




# Linking changes in landscape structure to population changes of an endangered primate

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## Abstract

**Context** Non-human primates are among the most threatened mammals on Earth. Although some species, such as howler monkeys, are thought to be resistant to initial phases of habitat disturbance, the lack of longitudinal studies prevents determining if this holds over time.

**Objectives** We assessed temporal changes in landscape structure in the Lacandona rainforest, Mexico, and how these changes relate to population trends of black howler monkeys (*Alouatta pigra*).

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**Methods** We surveyed primates in 22 forest sites in 2011 and 2017, and related temporal changes in primate abundance and immature-to-female ratio with changes in the spatial structure of local landscapes (forest cover, matrix openness, number of forest patches, and forest edge density) using a multi-scale approach.

**Results** Landscape changes occurring over a 6-year period were strongly associated with temporal changes in population parameters. Primate abundance increased as forest cover increased. Both primate abundance and immature-to-female ratio increased in sites located in landscapes where the number of patches increased over time, but where the proportion of open matrix decreased. Edge density showed a negative effect on immature-to-female ratio.

**Conclusions** This endangered primate might not be as tolerant to landscape disturbance as generally thought. Allowing forest patches to increase in number and/or size through active or passive restoration (reverse fragmentation), and preventing forest loss and an increase in matrix openness are key management strategies to preserve howler monkeys in this biodiversity hotspot.

**Keywords** Habitat loss · Habitat fragmentation · Human-modified landscape · Scale of effect · Tropical rainforest

## Introduction

Deforestation of tropical forests represents one of the biggest threats to biodiversity (Gibson et al. 2011). Tropical forests are being rapidly converted to human-modified landscapes, comprised of patches of native ecosystems surrounded by a matrix of anthropogenic land-cover types, such as crops, secondary forests and human settlements (Melo et al. 2013). Depending on the presence of different land-cover types and their proportions (i.e., landscape composition) as well as their spatial distribution and physiognomy (i.e., landscape configuration), landscapes can have a highly heterogeneous spatial structure, with variable impacts on wildlife (Fahrig et al. 2011). Whereas most species are negatively affected by the loss of forest cover, species' responses to other landscape attributes are highly variable (Fahrig 2003, 2017; Galán-Acedo et al. 2019a).

Human-modified landscapes are not only heterogeneous in their spatial dimension, but also temporally, as forest patches can increase or decrease in size, or change into another vegetation type (del Castillo 2015). However, few studies in anthropogenic landscapes have considered this temporal dynamism, which requires using longitudinal and multi-scale approaches (Ewers et al. 2013; Fahrig 2013). Longitudinal studies encompassing larger time periods are important for identifying lagged species' responses to changes in land-use and landscape structure (Metzger et al. 2009; Hanski 2013), particularly in the case of long-lived taxa, such as primates.

Primates play important ecological functions in the ecosystems they inhabit (da Silva et al. 2015; Andresen et al. 2018), but they are also among the most threatened groups of animals globally, mainly due to habitat loss, hunting and emergent diseases (Estrada et al. 2017). Several studies have assessed the importance of spatial characteristics of the habitat in determining primate abundance and distribution. These studies have found that both site-level variables (e.g., size, shape and isolation of forest patches; Anzures-Dadda and Manson 2007; Arroyo-Rodríguez et al. 2013; Benchimol and Peres 2013b; Puig-Lagunes et al. 2016), and landscape-level variables (e.g., forest cover, level of fragmentation, mean distance among patches and matrix quality; Arroyo-Rodríguez et al. 2013; Benchimol and Peres 2013b; da Silva et al. 2015; Galán-Acedo et al. 2019a), can affect

the presence and/or abundance of primates. However, as most studies have been carried out at single temporal and spatial scales, additional assessments of primates' responses to spatial changes through time are needed to design effective long-term conservation strategies (Chapman et al. 2018; Galán-Acedo et al. 2019a).

Southern Mexico represents the northernmost distribution limit of Neotropical primates and is inhabited by three species: *Alouatta pigra*, *A. palliata* and *Ateles geoffroyi* (Estrada and Coates-Estrada 1996). Among these species, the black howler monkey (*A. pigra*) has the most restricted distribution (Horwich and Johnson 1986). Throughout the geographic range of this primate, rainforests have been degraded, fragmented and converted into agricultural lands, threatening their populations (Estrada et al. 2002). It has been suggested that all howler monkeys (*Alouatta* spp.) are relatively resistant to the initial phases of habitat disturbance, due to their flexible diet and small area requirements (Silver et al. 1998; Kowalewski and Zunino 1999; Rangel-Negrín et al. 2014). However, they can be negatively affected by ongoing habitat loss and degradation, potentially becoming locally or regionally extinct in the long run (e.g., Van Belle and Estrada 2005; Dias et al. 2015; Puig-Lagunes et al. 2016). Potential negative effects of habitat disturbance on black howler monkeys include altered dispersal and reproductive patterns, and increased endogamy, stress levels, disease incidence and mortality rates (Arroyo-Rodríguez and Dias 2010).

Although longitudinal studies on primate responses to habitat changes—and in particular for howler monkeys—are scarce, they are becoming more frequent. One patch-scale study of *Alouatta caraya* in northern Argentina used a longitudinal approach (1984–1995) and concluded that these primates were resilient to deforestation (Kowalewski and Zunino 1999). Similarly, Cristóbal-Azkarate et al. (2017) showed that between 2000 and 2011 there was an increase in the number of individuals of *A. palliata* in forest patches at Los Tuxtlas, Mexico. However, a 7-year study of *A. pigra* in Campeche, Mexico, showed that population growth and infant survival were negatively related to habitat disturbance (Dias et al. 2015). Yet, to our knowledge, no study to date has linked the temporal changes in landscape-scale spatial patterns to changes in population parameters of these primates. As primates in general (Galán-Acedo

et al. 2019a, b) and howler monkeys in particular (e.g., Asensio et al. 2009; Pozo-Montuy et al. 2013) can travel in and out of habitat patches, they may be more strongly affected by the spatial structure of surrounding landscapes than by the characteristics of individual patches (see Fahrig 2013). Therefore, additional longitudinal landscape-scale studies are needed to better understand the impact of land-use change on this forest-specialist species.

