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Influence of Landscape Structure on Toucans and Parrots in the Fragmented Landscape of Los Tuxtlas, Mexico

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Abstract

Background and Research Aims: Habitat amount plays an important role in determining the presence and abundance of bird species in modified landscapes, whereas habitat fragmentation has shown little effects. Toucans (Ramphastidae) and parrots (Psittacidae) are large-bodied primary consumers and among the most representative birds in Neotropical forests. They are highly sensitive to habitat loss; nevertheless, their response to fragmentation has been poorly assessed leading to contradictory results. Here, we evaluate the influence of landscape structure on toucans and parrots in the tropical forest of Los Tuxtlas, Mexico. **Methods**: We censused birds in 12 landscapes of Los Tuxtlas and used a multi-scale landscape approach to assess the influence of landscape composition and configuration on the number of individuals of toucans and parrots. **Results**: We found that the most important and positive predictor of toucans and parrots was the amount of primary forest cover in the landscape. Forest fragmentation had positive effects on the number of toucan individuals, whereas parrots had negative responses to patch density but positive responses to edge density in the landscape. **Conclusion**: Our results suggest that primary forest loss is the main threat for toucans and parrots in Los Tuxtlas. **Implications for conservation**: Future conservation and land management must consider the protection of large and small remnants of primary forest and avoid additional forest loss in order to preserve toucan and parrots and their functional roles in human-modified Neotropical landscapes.

Keywords

forest loss, frugivores, habitat fragmentation, landscape configuration, landscape composition, seed eaters

Introduction

The majority of forests worldwide have been severely affected by human activities (Hansen et al., 2013; Newbold et al., 2016), with greater impact in tropical regions (Laurance et al., 2013). Tropical forest faces the greatest deforestation rate worldwide (Hansen et al., 2013), and it is expected that the continual human growth population and their demand for land and resources will increase the extension of tropical fragmented landscapes (Taubert et al., 2018). Thus, it is necessary to identify the main factors that contribute to biodiversity conservation in human-modified landscapes to guide conservation priority strategies (Arroyo-Rodríguez et al., 2020).

In anthropogenic landscapes, changes in landscape composition (i.e. the relative proportion of different land use and cover types) and configuration (i.e., the spatial arrangement of habitat and non-habitat remnants) can have different impacts on biodiversity (Dunning et al., 1992;

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Fahrig, 2003). Such changes are considered to be important factors for sustaining biodiversity in human-modified landscapes (Fahrig et al., 2011). There is a consensus that landscape composition, particularly habitat amount, has a stronger influence on biodiversity responses (richness and abundance) compared to landscape configuration (Fahrig, 2013). In this sense, the habitat amount hypothesis (HAH) posits that species richness can be predicted by the amount of habitat at the surrounding landscapes independent of patch size and isolation (Fahrig et al., 2013). On the contrary, the effects of landscape configuration (increasing landscape fragmentation) on biodiversity are more controversial and can be positive (Fahrig, 2017).

Several studies with a site-landscape approach have evaluated the relative importance of landscape composition and configuration on birds, but these are still scarce for tropical species. Previous studies demonstrated that landscape composition is more important than habitat configuration for forest birds in Neotropical forests (Cerezo et al., 2010; Carrara et al., 2015), and landscape composition also explains frugivorous bird occurrence (Cerezo et al., 2010; Morante-Filho et al., 2015; Walter et al., 2017). However, empirical evidence on the effects of landscape configuration on frugivorous birds shows contradictory results. Some studies have demonstrated no effects of small-scale landscape configuration in the presence of frugivorous birds in Brazil (Lasky & Keitt, 2012). Others have shown that the occurrence of some frugivores decreased with increasing fragmentation (Trzcinski et al., 1999). Similarly, terrestrial frugivorous birds increased in abundance with decreasing distance to the nearest forest patch in Malaysia (Azhar et al., 2013), while the abundance of large-bodied frugivorous birds responded positively to landscape fragmentation in Mesoamerica (Cerezo et al., 2010). Nevertheless, other studies have found that large-bodied frugivores such as toucan and parrots are absent in small forest patches in tropical regions (de Assis Bomfim et al., 2018), and functional richness of traits associated with seed dispersal in frugivorous birds decreased in small forest fragments (Bovo et al., 2017). As a consequence, this might lead to cascading effects on ecological services provided by these birds in human-modified landscapes.

Toucans (Ramphastidae) and parrots (Psittacidae) are large-bodied cavity-nesters of the tropics. Toucans are primarily frugivorous birds (Winkler et al., 2020a), and parrots feed on a variety of fruits and seeds (Winkler et al., 2020b). Toucans and parrots are most represented in Neotropical forests (Haugaasen & Peres, 2008; Terborgh et al., 1990) and highly sensitive to habitat loss (Sodhi et al., 2008). In this context, landscape structure (composition and configuration) should have an important role in the abundance of these birds since their functional traits (e.g., diet, size, and habitat association) influence their susceptibility to habitat modification (Burivalova et al., 2014). Due to the important ecological roles of toucans and parrots, including seed dispersal and predation (Blanco et al., 2016; Tella et al., 2015) plant gene flow and forest regeneration (Barreiros-Horta et al., 2018; Blanco et al., 2018; dos Santos, 2006), it is paramount to evaluate their responses to landscape structure change.

