

Regional context mediates the response of Mexican primates to landscape structure in fragmented rainforests

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ABSTRACT

Land use change is a major threat to species' persistence. Yet, landscape attributes that shape populations remain poorly understood. Landscape-scale forest cover and matrix quality can favor population persistence, while forest fragmentation per se usually has weak effects on species. The impact of these spatial changes can, however, be influenced by the regional context. To test these hypotheses, we assessed the abundance and immature-to-female ratio (reproductive success) of two endangered howler monkeys species and their relationships with forest cover, matrix quality and forest fragmentation (forest patch density) in four Mexican regions with different deforestation levels. Responses to landscape structure differed among regions. Forest loss was negatively related to primate abundance in two regions. Yet, in the most deforested region, forest loss was positively related to the immature-to-female ratio. Matrix quality was negatively related to monkey abundance and positively related to immature-to-female ratio in regions dominated by arboreal matrices. Fragmentation was negatively related to abundance but positively to immature-to-female ratio in the best preserved region, and negatively related to immature-to-female ratio in a region dominated by treeless matrices. Thus, given that the regional context influences the effects that landscape attributes have on primates, different conservation strategies could help maintain the populations of these arboreal mammals in different regions. Preventing forest loss and restoring forest cover are paramount in highly deforested regions. Increasing matrix quality is highly valuable, especially in regions dominated by treeless matrices. Finally, increasing the number of patches through restoration can have better conservation outcomes in more forested regions.

1. Introduction

Human activities transform natural ecosystems into landscapes with different spatial structures (Song et al., 2018; Taubert et al., 2018). In the tropics, agriculture (crops and cattle pastures) is responsible for 73% of forest loss (FAO, 2016), threatening the persistence of forest-dwelling species (Newbold et al., 2015). During the last decades, biodiversity has been lost at such dramatic rates that our planet is believed to be experiencing the sixth mass extinction in its geologic history (Ceballos et al., 2015). In this context, understanding the effects of landscape structure on wildlife is critical for designing effective management strategies that

can facilitate species' persistence in human-modified landscapes (Arroyo-Rodríguez et al., 2020).

Studies that assess species responses to landscape structure are generally carried out at a single spatial scale (Fahrig, 2005; Galán-Acedo et al., 2019b). This approach has serious limitations as it can miss significant species-landscape associations if these are not measured at the appropriate scale (Arroyo-Rodríguez and Fahrig, 2014; Galán-Acedo et al., 2019b; Jackson and Fahrig, 2012, 2015). Thus, species-landscape associations need to be evaluated across different spatial scales to identify the 'scale of effect', i.e., the scale at which these associations are the strongest (Galán-Acedo et al., 2019b; Jackson and Fahrig, 2012).

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Also, species-landscape associations can be affected by the regional context (e.g., land use history, regional forest cover), and hence, need to be evaluated in different regions (Lindenmayer et al., 2008; Pardini et al., 2010). However, as most studies are carried out in a single location, the role of the regional context in shaping species responses to landscape structure remains poorly known (Galán-Acedo et al., 2019b). Filling these gaps of information is particularly urgent for species strongly threatened with extinction, as is the case of most primates (Estrada et al., 2017).

Primates play key roles in ecosystem functioning, acting as herbivores, seed dispersers, predators and prey, and even ecosystem engineers (Andresen et al., 2018; Estrada et al., 2017; Stevenson and Guzman-Caro, 2010). As a result of habitat loss, degradation, and hunting ~60% of primate species are currently threatened with extinction (Estrada et al., 2017). The loss or decline of primate populations will likely trigger cascading effects with long-term negative consequences for plant diversity, forest regeneration, and ecosystem resilience (Andresen et al., 2018; Culot et al., 2017; Marsh and Chapman, 2013). Because most primate studies have been conducted at the patch scale, our understanding of how landscape attributes, such as forest cover, matrix quality or forest fragmentation per se affect primate populations is still scarce.

As most primates are forest-dependent (Galán-Acedo et al., 2019c), forest loss has strong negative effects on their distribution and abundance. Forest loss limits resource availability and connectivity, altering primate foraging behavior, and increasing the incidence of disease, competition, and stress (Arroyo-Rodríguez and Dias, 2010; Marsh, 2003). In a recent review, Galán-Acedo et al. (2019b) found that forest loss generally has negative effects on several primate responses, including the abundance of individuals, species richness, and patch occupancy. Furthermore, forest loss is often correlated to increased human presence and thus higher hunting pressure, as demonstrated for several primate species in the Amazon (Parry and Peres, 2015).

Due to deforestation and land-use change, primary primate habitat is reduced to forest remnants surrounded by an anthropic matrix. However, as forest edges do not represent absolute barriers to animal movement, most species (including primates) can use to some extent the surrounding matrix (e.g., secondary vegetation, crops; Galán-Acedo et al., 2019a; Watling et al., 2011). Although the conservation value of the matrix for primates has not been thoroughly studied, there is evidence that primates can use anthropic land covers for travelling, resting, and/or foraging (Anderson et al., 2007; Blanco and Waltert, 2013; Galán-Acedo et al., 2019a). The ability of a species to use the matrix, however, depends on the ecological traits of primates as well as the matrix type. For instance, arboreal primates may be more prone to use arboreal matrices, such as agroforestry systems and secondary vegetation, than treeless matrices, such as pastures and annual crops (Galán-Acedo et al., 2019a).

