Acta Oecologica 84 (2017) 57–63

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Landscape attributes as drivers of the geographical variation in density of *Sapajus nigritus* Kerr, 1792, a primate endemic to the Atlantic Forest

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A R T I C L E I N F O

Article history:
Received 23 December 2016
Received in revised form
21 August 2017
Accepted 21 August 2017
Available online 9 September 2017

Keywords:
Brown capuchin monkeys
Forest mammals
Forest patch
Habitat fragmentation
Matrix modification
Primates

A B S T R A C T

Neotropical primates are among the most well studied forest mammals concerning their population densities. However, few studies have evaluated the factors that influence the spatial variation in the population density of primates, which limits the possibility of inferences towards this animal group, especially at the landscape-level. Here, we compiled density data of *Sapajus nigritus* from 21 forest patches of the Brazilian Atlantic Forest. We tested the effects of climatic variables (temperature, precipitation), landscape attributes (number of patches, mean inter-patch isolation distance, matrix modification index) and patch size on the population density using linear models and the Akaike information criterion. Our findings showed that the density of *S. nigritus* is influenced by landscape attributes, particularly by fragmentation and matrix modification. Overall, moderately fragmented landscapes and those surrounded by matrices with intermediate indexes of temporal modification (i.e., crop plantations, forestry) are related to high densities of this species. These results support the assumptions that ecologically flexible species respond positively to forest fragmentation. However, the non-linear relationship between *S. nigritus* density and number of patches suggests that even the species that are most tolerant to forest cover changes seem to respond positively only at an intermediate level of habitat fragmentation, being dependent of both a moderate degree of forest cover and a high quality matrix. The results we found here can be a common response to fragmentation for those forest dweller species that are able to use the matrix as complementary foraging sites.

1. Introduction

Understanding the causes of spatial variation in the ecological attributes of species (e.g. abundance, density) is one of the main challenges of biogeography and macroecology (Gotelli et al., 2009). Although these patterns are often explored at the community level, some studies also have contributed to the knowledge of these patterns at the population level (Brown et al., 1995; Sagarin et al., 2006). General assumptions demonstrate that habitat suitability, environmental variation, plasticity in species' responses, interspecific interactions and anthropogenic effects play important roles in determining both the abundance and density of animal populations (see Brown et al., 1995; broad review of Sagarin et al., 2006).

It has been demonstrated that the population densities of forest mammals can vary widely according to the environmental heterogeneity influencing the quality of the forest habitat (Peres and Palacios, 2007). This include the effects of climatic factors (e.g., temperature, rainfall), elevation, floristic composition and resource availability (Link et al., 2010; Pinto et al., 1999; Stevenson, 2001). Recently, a large number of studies have also evaluated the isolated effects of habitat loss and fragmentation *per se* (Fahrig, 2003) on the density and persistence of forest mammals (Arroyo-Rodríguez et al., 2013a; Ethier and Fahrig, 2011; Michalski and Peres, 2007; Thornton et al., 2011). However, this issue seems to encompass a range of taxon-specific responses, which are also dependent from

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http://dx.doi.org/10.1016/j.actao.2017.08.007
1146-609X/

the variable chosen to measure habitat fragmentation (Arroyo-Rodríguez et al., 2013b). For instance, a meta-analysis showed that population density of forest-interior species was positively associated with patch size, whereas that the density of generalist and/or edge species showed a negative association (Bender et al., 1998). Controlling for patch size, Thornton et al. (2011) found negative responses to fragmentation *per se* for mid- and large-sized tropical mammals. Overall, forest specialist species have shown predominantly negative responses to habitat modification, while generalist species have shown positive responses (Pardini et al., 2009, 2010; Thornton et al., 2011). Interestingly some species may exhibit non-linear responses to fragmentation, which have been associated with their ability to access complementary resources across the landscape (i.e., landscape supplementation) (Dunning et al., 1992; Ethier and Fahrig, 2011).

Neotropical primates are among the most well studied forest mammals concerning their population densities. Climatic factors such as temperature and precipitation have been considered important predictors of primate density (Pinto et al., 1999). In terms of habitat modification, some evidences have shown that primates with more flexibles diets (e.g. *Sapajus* spp., *Alouatta* spp.) are not as sensitive to forest patch area as the large-bodied and frugivorous species (e.g. *Ateles* spp.) (Chiarello, 2003; Michalski and Peres, 2005, 2007; Thornton et al., 2011). However, the majority of studies have focused their attention in occupation patterns (presence and absence data) of primates in fragmented landscapes. To our knowledge, only one study directly evaluated the population responses of Neotropical primates to landscapes changes, revealing a positive correlation of density with the degree of fragmentation and matrix permeability (i.e., higher proportion of secondary forests and arboreal crops) for the folivory primate *Alouatta pigra* (Arroyo-Rodríguez et al., 2013a). Therefore, more inferences are essential to advance our understanding of how the populations of primates are surviving within human-modified landscapes in the Neotropical region (Arroyo-Rodríguez and Fahrig, 2014).

