

Occurrence and conservation of the Vulnerable titi monkey *Callicebus melanochir* in fragmented landscapes of the Atlantic Forest hotspot

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Abstract Tropical forest hotspots have a high diversity of species but have lost >70% of their original vegetation cover and are characterized by a multitude of small and isolated fragments. Paradoxically, conservation actions in these areas are still mainly focused on protection of large tracts of forests, a strategy now infeasible because of the small area of forest remnants. Here we use the Vulnerable black-handed titi monkey *Callicebus melanochir* as a model to study the effects of habitat loss, fragmentation and degradation on arboreal mammals and to provide insights for science-driven conservation in fragmented landscapes in tropical forest hotspots. We surveyed 38 Atlantic Forest fragments in Bahia State, Brazil and assessed the effects of patch area, quality and visibility, and landscape connectivity on the occurrence of our model species. Patch area was the single best model explaining species occurrence. Nonetheless, patch quality and visibility, and landscape connectivity, positively affect occurrence. In addition to patch area, patch quality, patch visibility and landscape connectivity are useful for predicting the occurrence of arboreal mammals in the fragments of tropical forest hotspots. We encourage the assessment of habitat quality (based on remotely sensed vegetation indices) and habitat visibility (based on digital elevation models) to improve discoverability of arboreal mammal populations and selection of fragments for conservation purposes across fragmented landscapes of tropical forest hotspots. Large remnants of tropical forest hotspots

are scarce and therefore we require baseline data to support conservation actions and management in small forest fragments.

Keywords Atlantic Forest, Brazil, *Callicebus melanochir*, degradation, ecological modelling, fragmentation, habitat loss, titi monkey

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Introduction

Biodiversity conservation is essential for the maintenance of ecosystem services that guarantee survival of wildlife and the quality of human life. To achieve biodiversity conservation, stakeholders must work under a common agenda to put in place actions to protect biodiversity (Bisseleua et al., 2009; Tilman et al., 2014). Effective conservation decision-making is guided by scientific information on species (Mace et al., 2012), the currency of conservation (Rylands & Mittermeier, 2014). Baseline data on species is therefore paramount for biodiversity conservation.

Deforestation is recognized as the major threat to terrestrial mammals (IUCN, 2019). Forest loss and fragmentation reduce the habitat of forest-dependent mammals and restrict their populations to small, isolated patches (Fahrig, 2003), leading to population declines and local extinctions (Estrada et al., 2017). Accordingly, conservation science has focused on the impacts of deforestation on species distributions and abundance, and one of the main practical outcomes has been the protection of large tracts of forests (e.g. Soulé & Simberloff, 1986): the patch area paradigm in conservation.

Large tracts of forests, however, are currently rare in tropical forest hotspots (areas with a high proportion of endemic plants and extensive vegetation loss; Myers et al., 2000) and the majority of remnants are small (< 100 ha) and embedded in human-modified landscapes (Turner & Corlett, 1996). In the absence of funding for large-scale reforestation, conservation of mammals in tropical forest hotspots thus needs to focus on a multitude of small forest fragments. The synergistic effects of habitat loss, degradation and fragmentation on arboreal mammals need to be examined, to inform strategies for population management and species conservation

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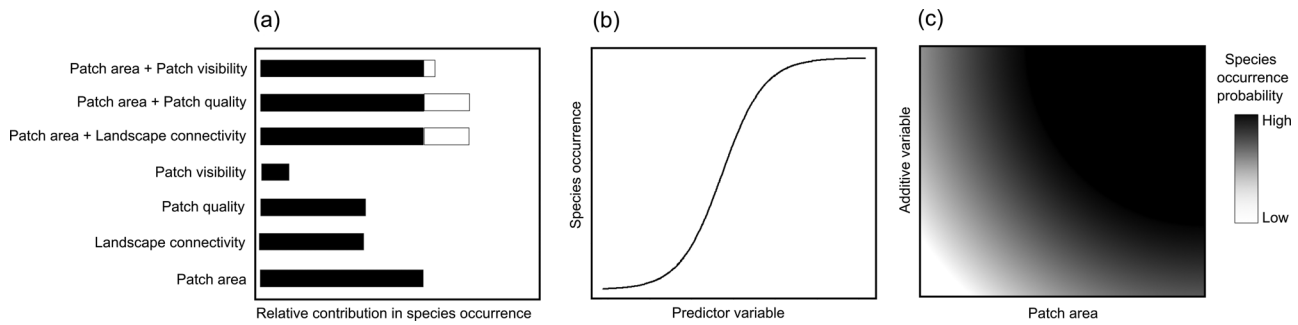