Here, we used a multi-scale landscape approach to evaluate the relative importance of landscape composition and configuration to explain the number of toucan and parrot individuals in 12 study landscapes of the tropical moist forest in Los Tuxtlas Biosphere Reserve (Los Tuxtlas hereafter), Mexico. Although the HAH deal primarily with species richness, we also predicted positive effects on the number of toucans and parrots. Since both toucans and parrots are bird species associated with forest cover (a proxy of habitat amount), we hypothesized that the numbers of these birds are primarily and positively influenced by forest cover in the landscape. Conversely, the number of toucans and parrots should be negatively influenced by non-forested land cover types, such as pasture lands in the landscape. Given their wide-ranging movements, and the overall neutral and positive effects of fragmentation found in previous studies, we expect that landscape fragmentation will have little or positive effects on toucans and parrots.

Methods

Study Area

The Los Tuxtlas region is located in the state of Veracruz, Mexico (18o05′ to 18o43′ N and 94o35′ to 95o25′ W; Figure 1a) and represents the extreme Neotropical limit of rainforests in the Americas. The region presents annual rainfall of 1500 to 4500 mm, with higher temperatures of 30 to 36°C in May and cooler temperatures of 10 to16°C in January (Soto & Gamma, 1997). The dominant vegetation type is tropical moist evergreen forest, which merges with mountain cloud forest at 700 masl and is replaced by cloud forest at 900 masl (Guevara et al., 2000).

The Los Tuxtlas region has been subjected to severe deforestation since the early 1960s, primarily for cattle pasture land expansion. By the end of the 1990s, only 7–10% of the original tropical moist forests that once covered the region remained (Guevara et al., 2004). The landscape is now composed of a large number of very small primary and well-developed secondary forest patches isolated by a homogeneous open matrix dominated by cattle pasture land (Guevara et al., 2004). Primary evergreen forest harbors large trees of 25–30 m canopy height, and common zoochoric tree species include *Lonchocarpus guatemalensis*, *Vatairea lundellii*, *Dialium guianense*, *Brosimum alicastrum*, *Poulsenia armata*, *Ficus yoponensis*, *F. cotinifolia*, *Spondias radlkoferi*, and *Terminalia amazonia* (Castillo-Campos & Laborde, 2004), whose fruits are consumed by toucans and parrots (De Labra-Hernández & Renton, 2019; Ragusa-Netto, 2006). Secondary forests are similar to primary ones in plant composition, but pioneer species

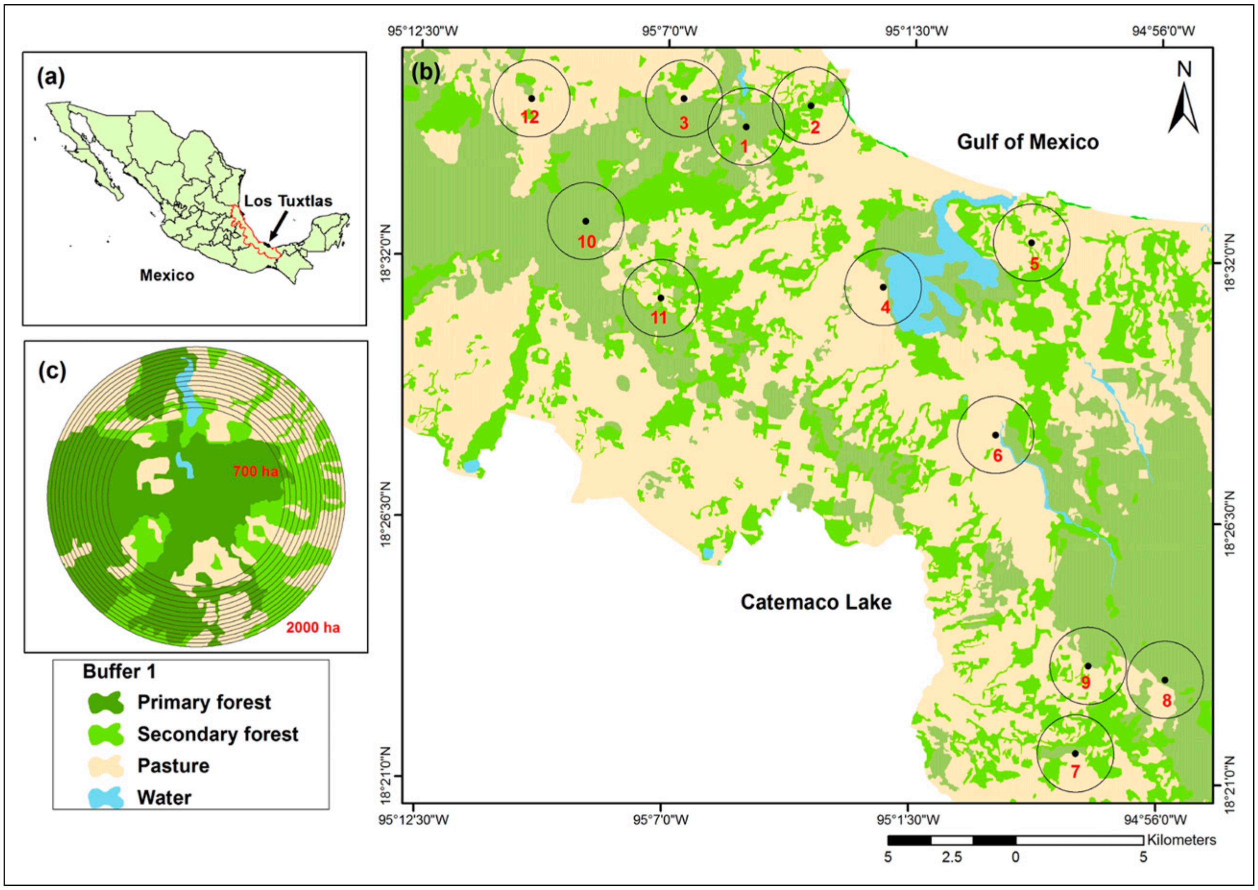

Figure 1. Study area (a) in Los Tuxtlas Biosphere Reserve, Mexico. Figure depicts the 12 study sites where survey transects were located (b) showing each buffer where landscape metrics where measured, and (c) example of one of the multi-scale analysis where landscape structure was measured (700 ha–2000 ha).