Here, we present the first longitudinal assessment of the effects of landscape changes on black howler monkeys in the Lacandona rainforest, a biodiversity hotspot that maintains the highest mammal biodiversity in Mexico (Medellín 1994). Despite its great ecological importance, the region has undergone an intense and continuous process of land-use change, with high deforestation and degradation rates throughout the last three decades, mainly due to agriculture (Carabias et al. 2015). In a period of 6 years we quantified structural landscape changes in terms of both its composition (i.e., forest cover and matrix openness) and configuration (i.e., number of forest patches and edge density). We then related these changes to those recorded in two important black howler monkey population parameters (i.e., number of individuals and immature-to-female ratio). Due to the relatively recent history of deforestation in the region, we expected to find high variability in the change of all landscape variables, as well as in the change of population parameters among study sites. We expected to find a positive effect of forest cover on both population parameters because this landscape metric is a proxy of resource availability and landscape connectivity. Number of patches (fragmentation level) and forest edge density are also predicted to have positive effects on both population parameters because these two metrics are negatively related to mean patch isolation distance (Fahrig 2003, 2017), and can therefore favor inter-patch animal movements and food availability through landscape supplementation dynamics (Dunning et al. 1992; Asensio et al. 2009). Following a similar rationale, we expected to find a negative impact of an increase in the proportion of the matrix covered by open (i.e., treeless) land uses because such increase is expected to limit landscape connectivity and resource availability for arboreal primates (Galán-Acedo et al. 2019a, b).

## Methods

### Compliance with ethical standards

This research is based on observational data. It adhered to national and international guidelines and was conducted in accordance with the legal requirements of the National Autonomous University of Mexico (UNAM), and the country of Mexico (NOM-059: SEMARNAT 2010). We were granted access to all study sites by landowners and authorities.

