# Evaluating extinction debt in fragmented forests: the rapid recovery of a critically endangered primate

Mónica Alcocer-Rodrígueza,\*, Víctor Arroyo-Rodríguezb, Carmen Galán-Acedob, Jurgi Cristóbal-Azkaratec, Norberto Asensiod, Kátia F. Ritob, Joseph E. Hawese,f, Joaquim J. Veàa, Jacob C. Dunne,g,h,\*

aCentre Especial de Recerca en Primats, Facultat de Psicologia, Universitat de Barcelona, Vall d’Hebron 171, Barcelona, 08035, Spain.

bInstituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México (UNAM), Morelia, México.

cOinarrizko Psikologia Prosezuak eta Garapena Saila, Psikologiako Fakultatea, Euskal Herriko Unibertsitatea, Tolosa Hiribidea 70, 20018, Donostia, Gipuzkoa, Spain.

dGizarte-Psikologia eta Portaera Zientzien Metodologia, Psikologia Fakultatea, Euskal Herriko Unibertsitatea, Tolosa Hiribidea 70, 20018, Donostia, Gipuzkoa, Spain.

eSchool of Life Sciences, Anglia Ruskin University, East Road, Cambridge, CB1 1PT, UK.

fFaculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, 1430 Ås, Norway.

gDivision of Biological Anthropology, University of Cambridge, Pembroke Street, Cambridge, CB2 3QY, UK.

hDepartment of Cognitive Biology, Althanstrasse 14, University of Vienna, Vienna, Austria.

**\*Corresponding authors:**

Jacob C. Dunn – Email: [jacob.dunn@anglia.ac.uk](mailto:jacob.dunn@anglia.ac.uk); Tel: +44 1223 698220; Twitter: @jacobcdunn

Mónica Alcocer-Rodríguez - Email: [aznevo28@hotmail.com](mailto:aznevo28@hotmail.com); Tel +34 699 54 06 07

# Abstract

Fragmented tropical forests can be highly dynamic, with the spatial configuration of forest patches changing through time. Yet, the lack of longitudinal studies limits our understanding of how patch dynamics affect biodiversity, especially when there is a time lag in species extinctions (extinction debt). We assessed how temporal changes in patch size, shape complexity, and isolation affect populations of the Mexican howler monkey (*Alouatta palliata mexicana*), hypothesizing that we would find an extinction debt in this relatively long-lived species. We assessed patch occupancy, subpopulation size and immature-to-female ratio in 39 forest patches from Los Tuxtlas, Mexico, in both 2001 and 2013. To identify time-lag responses to habitat disturbance, we related demographic attributes in 2013 to patch metrics in 2001 and 2013 and tested whether primate subpopulations were better predicted by current or historical patch characteristics. We also assessed how changes in patch metrics affected each demographic attribute between 2001 and 2013. Patch size and shape complexity increased over time, while isolation decreased. These positive spatial changes were accompanied by a 1.6-fold increase in mean subpopulation size over the same period. In addition, occupancy and immature-to-female ratio were similarly related to patch attributes in both years, suggesting that there is no extinction debt. Our findings are ‘good news’, suggesting that forest recovery over a relatively short period can promote the recovery of this Critically Endangered taxon. They also highlight the importance of preventing forest loss and promoting forest regeneration in human-modified tropical landscapes.

**Keywords:** *Alouatta* · Demography · Los Tuxtlas · Patch dynamics · Time-delayed extinctions · Restoration

# Introduction

With extensive deforestation across the tropics, the remaining tropical forests are increasingly fragmented (Taubert et al., 2018). Fragmented forests can be highly dynamic; therefore, they can increase, shrink, disappear or change into another vegetation type through time (del Castillo, 2015). However, fragmentation research has largely been focused on short-term and static studies, overlooking the importance of patch history and dynamics on biodiversity patterns and processes (Ewers et al., 2013; del Castillo, 2015). Longitudinal studies are not only needed to identify the effects of patch dynamics on species, but to identify species responses that may take some time to become evident, potentially leading to time-delayed extinctions (i.e., extinction debt) (Metzger et al., 2009; Lira et al., 2012).

Time delays in species’ responses to habitat spatial changes are determined by landscape dynamics, life history traits and interactions among species, amongst other factors (With, 2007; Kuussaari et al., 2009; Schwitzer et al., 2011; Hylander and Ehrlén, 2013; Sales et al., 2015). Species that are slow to respond to environmental fluctuations usually have large body sizes, long life-spans, slow life histories, low turnover rates, low dispersal capacities and/or resistance to environmental fluctuations (Nagelkerke et al., 2002; Ewers and Didham, 2006; Kuussaari et al., 2009; Hylander and Ehrlén, 2013). For example, Metzger et al., (2009) studied the response of trees, small mammals, birds and frogs to changes in patch area and connectivity through time in the Atlantic forest region of Brazil. They found that species richness and abundance both exhibited time-lagged responses to habitat spatial changes. However, the strength of these responses and specific responses to particular spatial attributes (e.g., patch size, connectivity), varied with dispersal capacity and longevity among taxa, so that past landscape structure was particularly relevant for long-lived trees (Metzger et al., 2009). Similarly, Krauss et al., (2010) found that the richness of vascular plants was better explained by past than current landscape patterns, while short-lived butterflies showed no evidence for such an extinction debt in a large-scale study across European grassland remnants.

