

# Scale Dependency of Arboreal Mammals' Responses to Landscape Spatial Changes in a Fragmented Rainforest

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## Research Article

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# Abstract

*Context.* Biodiversity patterns depend on landscape structure, but the spatial scale at which such dependence is strongest (scale of effect, SoE) remains poorly understood, especially for elusive species such as arboreal mammals.

*Objectives.* We assessed the SoE in arboreal mammals and evaluated whether it depends on which biological responses and landscape variables are measured. We expected the number of species to be more reliant on spatial patterns of larger landscapes than relative abundance, especially when considering larger bodied species, and connectivity-related landscape variables.

*Methods.* We sampled arboreal mammals during one year using camera traps placed in 100 trees within 20 forest patches in the Lacandona rainforest, Mexico. We measured forest cover, matrix openness, patch density, and edge density within 13 concentric buffers to identify the SoE of each landscape variable on the number of species, total abundance, and species-specific abundance.

*Results.* Unexpectedly, edge density tended to have larger SoE than forest cover and matrix openness, and the SoE did not differ between number of species and total abundance. Yet, the SoE tended to be positively related to body mass.

*Conclusions.* Mammal responses to edge density seem to be regulated by large-scale processes, such as an increasing dispersal in landscapes with higher edge density, and not by local-scale processes (e.g. edge effects). Species richness and total abundance seem to be moderated by ecological processes acting across similar spatial scales, but the SoE tends to increase with body mass. Therefore, conservation plans for larger mammals should be implemented across larger spatial extents.

## Introduction

Land-use change is rapidly transforming tropical ecosystems into anthropogenic landscapes. These emerging landscapes not only differ in the types and amounts of different land covers they contain (e.g. percentage of forest cover, Hansen et al. 2019), but also in the spatial arrangement of each land cover (e.g. number of forest patches; Taubert et al. 2018). These landscape spatial patterns can have contrasting effects on biodiversity (Tscharntke et al. 2012; Galán-Acedo et al. 2019; Arroyo-Rodriguez et al. 2020). However, detecting such effects is challenging because species' responses to landscape changes can only be evident at certain spatial extents (the so-called 'scale of effect', SoE hereafter; Jackson and Fahrig 2015; Miguet et al. 2016; Martínez-Ruiz et al. 2020). Therefore, to make accurate and more reliable inferences on the effect of landscape patterns on biodiversity, we need to use a multiscale approach measuring landscape variables across multiple scales to identify the scale that yields the strongest species-landscape response (Jackson and Fahrig 2015). Despite its importance, and some reviews on this topic (e.g. Jackson and Fahrig 2015; Miguet et al. 2016; Martin 2018; Yeiser et al. 2021), our understanding on the SoE is far from complete. Therefore, additional studies are required to better

understand species-landscape associations, and thus provide more accurate management and conservation initiatives.

Identifying the spatial extent at which a given biological response more strongly interacts with a given landscape variable is highly valuable to understand the ecological processes (e.g. dispersal, extinction, births and deaths) that may be regulating such response. As proposed by Miguet et al. (2016) and Martin (2018), responses regulated by local-scale processes are expected to be mainly associated with the spatial context of smaller landscapes, whereas responses driven by large-scale processes should be more strongly related to landscape patterns across larger spatial extents. For example, landscape variables affecting breeding and/or foraging (e.g. habitat fragmentation, edge density) could have smaller SoE than landscape variables related to dispersal success (e.g. habitat amount, matrix contrast; Miguet et al. 2016). In a similar rationale, the abundance of individuals is expected to be more strongly related to local-scale processes (i.e. those affecting the fitness of individuals), while the number of species is hypothesized to depend more on processes operating across larger spatial and temporal scales (e.g. dispersal, extinction; Miguet et al. 2016). Therefore, independently of the landscape variable, the SoE should be larger for the number of species than for the number of individuals. At the species population level, the SoE can be driven by certain species traits, especially by those determining the way species use their home ranges (Miguet et al. 2016). For example, body mass is often related to species' vagility, with larger species usually moving across larger territories than smaller species (Tucker et al. 2018). Therefore, large-bodied species are expected to have a larger SoE than small-bodied species (Miguet et al. 2016). However, these hypotheses remain poorly tested for most species (Jackson and Fahrig 2015; Miguet et al. 2016; Martin 2018), especially for strongly forest-dependent ones, such as arboreal mammals.

Given their strong dependence on forest canopy, arboreal mammals can be particularly sensitive to disturbances caused by land-use change (Whitworth et al. 2016; Bolt et al. 2018; Schüßler et al. 2018; Galán-Acedo et al. 2019). Arboreal mammals constitute a large proportion of mammal diversity in tropical forests (Kays and Allison 2001), and are involved in crucial ecological roles in the upper rainforest strata, such as pollination (e.g. Janson et al. 1981; Ganesh and Devy 2000), seed dispersal (e.g. Andresen et al. 2018), and herbivory (e.g. Chapman et al. 2013). In spite of their importance, several groups of arboreal mammals are highly threatened with extinction (e.g. primates, Estrada et al. 2017; marsupials, Wayne et al. 2006; sloths, Superina et al. 2010), while for others we do not have enough data to assess their population trends (e.g. anteaters and porcupines, IUCN 2019).