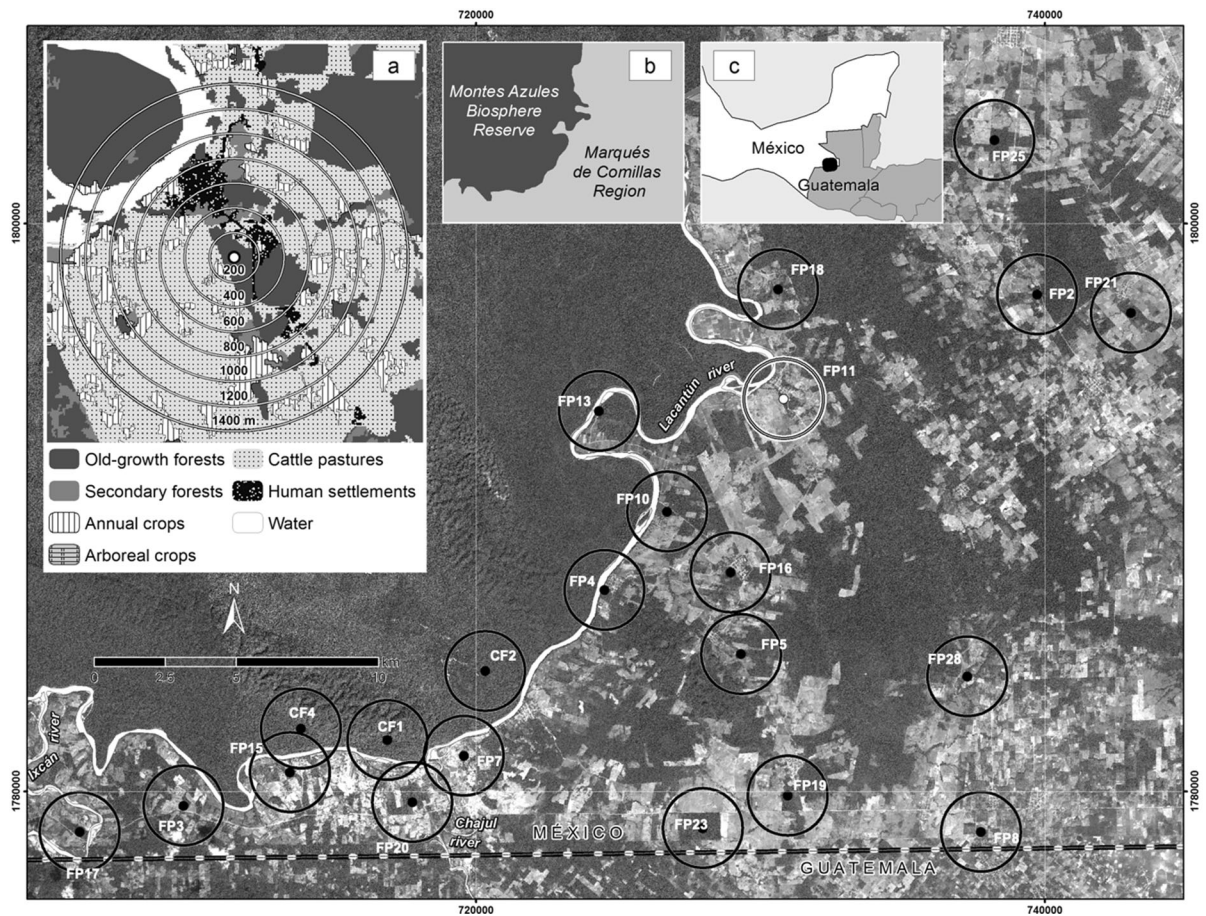
### Study area

The Lacandona rainforest, located in the northeast of the Mexican state of Chiapas (16°05'N, 90°25'W; Fig. 1), has a warm-humid climate, with average temperatures ranging from 24 to 26 °C and annual mean rainfall ranging from 2500 to 3500 mm (Instituto Nacional de Ecología 2000). The region, originally covered by old-growth tropical rainforest, has a high biodiversity and is considered of high conservation priority in Mexico (Arriaga et al. 2000). However, the area is highly threatened by anthropic pressures, such as land-use change and illegal extraction of fauna and flora (Carabias et al. 2015). To protect its biodiversity, the Montes Azules Biosphere Reserve was established in the northern part of the region, encompassing 331,200 ha of continuous tropical rainforest (Instituto Nacional de Ecología 2000). However, south from this reserve, the Marqués de Comillas Region comprises 203,999 ha of anthropic lands, where different-sized forest patches are surrounded by a matrix of agricultural lands, successional vegetation and human settlements. We conducted this study in 22 forest sites located at similar altitude (1–200 m a.s.l.): 19 forest patches (3–92 ha) in Marqués de Comillas and three continuous forest sites inside the biosphere reserve (Fig. 1).

### Study species

The black howler monkey (*Alouatta pigra*) has a restricted distribution, being endemic to Mexico, Belize and Guatemala. It mainly inhabits primary tropical forests but can also be found in disturbed forests (Arroyo-Rodríguez et al. 2013; Dias et al. 2015). Its diet is flexible (from highly folivorous to highly frugivorous, depending on food availability;





**Fig. 1** Location of the 22 forest sites in the Lacandona rainforest, Mexico. Points represent the center of each site. From the center of each site we estimated the spatial structure of seven different-sized landscapes of seven different-sized landscapes (radii of 200 m to 1400 m, at 200-m intervals, from the center of each forest site). Circles surrounding each point represent the largest buffer, i.e., 1400-m radius. **a** Close-up in white point, representing the land-cover classification used (i.e.,

old-growth forests, secondary forests, annual crops, arboreal crops, cattle pastures, human settlements and water) and the different-sized landscapes surrounding each site (radii of 200 m to 1400 m, at 200-m intervals, from the center of each forest site). **b** Schematic map, showing the Montes Azules Biosphere Reserve, and the Marqués de Comillas region. **c** Location map

Dias and Rangel-Negrín 2015). Group sizes range from 2 to 12 individuals (Crockett and Eisenberg 1987; Van Belle and Estrada 2008). According to the IUCN's Red List and Mexico's legislation, the species is considered Endangered, with declining populations (Marsh et al. 2008; SEMARNAT 2010).

#### Landscape metrics

We used a patch-landscape approach (sensu Fahrig 2013), in which we measured response variables in the 22 forest sites, whereas the explanatory variables were measured in the local landscapes containing each site. Given a home range size for black howler monkeys of

$6.3 \pm 1.1$  ha (mean  $\pm$  SD) and a daily ranging distance of  $393 \pm 74$  m (Fortes et al. 2015), we considered sites as independent, as forest patches were separated by more than 1.5 km and continuous forest sites by more than 2.5 km. We used high resolution (10 m) satellite images from 2010 (SPOT 5) and 2016 (Sentinel 2 A), produced by sensors with comparable radiometric features (Hagolle et al. 2015). Using Spring 3.3 (Camara et al. 1996), we identified six land-cover types: old-growth forest, secondary forest, cattle pasture, annual crop (e.g., chili pepper, corn), arboreal crop (e.g., rubber, oil palm), and human settlement (e.g., houses, roads) (see Step 1, Fig. A1). Following the map validation procedure proposed by Olofsson

et al. (2014), we obtained a classification accuracy of 80.0% in 2010 and 80.3% in 2016, with inaccuracies mainly caused by the differentiation between annual crops and pastures. As these two land cover types were pooled in our analyses, such inaccuracies did not affect our results.

We characterized landscape structure using five variables: three configurational variables (number of forest patches, edge density and mean inter-patch distance) and two compositional variables (percentage of forest cover and matrix openness in the landscapes containing each patch) (Step 2, Fig. A1). We tested these landscape predictors because they can have strong effects on primate populations (Galán-Acedo et al. 2019a), especially on black howler monkey abundance in the region (Arroyo-Rodríguez et al. 2013). The description and ecological justification of the selected landscape metrics are presented in Table 1. As species' responses to landscape structure may be scale-dependent (Jackson and Fahrig 2015), we assessed the effect of each landscape metric in seven different-sized landscapes containing each forest site (radii from 200 m to 1400 m, at 200-m intervals, from the center of each site), to determine

the scale of effect (see below). Except in two cases, the 1400 m radius was the largest radius that still avoided spatial overlap between the buffers of two sites, thus increasing independence between sample units (Eigenbrod et al. 2011). The smaller scales (200- and 400-m radius) were included following Jackson and Fahrig (2015), who recommend that to avoid measuring landscape structure at suboptimal scales, the scales at which landscape variables are measured should range widely, from the size of a single territory to well above the average dispersal distance. As stated above, the home range size of howler monkeys averages 6.3 ha, but larger sizes have been reported (reviewed by Galán-Acedo et al. 2019c). Therefore, the 200-m radius (12.6 ha) can represent the territory size of a black howler monkeys' group. Although relatively small, this landscape size was large enough to show a high variation in all explanatory variables (Supplementary Material, Table A1), which is needed to make accurate landscape-scale inferences (Eigenbrod et al. 2011). In eight fragmented sites close to the river, some buffers included a portion of the biosphere reserve, whereas buffers of two continuous forest sites presented some overlap with the fragmented area