Non-human primates (hereafter, ‘primates’) are among the most threatened taxa worldwide (Estrada et al., 2017). They play a critical role in maintaining tropical biodiversity and many ecosystem functions, processes, and services (Estrada et al., 2017). There is ample evidence that the abundance of primates inhabiting forest patches is determined by the characteristics of the patches they inhabit; namely their size, shape and isolation (Harcourt and Doherty, 2005; Cristóbal-Azkarate et al., 2005; Mandujano et al., 2006; Anzures-Dadda and Manson, 2007; Arroyo-Rodríguez and Dias, 2010; Benchimol and Peres, 2014; Puig-Lagunes et al., 2016). However, very few studies have looked into the temporal dynamic of these relationships. Primates are characterized by long lives, modest reproductive rates and extensive parental care. They grow more slowly, have later ages at first reproduction, longer life spans and lower fertility than most other mammals (Jones, 2011). Therefore, primate populations are predicted to show time-delayed responses to habitat modifications and, as a result, to show extinction debts (Tilman et al., 1994).

Based on a species-area modeling study, Cowlishaw (1999) suggested that in most African countries an extinction debt was present in over 30% of primate taxa. He also argued that the fact that no African country had lost a single primate species, in spite of massive deforestation during the 50 years prior to publication, represents a time lag between deforestation and extinction of primates. As different primate species have different life histories, the speed at which their populations will respond to changes in forest patch attributes will also vary. The demography of primate species with shorter generation times will fluctuate more readily, while the time lag between changes in habitat structure and population parameters will be longer for those species with slower life histories. We are, however, aware of only two studies that have empirically analysed time delayed responses in primates. In the first, Sales et al. (2015) assessed changes in patch occupancy for two primate species, using data before a dam construction and 11 years after. They found that black-pencilled marmosets (*Callithrix penicillata*) responded faster to habitat changes than black-fronted titi monkeys (*Callicebus nigrifrons*), probably as a result of differences in life history and habitat dependence. In the second, Arce-Peña et al. (2019) related changes in landscape structure occurring over a 6-year period to population trends of black howler monkeys (*Alouatta pigra*). They found that monkey abundance increased significantly in forest sites located in landscapes where forest cover and the number of forest patches increased over time. However, given the very limited number of studies, our understanding of time delayed responses in primates is far from complete.

Understanding the temporal dynamics of primate responses to habitat change, as well as identifying extinction debts, can help us to elucidate how long it takes for populations and communities to come into equilibrium with a given habitat spatial pattern following disturbance (Vellend et al., 2006; Hylander and Ehrlén, 2013). It can also provide an indicator of species’ responses to management strategies (e.g., reforestation and creation of corridors). This is particularly important when working with critically endangered taxa, such as the Mexican howler monkey (*Alouatta palliata mexicana*) (IUCN, 2019).

Here, we assessed the evidence for an extinction debt in a population of Mexican howler monkeys living in a highly fragmented landscape in the Los Tuxtlas rainforest, Mexico. We gathered data on patch occupancy and demography (i.e., subpopulation size and immature-to-female ratio) as well as patch size, shape complexity, and isolation in 2001 and 2013, to assess whether primate subpopulations are better predicted by current or historical patch attributes. This is a relatively long-lived primate species (25-30 years in the wild; Hakeem et al., 1996; Glander, 2006) compared with land-use change history in the region (a 60-year history of deforestation ﻿occurring predominantly between 1976 and 1986; Cristóbal-Azkarate et al., 2005). Therefore, we hypothesized that there may be a delayed response to changes in patch configuration. Thus, we predicted that past attributes would better predict current population demography than current patch attributes (e.g., Krauss et al., 2010; but see Arce-Peña et al. 2019). We also assessed whether and how changes in patch metrics between 2001 and 2013 promoted changes in each demographic attribute between years. In this case, we expected that subpopulation size and immature-to-female ratio (a proxy of reproductive output) would increase in larger, more complex-shaped, and less isolated patches, as all of these spatial changes promote patch connectivity and increase resource availability (Ewers and Didham, 2006).