Here, we evaluated the SoE of four landscape variables (forest cover, matrix openness, forest patch density, and forest edge density) on arboreal mammals in the Lacandona rainforest – a biodiversity hotspot from south-eastern Mexico. To our knowledge, only three studies have studied the scale of landscape effect in arboreal mammals, but all focused on primates (Ordóñez-Gómez et al. 2015; Galán-Acedo et al. 2018; Gestich et al. 2019). We measured each landscape variable in 13 spatial scales (circular landscapes with radii of 100 to 1300 m). We considered two responses at the community level (number species and total relative abundance). Following Miguet et al. (2016), we predicted that patch density and edge density would have smaller SoE than forest cover, matrix openness, and mean inter-

patch isolation. We also expected that SoE would be higher for the number of species than for total abundance. Finally, regarding species-specific responses, we predicted that SoE would increase with body mass.

## Methods

### Study region

The Lacandona rainforest, Chiapas, Mexico (91°6'42.8"–90°41'8.7" W; 16°19'17.1"–16°2'49.3" N) has a warm (mean annual temperature 24–26°C) and humid climate (mean annual precipitation ranges from 2500 to 3500 mm). The original vegetation is tall evergreen rainforest (Carabias et al. 2015). The Lacantún River separates a large protected forest tract on the western side of the study area, the Montes Azules Biosphere Reserve, from the Marqués de Comillas region on the eastern side, a heavily impacted area with approximately 50% of remaining forest cover (203,999 ha; Arce-Peña et al. 2019), dominated by cattle-ranches, annual crops and oil palm plantations. The study was conducted in 20 forest patches in the Marqués de Comillas region. Patches ranged in size from 5 to 2300 ha and were separated from each other by a distance of at least 2.5 km, measured from their geographical centres (Fig. 1).

### Arboreal mammal surveys

Mammal surveys are detailed elsewhere (Cudney-Valenzuela et al. 2020), but a brief overview is given here. At the geographical centre of each patch, and avoiding vegetation gaps, we selected five trees with suitable climbing conditions (branches  $\geq 20$  cm wide, preferably hard wood species) and whose architecture allowed to install a camera trap facing other main branches. At each tree, we established a single-rope climbing system. Focal trees in the same patch were separated by 30 – 150 m. Of the five focal trees per patch, four reached the canopy (mean  $\pm$  SD = 21.8  $\pm$  6.2 m, range = 10.2 to 36.6 m) and one the midstory (9.1  $\pm$  4.7 m, 3.4 to 19.6 m). This allowed us to capture a greater vertical range of strata potentially used by arboreal mammals.

We used one camera trap (Bushnell Trophy Cam HD Aggressor Low Glow ©) per patch. Cameras were placed at varying heights depending on the characteristics of the focal tree (camera height of canopy and midstory trees was 15  $\pm$  4.3 m and 2  $\pm$  0.6 m, respectively). Cameras were continuously active from May 2018 to May 2019, and they were serviced once a month (change of batteries, downloading of pictures, replacement of malfunctioning cameras). We rotated the location of the cameras once a month among the five focal trees in each patch, except from October to December when they remained on the same focal tree. Total sampling effort was 7,387 camera trap nights (average per patch = 369  $\pm$  11.6 nights), with 6,233 active camera trap nights (average per patch = 311.7  $\pm$  19.9 nights).

To increase the probability of photo-capture we used baits in the midstory trees (tuna fish, peanut butter with oatmeal and a banana). As revealed by photographs, bait was consumed during the first two nights in all cases. Since we did not provide more bait while the camera was active on that tree and no camera malfunctioned on the period the trees contained bait, all sites had the same bait sampling effort. We

processed all photographs with the program Digikam© and extracted photograph metadata with the package 'camtrampR' (Niedballa et al. 2016). We considered photo captures as independent events when there was at least a 24 h interval between captures of the same species, since individuals photographed on the same day are likely the same ones (Royle et al. 2009). We identified each mammal species using Reid's (2009) field guide, and obtained their body masses from Ceballos and Oliva (2006; Supplementary Material, Table S1). Except for the Mexican hairy porcupine (*Coendou mexicanus*) and squirrels, all other rodents were excluded from the analyses, due to imprecision in identification. For further analyses, we excluded rare species that appeared in less than half of the sites (i.e. *Eira barbara*,  $n = 4$  patches; *Leopardus wiedii*,  $n = 2$  patches; *Procyon lotor*,  $n = 1$  patches) to avoid spurious relationships. We finally included 12 species in the analyses that are described below.