**Table 1** Definition and ecological justification of the landscape metrics assessed in the study

Landscape metric	Metric description	Ecological interpretation	Refs. <sup>a</sup>
Forest cover	Percentage of landscape area covered by old-growth forest cover	A proxy of landscape-scale habitat amount, resource availability and landscape connectivity	1,2,3
Matrix openness	Percentage of the matrix composed of treeless areas (i.e., cattle pastures, annual crops and human settlements)	Open-area matrices increase negative edge effects and limit inter-patch movements. These matrices also limit landscape supplementation dynamics	2,3,4
Number of patches	Number of forest patches in the landscape	Positively related to landscape connectedness and the number of subpopulations in the landscape. Also, landscape supplementation dynamics may be enhanced in landscapes with more patches	2,5
Edge density	Length of all old-growth forest edges divided by total landscape area (m/ha)	Positively related to landscape connectedness and availability of pioneer tree species (which can be important food resources for howler monkeys, such as <i>Cecropia obtusifolia</i> ). But it can also have negative impacts on primates through negative edge effects, such as an increased mortality of emergent trees at forest edges	2,5,6
Inter-patch distance	Average value (m) of the shortest edge-to-edge distance between all possible pairs of patches in the landscape	Inversely related to landscape connectedness, with potential negative effects on inter-patch animal movements	2,6

<sup>a</sup>1. Fahrig (2003); 2. McGarigal et al. (2012); 3. Fahrig (2017); 4. Galán-Acedo et al. (2019a); 5. Dunning et al. (1992) and 6. Bennet and Saunders (2010)

(Fig. 1). In all these cases, as the river represents a barrier for howler monkey populations, we excluded the spatial information from the other side of the river, i.e., for the forest patches whose buffers included the continuous forest, we excluded the area covered by continuous forest from the spatial characterization of the patches' matrix, and vice versa for the two continuous forest sites whose buffers included the fragmented region.

### Primate surveys

We conducted surveys between April and October in 2011 and 2017, using the same methods applied in previous research on the species (e.g., Rosales-Meda et al. 2008; Arroyo-Rodríguez et al. 2013). Briefly, two people walked slowly (1 km/h) inside and around each forest site, starting at 6:00 h, looking for groups and locating them by their long-distance vocalizations. Survey duration in each site varied according to area: 2 days for 3–4 h each day in small patches (< 10 ha), 3 days for 5–6 h daily in medium-sized patches (10–50 ha), 4 days for 7–8 h daily in larger patches (> 50 ha), and 5 days for 9–10 h daily in continuous forest sites. Surveys in the continuous forest sites were restricted to an area of approximately 100 ha to standardize sampling area. Once we established visual contact with howler monkeys, we registered the geographical position of the group with a GPS and counted individuals, classifying each one as adult male, adult female, juvenile or infant (Rosales-Meda et al. 2008). We then obtained primate abundance from the total number of individuals observed during the surveys and calculated the immature-to-female ratio as the number of infants and juveniles divided by the number of adult females. The ratio of immatures to females is a measure of successful reproduction commonly used in howler monkey studies (e.g., Cristóbal-Askarate et al. 2005; Arroyo-Rodríguez et al. 2008); yet, it is not only affected by female reproductive output and immature survival, but also by variations in the abundance of adult females.

### Data analyses

All analyses were carried out using R version 3.5.1 (R Core Team 2018). We first tested for differences in population parameters between continuous forest sites and forest patches with t-Student tests. We then

obtained the differences between years (2016 values–2010 values) for each landscape metric (forest cover, matrix openness, number of patches, edge density and mean inter-patch distance; Table A1) and used generalized linear mixed models to evaluate such differences at the largest scale (1400-m radius landscape; Fig. A2). We used the same analysis for assessing differences in each primate population parameter (primate abundance and immature-to-female ratio) between years (2011–2017). For percentage of forest cover and matrix openness we selected a binomial distribution with a logit link-function. All other variables were log-transformed to normalize their residuals and analyzed with a normal error distribution and identity link-function. We assessed model fit with a Shapiro–Wilk test on model residuals. For all models, we used year as a fixed factor, and site ID as a random factor. To assess whether complete models (i.e., with both fixed and random factors) were a better fit for dependent variables than solely the random factors, we used likelihood ratio tests. In these tests we compared null models including only the random factor with the complete models (Pinheiro and Bates 2000). We evaluated the change in landscape drivers (landscape  $\Delta$ s = 2016 values–2010 values) and the changes in howler monkeys' demographic attributes (primate  $\Delta$ s = 2017 values–2011 values) (Steps 3–4, Fig. A1). Positive delta values ( $\Delta$ ) indicate that a variable increased through time, i.e., it showed a higher value in 2017/2016 than in 2011/2010, whereas negative values indicate the opposite.

As we did not know a priori the landscape size that better predicted primate population responses to changes in landscape structure, we followed Jackson and Fahrig (2015) to determine the scale of effect of each landscape metric change (Step 5, Fig. A1). We used generalized linear models to quantify the association between the change in each landscape metric (landscape  $\Delta$ s) and the change in each demographic attribute (primate  $\Delta$ s). We obtained the AIC (Akaike's Information Criterion) and the percentage of explained deviance of each univariate model to identify the spatial scale (i.e., length of the radius of the circular landscape, measured from the center of each forest site) at which the strongest relationship occurred (lowest AIC and highest percentage of explained deviance). Most scales of effect were relatively small (Table A2). In 3 out of 8 cases, monkeys responded most strongly to landscape

metrics measured at the 200-m radius, and in another 3 cases, to metrics measured at the 400-m radius. These scales of effect are within the range reported in other studies (Ordóñez-Gómez et al. 2015; Galán-Acedo et al. 2018; Gestich et al. 2019), and can be related to the relatively small home-range size of the species.

