black howler monkeys (*Alouatta pigra*). Folia Primatol 89:111–122

Rangel-Negrín A, Coyohua-Fuentes A, Chavira-Ramírez DR, Canales-Espinosa D, Dias PAD (2018b) Energetic constraints on the reproduction of female mantled howlers. Am J Primatol 81:e22925

Rios E, Benchimol M, De Vleeschouwer K, Cazetta E (2022) Spatial predictors and species' traits: evaluating what really matters for medium-sized and large mammals in the Atlantic Forest, Brazil. Mamm Rev 52:236–251

Rocha R, Ovaskainen O, López-Baucells A, Farneda FZ, Sampaio EM, Bobrowiec PED, Cabeza M, Palmeirim JM, Meyer CFJ (2018) Secondary forest regeneration benefits old-growth specialist bats in a fragmented tropical landscape. Sci Rep 8:1–9

Russildi G, Arroyo-Rodríguez V, Hernández-Ordóñez O, Pineda E, Reynoso VH (2016) Species- and community-level responses to habitat spatial changes in fragmented rainforests: assessing compensatory dynamics in amphibians and reptiles. Biodivers Conserv 25:375–392

Rybicki J, Hanski I (2013) Species–area relationships and extinction caused by habitat loss and fragmentation. Ecol Lett 16:27–38

San-José M, Arroyo-Rodríguez V, Meave JA (2020) Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. Ecol Appl 30:e02033

Shimooka Y, Campbell CJ, Di Fiore A, Felton AM, Izawa K et al (2008) Demography and group composition of *Ateles*. In: Campbell CJ et al (eds) Spider monkeys: behavior, ecology and evolution of the genus *Ateles*. Cambridge University Press, Cambridge, pp 329–348

Smith CC, Healey JR, Berenguer E, Young PJ, Taylor B et al (2021) Old-growth forest loss and secondary forest recovery across Amazonian countries. Environ Res Lett 16:085009

Supriatna J, Shekelle M, Fuad HAH, Winarni NL, Dwiyahreni AA, Farid M, Mariati S, Margules S, Prakoso B, Zakaria Z (2020) Deforestation on the Indonesian Island of Sulawesi and the loss of primate habitat. Glob Ecol Conserv 24:e01205

Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. Biol Rev 85:35–53

Thompson ME, Donnelly MA (2018) Effects of secondary forest succession on amphibians and reptiles: a review and meta-analysis. Copeia 106:10–19

Vallejos MAV, Padial AA, Simoes JR, Moteiro-Filho ELA (2019) Effects of crowding due to habitat loss on species assemblage patterns. Conserv Biol 34:405–415

Van Belle S, Kulp AE, Thiessen-Bock R, Garcia M, Estrada A (2010) Observed infanticides following a male immigration event in black howler monkeys, *Alouatta pigra*, at Palenque National Park, Mexico. Primates 51:279–284

Wallace RB (2008) Factors influencing spider monkey habitat use and ranging patterns. In: Campbell CJ (ed) Spider monkeys: behavior, ecology and evolution of the genus *Ateles*. Cambridge University Press, Cambridge, pp 138–154

Watling JI, Arroyo-Rodríguez V, Pfeifer M, Baeten L, Banks-Leite C, Cisneros LM, Fang R, Hamel-Leigue AC, Lanchat T, Leal IR, Lens L, Possingham HP, Raheem DC, Ribeiro DB, Slade EM, Urbina-Cardona JN, Wood E, Fahrig L (2020) Support for the habitat amount hypothesis from a global synthesis of species density studies. Ecol Lett 23:674–681

Wies G, Arzeta N, Martínez-Ramos M (2021) Critical ecological thresholds for conservation of tropical rainforest in human-modified landscapes. Biol Conserv 255:109023

Wright SJ, Muller-Landau HC (2006) The uncertain future of tropical forest species. Biotropica 38:443–445

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. In: Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W (eds) Statistics for biology and health, vol 574. Springer, New York, pp 209–236