predominate, such as *Cecropia obtusifolia*, *Croton schiedeanus*, and *Schizolobium parahyba,* whose fruits are also consumed by parrots (De Labra-Hernández & Renton, 2019). The pasture land in Los Tuxtlas contains live fences, which are used to hold the barber wire to enclose cattle and to delimit the boundaries of the land. These fences are conformed of single planted rows of *Bursera simaruba* and *Gliricidia sepium* (among others), and large frugivores like the Red-lored Amazon have been observed to be present in these live fences (Estrada et al., 2000).

Toucans and Parrots in Los Tuxtlas

Toucans and parrots are among the most represented large-bodied frugivorous bird species in Los Tuxtlas and are common in tropical modified landscapes. Three toucan species occur in Los Tuxtlas: the Emerald Toucanet (*Aulacorhynchus prasinus warneri*), which is an endemic subspecies for the region; Winkler et al., 2020a), the Collared Aracari (*Pteroglossus torquatus*), and the Keel-billed Toucan *(Ramphastos sulfuratus*) (Howell & Webb, 1995). By the end of the 1990s, the Emerald Toucanet was reported as uncommon, the Collared Aracari was reported as common, and the Keel-billed Toucan was reported as highly common in our study area (Schaldach & Escalante-Pliego, 1997). Toucans are associated with tropical evergreen forest, and the Emerald Toucanet can be seen in the cloud forest. Also, the Collared Aracari and the Keel-billed Toucan may use secondary forests and open areas (Schaldach & Escalante-Pliego, 1997). For parrots, nine species have been reported in the Los Tuxtlas region (see Schaldach & Escalante-Pliego, 1997), and recent assessments of parrot populations in the region indicate that the most abundant species are the Red-lored Amazon (*Amazona autumnalis*), the White-fronted Amazon (*Amazona albifrons*), and the Olive-throated Parakeet (*Eupsittula nana*) (De Labra et al., 2010). In general, these parrot species use both preserved and disturbed areas of the evergreen forest, secondary forest, and mangrove (De Labra et al., 2010).

Bird Surveys

We used a map of the study region and a 3 × 3 km grid to randomly select 12 forest fragments to conduct bird surveys.

In each of the 12 survey sites, we randomly established a 3 km line transect to sample toucans and parrots (Figure 1b). Due to the extension of transects, these included mainly forest habitats, but also some extension of open areas (cattle pasture land, crop fields) surrounding the fragments. Each transect was surveyed four times during 2 years: September–November 2008–2009 and March–May 2009–2010, totaling 144 km of line transect observation. Censuses were conducted during the first 4 hour after sunrise, walking at a steady, slow pace of approximately 0.75 km/h in one direction along the transect. Surveys were conducted only in favorable weather conditions to avoid bias on bird detectability. We recorded all toucans and parrots observed (perched and flying) or heard without distance restriction (Bibby et al., 2000). As we could not accurately estimate the number of birds heard due to low visibility in the canopy, we considered birds heard as a single individual regardless of group size to avoid overestimating the number of birds. Auditive detections account for <20% of all observations; thus, we believe this approach did not influence our results. All surveys were conducted by the same observer (MADLH). Based on results from bird surveys, we estimated the number of individuals of (1) all toucan species detected (Emerald Toucanet, Collared Aracari, and Keel-billed Toucan); (2) the historically more abundant Keel-billed Toucan; (3) all parrots detected (Red-lored Amazon, White-fronted Amazon, and Olive-throated Parakeet); and (4) the historically more abundant Red-lored Amazon as the sum of all observations made during the four survey periods.

Landscape Metrics and the Scale of Effect of Landscape Structure

We used a site-landscape approach (sensu Fahrig, 2013) where the response variables were recorded at the site scale, and landscape structure was measured at the landscape scale. We used Spring 5.2.2 (Câmara et al., 1996) from year 2008 to develop a land cover map from a high resolution (20 m) satellite image (SPOT 5) of the study area. We defined five land cover types: water, pasture land, tropical primary forest, tropical secondary forest, and human settlements to characterize landscape structure. We used ArcGis 10.5 software to measure landscape compositional variables of primary forest, secondary forest, and pasture land cover as the percentage of the landscape covered by each of these land cover types. Primary and secondary forests were considered as suitable habitat for both toucans and parrots, and they were used as proxies of habitat amount. Regarding landscape configuration, we calculated two predictors that represent habitat fragmentation: patch and edge density (Fahrig, 2017). Forest patch density is positively related to landscape connectivity and landscape supplementation dynamics may be enhanced in landscapes with higher patch density (Dunning et al., 1992; McGarigal et al., 2012). Edge density can have negative effects on birds through negative edge effects, such as an increased mortality of emergent trees at forest edges (Bennet & Saunders, 2010; Dunning et al., 1992; McGarigal et al., 2012) and the more extreme local climates occurring in human-dominated land uses (Williams et al., 2020). For habitat fragmentation, we used an estimation of forest patch density, calculated as the number of forest patches in the landscape divided by landscape area (Fahrig, 2017). Forest edge density was estimated as the total perimeter length of all forest patches (primary forest + secondary forest) within the landscape divided by landscape area (m/ha). We combined both primary and secondary forests to calculate patch and edge density since these land covers occur contiguously at the study site and edges from only one of those covers do not represent real edges of forest–non-forest habitat.