Another common consequence of deforestation is forest fragmentation. Although forest fragmentation per se (i.e., independent of forest loss) generally has weak or no effect on biodiversity (Fahrig, 2003), when significant, most responses (76%) to fragmentation per se are positive (Fahrig, 2017). Primates are no exception: a comprehensive review only detected seven studies assessing primate responses to landscape structure, and of these, three found no significant responses to fragmentation per se, and three reported positive effects (Galán-Acedo et al., 2019b). Among the mechanisms that can explain this pattern (reviewed by Fahrig et al. (2019), mean inter-patch distance typically decreases with increasing patch density, potentially increasing dispersal opportunities and resource availability through landscape supplementation dynamics (Dunning et al., 1992; Asensio et al., 2009). Yet, given the small number of primate studies using a proper landscape design (Galán-Acedo et al., 2019b), our understanding on this topic is far from complete.

Here, we evaluated the effects of three landscape structural attributes (forest cover, matrix quality, and forest fragmentation per se) on

the abundance and immature-to-female ratio (a proxy for reproductive success) of howler monkeys (*Alouatta palliata* and *A. pigra*) inhabiting forest fragments in four rainforest regions of Mexico. Study regions differed in the time since the onset of human disturbance, the degree of deforestation, and the dominant type of anthropic land cover in the matrix. Prior to assessing the effects of landscape attributes on primates, we identified the scale of effect of each predictor on each response variable in each region (Galán-Acedo et al., 2018). As howler monkeys are arboreal, we expected that forest cover would be positively related to abundance and immature-to-female ratio. Additionally, as arboreal elements in the matrix (e.g., living fences, isolated standing trees, tree crops) can be used by arboreal primates for travelling, resting, and/or foraging (Blanco and Waltert, 2013; Galán-Acedo et al., 2019a), we predicted that howler monkey abundance and immature-to-female ratio could increase with the proportion of these elements in the matrix (i.e., higher matrix quality). Finally, following previous studies (Fahrig, 2017, 2019; Galán-Acedo et al., 2019b), we predicted a non-significant or positive relationship between fragmentation per se and both responses.

2. Methods

2.1. Study regions

We worked in four regions with different land-use change histories and deforestation levels in southeastern Mexico, all of which have tropical rainforest as the primary vegetation type, with similar hot and wet climate (Table 1; Fig. 1). For the purpose of our study, we defined each region as a ~116,000-ha territory. The region with the lowest deforestation level (LDL, ~50% of deforestation) is the Marqués de Comillas rainforest, whereas the region with highest deforestation level (HDL, ~95% of deforestation) is the 8th North region, both located in the state of Chiapas. The other two regions have intermediate deforestation levels (IDL), Uxpanapa (IDL-1, ~70% of deforestation) and Los Tuxtlas (IDL-2, ~83% of deforestation), both in the state of Veracruz (Fig. 1). Deforestation began earlier in HDL (early 1950s), followed by IDL-1 (late 1950s), IDL-2 (1960s), and LDL (1970s). Arboreal matrix covers (e.g., rubber, orange, oil palm crops, secondary forest) are more common in the LDL and IDL-1 regions, while the IDL-2 and HDL regions are dominated by open matrices such as pastures and annual crops (Table 1). In 1998 there was a fire in IDL-1 in which 35,000 ha of forest were lost, of which 21% had regenerated by the time we conducted our study (Hernández-Gómez, 2014). As a consequence, this region is composed of old-growth forest patches embedded in a matrix of regenerating vegetation and other land covers, such as arboreal crops, annual crops, and pastures.

2.2. Study species

Howler monkeys are diurnal, arboreal, and forest specialist primates (Galán-Acedo et al., 2019c). In Mexico, where they reach their northern geographic distribution limit, two species occur: mantled howler monkeys (*Alouatta palliata*) and black howler monkeys (*Alouatta pigra*). In Mexico, mantled howler monkeys have a mean home range of 13 ha (Cristóbal-Azkarate and Arroyo-Rodríguez, 2007), a mean group size of 8 individuals (Cristóbal-Azkarate et al., 2017), and a body mass of 5.1 kg (Kelaita et al., 2011). Black howler monkeys have a mean home range of 9.2 ha, a mean group size of 5.3 individuals, and a body mass of 6.6 kg (Kelaita et al., 2011). In both species, male and female juveniles and young adults commonly disperse to join existing groups or to form new groups with other individuals (Clarke et al., 1997; Clarke and Glander, 2001; Dias et al., 2015). However, there is also evidence that in disturbed habitats they may remain in their natal groups (Dias et al., 2015; Nidiffer and Cortés-Ortiz, 2015; Van Belle et al., 2012). Due to deforestation, howler monkey populations are declining in Mexico, and are currently classified as Engangered by the IUCN 2020 (The IUCN Red List of Threatened Species). Of the regions studied, *A. pigra* inhabits LDL,

Table 1
Characteristics of the study regions in southeastern Mexico. Regions are ordered from least to most deforested: LDL (lowest deforestation), IDL-1 and IDL-2 (intermediate deforestation), and HDL (highest deforestation).

	LDL	IDL-1	IDL-2	HDL
Coordinates	90°41'8.7"W 16°2'49.3"N	94°24'30.216"W 17°8'46.1"N	98°38'00"W 18°03'00"N	93°08'00"W 17°45'15"N
Mean annual temperature (°C)	24	25	22	25
Mean annual precipitation (mm)	2,143	3,640	4,900	2,600
Onset of deforestation	1970's	1950's	1960's	1950's
Dominant anthropic land covers in matrix	Crops and cattle pastures	Crops and cattle pastures	Crops	Crops
Deforestation (%)	~50% ^a	~70% ^b	~83% ^c	~95% ^d

References.