## Landscape variables

We adopted a site-landscape approach (*sensu* Brennan et al. 2002), with response variables measured in same-sized sample sites (i.e. 5 focal trees at the centre of each forest patch), and landscape variables measured within 13 concentric circular landscapes (100- to 1300-m radius, at 100 m intervals, measured from the geographical centre of each site; Fig. 1). We used recent and high-resolution Sentinel S2 satellite images (from 2016) to produce land cover maps of each landscape surrounding the focal patches using ENVI 5.0 software. Land covers were classified into six types: (i) old-growth forest cover; (ii) secondary vegetation; (iii) tree crops (e.g. oil palm plantations); (iv) annual crops and cattle pastures; (v) human settlements; and (vi) water bodies (Fig. 1). The area covered by each land cover type was calculated using ArcGIS software with the 'Patch Analyst' extension. We then estimated the following landscape variables: (i) the percentage of old-growth forest cover (i.e. area covered by old-growth forest divided by landscape size  $\times 100$ ), (ii) matrix openness (i.e. area covered by treeless land divided by matrix area  $\times 100$ ), (iii) patch density (i.e. number of old-growth forest patches divided by landscape size), and (iv) edge density (i.e. the sum of the length of all old-growth forest edges within the landscape, divided by landscape size).

## Data analyses

We calculated the number of species per forest patch. We also calculated each species' relative abundance index (O'Brien 2011) by dividing the number of events for a given species by the number of days the camera was active in the patch, and multiplied by 100. This index is widely recommended as a proxy of mammal abundance in studies using camera traps (Mandujano and Pérez-Solano 2019; Benchimol and Peres 2020). We rounded up each species' relative abundance to the nearest whole number to calculate species-specific abundance per patch, and summed the relative abundance of all species in each patch to calculate total abundance per patch.

To identify the SoE, i.e. the scale at which each landscape variable best predicted each response (total relative abundance, number of species, and relative abundance of each mammal species), we used generalized linear models with a Poisson distribution error. We excluded the smallest scale from the analysis (100-m radius) since it did not show variation in forest patch density (Fig. S1). We first

quantified the relationship between each landscape variable and each response at each scale (4 landscape variables × 12 landscape buffers × 14 response variables = 672 models). To identify the SoE, we calculated the percentage of explained deviance by each landscape variable measured at each scale to identify the scale at which each variable best predicted each response variable (Fig. 2). For the analyses at the species level, we only considered this scale as the SoE if it showed a relatively higher empirical support (i.e. it showed a difference in Akaike Information Criterion ( $\Delta\text{AIC}$ ) > 2) when compared with the null model (i.e. including only the intercept) (see Table S2). Then, following the protocol proposed by Galán-Acedo et al. (2018), San-José et al. (2019) and Martínez-Ruiz et al. (2020), we used ANOVA to test whether the SoE differed among landscape variables, and a *t*-test to test whether the number of species had greater SoE than total relative abundance. We finally used a linear regression to assess whether the SoE increased with increasing body mass.

## Results

We obtained 1,672 independent photo-captures of 15 species. The most frequently recorded species were the Deppé's squirrel (*Sciurus deppei*), the kinkajou (*Potos flavus*), and the black howler monkey (*Alouatta pigra*), together representing ~ 50% of all records. Rarely recorded species were the margay (*Leopardus wiedii*), the Northern raccoon (*Procyon lotor*) and the tayra (*Eira barbara*), together representing 0.9% of the records.

We found a large variation in SoE among species and landscape variables and there was not a unique landscape variable that had empirically supported SoE models for all species (Fig. 2, Table S2). Twenty out of 48 SoE models showed a greater empirical support than the null model (i.e.  $\Delta\text{AIC} > 2$ ), and only 3 out of 12 species – the common opossum (*Didelphis marsupialis*), the white-nosed coati (*Nasua narica*), and the Mexican mouse opossum (*Marmosa mexicana*) – did not show empirically supported SoE models with any landscape variable (Fig. 2).

The SoE did not differ among landscapes metrics ( $F = 1.39$ ,  $p = 0.28$ ; Fig. 3). However, the median value of SoE of edge density was >2 times higher than the SoE of forest cover and matrix openness and >3 times higher than the SoE of patch density (Fig. 3). We also found no differences in SoE between response variables at the community level, with the number of species and species abundance showing similar SoE ( $t = -0.58$ ,  $p = 0.59$ ; Fig. 4). However, after excluding the cases in which the model with highest explanatory power did not show stronger empirical support than the null model, the SoE at the population level tended to be positively related to body mass ( $R^2 = 0.16$ ;  $F_{(1,18)} = 3.56$ ,  $p = 0.07$ ; Fig. 5).

## Discussion

This study assesses the potential determinants of the scale of landscape effect (SoE) on arboreal tropical mammals – a threatened and understudied group. Although we did not find significant differences in SoE among landscape variables, the SoE of edge density was notably higher than the SoE of forest cover, matrix openness and patch density. Unexpectedly, the SoE was also independent of the

response variable at the community level. Nevertheless, at the population level, we found that, as predicted, SoE depends on body mass, with larger species showing larger SoE. As discussed below, these findings have important ecological and conservation implications.