# Materials and methods

## Compliance with ethical standards

This study is based on observational data and there was no direct interaction with the study subjects. We were granted access to the study site by local communities, landowners, and the Los Tuxtlas Biosphere Reserve – part of the National Commission of Natural Protected Areas of Mexico (CONANP). All research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non‐Human Primates and to the legal requirements of Mexico.

## Study site

We conducted this study in the northern part of Los Tuxtlas Biosphere Reserve, Veracruz, Mexico (18°39’21.5’’ - 18°31’20.4’’N; 95°09’14.9’’ - 95°01’45.3’’W; elevation 0-730 m a.s.l.; Fig. 1), in lowland areas with a warm and humid climate (mean annual temperature = 25 °C, mean annual precipitation = 4 900 mm; Soto 2004). The vegetation type is evergreen rainforest (Castillo-Campos and Laborde 2004) with some areas of secondary forest. In the past, this region has undergone intense deforestation. At the end of the 1970’s, the northern part of Los Tuxtlas lost more than 80% of its original vegetation (Dirzo and Garcia, 1992). At present, large-scale deforestation is controlled and some agricultural lands have been abandoned due to poor soil productivity. Nevertheless, illegal tree-felling is still common, due principally to the expansion of cattle pastures. The current landscape is composed of a mosaic of rainforest patches, with different spatial configurations, embedded in a mostly homogeneous matrix of cattle pasture (Cristóbal-Azkarate et al., 2017; Fig. 1).

## Landscape surveys

As part of a long-term program of primate research in the Los Tuxtlas region (Cristóbal-Azkarate and Dunn, 2013; Cristóbal-Azkarate et al., 2017), we analysed the spatial configuration of 39 forest patches, spread over an area of approximately 7 500 ha (Fig. 1). We considered patch size, shape complexity, and isolation for the analysis, as they can be strong drivers of biodiversity patterns in fragmented landscapes (Ewers and Didham, 2006; Hanski, 2015), especially when considering forest specialist species such as most primates (Harcourt and Doherty, 2005; Benchimol and Peres, 2014; Carretero-Pinzón et al., 2017). For example, patch size has been shown to be positively related to food availability, number of individuals, and patch occupancy (Arroyo-Rodríguez and Dias, 2010; Puig-Lagunes et al., 2016); more complex shaped patches can be colonised more frequently than more uniform patches (Ewers and Didham, 2006); and a greater distance between patches can restrict animal dispersal patterns (Fischer and Lindenmayer, 2007), both for the purposes of reproduction and for supplementing food intake by using resources from different landscape elements (Asensio et al., 2009).

Patch attributes were assessed in 2001 using aerial photographs (1:20 000 scale) provided by the Mexican National Institute of Statistics and Geography (INEGI), and in 2013 using imagery from the Environmental Systems Research Institute (ESRI). We used ArcView GIS software (version 10, ESRI®) and the Patch Analyst 4 extension (Rempel and Elkie, 1999) to obtain each patch metric (Table 1). We also estimated the change (Δ) in each patch metric between years (2001-2013). Patch shape complexity was estimated using the shape index (SI) proposed by Patton (1975): ; where *P* and *A* are the perimeter and area of the patch measured in meters and meters squared, respectively. The SI = 1 for square patches of any size, and increases without limit as the patch becomes increasingly non-square (i.e., geometrically more complex). Patch isolation was simply measured as the minimum Euclidian distance from each patch to its nearest neighbouring patch (edge-to-edge distance).

## Study species

*Alouatta palliata mexicana* is a subspecies that is paleoendemic to Mexico (Dunn et al., 2014). It is arboreal, and has a limited ability to move between forest patches, particularly when the surrounding matrix is composed of cattle pastures or croplands (Arroyo-Rodríguez and Dias, 2010). It has a folivore-frugivore diet with a high degree of dietary flexibility that is affected by both environmental and social factors (Cristóbal-Azkarate and Arroyo-Rodríguez, 2007; Dunn et al., 2009, 2010, 2012; Arroyo-Rodríguez et al., 2015b; Dias and Rangel-Negrín, 2015). The average age at first birth for female *A. palliata* is 43 months (Domingo-Balcells and Veà, 2009) and gestation lasts approximately 6 months (Glander, 1980). The species is characterized by bisexual emigration of juveniles (Cristóbal-Azkarate et al., 2017).

The Mexican howler monkey is listed as Critically Endangered by the IUCN as it is predicted that this subspecies will experience a decline exceeding 80% over 3 generations (36 years), largely owing to past and ongoing rates of habitat loss (IUCN, 2019). The subspecies also exhibits extremely low genetic diversity compared to other Neotropical primates (Dunn et al., 2014; Mello-Carillo et al., 2020).