- ^a Zermeno (2008).
- ^b Hernández et al. (2013).
- ^c Castillo-Campos and Laborde (2004).
- ^d Anzures-Dadda and Manson (2007).

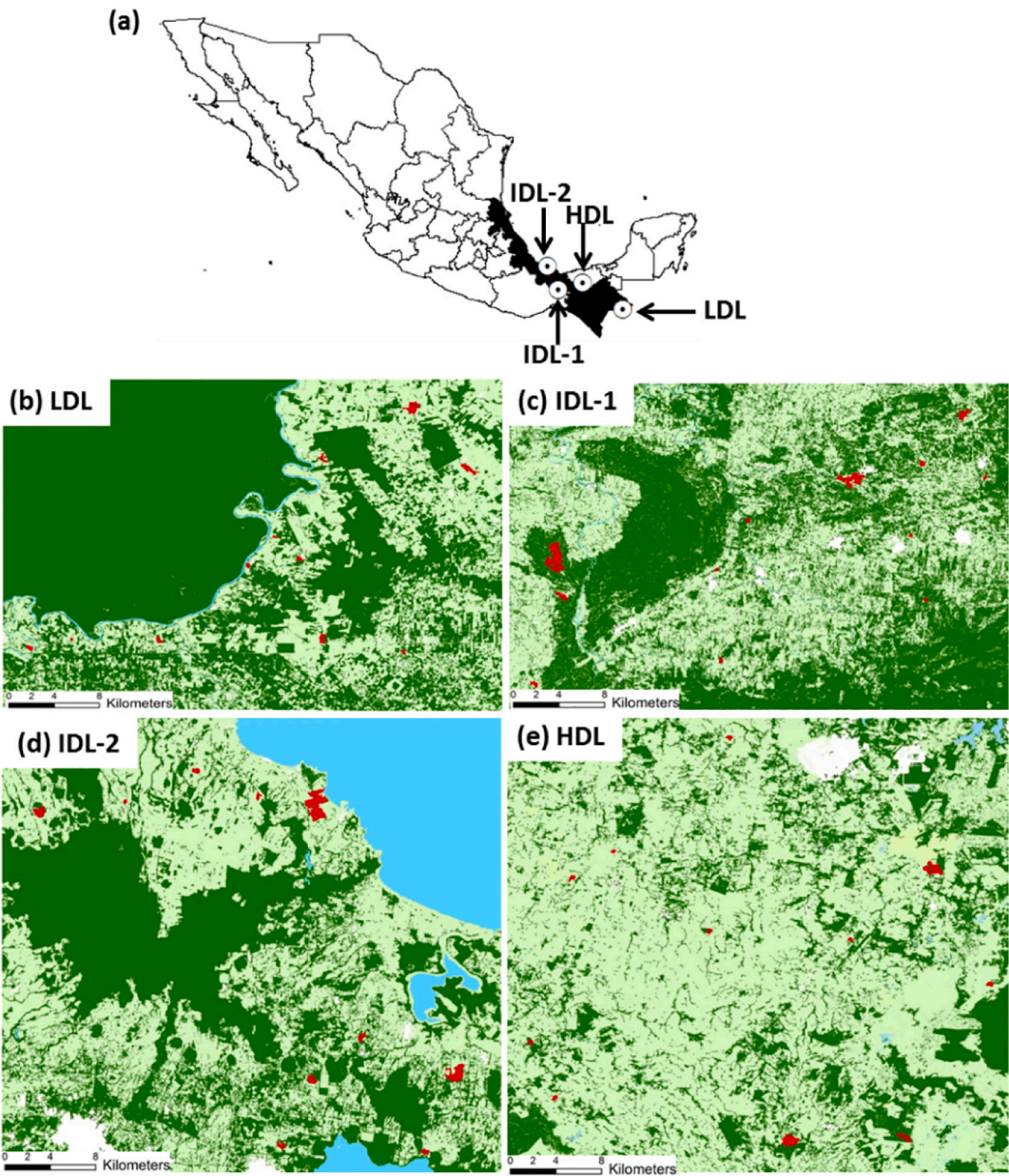


Fig. 1. Location of the study regions in southeastern Mexico (a). Study regions are ordered from the least to the most deforested: (b) LDL, lowest deforestation level (Marqués de Comillas, Chiapas); (c) IDL-1, intermediate deforestation level (Uxpanapa, Veracruz); (d) IDL-2, intermediate deforestation level (Los Tuxtlas, Veracruz); and (e) HDL, highest deforestation level (8th North, Chiapas). The 12 forest patches in which primate response variables were measured in each region are shown in red. Forest cover is represented in dark green, open areas in light green, water bodies in blue and human settlements in white. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

whereas *A. palliata* is found in the other three.

2.3. Study patches and primate surveys

In each region, we randomly selected 12 old-growth isolated forest patches separated by at least 2.7 km from each other in three size categories: 6 small patches (1–10 ha), 4 medium patches (11–50 ha), and 2 large patches (51–100 ha). We selected these patch sizes to increase the probability of studying landscapes with different amounts of forest cover. As the most deforested region (HDL) had no large patches and few medium patches, we selected 10 small and 2 medium patches. Although the percentage of forest cover at the landscape scale also tended to be lower in this region, we were able to find a wide range of values (1.5–98.7%) for remaining forest cover (Galán-Acedo et al., 2018).