Contrary to our predictions, the SoE does not differ significantly among landscape variables. However, it is important to note that forest edge density tends to have larger SoE than forest cover, matrix openness and patch density. This is consistent with previous studies of arboreal primates (Galán-Acedo et al. 2018) and suggests that, contrary to what it is usually argued (see e.g. Fletcher et al. 2018), the effects of edge density on biodiversity can be more strongly related to large-scale processes, such as the increasing dispersal of individuals (higher connectivity) in landscapes with higher edge density (reviewed by Ewers and Didham 2006), than to local-scale processes, such as negative edge effects. This issue is particularly relevant in the context of fragmentation studies, which usually extrapolate empirical evidences obtained at the local scale to the landscape scale (Fahrig et al. 2019). For example, a common extrapolation in these studies is that the species that have a lower abundance along forest edges than forest interior cannot persist in fragmented landscapes with higher edge density (Fletcher et al. 2018; Phalan 2018). Nevertheless, our findings suggest that, in agreement with Fahrig et al. (2019), this extrapolation is unreliable because it overlooks other mechanisms at large scales (e.g. increased landscape connectivity and habitat heterogeneity, enhanced landscape complementation and supplementation dynamics) that can counteract local edge effects. In fact, edge density is largely moderated by shape complexity of remaining patches in the landscape, and shape complexity is known to facilitate the movements of individuals among habitat patches and between patches and the surrounding anthropogenic matrix (Collinge and Palmer 2002; Ewers and Didham 2006). Therefore, as argued by Galán-Acedo et al. (2018), it seems reasonable to consider edge density as a connectivity-related landscape variable, whose effects can be more evident at relatively large spatial extents.

The lack of differences in SoE between the number of species and total abundance is not totally surprising. Although these findings contradict our predictions based on previous theoretical models (Miguet et al. 2016), they align with a recent review showing that the SoE of richness-related response variables is not always larger than the SoE of abundance-related responses (Martin 2018). Such a lack of differences in SoE between total abundance and species richness can be explained by three factors. First, it could be possible that the landscape-scale processes regulating these two responses may act at similar scales. For example, both species richness and abundance may depend on migrations across short and large scales, and the landscape processes affecting the fitness of individuals at the population level can ultimately affect species richness. Second, species richness could actually be regulated by processes acting at larger scales, but the extinction debt in the study region does not allow to find significant differences in SoE between species richness and total abundance. In particular, we know that species extinctions in human-modified landscape may take time to become evident, potentially leading to time-delayed extinctions (i.e. extinction debt) (Metzger et al. 2009; Lira et al. 2012). Thus, given the relatively short history of land-use change in the region (<40 years), it is reasonable to expect that there is a relatively high extinction debt, which means that the effects of extinctions (i.e. a process usually associated to large temporal and spatial scales; Miguet et al. 2016) on species richness has not been

fully expressed. Finally, another non-exclusive possibility of the lack of differences in the SoE between community responses is related to the confounding effect of including in these response variables species with contrasting dispersal abilities, as they are expected to have different SoE (Miguet et al. 2016). In fact, as discussed below, we found that large-bodied species tend to have larger SoE than small-bodied species. Therefore, when assessing the SoE of total abundance and species richness we are including species with different body mass and thus with contrasting SoE, increasing the variation in the data, and thus preventing to find significant differences between these two community-level responses.

Our results support the hypothesis that body mass can determine the SoE of arboreal mammals. In particular, larger species have larger SoE. This finding aligns with numerous studies of different animal groups that demonstrate the positive association between body mass and the landscape size that is used by the species (e.g. mammals = Tucker et al. 2014; birds = Thornton and Fletcher 2014; reptiles = Mitrovich et al. 2011; fishes = Nash et al. 2015). This can be related to the fact that larger species can travel further than smaller ones (Jetz et al. 2004), as this implies that they interact with the spatial structure of larger territories.

In summary, our findings suggest that the SoE depends more strongly on landscape variables than on response variables at the community level. However, the biological responses at the population level can also be critical, with large-bodied species showing larger SoE than small-bodied species. These findings have important conservation implications. First of all, the fact that the SoE of edge density is relatively higher than the SoE of other landscape variables implies that to prevent negative responses of biodiversity to edge density, the management and conservation actions should be designed and implemented across relatively large spatial extents. Similarly, the fact that SoE is positively related to body mass implies that conservation actions for larger species is likely more challenging, as it needs to be planned and implemented across larger scales than those focused on preserving small-bodied species.

## **Declarations**

### **Author contributions**

SCV and VAR developed the idea of the study, with support from EA and TTA. SCV collected and analysed the data with guidance from VAR. All authors made substantial contributions to the intellectual content, interpretation and editing of the manuscript.