## Primate surveys

Details of our primate survey methods have been given elsewhere (Cristóbal-Azkarate et al., 2005, 2017), but a brief overview is provided here. We carried out two censuses of howler monkey subpopulations in 39 forest patches, one from March 2000 to December 2001, and another from January 2012 to May 2013, using the same methods and sampling efforts in both periods. Our census method involved at least two observers positioning themselves for several days (depending on the size of the patch) in strategic spots (inside and/or outside the patch) before sunrise, waiting for the monkeys to howl (groups of howler monkeys howl daily at dawn and dusk; ﻿Baldwin and Baldwin 1976; Carpenter 1934; Cornick & Markowitz, 2002). These methods allowed us to determine whether a patch was inhabited, and, if so, further investigate the number and localization of the groups. In addition, we interviewed the local people who lived and worked in the proximity of the forest patch about the presence or absence of howler monkeys in the patches. If after several days none were heard in a patch, and the local people reported that the fragment was not occupied by howler monkeys, it was considered empty.

Once we had located a group, we recorded its location and the number of males, females, juveniles and infants. We followed each study group until we were sure that we had censused every group member. For this we payed special attention to group travelling instances. These allow for the detection of individuals that may be in the periphery of the group, as howler monkeys are group living and show conspicuous and relatively cohesive group movement patterns (Ceccarelli et al., 2020; Van Belle et al., 2013). Typically, we would spend a complete day (never less) with each study group, but if required, and particularly with larger groups and/or if less than two travelling instances were observed, we spent additional days observing them. We used the classification system devised by Domingo-Balcells and Veà (2009) to categorize the howler monkeys into age/sex classes. To simplify the analyses, we grouped juveniles and infants into a single category of ‘immatures’. To avoid recording the same group or individual more than once, we identified each member of the group according to the colour patterns on their hind legs and tails, which are typical of this subspecies (c.f. Cristóbal-Azkarate et al., 2017). We also recorded any distinctive morphological characteristics (scars, injuries, mutilations or malformations).

## Response variables

We assessed patch occupancy (i.e., presence or absence of howler monkeys) as a proxy of population distribution in the landscape. We also estimated subpopulation size (i.e., total number of individuals) in each patch and immature-to-female ratio (i.e., number of infants and juveniles/number of females). As the number of immatures per female is related to the reproductive rate (or ‘replacement rate’; Wilson and Bossert, 1971) in a population (though it will also be affected, to some degree, by mortality and migration of both adult females and immatures), this index is widely used in primate studies as a proxy of reproductive output (e.g., Arroyo-Rodríguez et al., 2013; Galán-Acedo et al., 2018; Wilson and Bossert, 1971; Zucker et al., 2003).

## Data analysis

We first tested for differences between years in both forest patch attributes and demographic attributes with linear mixed-effects models, using the *lme* function in the *nlme* package (Pinheiro et al., 2016) in R (R Team Development Core, 2014), and setting an alpha level of 0.05 to assess significance. In all models, we included the year (2001 and 2013) as a fixed categorical factor and patch identity within each year as a random factor. We verified that we did not violate the normality assumption by using a Shapiro-Wilk test of residuals and log-transformed the response variables as necessary. To assess whether models including both fixed (i.e., year) and random (i.e., patch identity within each year) factors showed a better fit for each response variable than solely the random factor, we compared null models (i.e., including only the random factor) with the complete model by using likelihood ratio tests (Pinheiro and Bates, 2000). The null model was not significantly better than the complete model for any of the response variables.

To assess whether historic (2001) or current (2013) patch attributes better predicted current (2013) patch occupancy and demographic attributes, and whether changes (Δ) in demographic attributes between years (2013-2001) were associated with changes in patch attributes between years, we used generalised linear models. We assessed patch occupancy considering all (n = 39) forest patches by fitting a GLM with a binomial distribution (binary response: occupied/unoccupied) (Crawley, 2012). However, when assessing the predictors of demographic variables (subpopulation size and immature-to-female ratio), we excluded unoccupied patches (n = 24 patches) and focused only on occupied patches (n = 15 patches) to avoid any bias/error associated with the high number of zeros in our database. Demographic and patch attributes for all forest patches studied are provided in Table S1.

To evaluate the relative effect of each predictor on each response variable we used a multimodel inference approach (Burnham and Anderson, 2002) with the *glmulti* package for R (Calcagno and Mazancourt, 2010). To avoid problems with multicollinearity among predictors, we first verified that all our predictor variables were independent using the Variance Inflation Factor (VIF) in the *car* package for R (Fox and Weisberg, 2011). All VIF values were ≤ 2.4, indicating independence among our predictors (Jou et al., 2014). We thus retained all predictors in the models, and constructed 8 models per response variable for each year, which included the isolated and additive effects of all patch variables (Tables S2-S5). For each model, we calculated the Akaike’s information criterion corrected for small samples (AICc) and obtained model-averaged parameter estimates using Akaike weights (*wi*). To correct for the overdispersion usually associated with count data, models for subpopulation size were assessed with qAICc instead of AICc values (Calcagno and Mazancourt, 2010). The set of models for which Σ*wi* was 0.95 represents a set that has 95% probability of containing the best model (Burnham and Anderson, 2002). The best predictors of a given response variable were those that: (i) showed a high Σ*wi* (i.e., considering all candidate models in which it appeared); (ii) showed a model-averaged parameter estimate higher than its unconditional variance (i.e., the unconditional variance around the parameter estimate did not include zero). We also calculated the percentage of explained deviance for each complete model (i.e., the model that includes all predictors) as a measure of the goodness-of-fit of the models (Crawley, 2012).