Primate surveys in all regions were carried out by C.G-A and a field assistant with extensive experience in monkey surveys. To determine the presence of primates in each focal patch, we followed a sampling protocol widely used in primatological studies. We walked slowly (~1–2 km/h) inside and around each focal patch from 6 am to 5 pm, which encompasses the hours in which monkeys are active. We only worked during sunny days of the 2015 and 2016 dry seasons (January to June) to avoid the difficulties of detecting and counting monkeys under bad weather conditions. Loud call vocalizations helped us locate groups within patches. When we made visual contact with a group, we recorded its position with a GPS, and counted all individuals. Individuals were classified as adult males, adult females, juveniles, or infants (Domingo-Balcells and Veà-Baró, 2009; Rosales-Meda, 2003). We surveyed each patch once, but search times were proportional to patch size, with 3 consecutive days for small patches, 5 days for medium patches, and 7 days for large patches. This helped us reduce potential errors in population estimates, as counting all groups and individuals in large patches can be more difficult than in small patches. In total, we conducted 196 sampling days (~1,900 h of field observations) and we walked 1,020 km (3.9 km to 84 km/patch). To avoid recording the same group or individual more than once, we identified each group according to its composition, location within the patch, and distinctive morphological characteristics of individuals (e.g., scars, the colour patterns on their hind legs and tails, Supplemental material Fig. S1).

As response variables, we calculated the abundance (i.e., total number of individuals) and the immature-to-female ratio for each focal patch. Immature-to-female ratio is a proxy for successful reproduction (i.e., female fecundity and/or immature survival) commonly used in howler monkey studies (Arroyo-Rodríguez et al., 2013; Zucker and Clarke, 2003). Immatures individuals are juveniles and infants and the ratio was calculated considering the total number of immatures and adult females in each focal patch.

2.4. Landscape metrics

We obtained land-cover maps of circular landscapes surrounding the focal patches using radii in 100 m increments (up to a maximum radius of 1,300 m) measured from the geographic center of patches, using recent high-resolution Sentinel S2 satellite images (from 2015 and 2016). We conducted a supervised land-cover classification with the software ENVI 5.0, using control points obtained through field observations in each region. We distinguished seven types of land covers: (i) old-growth forest; (ii) secondary vegetation; (iii) connectors; (iv) arboreal crops (e.g., rubber plantations); (v) annual crops and cattle pastures; (vi) human settlements; and (vii) water bodies (Fig. 1). We defined secondary forests as naturally regenerating vegetation following forest loss. To identify secondary vegetation, we monitored deforestation from 1997 to 2017 in the four regions using Landsat images and the CLASlite software (Asner et al., 2009). Landscape classification performed well, with 90% of accuracy (Kappa index ≥ 0.9).

We analyzed the effects of three landscape predictors: two metrics of landscape composition (forest cover and matrix quality) and one metric

of landscape configuration (fragmentation per se). We chose these landscape predictors because they have been demonstrated to influence a variety of vertebrate taxa (Ewers and Didham, 2006; Smith et al., 2011), including primates (Arroyo-Rodríguez et al., 2013; Galán-Acedo et al., 2019b; Thornton et al., 2011). We measured landscape predictors using the ArcGIS 10.5 software with the Patch Analyst extension (Rempel et al., 2012). Forest cover was calculated as the percentage of old-growth forest in a landscape. To estimate matrix quality, we first ranked the quality of all land cover types that were not the original habitat of howler monkeys (i.e., old-growth forest), from 1 (lowest quality) to 6 (highest quality). We included water bodies because howler monkeys may use it for drinking (Almeida-Silva et al., 2005) or even swimming (Chaves and Stoner, 2010; Gonzalez-Socoloske and Snarr, 2010). Our ranking was based on our understanding of the ability of howler monkeys to use different land covers in the matrix for feeding and/or travelling (Pozo-Montuy et al., 2013): 1 (water bodies), 2 (human settlements), 3 (annual crops and cattle pastures), 4 (arboreal crops), 5 (connectors), and 6 (secondary vegetation). We then calculated a matrix quality index as $[(1 \times \% \text{ of water bodies}) + (2 \times \% \text{ of human settlements}) + (3 \times \% \text{ of annual crops and cattle pastures}) + (4 \times \% \text{ of arboreal crops}) + (5 \times \% \text{ of connectors}) + (6 \times \% \text{ of secondary vegetation})]$. To make this index independent of forest cover, we calculated all percentages considering the area covered by all land covers in the matrix, and not by total landscape area (Garmendia et al., 2013). This index varies between 100 (100% composed of water) and 600 (100% composed of secondary vegetation) and therefore is positively related to resource availability in the matrix and to matrix permeability (Garmendia et al., 2013). Finally, we measured fragmentation as forest patch density, i.e., the number of isolated forest patches (≥ 1 ha) within the landscape divided by total landscape area (n/ha). This is a widely used forest fragmentation metric, and we statistically controlled for the effect of forest cover (see the statistical analyses section), so that this variable can be considered a metric of fragmentation per se (Fahrig, 2017).

We followed Jackson and Fahrig (2015) to identify the scale at which the relationship between a landscape predictor and a species' response is strongest, i.e., the scale of effect. We did this separately for each predictor-response combination in each region (Galán-Acedo et al., 2018). Using regression analyses, we tested 13 scales, varying the radius of the circular landscapes (measured from the center of the focal patch) in 100 m increments, with the smallest radius being 100 m and the largest 1300 m (with no overlap between the radii of adjacent landscapes). As suggested by Jackson and Fahrig (2015), the largest landscape size (i.e., 531-ha landscape) was much larger than the home range of the studied species. The smallest radius (100-m radius) corresponds to a landscape of ~3 ha, which is smaller than the mean home range size of both species, but larger than the smallest forest patch inhabited by howler monkeys (i.e., ~1 ha; Arroyo-Rodríguez et al., 2008, 2013; Boyle and Smith, 2010). The scale of effect was the landscape size that yielded the strongest associations between each response variable and each predictor (Table A1; Galán-Acedo et al., 2018).