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## Figures

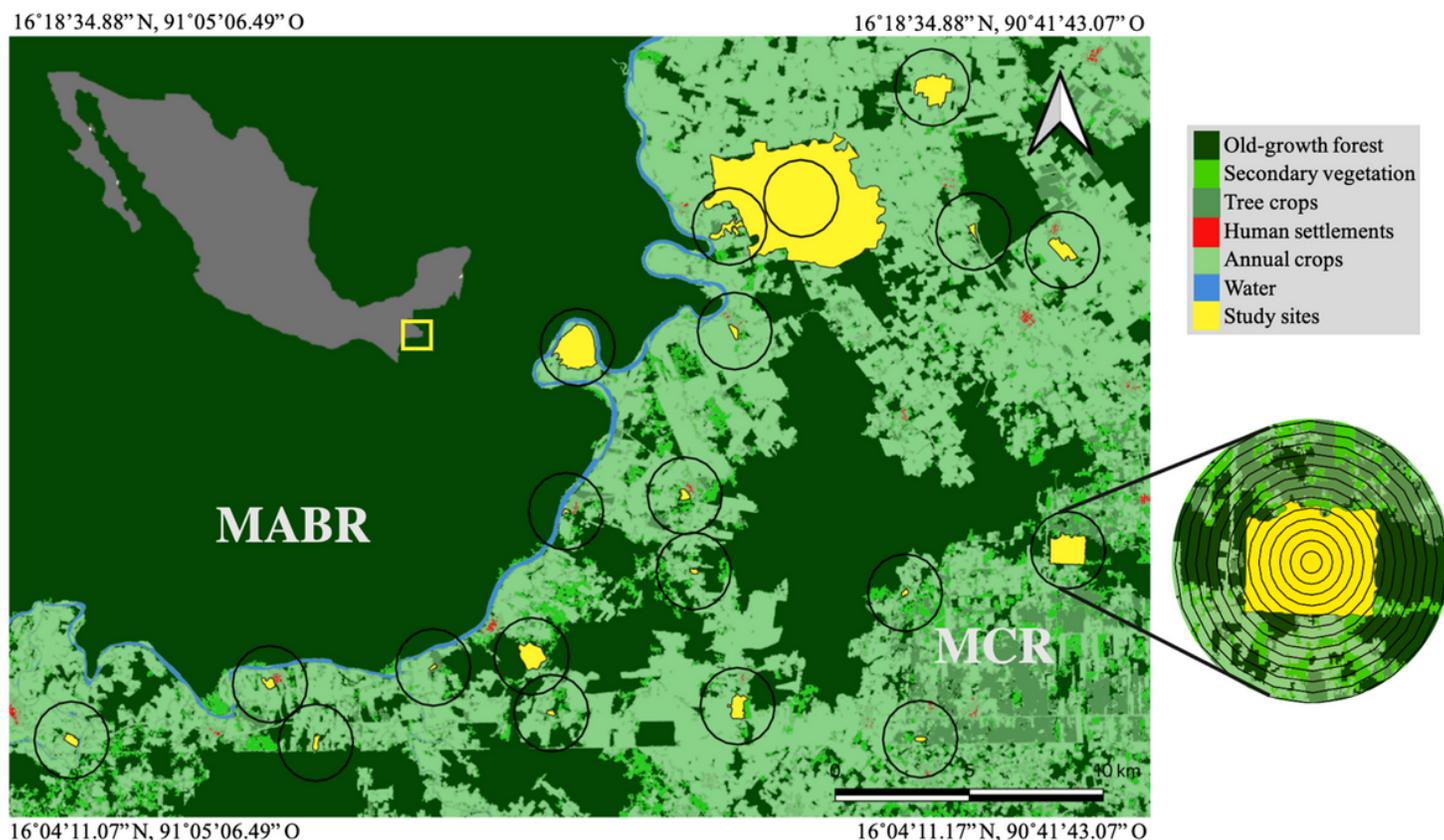
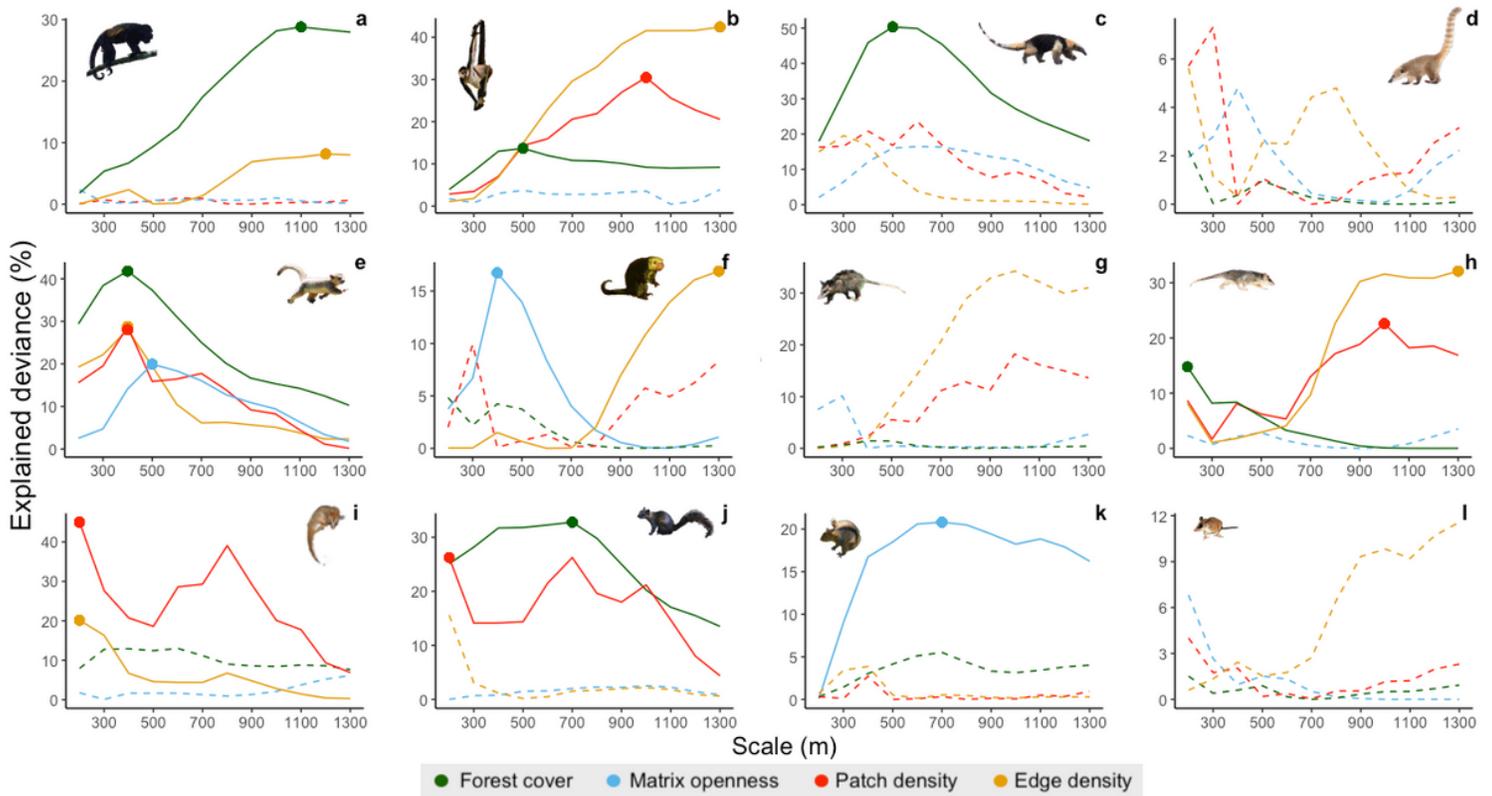