Considering that the response of species to landscape structure can be scale-dependent, and as we did not know a priori the landscape that best predicts the number of toucan and parrot individuals to landscape patterns, we first assessed the so-called “scale of effect” of each landscape metric following Jackson and Fahrig (2015). For this, we traced a total of 14 concentric landscapes at 100 ha intervals from 700 ha (1493 m radii) to 2000 ha (2523 m radii) from the midpoint of each survey site (Figure 1c) using ArcGis 10.5 software. We calculated the described five landscape structure metrics within each landscape. We then used Generalized Linear Models (GLMs) to assess the association between each landscape metric and each response variable at each spatial scale (i.e., different size radii). Then, following Fahrig (2013), we plotted the percent of explained deviance (i.e., measure of the effect size) as a dependent variable against landscape size (each radii) to identify the spatial scale that yields the strongest response-predictor relationship (i.e., the highest percent of explained deviance; Online Appendix A).

Data Analyses

We used the ape package (Paradis et al., 2004) and letsR package (Vilela & Villalobos, 2018) of R (R Core Team, 2020) to assess the spatial independence of our samples by computing correlogram plots based on Moran’s Index. We found significant spatial autocorrelation in five out of 20 models, but these showed very small Moran’s Index values (<0.12, in all cases; Online Appendix B), which may be spurious correlations (Fortin et al., 2002). However, we constructed General Least Square (GLS) spatial models (Dormann et al., 2007) for those response variables that showed significant Moran’s Index. Nevertheless, comparisons of GLS versus GLS spatial models showed that the first performed better than models including spatial correlation by comparison of their Akaike Information Criterion AIC (Online Appendix C). Thus, we decided to continue all further analysis using GLMs.

Then, we constructed GLMs using Poisson error distribution for each response variable and all landscape metrics calculated at the scale of effect. We used “dredge” function from library MuMIn (Bartón, 2020) on R to generate all possible combinations of the independent variables starting with the full model and to select the best model explaining the number of individuals of toucans and parrots. We acknowledge our small sample size, but this approach resulted to be more accurate since performing individual models did not meet for linear model assumptions after verifying residuals versus fitted values (Appendix C). We interpreted best models indicated by ΔAICc <2 (Burnham & Anderson, 2002). All analyses were performed using R (R Core Team 2020).

Results

Toucan and Parrot Total Observations

In the four surveyed periods, we registered the three species of toucans (Keel-billed Toucan, Collared Aracari, and Emerald Toucanet) and only three out of nine species of parrots reported to occur in the study area (Red-lored Amazon, White-fronted Amazon, and Olive-throated Parakeet). We recorded a total of 1134 toucans and parrots over the four survey periods. A total of 280 toucans were recorded during our surveys (Table 1). The Keel-billed Toucan was the most common species (total = 239), representing 85.3% of all toucans observed (Table 1). Regarding parrots, we observed a total of 854 parrots of the three species (Table 1). The Red-lored Amazon was the most abundant parrot species (Total = 660) representing 77.2% of all parrots observed (Table 1).

Toucan and Parrot Response to Landscape Structure

We found a high association of landscape structure variables with the numbers of individuals of all toucans (68.2% explained deviance), the Keel-billed toucan (57.8% explained deviance), all parrots (76.7% explained deviance), and the Red-lored Amazon (84.7%).

Regarding landscape composition variables, model selection showed that the amount of primary forest cover was present in all models explaining the number of individuals of toucans and parrots. In all cases, the number of individuals of these birds increased with the amount of primary forest cover in the landscape (Table 2; Figures 2 and 3). Secondary forest cover was also an important landscape predictor for all parrot species only, resulting in increasing their number of individuals as secondary forest amount increases in the landscape. The amount of pasture land in the landscape was only important in explaining the abundance of the Keel-billed Toucan, resulting in a negative effect on the abundance of this species.

For bird responses to landscape configuration variables, the number of individuals of all toucans and the number of individuals of the Keel-billed Toucan increased with higher patch density in the landscape, whereas this predictor

Table 1. Total Numbers of Toucans and Parrots Registered in Los Tuxtlas (2008–2010).

Species	Number of Toucans and Parrots Observed
Keel-billed Toucan (*Ramphastos sulfuratus*)	239
Collared Aracari (*Pteroglossus torquatus*)	31
Emerald Toucanet (*Aulacorhynchus prasinus*)	10
All toucans	280
Red-lored Amazon (*Amazona autumnalis*)	660
White-fronted Amazon (*Amazona albifrons*)	137
Olive-throated Parakeet (*Eupsittula nana*)	57
All parrots	854

Table 2. Results of Generalized Linear Models for Assessing the Impact of Landscape Structure in the Number of Individuals of Toucans and Parrots in Los Tuxtlas, Mexico. We Present Standardized Parameter Estimates (β) for the Best Models (ΔAICc <2) Obtained by Model Selection, AICc, ΔAICc, and Akaike Weights for Each Model.