2.5. Statistical analyses

We used the software R ver. 3.0.1 for all analyses (R Core Team, 2013). Analyses were conducted separately for each region. We assessed the collinearity among landscape predictors with the variance inflation factor (VIF) using the 'car' package (Fox et al., 2019). We found significant collinearity among predictors in the IDL-2 region, when assessing abundance. Thus, to assess the response of abundance to landscape structure in this region, we did not use the value of patch density at the best scale (scale of effect), but at the second best scale, at which we did not find collinearity among predictors (Table A1), i.e., all VIF values were < 3.34 (Neter et al., 1996).

To evaluate the effects of landscape variables on each response variable we built generalized linear models with the package 'glmulti' (Calcagno and de Mazancourt, 2010). We used an information-theoretic

approach and multimodel inference to assess the relative effect of each predictor on each response variable (Burnham and Anderson, 2002). For each response variable we constructed eight models, representing all combinations of the three explanatory variables plus the null model, which includes only the intercept. For each model we computed Akaike's information criterion corrected for small samples (AICc), and we ranked the models from best to worst (Supplemental material Table S2). We used Akaike weights (w_i) to evaluate the importance of each predictor and produce model-averaged parameter estimates (Anderson, 2007). We summed w_i of ranked models until the total was >0.95 (Whittingham et al., 2005). The set of models for which Σw_i is 0.95 represents a set that has at least a 95% probability of containing the true best model (Whittingham et al., 2005). Following Crawley (2007), the goodness-of-fit of the models was estimated as: (deviance explained by the complete model/deviance explained by the null model) $\times 100$. A given landscape variable was considered a relatively important predictor for a given response if the following four criteria were met: (i) the complete model in which such predictor appeared had a relatively high goodness-of-fit; (ii) the predictor showed a relatively high Σw_i (i.e., considering all candidate model in which it appeared); (iii) it was present in at least one of the most plausible models (i.e., $\Delta AICc < 2$); and (iv) the model-averaged parameter estimate was higher than its unconditional variance (i.e., it did not include zero).

3. Results

Of the 48 forest patches studied in the four regions, 29 (60.4%) were inhabited by howler monkeys, with a total of 579 individuals (range = 1–68 individuals per patch; Table 2). The highest values for both abundance and immature-to-female ratio were found in the region with lowest deforestation, followed by the region with highest deforestation (Table 2).

Complete models (those including the three landscape metrics) had relatively high explanatory power (31.6% to 78.1% of deviance explained), except for the models of abundance in IDL-1 and in HDL (Fig. 2). Values of model-averaged parameter estimates and unconditional variances are in Table 3. In LDL, monkey abundance was positively related to forest cover ($\Sigma w_i = 0.7$) and negatively related to matrix quality ($\Sigma w_i = 0.7$) and forest patch density ($\Sigma w_i = 0.6$; Figs. 2a, 3a, b), while immature-to-female ratio increased with matrix quality ($\Sigma w_i = 0.8$) and forest patch density ($\Sigma w_i = 0.5$; Figs. 2b, 3c). In IDL-1, matrix quality was also positively related to immature-to-female ratio ($\Sigma w_i = 0.5$; Fig. 2d). In IDL-2 abundance was positively related to forest cover ($\Sigma w_i = 0.9$) but negatively to matrix quality ($\Sigma w_i = 0.5$, Figs. 2e, 3d) and immature-to-female ratio was negatively related to patch density ($\Sigma w_i = 0.9$; Figs. 2f, 3e). Finally, in the most deforested region (HDL), immature-to-female ratio was negatively related to forest cover ($\Sigma w_i = 0.6$; Figs. 2h, 3f).

Table 2

Results of howler monkey surveys in each study region ($n = 12$ forest patches per region). LDL = region with lowest deforestation level, IDL-1 = intermediate deforestation level 1, IDL-2 = intermediate deforestation level 2, HDL = highest deforestation level. Total and range values per patch (in parentheses) are indicated.

	LDL	IDL-1	IDL-2	HDL
Primate species	<i>A. pigra</i>	<i>A. palliata</i>	<i>A. palliata</i>	<i>A. palliata</i>
# Occupied patches	9	6	5	9
Abundance	244 (4–68)	51 (3–12)	116 (1–51)	168 (10–47)
Immature-to-female ratio ^a	1.26 (0.67–2)	0.61 (0–1)	0.33 (0–0.52)	0.69 (0.5–1)
# Groups	44 (0–15)	6 (0–1)	11 (0–5)	13 (0–13)
Mean group size	5.26 (2–11)	8.50 (3–12)	10.18 (2–17)	12.92 (2–25)

^a Considering only patches occupied by at least one adult female.

4. Discussion

Our findings indicate that howler monkey responses to landscape structure can depend on the regional context in which the landscape is embedded. As predicted, landscape forest cover was positively related to primate abundance, but only in two of the four regions. Contrary to our expectations, forest cover was negatively related to immature-to-female ratio in the region with highest deforestation level (HDL region). Also surprising was the fact that in HDL we recorded a similarly high number of inhabited patches ($n = 9$) as in the region with lowest deforestation level (LDL), and the second highest abundance of howler monkeys. On the other hand, matrix quality was negatively related to monkey abundance in LDL, and in a region with intermediate deforestation level (IDL-2), and positively related to the immature-to-female ratio in LDL and IDL-1. Finally, fragmentation was negatively related to abundance, but positively to immature-to-female ratio in the LDL region, and negatively related to immature-to-female ratio in IDL-2 (Table 3).