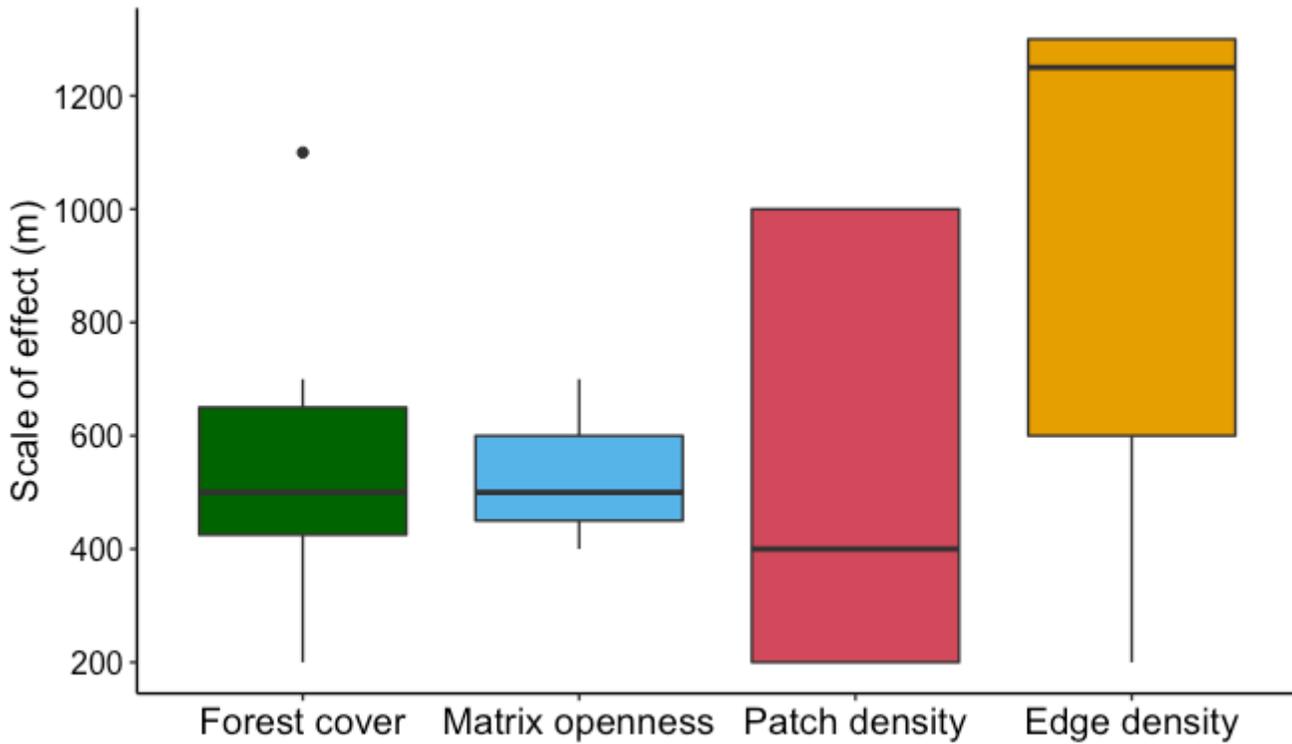
Figure 1

Location of the 20 study patches (yellow polygons) in the Lacandona rainforest, Mexico. The circles around the patches indicate the maximum spatial extent (landscape size), and the inset shows an example of the 13 concentric buffers (range = 100 – 1300 m radius) where landscape variables were measured. MABR = Montes Azules Biosphere Reserve; MCR = Marqués de Comillas Region



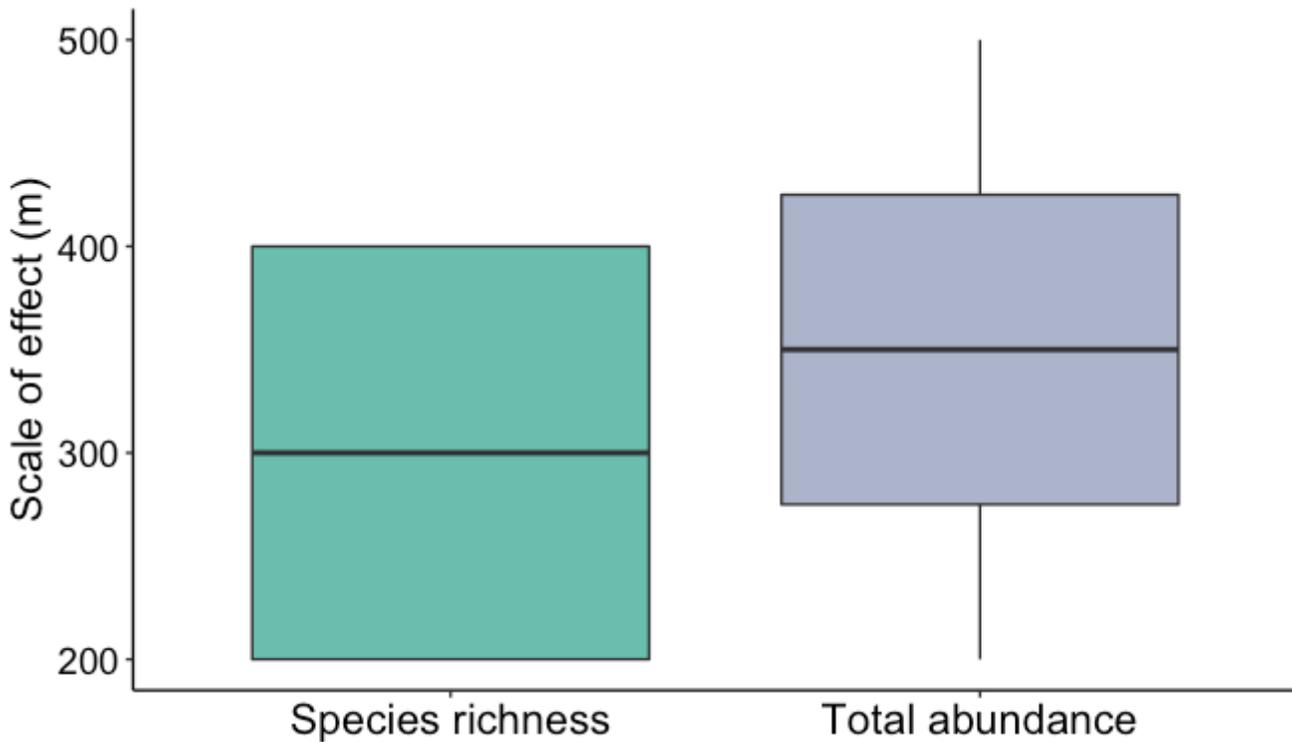
**Figure 2**

Effect of four landscape variables (indicated with different colors) measured across different spatial scales on the abundance of 12 arboreal mammals in the Lacandona rainforest, Mexico. The strength of landscapes effects is measured with the explained deviance (%) of each generalized linear model. Species = *Alouatta pigra* (black howler monkey; a), *Ateles geoffroyi* (spider monkey; b), *Tamandua mexicana* (northern tamandua; c), *Nasua narica* (white-nosed coati; d), *Potos flavus* (kinkajou; e), *Coendou mexicanus* (Mexican hairy porcupine; f), *Didelphis marsupialis* (common opossum; g), *Philander opossum* (four-eyed gray opossum; h), *Caluromys derbianus* (wooly opossum; i), *Sciurus aureogaster* (gray squirrel; j), *Sciurus deppei* (Deppé's squirrel; k), *Marmosa mexicana* (Mexican mouse opossum; l). The scale of effect (SoE) of each landscape attribute on each species is indicated with big colored points. Dashed lines indicate the cases in which the model with highest explained deviance showed a similar plausibility than the null model (i.e.  $\Delta AIC < 2$ )