# Results

The total area of forest habitat across our sample of 39 patches increased from 2,149 ha to 2,742 ha between 2001 and 2013, with our linear mixed-effects models showing a significant increase in mean patch size over this time period (Table 1). This increase was accompanied by a significant increase in mean patch shape complexity and a significant decrease in mean patch isolation (Table 1). As patches became larger, their perimeter shape became more irregular, and the mean distance from neighbouring patches was approximately halved.

The total surveyed howler monkey population size increased from 344 individuals (45 groups in 12 patches) in 2001 to 565 individuals (49 groups in 14 patches) in 2013, with a significant increase in mean subpopulation size per patch (Table 1). Three patches were colonised, and one patch was abandoned by howler monkeys between the two periods; the remaining forest patches were unoccupied in both time periods. Mean immature-to-female ratio was two times higher in 2013 than in 2001, but this difference was only close to statistical significance (p = 0.07; Table 1).

Patch occupancy was positively related to both patch size and isolation in both surveys (Table 2), with a similar percentage of explained deviance in 2001 (36.1%) and 2013 (35.7%) (Fig. 2a-b, Table S2). The explanatory power of patch geometry was higher for subpopulation size, although again, the percentage of explained deviance was similar in 2001 (85.0%) and 2013 (73.7%) (Fig. 2c-d). Based on the sum of Akaike weights (Σ*wi*), the most important patch characteristic differed between years (Fig. 2c-d). In 2001, subpopulation size was mainly positively related to patch shape complexity, whereas in 2013 it was positively related to both patch area and shape complexity (Table 2 and Table S3). In contrast to both occupancy and subpopulation size, immature-to-female ratio was poorly related to patch characteristics in both surveys (i.e., 3.0% – 14.3% of explained deviance; Fig. 2e-f; Table 2 and Table S4). Finally, when assessing changes in demographic characteristics and patch metrics between the two surveys, we detected a positive effect of patch size on subpopulation size (72.4% of explained deviance), but changes in patch metrics over time were poorly related to temporal changes in immature-to-female ratio (13.4%; Fig. 3; Table 3 and S5).

# Discussion

This study represents the first temporal analysis of the spatial drivers of population demography in the Mexican howler monkey. In fact, we are only aware of two other studies that have conducted a similar analysis in primates (Sales et al., 2015; Arce-Peña et al. 2019). With such a longitudinal approach, we were able to improve our understanding of the impact that forest patch dynamics have on this critically endangered subspecies. Interestingly, we recorded the rapid recovery of this subspecies following positive habitat changes in the landscape over a relatively short period of 12 years – a finding consistent with a previous assessment of a sister species, the black howler monkey, in the Lacandona rainforest, Mexico (Arce-Peña et al. 2019). In particular, between 2001 and 2013, we observed a significant increase in patch size and shape complexity, and a significant decrease in patch isolation. These spatial changes were followed by a 1.6-fold increase in the overall population size of howler monkeys (and a significant increase in subpopulation size per patch), as well as a 2-fold increase in the number of immatures per female. Also, patch occupancy and immature-to-female ratio were similarly related to patch attributes in both years, thus suggesting that there is no extinction debt.

## Forest recovery provides habitat, food resources and landscape connectivity

At the end of the 1970s, the Los Tuxtlas rainforest, in southeastern Mexico, experienced a dramatic loss of 80% of its original rainforest (Dirzo and Garcia, 1992), which was primarily converted to cattle pasture (Durand and Lazos, 2008). In response, this region was designated as a Biosphere Reserve in 1998 (IUCN Category VI), providing habitat protection but permitting the sustainable use of natural resources by local communities. Our results confirm that this protection has had a positive ecological impact on the remaining forest patches, in terms of patch area, shape complexity and relative isolation. Recovery across these patch metrics is probably explained by the so-called ‘forest transition’ process (Melo et al., 2013), i.e., the abandonment of pastoral land as people left in search of better economic opportunities, with this emigration likely stimulated by a combination of deteriorating soil quality and increased restrictions on deforestation (Gerez-Fernández and Pineda-López, 2011). Whatever the cause of the forest transition phenomenon in the region, secondary forest regeneration promoted an average increase of 2.9% per year in mean patch size over a 12-year period. This is consistent with other human-modified landscapes across the Neotropics, where secondary forests are expanding (Aide et al., 2013), providing habitat, complementary and supplementary resources, and landscape connectivity for many species (Asensio et al., 2009; Melo et al., 2013; Chazdon, 2014; Arroyo-Rodríguez et al., 2017; Galán-Acedo et al., 2019).