Forest cover was positively related to monkey abundance in two regions (i.e., LDL and IDL-2). This is not surprising because forest cover determines the amount of habitat for arboreal mammals, and it is positively related to landscape connectivity and resource availability (e.g., food, shelter; Carretero-Pinzón et al., 2017; Fahrig, 2003, 2013; Marsh and Chapman, 2013). But why can forest cover be relatively more important for howler monkeys in IDL-2 than in IDL-1? Although these two regions have intermediate deforestation levels (83% and 70% of deforestation, respectively), matrix quality differs between them. The matrix in IDL-2 is mainly composed of pastures, which do not provide supplementary resources to howler monkeys, probably making them more dependent on variations in forest cover. In contrast, the matrix in IDL-1 includes arboreal elements (e.g., secondary vegetation, tree crops) that can be used as temporary and supplementary habitat (Asensio et al., 2009; Galán-Acedo et al., 2019a; Pozo-Montuy et al., 2013). This can diminish primate dependence on forest cover, while strengthening the relationship with matrix quality (see below).

Contrary to our expectations, in HDL (95% of deforestation) forest cover was negatively related to immature-to-female ratio. Howler monkeys are frequently considered to have high behavioral flexibility to cope with degraded habitats, adjusting, for instance, the size of their home ranges or activity budgets (Arroyo-Rodríguez and Dias, 2010). In mantled howler monkeys, juveniles and young adults of both sexes disperse away from their natal groups (Clarke et al., 1997; Clarke and Glander, 2001). However, evidence shows that howler monkeys could limit their dispersal in highly deforested landscapes, as these provide less opportunity for colonization by new groups (Arroyo-Rodríguez and Dias, 2010; Arroyo-Rodríguez et al., 2008). Furthermore, dispersal events in such landscapes can entail high mortality risks for individuals (Fahrig, 2002). Thus, to persist in highly deforested landscapes, mantled howler monkeys could be limiting their dispersal, which could increase the number of juveniles in the groups and therefore the immature-to-female ratio. Although this needs to be tested in future research, if confirmed, the lack of dispersal could pose serious conservation risks, as it associates with loss of genetic variability (Pope, 1996), disrupted metapopulation dynamics (Mandujano et al., 2004), infectious disease dynamics (Baudouin et al., 2019), and changes to biotic interactions that affect ecosystem structure and function (López et al., 2005).

The relatively high abundance of howler monkeys in HDL was also surprising. This finding does not support the extinction threshold hypothesis, which predicts that populations can decrease sharply in landscapes with <10 – 30% of remaining habitat (Andren, 1994; Swift and Hannon, 2010). The persistence of monkeys in a landscape with only 5% of forest cover can be explained by the high behavioral flexibility of howler monkeys which may allow them to accumulate individuals in forest patches (Bicca-Marques, 2003; Arroyo-Rodríguez and Dias, 2010). This crowding effect has been suggested as a key mechanism for explaining the abundance of other tropical forest-specialist species in fragmented forest landscapes, including non-volant mammals