Response	Primary Forest Cover	Secondary Forest Cover	Pasture Land	Patch Density	Edge Density	AICc	ΔAICc	*wi*
All toucans	0.478			0.161		95.1	0	0.338
	0.535				0.162	97.0	1.85	0.134
Keel-billed Toucan	0.469			0.148		101.3	0	0.252
	0.396		−0.193	0.180		101.7	0.37	0.210
	0.441					102.3	1.01	0.152
All parrots	0.636	0.290		−0.310	0.179	250.6	0	0.974
Red-lored Amazon	0.516			−0.325	0.373	160.1	0	0.776

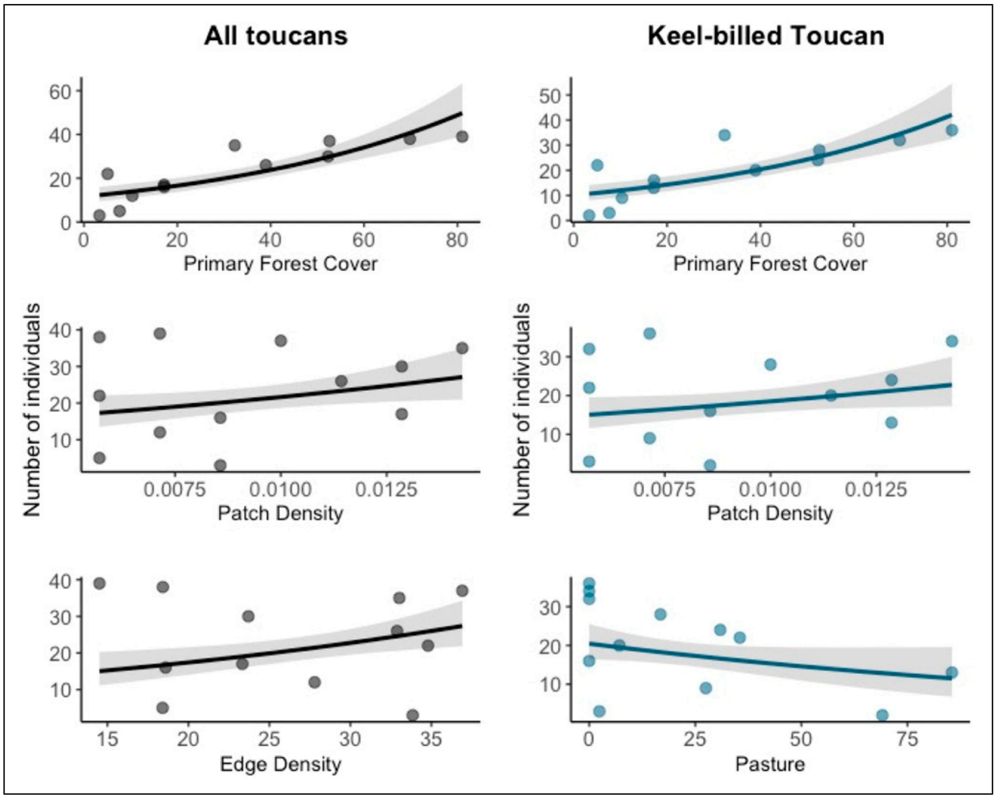

Figure 2. Effect plots showing the influence of each landscape predictor included in best models of the number of individuals of toucans in Los Tuxtlas, Mexico.

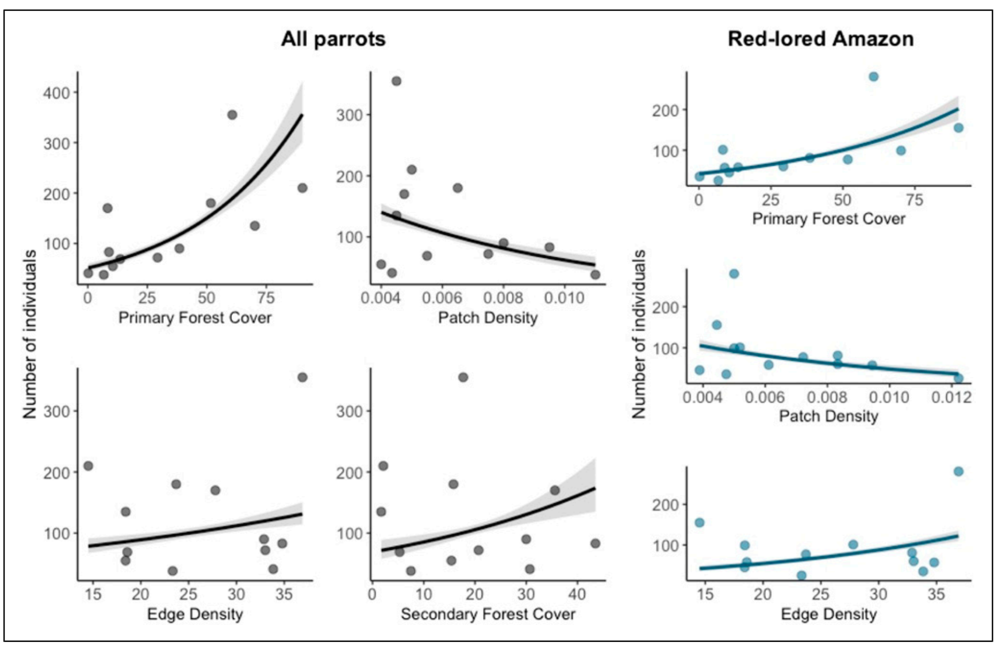

Figure 3. Effect plots showing the influence of each landscape predictor included in best models of the number of individuals of parrots in Los Tuxtlas, Mexico.

decreased numbers of all parrots and the Red-lored Amazon (Table 2; Figure 3). Finally, edge density had positive effects for the number of individuals of all toucans, all parrots and the number of individuals of the Red-lored Amazon (Table 2; Figures 2 and 3).