Finally, we used a multimodel averaging approach (Burnham and Anderson 2002) with generalized linear models to assess the relationship between the landscape  $\Delta$ s (measured at their scale of effect; Table A2) and the primates  $\Delta$ s (Step 6, Fig. A1). We used the ‘glmulti’ package (Calcagno and de Mazancourt 2010), selecting a normal distribution with an identity-link function. To avoid multicollinearity among multiple models, we estimated the Variance Inflation Factor (VIF) for each predictor, using the ‘car’ package (Fox and Weisberg 2011). In several cases VIF values for mean inter-patch distance were higher than 4, indicating collinearity (Neter et al. 1996). Since this landscape predictor was negatively correlated with forest cover ( $r = -0.91$ ), we excluded it from analyses. For each response variable (primate  $\Delta$ s) we then constructed 16 models, representing all combinations of the four explanatory variables ( $\Delta$ forest cover,  $\Delta$ matrix openness,  $\Delta$ edge density and  $\Delta$ number of patches) and the null model (which includes only the intercept). We calculated the Akaike Information Criterion of each model corrected for small samples (AICc) and arranged the models from best to worst (i.e., lowest to highest AICc). We obtained model-averaged parameter estimates using Akaike weights ( $w_i$ ). Then, we calculated the sum of Akaike weights ( $\sum w_i$ ) of each  $\Delta$  landscape predictor, which represents the probability that this predictor is within the true best model (Burnham and Anderson 2002). To be conservative, we considered a landscape attribute as an important explanatory variable if the following three criteria were met: (i) it showed a relatively high sum of Akaike weights; (ii) the model-averaged unconditional variance was lower than the model-averaged parameter estimate; and (iii) the complete model showed a relatively high percentage of explained deviance (i.e., relatively high goodness-of-fit; Burnham and Anderson 2002).

## Results

Population parameters did not differ between continuous and fragmented forests (primate abundance:  $t = 0.39$ ,  $p = 0.70$ ; immature-to-female ratio:  $t = 0.56$ ,  $p = 0.58$ ). Landscape structure changed through time, with high variability in those changes among sites (Table A1; Fig. A2). The percentage of forest cover (full model vs. null model:  $\chi^2 = 5.6$ ,  $p < 0.02$ ) and matrix openness ( $\chi^2 = 7.5$ ,  $p < 0.01$ ), showed a significant increase from 2010 to 2016 (Table 2). Total primate abundance ( $\chi^2 = 4.2$ ,  $p < 0.04$ ) and the immature-to-female ratio ( $\chi^2 = 11.3$ ,  $p < 0.001$ ) also differed between years, with an increase of 27% in the number of monkeys between 2011 and 2017, and a decrease of 35% in the immature-to-female ratio (Tables 2, 3). Three forest patches did not present any individuals in both years (Table 3).

We found clear associations between the temporal changes in landscape structure (measured at their scale of effect, Table A2) and the temporal changes in primate population parameters (Fig. 2). Yet, based on the goodness-of-fit of the models, changes in the immature-to-female ratio (59% of explained deviance) were better predicted by changes in landscape structure than changes in primate abundance (34%). All model-averaged parameter estimates (slopes) were higher than their respective unconditional variances, suggesting confidence in the estimations (Table A3). Considering the sum of Akaike weights ( $\sum w_i$ ), changes in howler monkey populations were better predicted by changes in the number of patches and changes in forest edge density than by changes in matrix openness and forest cover. In particular, both demographic variables increased in forest sites found in landscapes where the number of forest patches increased through time (Fig. 2a, b). Yet, the immature-to-female ratio decreased in sites found in landscapes in which the density of forest edges increased (Fig. 2b; Table 4). Changes in matrix openness were also negatively related to changes in immature-to-female ratio (Fig. 2a, b; Table A2). The association between changes in forest cover and changes in population parameters was positive, being more important for primate abundance than for immature-to-female ratio (Fig. 2a; Table 4).



**Table 2** Landscape composition and configuration metrics and *Alouatta pigra* population parameters sampled in two different years in the Lacandona rainforest, Mexico. Mean ( $\pm$  SD) values are indicated

Variables	Year		$\beta$	SE	<i>t</i>	p
	2010	2016				
Landscape metrics						
Compositional metrics						
Forest cover (%)	52.5 $\pm$ 23.9	53.5 $\pm$ 23.1	0.011	0.005	2.36	0.02
Matrix openness (%)	70.4 $\pm$ 29.6	73.0 $\pm$ 31.7	0.081	0.008	10.7	< 0.001
Configurational metrics						
Number of patches	18.0 $\pm$ 12.5	16.5 $\pm$ 10.7	- 0.371	0.192	- 1.94	0.07
Edge density (m/ha)	65.9 $\pm$ 30.1	64.1 $\pm$ 34.1	- 0.009	0.008	- 1.06	0.30
Demographic attributes	2011	2017				
Number of individuals	11.7 $\pm$ 8.7	16.0 $\pm$ 10.9	0.045	0.021	2.14	0.047
Immature-to-female ratio	0.9 $\pm$ 0.5	0.6 $\pm$ 0.4	- 0.105	0.029	- 3.67	0.002