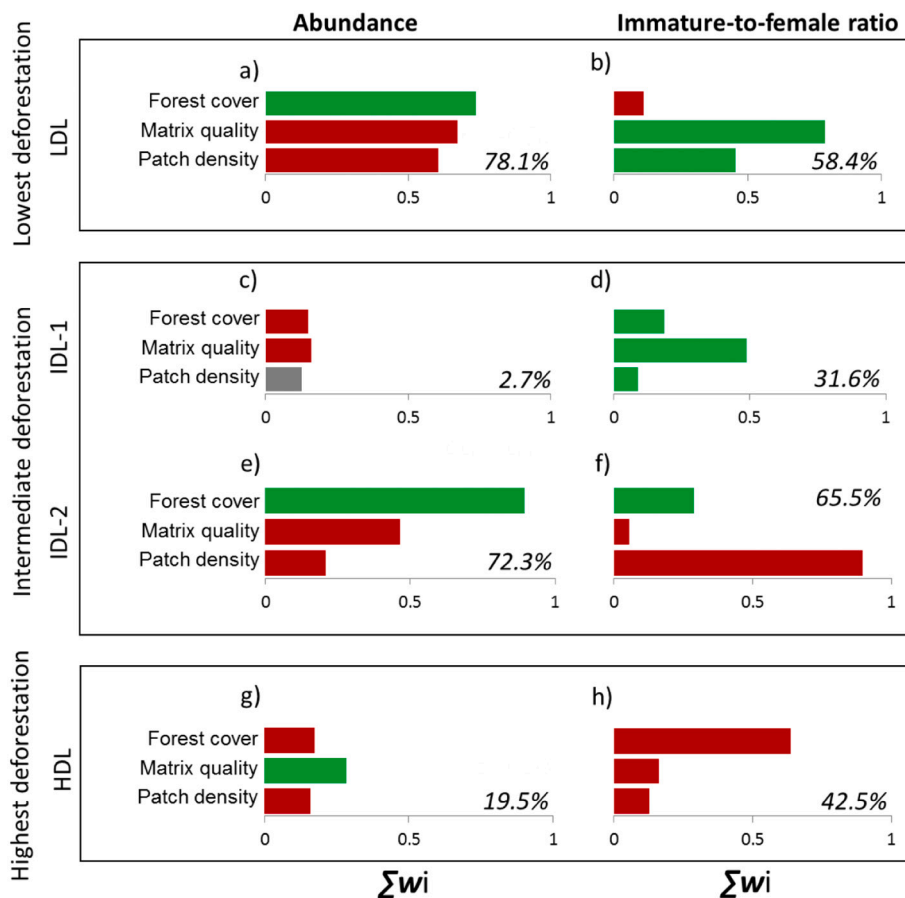


Fig. 2. Predictor variables included in the set of models for which Σw_i was 0.95, for the two response variables of howler monkeys, abundance (left) and immature-to-female ratio (right). We assessed four regions: LDL, lowest deforestation level, IDL-1, intermediate deforestation level 1, IDL-2, intermediate deforestation level 2, HDL, highest deforestation level. The importance of predictor variables is represented by the length of bars, which corresponds to the sum of Akaike weights (Σw_i). The percentage of deviance explained by each complete model is indicated in each panel. Positive (green bars) or negative (red bars) responses to each predictor are indicated. The gray bar represents a case in which the unconditional variance was higher than the model-averaged parameter estimate, indicating that such parameter can include zero (i.e., a null effect). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Laurance, 1994), terrestrial rodents (Arce-Peña et al., 2019a), and howler monkeys (Terborgh et al., 2001; Arce-Peña et al., 2019b). Crowding can, however, have negative consequences. In howler monkeys, high population densities have been associated with reduced food availability and reproduction, and increased inter- and intra-specific food competition (Arroyo-Rodríguez and Dias, 2010; Cristóbal-Azkarate and Arroyo-Rodríguez, 2007; Rose et al., 2003). Thus, this region may be facing an extinction debt (Tilman et al., 1994), as howler monkeys have a long life-span (>30 years) and slow life-histories (e.g., mean interbirth interval of 22 months in *A. palliata* and 18 months in *A. pigra*; Rangel-Negrín et al., 2016; Rangel-Negrín et al., 2018) – a hypothesis that needs to be tested through long-term monitoring.

Interestingly, matrix quality was negatively related to monkey abundance in LDL and IDL-2. These apparently counterintuitive findings could be interpreted as a positive effect of matrix quality. Landscapes with high quality matrices have higher availability of arboreal covers (e.g., successional vegetation, riparian corridors or arboreal crops), which increase landscape connectivity and offer dispersal opportunities for arboreal species (Anderson et al., 2007; Blanco and Waltert, 2013; Galán-Acedo et al., 2019a). Thus, howler monkeys in landscapes dominated by these matrices may leave forest patches more frequently to use resources from the matrix, which may explain a lower number of individuals in patches surrounded by higher quality matrices.

Opposite to abundance, matrix quality was positively related to immature-to-female ratio in regions LDL and IDL-1. These two regions have higher quality matrices than the other two regions (i.e., structurally more similar to species' natural habitat; Fahrig et al., 2011), such that monkeys can more easily move and find food resources (Asensio et al., 2009; Galán-Acedo et al., 2019a; Pozo-Montuy et al., 2013; Watling et al., 2011). This, in turn, could increase survival rates of immature individuals, and thus the immature-to-female ratio.

Supporting this possibility, Reider et al. (2018) found in their meta-analysis that species-area relationships are shallower (less extinction driven) where matrix quality is higher, likely because of the supplementary resources provided by the matrix. This process, called landscape supplementation (Dunning et al., 1992), presumably plays an important role for the persistence of primates in altered landscapes (Asensio et al., 2009; Galán-Acedo et al., 2019a; Pozo-Montuy et al., 2013).

The effect of forest fragmentation was important in two of the four regions. This landscape variable was negatively related to the abundance of howler monkeys and positively related to immature-to-female ratio in the best-preserved region (LDL, ~50% deforestation). Similar to the negative effect of matrix quality discussed above, it is possible that the high density of forest patches in this well-preserved region is associated with a decrease in patch isolation (Fahrig, 2003, 2013). Such spatial configuration can favor inter-patch movements, allowing for a more evenly distribution of individuals across the landscape and reducing population density in the focal patches. This, in turn, could increase the survival of immature individuals, and thus the reproductive rate in this region. If this were the case, the negative association between forest fragmentation and monkey abundance in LDL would not imply a negative effect of fragmentation on monkey population dynamics. However, the immature-to-female ratio was also negatively associated to fragmentation in IDL-2, which had 83% of deforestation. Because the matrix in IDL-2 is mainly composed of open areas, and little forest cover remains, fragmentation in this region could increase howler monkeys' exposure to different threats, such as hunting and illegal trade.