Secondary vegetation can be used by primates as permanent and temporary habitat (Galán-Acedo et al., 2019). The proliferation of light-demanding plant species (e.g., lianas and pioneer tree species) across secondary forests and forest edges, can provide supplementary food resources for howler monkeys and other primates (Asensio et al., 2009; Cristóbal-Azkarate and Arroyo-Rodríguez, 2007; Dunn et al., 2012; Arroyo-Rodríguez et al., 2015b). Forest recovery along riparian vegetation and living fences (i.e., tree lines delimiting property margins) also contribute to decreased inter-patch isolation distances (Arroyo-Rodríguez et al., 2020). These landscape elements can be used by howler monkeys and other taxa (e.g., terrestrial mammals, bats, birds) as food resources and to facilitate movement through the landscape (Estrada et al., 2000; Estrada and Coates-Estrada, 2001; Asensio et al., 2009; Galán-Acedo et al., 2019), thus maintaining ecological connectivity between remaining patches (Fahrig and Merriam, 1985; Arroyo-Rodríguez et al., 2020). Therefore, as discussed below, the rapid recovery of primate populations in the Los Tuxtlas landscape can likely be related to increasing habitat and food availability, as well as improved landscape connectivity.

## Primate population recovery

Our findings indicate an annual increase of 5.2% in subpopulation size and an increase in the immature-to-female ratio, suggesting improved reproductive output (Zucker and Clarke, 2003). The improvements observed in the quality of forest patches (i.e., larger, more complex and less isolated; see Table 1) may help to explain this pattern. For example, in the spatially explicit metapopulation model proposed by Hanski (2000), the biggest positive factor for enhanced forest quality and facilitation of species migration between forest patches, is the restoration of patches located close to existing high-quality forest. The changes in patch attributes that we recorded at Los Tuxtlas include decreased inter-patch isolation distances, which helps explain our finding of re-colonization in three patches, compared to only one local extinction in 2013. Fahrig (2013) suggests that patchy habitats do not limit population distribution, and therefore, that subpopulation growth could be due to the immigration of howler monkeys from other areas. Indeed, Cristóbal-Azkarate et al. (2017) observed that migration was the principal cause of changes in group size in their long-term study (10 years) of 11 howler groups inhabiting nine forest patches from our present study. Another factor that may have contributed to howler monkey recovery in our study region is the local extinction of almost all of their principal predators (e.g., *Panthera onca* and *Harpia harpyja*), as abundances of howler monkeys and other herbivores are known to be 10 to 100 times greater in islands unoccupied by predators than in forest areas with predators (Terborgh et al., 2001).

In accordance with metapopulation theory (Hanski, 1999), our results show that patch occupancy is positively related to patch size. This may be related to lower extinction rates and higher colonization rates in larger patches (Hanski, 1999). Yet, we found that patch occupancy was positively related to patch isolation, not negatively as predicted by metapopulation theory (Hanski, 1999). Although this finding is somewhat counterintuitive at first, the best models indicate that the probability of patch occupancy was driven by the combined effect of isolation and size (see Table S1). In particular, patch occupancy increased in more isolated, but also larger patches. Thus, the higher probability of extinction that is usually associated with increasing isolation may be counteracted by lower extinction rates in larger patches. In contrast, smaller patches are more likely to have seen extinctions and less likely to be permanently colonised (due to the low availability of food resources) even if they are closer to other patches (Arroyo-Rodríguez et al., 2007).

Our findings are consistent with previous studies suggesting that howler monkeys are able to adapt to altered landscapes (Bicca-Marques, 2003; Arroyo-Rodríguez and Dias, 2010; Arce-Peña et al., 2019), largely because of their high dietary plasticity (Dunn et al., 2010; Cristóbal-Azkarate and Dunn, 2013; Dias and Rangel-Negrín, 2015). As stated above, their use of secondary vegetation as temporary or permanent habitat can also explain their ability to persist and increase their abundance in this fragmented landscape. For example, a 7-fold population increase of mantled howler monkeys (*A. palliata*) was reported after 28 years of forest recovery in Santa Rosa National Park, Costa Rica (Fedigan and Jack 2001), and the number of Mexican howler monkeys on the reforested island of Agaltepec, Veracruz, grew from 9 to 95 individuals in 14 years (Carrera-Sánchez et al., 2003). However, the current study is the first to examine the potential for an extinction debt, while determining the habitat spatial changes that can promote population increases in fragmented landscapes.