Discussion

Our study highlights the effects of landscape structure on the number of toucans and parrots, demonstrating similar responses of both groups to landscape composition but not configuration in Los Tuxtlas. As hypothesized, primary forest cover was the best predictor explaining toucan and parrot number of individuals in the study area. In this context, our results add support to the habitat amount hypothesis (Fahrig, 2013), which posits that habitat amount (forest cover) is more important than landscape configuration. By teasing apart the effects of landscape composition and configuration, our results suggest that despite toucan and parrot movement ability, these species depend on higher amount of primary forest cover within modified landscapes. Thus, averting deforestation should be the focus of conservation and management initiatives of this particular land cover in this vanishing tropical forest.

Influence of Landscape Composition on Toucan and Parrots

As expected, primary forest cover in the landscape increased the number of individuals of toucans and parrots. Our results are consistent with other studies that demonstrated that forest cover—a proxy of habitat amount and the most used landscape composition variable—has stronger effects on the abundance or occurrence of bird species in tropical forests (Bonfim et al., 2021; Carrara et al., 2015; Cerezo et al., 2010; Morante-Filho et al., 2021). Results from this study also support other studies which have demonstrated that some parrot species are more abundant within preserved sites with highest forest cover (De Labra-Hernandez & Renton, 2017; Legault et al., 2011). An increasing number of individuals of both toucans and parrots with higher amount of forest is likely explained by the high resource availability for large-bodied cavity nesting birds, like toucans and parrots, in forest habitats (Cornelius et al., 2008; De Labra-Hernández & Renton, 2016; Zanette et al., 2000). In addition, studies have shown that forest loss decreased the biomass and quality of fruits in fragmented landscapes in Brazil (Pessoa et al., 2017a, 2017b) and reduced the complexity of forest structure (DBH, tree density, height; Morante-Filho et al., 2018; Rocha-Santos et al., 2016), resulting in decreased diversity of forest-dependent frugivores (Morante-Filho et al., 2018). Forest structure simplification in deforested landscapes may influence the availability of nests for large-bodied cavity nesting birds, which depend on nest-cavities of old-growth forest trees (De Labra-Hernández & Renton, 2016; Renton et al., 2015), and cavity characteristics highly influence nest survival of cavity nesting birds (Cockle et al., 2015). Consequently, our results and previous evidence suggest possible indirect cascading effects of forest loss in food and nesting resource availability for forest-dependent frugivorous birds (Morante-Filho et al., 2018).

Secondary forest was also an important predictor, but only for parrots. These forests in Los Tuxtlas harbor old, well-preserved second-growth vegetation and may therefore be functional in terms of resource availability for forest-dependent species such as parrots, as previous studies have observed these birds occurring within secondary forests (De Labra-Hernández & Renton, 2019; De Labra et al., 2010; Marsden & Symes, 2006; Urquiza-Haas et al., 2011). The fact that secondary forest cover was not an important predictor for the abundance of the Red-lored Amazon could be related to its larger size compared to the other parrots registered in this study (White-fronted Amazon and Olive-throated Parakeet). It is likely that the structural characteristics of secondary forests may not harbor optimal nesting resources for this species since other studies have observed lower densities of cavities in secondary forest compared to primary forest for the large-bodied Northern Mealy Amazon (De Labra-Hernández & Renton, 2016), suggesting that secondary forests are less important for large-bodied parrots in Los Tuxtlas. Nevertheless, we acknowledge that the lack of data on the quality of vegetation in forest patches along with fruit composition, and fruit availability in the studied landscapes may represent a bias in our results of landscape composition influence on toucans and parrots.

Similarly as secondary forests, cattle pasture land only influenced the abundance of the larger Keel-billed Toucan, thus indicating that this species is highly associated with primary forest and avoids open areas. The fact that cattle pasture land was not an important landscape predictor for parrots and toucans could be related to the high heterogeneity of this land cover in Los Tuxtlas. Cattle pasture land in Los Tuxtlas is usually composed by live fences which resemble corridors of vegetation across pasture land, and these have been observed to support a high number of species in the region (Estrada et al., 1997) including the Red-lored Amazon (Estrada et al., 2000). Additionally, isolated trees are considered important for animals when crossing pasture land between forest fragments in Los Tuxtlas (Guevara & Laborde, 2014), where 47 frugivorous bird species have been observed visiting these trees for feeding, perching, and resting (Guevara & Laborde, 1993). These friendly elements within cattle pasture land may be the reason why we did not observe the expected negative effect of these non-forest land in toucans and parrots in Los Tuxtlas.

Influence of Landscape Configuration on Toucans and Parrots

As predicted, landscape fragmentation had smaller effects than landscape composition on toucan and parrot numbers, with most of the responses being positive. These results corroborate the observed pattern of larger effects of landscape composition on species responses than changes in landscape configuration, such as fragmentation (Carrara et al., 2015; Fahrig, 2017; Klingbeil & Willig, 2016). This result adds support to the growing evidence of positive effects of fragmentation for biodiversity (Fahrig et al., 2019). Interestingly, patch density in the landscape had contrary effects for toucans and parrots. We suggest that toucans are positively influenced by patch density in the landscape due to their wide-ranging movements (900 ha; Holbrook, 2011). Additionally, although considered primarily as frugivores, toucans can supplement their diets with vertebrates, insects, eggs, and nestlings (Jones & Griffiths, 2020), which may be well supported in several patches of habitat within the landscape in Los Tuxtlas.