5. Conservation implications

Even though our sample size to detect inter-regional differences was

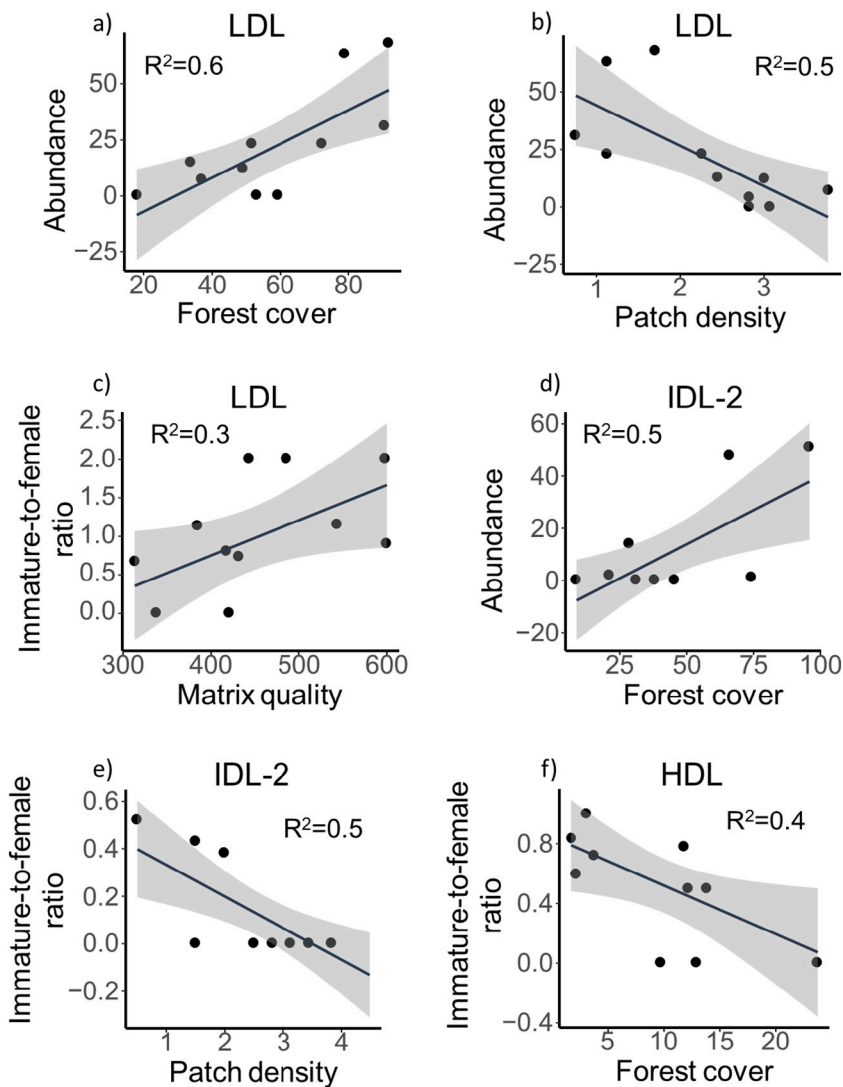


Fig. 3. Most important univariate relationships between abundance and immature-to-female ratio of howler monkeys and three landscape variables (forest cover, matrix quality and patch density) in three rainforest regions with different deforestation level (LDL = lowest deforestation, IDL-1 = intermediate deforestation, HDL = highest deforestation). Only predictors with a relatively high sum of Akaike weights and in models with high explanatory power (high deviance explained) are included. Points represent the forest sites in each region ($n = 12$). Black lines show the predicted estimates from the binomial regression using a generalized linear model and gray areas indicate 95% confidence intervals.

relatively low (12 landscapes per region), our findings showed that species' responses to changes in landscape structure are influenced by the regional context. Thus, whereas some effects of the regional context might have gone undetected due to small sample size, the effects that we did detect can give us valuable insights that can inform management decisions. Forest fragmentation generally shows weaker effects in regions with high quality matrices or in strongly deforested regions. This could imply that in such regions, conservation plans may improve howler monkey maintenance through preventing forest loss and increasing forest cover (i.e., restoration). The spatial configuration of the remaining forest might be relatively more important in regions with high forest cover and low quality matrices. Improving matrix quality with arboreal elements could also be an effective management strategy, especially for arboreal mammals, such as most primates. Although the study species seem to be relatively resilient to forest loss, with the most deforested region showing a high number of individuals, we believe that this pattern could be related to time-lagged responses to habitat loss (Metzger et al., 2009; Arce-Peña et al., 2019b; but see Alcocer-Rodríguez et al., 2020). Thus, additional long-term studies are needed to better understand the impact of extreme deforestation on the persistence of these and other species that seem resistant to forest loss. Increasing the sample size in each region could also be valuable to improve the predictive power of the models, and to allow for the inclusion of additional predictor variables (e.g., landscape connectivity, land-use history) that

can also drive primate population dynamics in fragmented forests. These improvements to the methods used here could contribute to increasing our understanding of how primate populations may be able to persist in the long term in fragmented rainforests.

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CRediT authorship contribution statement

CGA and VAR developed the idea of the study. CGA collected and analyzed the data, with significant guidance from VAR. All authors made substantial contributions to the intellectual content, interpretation of results and editing of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

Table 3

Values of model-averaged parameter estimates (β) and unconditional variances (UV) of information-theoretic-based model selection and multimodel inference of the effects of three landscape predictors on the abundance and immature-to-female ratio of howler monkeys in four rainforest regions (see all model sets in Table A2). LDL = region with the lowest deforestation level, IDL-1 = intermediate deforestation level 1, IDL-2 = intermediate deforestation level 2, HDL = highest deforestation level.

Region/predictors	Abundance		Immature-to-female ratio	
	β	UV	β	UV
LDL				
Forest cover	0.023	0.0002	-0.002	0.00007
Matrix quality	-0.007	0.00002	0.005	0.000008
Patch density	-0.419	0.131	0.145	0.038
IDL-1				
Forest cover	-0.00008	0.00002	0.002	0.00002
Matrix quality	-0.0003	0.000009	0.002	0.000006
Patch density	0.0002	0.003 ^a	0.002	0.001
IDL-2				
Forest cover	0.045	0.0003	0.0009	0.000003
Matrix quality	-0.011	0.0001	-0.00003	0.0000003
Patch density	-0.143	0.123	-0.116	0.003
HDL				
Forest cover	-0.006	0.0002	-0.021	0.0004
Matrix quality	0.0008	0.000002	-0.0005	0.000005
Patch density	-0.038	0.009	-0.016	0.003

^a Cases in which the unconditional variance (UV) was higher than the model-averaged parameter estimates (β).

the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109006>.

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