Although immature to female ratio doubled between years, this proxy of reproductive output was only weakly related to patch attributes. This suggests that habitat spatial patterns alone are not responsible for temporal changes in demography, and that other important factors relating to habitat quality, such as floristic composition and food availability, may also play an important role (e.g., Milton et al. 2019). Indeed, large tree density has previously been shown to be an important predictor of howler monkey presence in forest patches (Arroyo-Rodriguez et al. 2007). This presents a very interesting avenue for future research.

## Is there an extinction debt?

The howler monkey population in our study area does not seem to show any evidence of an extinction debt. First, we found increases in patch occupancy, subpopulation size and immature-to-female ratio. Second, all three of these response variables were similarly related to patch attributes in both years. Finally, current occupancy was not better predicted by past patch characteristics than present conditions. Previous studies concluded that the howler monkey population in Los Tuxtlas was in decline from the beginning of the 1980s until 2001 (Estrada and Coates‐Estrada, 1988; Estrada and Coates-Estrada, 1996; Cristóbal-Azkarate et al., 2005; Cristóbal Azkarate et al., 2017). The probability that an extinction debt has been paid increases with time since the landscape perturbation occurred (Hanski, 2000; Vellend et al., 2006; Kuussaari et al., 2009) and the major habitat loss at Los Tuxtlas was approximately 30 years ago. As argued above, it is therefore highly likely that, consistent with previous studies (Arce-Peña et al. 2019), this population has already paid its extinction debt, and it is now responding positively to forest recovery.

## A case of conservation optimism?

Our study provides strong evidence that forest recovery over a relatively short period (12 years) can promote the recovery of a critically endangered taxon. Despite their relatively slow life history, we found positive trends in the population responses of Mexican howler monkeys in the Los Tuxtlas landscape and a lack of evidence for a continuing extinction debt. These findings are very good news for the conservation of this and potentially other forest dwelling mammal species living in a similar situation of habitat fragmentation. Of particular significance is the fact that howler monkeys represent ecologically important fauna in the Neotropics, as they play an important role in seed dispersal (Estrada and Coates-Estrada, 1991; Arroyo-Rodríguez et al., 2015a) and nutrient cycling (Dos Santos Neves et al., 2010). Natural regeneration can considerably reduce the high cost of forest restoration (Rezende et al., 2015), and howler monkeys can help improve vegetation quality and diversity in secondary forests and fragmented landscapes (Arroyo-Rodríguez et al., 2015a). Their preservation, therefore, has an even broader importance for tropical biodiversity conservation.

The rapid response of howler monkeys to habitat recovery in Los Tuxtlas certainly provides grounds for optimism. However, it is important to consider variable and species-specific responses to habitat spatial patterns (Keinath et al., 2017). For example, other primate species, including the Geoffroy’s spider monkey (*Ateles geoffroyi*), which also persists within the fragmented Los Tuxtlas landscape, are often less tolerant of human disturbance than howler monkeys (Michalski and Peres; Boyle and Smith 2010). This serves to highlight the continued importance of preventing forest loss and promoting forest regeneration in human-modified tropical landscapes (Arroyo-Rodríguez et al., 2020). Although the Mexican howler monkey seems to be relatively resilient to habitat disturbance, their long-term conservation will still depend on preventing further forest loss and promoting ‘reverse fragmentation’ (i.e., increasing the number of forest patches in the landscape and connecting the existing ones; sensu del Castillo, 2015). Introducing a restoration plan to conserve and restore the fragmented forest landscape in the Los Tuxtlas Biosphere Reserve remains a conservation priority that will benefit hundreds of vertebrate species and thousands of plant species (Reynoso et al., 2017).

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# Conflict of interest

The authors declare that they have no conflict of interest.

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Table 1. Differences in each forest patch attribute and Mexican howler monkey demographic attributes between sampling years at Los Tuxtlas, Mexico. Mean value and standard deviations are indicated for each year, as well as the results of linear mixed-effects models, testing for significant (p<= 0.05) differences between years.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Variables | 2001 | 2013 | t | p |
| *Patch attributes* |  |  |  |  |
| Size (ha) | 55.1 ±104.8 | 70.3 ± 126.1 | 3.21 | 0.01 |
| Isolation (m) | 447.0 ± 440.6 | 218.8 ± 319.9 | -3.34 | 0.00 |
| Shape index | 6.2 ± 3.7 | 7.2 ± 4.3 | 2.62 | 0.02 |
| *Demographic attributes* |  |  |  |  |
| Subpopulation size (n) | 22.9 ± 41.5 | 37.3 ± 63.5 | 2.28 | 0.04 |
| Immature-to-female ratio | 0.3 ± 0.4 | 0.6 ± 0.3 | 1.99 | 0.07 |