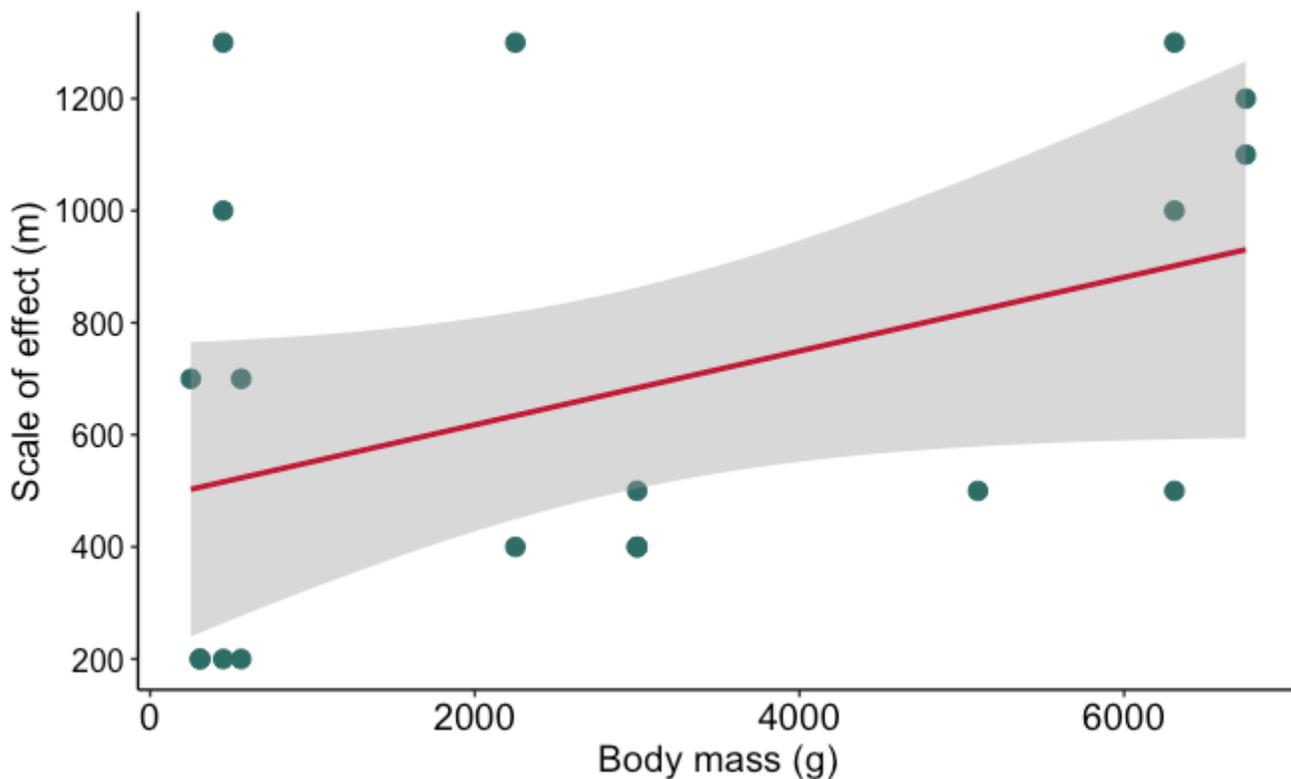
**Figure 3**

Differences among landscape variables in the scale of effect on arboreal mammals. The boxplots indicate the median (thick lines), the first and third quartiles (boxes) and the range (vertical lines). Dots are outliers



**Figure 4**

Differences in the scale of landscape effect on species richness and total abundance of arboreal mammals. Boxplots indicate the median (thick lines), the first and third quartiles (boxes) and the range (vertical lines)



**Figure 5**

Effect of body mass on the scale of effect of landscape structure on the relative abundance of arboreal tropical mammals in the Lacandona rainforest, Mexico. The gray area indicates the standard error of the linear regression model. We only include the cases in which the model with highest explained deviance (i.e. scale of effect) showed a higher plausibility than the null model (i.e.  $\Delta AIC < 2$ ). Also note that we assessed four landscape variables, so a single mammal species can have up to four data points depending on the number of landscape variables for which we detected the scale of effect

## Supplementary Files

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