Landscape metrics were recorded in buffers with 1400-m radii measured from the center of each forest site (N = 22). Demographic attributes come only from forest sites occupied by howler monkeys (N = 19). Differences between years were evaluated with generalized linear mixed models and a likelihood ratio test. We show the  $\beta$ -estimate and standard error (SE) of each model

## Discussion

This longitudinal study is the first to assess the effects of temporal and spatial changes in landscape structure on demographic attributes of the black howler monkey—an endangered primate with a highly restricted distribution (Marsh et al. 2008). Our findings indicate that the Mexican portion of the Lacandona rainforest is highly dynamic, with different sites undergoing contrasting changes in landscape structure through time. Howler monkeys responded strongly to such changes, including those describing landscape configuration (i.e., number of forest patches and forest edge density) and those associated with landscape composition (i.e., forest cover and matrix openness). As predicted, the number of individuals increased in sites located in landscapes in which forest cover increased. Additionally, both the number of individuals and immature-to-female ratio increased in sites surrounded by landscapes with increasing number of patches over time, but where the proportion of treeless land decreased in the matrix. Yet, in contrast to our predictions, the immature-to-female ratio decreased in sites with an increasing density of forest edges. These novel findings indicate that this primate species might not be as tolerant to landscape disturbance as generally thought (e.g., Silver et al. 1998; Rangel-Negrín et al. 2014), as both population parameters were clearly

associated with landscape changes occurring over a relatively short (6 years) time period.

The number of individuals increased through time. This finding is unexpected because this species has a relatively long life-span (> 30 years: Glander 2004) and a slow life-history (e.g., mean interbirth interval = 18 months: Dias et al. 2016)—attributes that can result in time-lagged responses to habitat disturbance (Metzger et al. 2009). Such a relatively rapid increase can be related to two non-exclusive mechanisms. First, the continuous deforestation in the region could be pushing the remaining individuals to take refuge in remnant forest patches, causing them to concentrate there. This phenomenon is known as the ‘crowding effect’, and has been shown to occur in forest-specialist species, including insects (Grez et al. 2004), terrestrial mammals (Laurance 1991; Arce-Peña et al. 2019), and howler monkeys (Arroyo-Rodríguez and Dias 2010). The second mechanism is related to the social system of this primate. Howler monkeys live in groups that constantly move around the landscape in the search of resources (Estrada 1984; Crockett and Eisenberg 1987). Both males and females immigrate from their natal groups to enter other groups or form new groups (Crockett and Eisenberg 1987). Thus, it could be possible that individuals in forest patches are not being able to disperse from their natal group due to an increasingly open and inhospitable matrix (Arroyo-Rodríguez and



**Table 3** Results of *Alouatta pigra* population monitoring in the Lacandona rainforest in 2011 and 2017, and the deltas between years (2017 values–2011 values) in three continuous forest sites (CF) and 19 forest patches (FP)

Site	2011						2017						Deltas					
	AM	AF	J	IN	I/F	TA	AM	AF	J	IN	I/F	TA	AM	AF	J	IN	I/F	TA
CF1	4	3	1	1	0.67	9	2	2	1	0	0.5	5	-2	-1	0	-1	-0.2	-4
CF3	6	3	3	0	1	12	4	5	1	0	0.2	10	-2	2	-2	0	-0.8	-2
CF4	4	3	2	1	1	10	9	9	6	0	0.67	24	5	6	4	-1	-0.3	14
FP2	2	3	2	1	1	8	6	4	2	1	0.75	13	4	1	0	0	-0.3	5
FP3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FP4	3	2	0	0	0	5	7	4	3	1	1	15	4	2	3	1	1	10
FP5	3	2	3	0	1.5	8	2	2	2	1	1.5	7	-1	0	-1	1	0	-1
FP7	2	1	1	0	1	4	1	3	1	0	0.33	5	-1	2	0	0	-0.7	1
FP8	0	0	0	0	0	0	1	4	1	0	0.25	6	1	4	1	0	0.25	6
FP10	4	1	2	0	2	7	3	4	2	0	0.5	9	-1	3	0	0	-1.5	2
FP11	8	7	5	3	1.14	23	6	8	1	1	0.25	16	-2	1	-4	-2	-0.9	-7
FP13	3	3	3	1	1.33	10	5	5	1	1	0.4	12	2	2	-2	0	-0.9	2
FP15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FP16	1	2	0	1	0.5	4	7	5	6	3	1.8	21	6	3	6	2	1.3	17
FP17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FP18	10	12	11	2	1.08	35	11	15	8	2	0.67	36	1	3	-3	0	-0.4	1
FP19	2	6	2	0	0.33	10	5	9	1	1	0.22	16	3	3	-1	1	-0.1	6
FP20	5	3	2	0	0.67	10	4	7	1	2	0.43	14	-1	4	-1	2	-0.2	4
FP21	8	10	5	2	0.7	25	19	13	6	1	0.54	39	11	3	1	-1	-0.2	14
FP23	2	5	3	2	1	12	3	7	1	2	0.43	13	1	2	-2	0	-0.6	1
FP25	7	9	5	2	0.78	23	14	15	6	2	0.53	37	7	6	1	0	-0.2	14
FP28	3	1	1	1	2	6	2	2	1	0	0.5	5	-1	1	0	-1	-1.5	-1