Table 2. Results of information-theoretic based model selection and multimodel inference for assessing the impact of three forest patch attributes (patch size, shape and isolation) on the occupancy, subpopulation size, and immature-to-female ratio of Mexican howler monkeys in Los Tuxtlas, Mexico. The model-averaged parameter estimates (β) and the unconditional variance (UV) are indicated. The sign of each parameter represents the direction of the effect (positive or negative) of each predictor on each response variable. Note that most β values are relatively accurate, as they were higher than their respective UV (i.e., they did not include zero) in all but one case.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Response variables |  | Size | |  | Isolation | |  | Shape | |
| 2001 | 2013 |  | 2001 | 2013 |  | 2001 | 2013 |
| Occupancy | β | 4.82 10-2 | 3.57 10-2 |  | 5.09 10-3 | 8.23 10-3 |  | -1.02 10-2 | -5.15 10-2 |
| UV | 1.06 10-3 | 4.10 10-4 |  | 5.92 10-6 | 2.15 10-5 |  | 2.71 10-2 | 2.01 10-2 |
| Subpopulation size (n) | β | -1.04 10-4 | 3.62 10-3 |  | 4.81 10-5 | -4.72 10-4 |  | 3.38 10-1 | 9.83 10-2 |
| UV | 1.08 10-7 | 5.42 10-6 |  | 1.27 10-8 | 6.56 10-7 |  | 3.67 10-4 | 1.04 10-2 |
| Immature-to-female ratio | β | -1.13 10-5 | -1.51 10-5 |  | 1.76 10-5 | 6.26 10-5 |  | 1.21 10-3 | 3.91 10-3 |
| UV | 1.61 10-7 | 1.18 10-7 |  | 8.81 10-9 | 3.04 10-8 |  | 1.33 10-4 | 1.67 10-4 |

Table 3. Results of information-theoretic based model selection and multimodel inference for assessing the impact of the difference (Δ) between sampling years (2013-2001) in three forest patch attributes on the difference in subpopulation size and immature-to-female ratio of Mexican howler monkeys in Los Tuxtlas, Mexico. The model-averaged parameter estimates (β) and the unconditional variance (UV) are indicated. The sign of each parameter represents direction of the effect (positive or negative) of each predictor on each response variable. Note that most β values are accurate, as they were higher than their respective UV (i.e., they did not include zero) in all but one case.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Variables | Δ Size | |  | Δ Isolation | |  | Δ Shape | |
| β | UV |  | β | UV |  | β | UV |
| Δ Subpopulation size | 0.90 | 2.81 10-2 |  | -1.20 10-3 | 3.91 10-5 |  | -0.40 | 1.86 |
| Δ Immature-to-female ratio | -4.79 10-4 | 8.00 10-6 |  | 2.47 10-4 | 2.15 10-7 |  | 4.59 10-2 | 6.90 10-3 |

# Figure legends

Fig. 1 The location of our study area in the Los Tuxtlas Biosphere Reserve, Veracruz State, Mexico. Forest patches occupied by Mexican howler monkeys are shown in dark grey and unoccupied patches are shown in white. Light grey areas highlight forest patches that did not form part of the study. Increases in patch size between 2001 and 2013 are indicated in black.

Fig. 2Response of patch occupancy (a-b), subpopulation size (c-d), and immature-to-female ratio (e-f) of Mexican howler monkeys to three forest patch attributes (patch size, shape and isolation) in Los Tuxtlas, Mexico. Response variables were sampled in 2013; patch predictors were recorded in 2001 and 2013. The explanatory variables included in the 95% set of models are indicated. The sum of Akaike weights (Σ*wi*) is a proxy of the importance of each variable. The mean percentage of deviance explained by the most parsimonious models for each response variable is included as a measure of goodness-of-fit.

Fig. 3 Response of the difference (Δ) between sampling years (2013-2001) in subpopulation size, density (ind/ha), immature/female ratio and mean group size of Mexican howler monkeys to differences between sampling years (2013-2001) in three forest patch attributes (patch size, shape and isolation) at Los Tuxtlas, Mexico. The explanatory variables included in the 95% set of models are indicated. The sum of Akaike weights (Σ*wi*) is a proxy of the importance of each variable. The mean percentage of deviance explained by the most parsimonious models for each response variable is included as a measure of goodness-of-fit.



# Figure 1

Figure 2

# Figure 2

**Figure 3**

# Figure 3

**Graphical Table of Contents**

**image of study species which we would like to be used for the table of contents and considered for the publication cover.**

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Figure 4.A mantled howler monkey (*Alouatta palliata*). Copyright Cephas CC-BY-SA-4.0 (<https://commons.wikimedia.org/wiki/File:Alouatta_palliata_4_CR.JPG>)