Even though parrots are also wide-ranging species, which undertake both local and long-distance movements (Renton et al., 2015), their negative response to patch density could be related to the fact that these birds are mostly seed eaters and fruit eaters. Some species have shown dietary selectivity within the primary forest (De Labra-Hernández & Renton, 2019), and particular food-resources for these birds could be more abundant in continuous extensions of habitat rather than several habitat patches. Moreover, although parrot species in this study are frequently located in human-modified landscapes, they show larger movements through the landscape when the forest is dispersed (Salinas-Melgoza et al., 2013). This would involve higher investment of energy for parrots, and when inhabiting these landscapes they may be more prone to be captured for the pet trade, which is the main threat to parrot populations in the Neotropics (Berkunksy et al., 2017). The fact that we did not observe six of the nine parrot species could be related to the high rates of poaching that these birds suffer, resulting in the decline of their populations. It is likely that individuals of the missing species remain in more continuous forested areas like the Volcan de Santa Marta, southeast of Los Tuxtlas (MADLH, unp. Data). This is the case of the larger Scarlet Macaw and the Northern Mealy Amazon; the first extirpated for decades from Los Tuxtlas (but now reintroduced) and the second being absent for several years due to logging and nest poaching (De Labra et al., 2010).

Implications for Conservations

Globally, there is a consensus that forest loss is the main threat to biodiversity in human-modified landscapes (Fahrig, 2003), including large-bodied birds, which are severely affected due to forest loss (Sodhi et al., 2008). Our study demonstrates that primary forest cover was the most important landscape factor explaining toucan and parrot numbers in the landscape, indicating that continual primary forest loss will represent the greatest threat to these large-bodied birds. Overall, our results suggest that the availability of primary forest in the landscape represents a limiting factor for toucans and parrots, thus adding evidence to the high conservation value of primary forest patches, including the small ones (Fahrig et al., 2019; Wintle et al., 2019). We recommend maintaining primary forest in the landscape, which is consistent with the findings of numerous studies in fragmented tropical landscapes to conserve tropical forest birds (Cerezo et al., 2010; Graham, 2001a, 2001b; Pizo & dos Santos, 2011), including frugivores (Bonfim et al., 2021). Moreover, for preserving forest species, landscapes should at least maintain 40% of forest cover, with 30% of forest evenly dispersed (Arroyo-Rodríguez et al., 2020). Additionally, conservation actions should be focused on preserving both continuous forest and habitat patches in the landscape since toucans and parrots showed contrasting response to patchiness. Further studies should evaluate such responses in terms of patch quality of primary and secondary forests for these birds since the quality of forest patches highly influences the abundance of toucans and parrots (Pizo et al., 1995; Ragusa-Netto, 2008). We strongly recommend that studies involving frugivorous birds should be coupled with data acquisition on fruit composition availability to avoid potential bias when relating responses of these birds with landscape features. Therefore, conservation efforts should also include the strengthening of the quality of secondary forests in order to reduce the habitat-matrix contrast (Levey et al., 2021) and to promote landscape supplementation/complementation dynamics (Dunning et al., 1992) for toucan and parrot populations. Fortunately, deforestation rates in Los Tuxtlas have decreased since the decree of the Los Tuxtlas Biosphere Reserve in 1998, with deforestation in the nucleus zones of the reserve halved since 1998–2011 (Von Thaden et al., 2018) and reforestation efforts have taken place in the area (Von Thaden et al., 2020). Nevertheless, a substantial loss of forest cover is predicted by 2025, particularly in the buffer areas of the reserve (Von Thaden et al., 2018). Additionally, a more recent and long-term monitoring of toucans and parrots in Los Tuxtlas is necessary to determine the actual status of populations of these birds. Continual monitoring of these birds and their habitat associations can be helpful when using birds as indicators of habitat quality through the process of habitat restoration (Ramírez-Soto & Gama, 1997). This is the case of toucans and parrots due to being large-bodied species and easy to observe. They are also charismatic bird species, which also confers them the potential use as flagship species in conservation management by increasing concern on the target species and its habitat. Finally, any landscape level management actions for these birds should be accompanied by an enforcement of federal laws against trade of toucans and parrots. According to local people from Los Tuxtlas, species in this study (Red-lored Amazon and White-fronted Amazon) were found to be the most trafficked into the region (De Labra et al., 2010). Moreover, Psittacidae and Ramphastidae are among the most represented birds in the Mexican bird pet trade (Roldán-Clarà et al., 2017).

Appendix A

Martínez-Ruiz, M., De Labra-Hernández, M. A., Bonfim F. G., & Cazetta, E. Influence of landscape structure on toucans and parrots in the fragmented landscape of Los Tuxtlas, Mexico. Tropical Conservation Science.