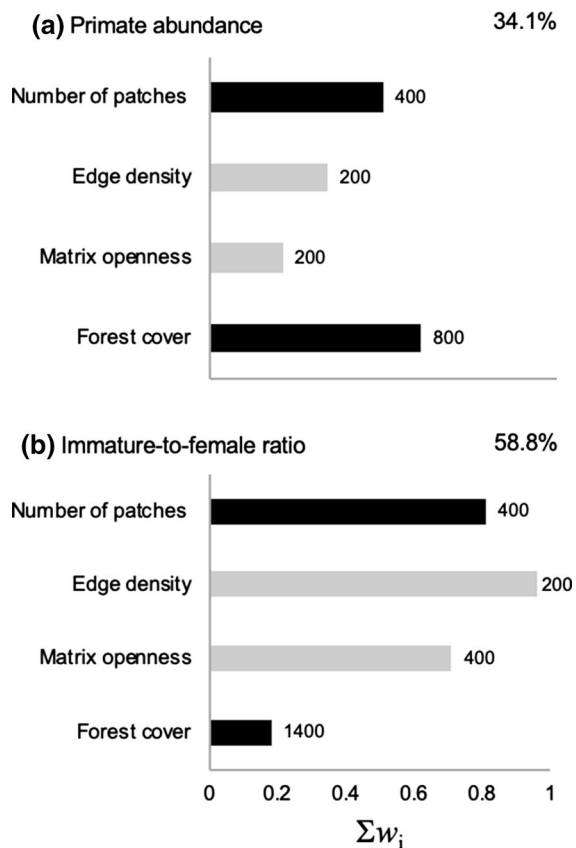
Sites IDs correspond to those showed in Fig. 1 and Table A1

AM adult males, AF adult females, J juveniles, IN infants, I/F immature-to-female ratio, TA total abundance

Dias 2010). Whatever the cause of such accumulation of individuals, it could have negative impacts on the long-term persistence of howler monkey populations. For example, high population densities can cause a reduction in food availability and an increase in competition (Cristóbal-Azkarate and Arroyo-Rodríguez 2007). Furthermore, high densities can cause higher levels of disease and parasitism (Arroyo-Rodríguez and Dias 2010), which are important mortality causes in howler monkeys (Holzmann et al. 2010). Therefore, increasing landscape connectivity can be critical for primate conservation in the region (see below).

The disruption of female emigration from natal groups could explain the observed decrease in immature-to-female ratio. The number of immature

individuals was similar in both years, averaging 3.6 individuals in 2011 and 2017 (Table 3). Yet, the mean number of adult females was 38% higher in 2017 (6.5 individuals) than 2011 (4 individuals) (Table 3). Dias et al. (2015) show that the number of immature individuals is usually stable through time in a fragmented forest, and that females migrate from natal groups at the age of  $\sim 4$  years. Thus, the observed decrease in immature-to-female ratio in our study could be caused by a lack of female migration due to spatial changes in landscape structure, such as the increase in matrix openness. Consistent with this idea, the number of females increased more in forest patches surrounded by increasing matrix openness (Table A1). However, the number of females also increased in two continuous sites where dispersal



**Fig. 2** Effect of landscape structure change (landscape  $\Delta$ s) between 2016 and 2010 on changes in population parameters (primate  $\Delta$ s) of black howler monkeys (*Alouatta pigra*) between 2017 and 2011 in the Lacandona rainforest, Mexico. We assessed changes in primate abundance (a), and immature-to-female ratio (b). We present the sum of Akaike weights ( $\Sigma w_i$ ) of each landscape predictor, showing both positive parameter estimates (black), and negative parameter estimates (grey). We also indicate the values of pseudo- $R^2$ , i.e., the percentage of deviance explained by complete models. Values at the right side of each bar are the scale of effects (i.e., radius in meters of landscape buffers) of each landscape metric on each response (see details in Table A2)

movements are not limited. In these cases, the increase in female abundance could actually be associated to immigrations of females from other landscapes.

The number of individuals, but more importantly the immature-to-female ratio, increased with increasing the number of fragments, i.e., increasing fragmentation. These results support a recent review of species' responses to habitat fragmentation per se by Fahrig (2017), which suggests that significant responses to fragmentation are mostly positive. Galán-Acedo et al. (2019a) also found a similar

pattern in a review of primate responses to fragmentation, and other case studies indicate that howler monkeys are not the exception (Anzures-Dadda and Manson 2007; Arroyo-Rodríguez et al. 2013). Therefore, our findings support that mechanisms resulting in positive responses to fragmentation may be more important than those resulting in negative responses (reviewed by Fahrig et al. 2019). For example, a high number of patches remaining in the landscape can reduce inter-patch isolation distances and facilitate animal movements between patches (Anzures-Dadda and Manson 2007; Fahrig 2017). Decreasing isolation distances can also reduce movement-related risks and favor landscape-scale processes critical for population maintenance in fragmented landscapes, such as source/sink dynamics and landscape supplementation dynamics (sensu Dunning et al. 1992). Finally, as the number of patches increases, the number of sub-populations can also increase, which can facilitate metapopulation persistence (Hanski 1999). Therefore, increasing the number of forest patches while simultaneously maintaining or increasing forest cover in the landscape could favor primate conservation in the region. Of course, this does not mean that we should break apart the remaining patches because this would result in habitat loss—a critical threat to howler monkeys (present study), and other primates (Galán-Acedo et al. 2019a). We rather suggest increasing the number of forest patches through active or passive restoration (the so-called 'reverse fragmentation'; sensu del Castillo 2015), which would result in an increase in both habitat amount and landscape connectedness.