Sapajus nigritus Kerr, 1792 (brown capuchin monkeys) is a primate endemic to and widely distributed in Atlantic Forest, from the south of Rio Doce in Brazil to Misiones in Argentina (Alfaro et al., 2012). Their ecological flexibility allows for adaptation to a variety of habitats, from continuous to small forest patches, including agroecosystems and urban areas (Aguiar et al., 2014; Estrada et al., 2012; Fragaszy et al., 2004). Hence, in many localities of the Atlantic Forest, brown capuchin monkeys have been treated as "problem-populations" due their high densities (Ludwig et al., 2005; Mikich and Liebsch, 2014; Vidolin and Mikich, 2004). Nevertheless, the factors influencing the variation in the density of *S. nigritus* remain underexplored, which hinders the design appropriate management plains. Pinto et al. (1999) showed that temperature, precipitation and industrialization had a positive impact on the density the brown capuchin monkeys. Although these findings suggest that habitat modification could increase the densities of this species, no study has yet explored the direct impact of landscape attributes in the density variation of *S. nigritus*. More importantly, even if some ecological traits of this species suggest positive responses to habitat fragmentation (Pardini et al., 2009; Thornton et al., 2011), we also do not know if the populations could show a response threshold to habitat loss in fragmented landscapes (Fahrig, 1999).

Here we aim to investigate the effects of climatic variables (temperature, precipitation), landscape attributes (number of patches, patch density, mean inter-patch isolation distance, matrix modification index) and patch size on the spatial variation of the population density of *S. nigritus*. We predict that both climatic and landscape factors should influence the density of this species (Arroyo-Rodríguez and Fahrig, 2014; Pinto et al., 1999). However, a strongest effect of landscape attributes should be expected due its high ecological flexibility and ability to move through and use resources in the matrix (Fragaszy et al., 2004; Ludwig et al., 2005; Michalski and Peres, 2005). Moreover, brown capuchin monkeys have large home ranges and long daily path lengths (c.a. 268 ha, 550 to 3.000 m per day: Rímoli et al., 2008). These characteristics also would make them potentially dependent on the landscape attributes instead of the size of forest patches (Bender et al., 1998; Thornton et al., 2011).

2. Material and methods

2.1. Study area

The *Sapajus nigritus* data compiled in this study represent the entire geographic distribution of this species in Brazilian Atlantic Forest according to IUCN (Fig. 1).

The Atlantic Forest extends from the northeast coast of Brazil to northern Argentina and eastern Paraguay (Tabarelli et al., 2005). Originally covering more than 1.5 million km^2, historical anthropogenic disturbances have occasioned large forest loss. Currently, more than 80% of the remaining Atlantic Forest patches are smaller than 50 ha, and mostly located inside a human-dominated matrix with pastures, plantations, urban centers and roads (Ribeiro et al., 2009). Nevertheless, it remains a biodiversity hotspot, with high levels of species diversity and endemism (Myers et al., 2000).

The remaining Atlantic Forest patches include rainforests along the Atlantic coast, mixed *Araucaria* pine forests in high altitudes of its southern portion, deciduous and semideciduous forests towards the mainland, plus other associated formations such as dry forests, mangroves and upland grasslands (Tabarelli et al., 2005). The climate in the region ranges from tropical to subtropical with high temperature fluctuations (around 12° to 25 °C, Colombo and Joly, 2010).

2.2. Density data acquisition

We compiled a database of population densities of *S. nigritus* obtained from 21 forest patches of 18 different localities in Brazilian Atlantic Forest (Fig. 1; Table S1). In order to standardize the dataset and to avoid possible bias caused by variation among sampling methods we selected only studies that used the line-transect method and the software Distance to perform density estimates (Buckland et al., 2010).

2.3. Environmental and landscape variables

For each site, we extracted two environmental variables with 2.5 arc-minutes resolution from the WorldClim raster database (Hijmans et al., 2005): temperature seasonality and precipitation seasonality using the DIVA-GIS 7.5 software (http://www.divagis.org/download). These variables were previously suggested as predictors of the distribution and the densities of primates in the Atlantic Forest (Pinto et al., 1999).

To measure the landscape predictors, we needed to estimate the correct species 'scale of effect', i.e., the spatial extent at which landscape structure best predicts population response (Jackson and Fahrig, 2012). We estimated the scale of effect considering the home range size of 2.68 km^2 for *S. nigritus* (Rímoli et al., 2008). The home range was converted into maximal dispersal distance using 40*(linear dimension of home range) according to Bowman et al. (2002). We used these estimated dispersal distances to obtain the scale of effect as 0.3*(maximal dispersal distance), according to Jackson and Fahrig (2012). Then, we calculated the scale of effect as:

$$\textit{Scale of effect} = [(\sqrt{2.68})^{*}40]^{*}0.3$$