Association (i.e., percentage of explained deviance and Generalized Linear Models) between the number of

Landscape Predictor/Scale	All Toucans	Keel-Billed Toucan	All Parrots	Red-Lored Amazon
Primary forest				
700	74.92	74.92	**47.85**	**49.40**
800	75.35	66.09	46.04	47.39
900	75.41	65.82	45.06	46.30
1000	75.85	66.03	44.01	44.99
1100	76.16	66.31	42.66	44.99
1200	76.33	66.52	41.52	41.68
1300	**76.37**	**76.37**	40.49	40.32
1400	76.30	66.75	39.38	44.99
1500	76.23	66.87	44.01	38.09
1600	76.28	67.18	37.92	37.26
1700	76.21	67.25	47.80	36.62
1800	76.14	67.38	36.58	35.72
1900	76.14	67.59	35.81	34.78
2000	76.14	67.78	34.88	33.67
Secondary forest				
700	14.18	12.80	**1.94**	**2.70**
800	14.25	12.73	1.91	2.44
900	14.93	13.34	1.93	2.01
1000	**15.27**	**13.75**	1.88	1.68
1100	14.64	13.29	1.73	1.26
1200	13.75	12.62	1.53	0.86
1300	12.48	11.56	1.25	0.47
1400	10.77	10.01	0.93	0.18
1500	8.83	8.14	0.67	0.06
1600	7.09	6.30	0.64	0.04
1700	6.14	6.14	0.62	0.03
1800	5.20	4.39	0.64	0.02
1900	4.58	3.79	0.54	0.00
2000	4.14	3.38	0.42	0.02
Pasture				
700	**21.81**	**24.98**	**10.06**	**16.03**
800	21.55	24.92	9.24	15.39
900	20.73	24.19	8.11	14.32
1000	20.13	23.54	7.38	13.63
1100	19.96	23.33	6.79	12.92
1200	10.49	13.38	2.66	8.38
1300	19.13	19.13	5.26	11.51
1400	19.02	19.02	5.31	11.59
1500	18.88	22.16	5.05	11.30

(continued)

(continued)

Landscape Predictor/Scale	All Toucans	Keel-Billed Toucan	All Parrots	Red-Lored Amazon
1600	19.31	22.51	5.14	11.17
1700	19.08	22.33	4.69	10.45
1800	18.58	21.90	4.26	10.04
1900	18.49	21.82	4.11	9.83
2000	18.59	21.93	4.19	9.98
Forest patch density				
700	**5.68**	**4.23**	0.13	0.63
800	1.73	0.71	2.06	3.38
900	2.94	1.79	5.39	6.60
1000	4.82	3.24	7.12	8.02
1100	2.72	2.17	13.17	13.46
1200	2.87	2.57	12.97	12.83
1300	2.45	1.83	8.87	9.51
1400	3.29	3.09	8.84	12.51
1500	2.01	2.01	9.87	13.79
1600	0.45	0.91	14.75	18.86
1700	0.29	0.71	15.72	19.60
1800	0.24	0.24	18.92	**22.56**
1900	0.29	1.01	17.80	21.29
2000	0.24	0.97	**19.06**	21.89
Forest edge density				
700	0.84	0.75	0.00	0.11
800	1.09	0.90	0.04	0.49
900	2.49	2.90	0.08	0.81
1000	1.84	2.31	0.49	1.57
1100	2.74	3.60	0.16	1.15
1200	4.74	6.25	0.63	1.68
1300	**24.94**	**23.68**	**12.35**	**9.69**
1400	1.77	2.68	0.50	1.92
1500	0.81	1.38	0.58	1.99
1600	0.36	0.75	0.41	1.67
1700	0.23	0.64	0.72	2.05
1800	0.32	0.79	0.78	2.18
1900	0.10	0.45	1.45	3.54
2000	0.12	0.41	1.64	4.08

individuals of toucans and parrots and landscape composition (primary forest, secondary forest, and pasture) and landscape configuration (forest patch density and forest edge density). Landscape structure was measured considering 13 different-sized radii for each survey site to identify the landscape size that yields the strongest association between each response variable and each predictor (i.e., the scale of landscape effect, in bold)

Model	Moran's Index	*p*-Value
All toucans		
Num. individuals~Primary forest$_{1300}$	0.0416	0.1441
Num. individuals~Secondary forest$_{1000}$	0.0314	0.2055
Num. individuals~Pasture$_{700}$	−0.0935	0.1666
Num. individuals~Forest patch density$_{700}$	−0.0262	0.4936
Num. individuals~Forest edge density$_{1300}$	−0.0935	0.9779
Keel-billed toucan		
Num. individuals~Primary forest$_{1300}$	0.0880	**0.0381**
Num. individuals~Secondary forest$_{1000}$	0.0452	0.1564
Num. individuals~Pasture$_{700}$	0.0386	0.1560
Num. individuals~Forest patch density$_{700}$	0.1025	**0.0294**
Num. individuals~Forest edge density$_{1300}$	−0.0691	0.8140
All parrots		
Num. individuals~Primary forest$_{700}$	0.1232	**0.0119**
Num. individuals~Secondary forest$_{700}$	0.0546	0.0923
Num. individuals~Pasture$_{700}$	0.1171	**0.0149**
Num. individuals~Forest patch density$_{2000}$	0.1025	**0.0294**
Num. individuals~Forest edge density$_{1300}$	0.0141	0.2217
Red-lored amazon		
Num. individuals~Primary forest$_{700}$	−0.0043	0.2406
Num. individuals~Secondary forest$_{700}$	−0.0401	0.5034
Num. individuals~Pasture$_{700}$	0.0252	0.0947
Num. individuals~Forest patch density$_{1800}$	0.0053	0.2194
Num. individuals~Forest edge density$_{1300}$	−0.0252	0.9254

Appendix B

Moran's spatial autocorrelation index for 12 survey sites, and p values for the residuals of the best models for the number of individuals of toucans and parrots as a function of each landscape predictor at the selected scale of effect in Los Tuxtlas, Mexico. Significant values are indicated in bold ($p < 0.05$). Sub-indices indicate the landscape size (ha) at which scale of effect was detected.

Appendix C

Plots of residual versus fitted values of complete GLMs explaining the number of individuals of toucans and parrots.

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