The fact that the number of individuals increased in sites that showed an increase in forest cover over time is not surprising. For arboreal primates, forest cover is a proxy of habitat amount in the landscape, as they depend on forest for finding food, shelter, and sites for reproduction (Da Silva et al. 2015). Arroyo-Rodríguez et al. (2008) also report that landscapes with higher forest cover have a higher number of howler monkeys (*A. palliata*) in the Los Tuxtlas rainforest, Mexico. In fact, this landscape variable is an important predictor of primate distribution, abundance and richness in fragmented forests across the world (da Silva et al. 2015; Dias et al. 2015; Puig-Lagunes et al. 2016; Galán-Acedo et al. 2019a). Percentage of forest cover also has positive effects on many other forest-dependent taxa (Benchimol and Peres 2013a; Morante-Filho

**Table 4** Additive models assessing the relationship between changes in the abundance of howler monkeys and immature-to-female ratio (primate  $\Delta s = 2017$  values–2011 values), andchanges in landscape structure (landscape  $\Delta s = 2016$  values–2010 values). We show the five best models for both primate response variables

Model		AICc	$w_i$	$\Delta AICc$	%ED
Primate abundance	1 + FC + NP	146.76	0.21	0	26.73
Primate abundance	1 + FC	147.77	0.12	1.01	11.99
Primate abundance	1	147.88	0.12	1.12	0
Primate abundance	1 + FC + NP + ED	148.36	0.09	1.6	32.47
Primate abundance	1 + NP	148.61	0.08	1.85	8.56
Immature-to-female ratio	1 + NP + MO + ED	37.87	0.46	0	58.09
Immature-to-female ratio	1 + NP + ED	39.75	0.18	1.88	46.48
Immature-to-female ratio	1 + MO + ED	40.76	0.11	2.89	43.92
Immature-to-female ratio	1 + FC + NP + MO + ED	41.06	0.09	3.19	59.36
Immature-to-female ratio	1 + FC + NP + ED	42.71	0.04	4.84	47.55

We present results of Akaike's Information Criterion for small samples (AICc), the sum of Akaike Weights ( $w_i$ ), the difference between each model and the best model ( $\Delta AICc$ ), and the percentage of deviance explained by each model (%ED)

FC Forest cover, NP number of patches, MO matrix openness, ED edge density

et al. 2018), probably due to its positive association with landscape connectedness and resource availability (Fahrig 2003, 2013). Therefore, prevention of forest loss and increase in forest cover (e.g., through restoration) are needed to preserve howler monkeys.

Our findings also highlight the key role played by matrix quality in maintaining howler monkey populations. Matrix openness was negatively related to both population parameters, but more importantly to the immature-to-female ratio. The importance of the matrix for primate populations had been reported in a previous study of black howlers in the region (Arroyo-Rodríguez et al. 2013), as well as in a global review of primate responses to landscape structure (Galán-Acedo et al. 2019a). As other primates (Arroyo-Rodríguez et al. 2017; Galán-Acedo et al. 2019b), black howler monkeys can use the matrix for feeding and traveling, but such use depends on matrix quality, which in this case was related to the availability of trees in the matrix (Arroyo-Rodríguez et al. 2017). Thus, the increase of treeless areas in the matrix limits resource availability and landscape connectedness, and 'forces' primates to inhabit the remaining forest patches (Dias et al. 2015). Although howler monkeys can move through highly disturbed matrices to reach isolated food patches (Fortes et al. 2015), these movements involve risks such as road kills, predation, and hunting, especially for immature individuals. Therefore, consistent with previous studies (Arroyo-Rodríguez et al.

2017; Galán-Acedo et al. 2019a, b), matrix enrichment with native food-plant trees and creation of wooded corridors may be critical for primate conservation. Decreasing matrix openness by changing open-area matrices (e.g., annual crops, cattle pastures) to different arboreal crops (e.g., mango, guava) and agroforests (e.g., shade coffee and cacao plantations) can have numerous benefits for both primates and humans (see Arroyo-Rodríguez et al. 2017).

Finally, in contrast to our prediction, the immature-to-female ratio decreased in landscapes where edge density increased through time. This result could represent two non-exclusive effects of edge density on primate populations: (i) a positive effect on the number of adult females, and (ii) a negative effect on the number of immatures. Positive effects on adult individuals have been previously reported (Arroyo-Rodríguez et al. 2013), probably because sites surrounded by higher edge density can be better connected to other patches. In particular, edge density is higher in landscapes dominated by patches with more complex shapes, and such patches can be more frequently colonized by dispersing fauna (Ewers and Didham 2006). Edge density can also increase food availability through landscape supplementation dynamics (Dunning et al. 1992; Asensio et al. 2009), as the amount of forest that is in contact with the anthropogenic matrix increases with edge density. In fact, forest edges are typically dominated by fast-

growing light-demanding tree species, and these highly productive trees (e.g., *Cecropia*, *Ficus*) are known to be top food species for howler monkeys (Dias and Rangel-Negrín 2015). Yet, immature individuals could be negatively affected by increasing edge density because of an increased vulnerability to predation and human-related activities (e.g., hunting, extraction for illegal trade, road-kills) at forest edges (Michalski and Peres 2005). Accurately testing the relative importance of these processes is necessary to better understand the role of edge density in maintaining primate populations, and thus improving conservation strategies.

## Conclusions

The rapid response of howler monkeys to landscape spatial changes suggests that this species may not be as tolerant to landscape disturbance as previously proposed (Silver et al. 1998; Rangel-Negrín et al. 2014). Although we did not assess temporal changes in patch-scale characteristics such as patch size, quality and history—a very interesting topic that needs to be assessed in future studies—our research indicates that relatively short-term landscape-scale changes can have important effects on black howler monkey populations. To improve landscape quality for this endangered primate species, conservation actions should include: (i) preventing forest loss and increasing forest cover (passive or active restoration); (ii) generating or increasing the size of forest patches in the landscape (i.e., reverse fragmentation); and (iii) decreasing the amount of treeless areas by enriching the matrix with native tree species, wooded corridors and different arboreal crops and agroforests. Overall, these management strategies can contribute to increasing both resource availability and landscape connectedness for howler monkeys and many other forest-dependent species in this important but vanishing biodiversity hotspot.

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