FIG. 1 Hypothesized influence of patch area, quality and visibility, and landscape connectivity, on the occurrence of the arboreal black-handed titi monkey *Callicebus melanochir* in a fragmented Atlantic Forest landscape (Fig. 2): (a) relative contribution of univariate (black bars) and compound models (black, patch area contribution; white, additive variable contribution) in explaining species' occurrence; (b) expected response of the species occurrence to predictor variables in univariate models; (c) expected response of species occurrence synthesized for the three compound models having patch area and an additive variable.

(Cassano et al., 2012; Gestich et al., 2019), especially in small forest fragments.

Such information is fundamental for facilitating conservation actions beyond the creation of protected areas and for understanding how forest degradation affects arboreal mammals in fragmented landscapes, a relationship little studied (Mortelliti et al., 2010). For mammals that depend on high quality forests, the availability of well conserved habitats may be critical (Henle et al., 2004).

Here we investigate the influence of patch and landscape structure on the occurrence of the coastal black-handed titi monkey *Callicebus melanochir* in the Atlantic Forest hotspot (sensu Myers et al., 2000), using this species as a model for arboreal mammals inhabiting fragmented landscapes in tropical forest hotspots. Neotropical primates are strictly forest-dependent (Cowlshaw & Dunbar, 2000), directly and negatively affected by deforestation (Estrada et al., 2017), and thus are appropriate models to study the impacts of forest reduction and fragmentation on the occurrence of forest-dependent mammals.

We hypothesize that (1) patch area, quality and visibility, and landscape connectivity, affect the probability of occurrence of our model species, with patch area having the strongest influence (Fig. 1a); (2) all four patch–landscape metrics positively influence the probability of the species' occurrence (Fig. 1b); and (3) compound models (patch area plus each of the other metrics) will significantly increase model weights (Fig. 1c). Based on our findings, we discuss the usefulness of patch–landscape metrics in predicting the occurrence of titi monkeys and potentially other arboreal mammals in tropical forest hotspots and the application of such metrics for science-based conservation action.

Study area

This study was conducted in fragmented landscapes of the Atlantic Forest hotspot, southern Bahia State, Brazil (Fig. 2). The study area encompasses semi-deciduous forests

in a transition zone between coastal wet forests and inland deciduous forests within the Atlantic Forest domain (Thomas, 2003). Anthropogenic land-use conversion since the 1970s has transformed the originally continuous wet forests of the interior of southern Bahia into small fragments embedded in a matrix of pastures for cattle ranching (Coimbra-Filho & Câmara, 1996; Landau, 2003). The study area is therefore similar to other landscapes in the Atlantic Forest (Landau, 2003; Ribeiro et al., 2009) and other tropical forest hotspots (Turner & Corlett, 1996) regarding past processes and current patterns of forest loss and fragmentation.

Methods

Model species The coastal black-handed titi monkey *Callicebus melanochir* (Plate 1) is endemic to the Atlantic Forest of north-east Brazil (Culot et al., 2019). It is an arboreal species that occasionally moves on the ground and can disperse over short distances in non-forested areas (Mason, 1986; Souza-Alves et al., 2019), lives in groups comprising a monogamous pair and offspring, and occupies home ranges of 22–24 ha (Müller, 1995; Heiduck, 2002). The species is categorized on the IUCN Red List as Vulnerable to extinction as a result of habitat loss and fragmentation (Veiga et al., 2008) but the response of individuals to such habitat modifications has not been studied.

Field surveys During March 2013–December 2014 (72 field days) surveys of the titi monkey were carried out in 38 fragments using playback censuses and interviews (following Jerusalinsky et al., 2006; Printes et al., 2011). The fragments studied were randomly selected to ensure complete coverage of the variation in the area of fragments. For playback censuses, recordings of the long-calls of *C. melanochir* were played along pre-existing trails and forest edges using a mini amplifier connected to an MP3 player (Jerusalinsky et al., 2006; Printes et al., 2011). We successfully used



PLATE 1 A typical group of *Callicebus melanochir*, observed in the study area (Fig. 2). Photo: Rodrigo Costa-Araújo.

Callicebus barbarabrownae calls during a short pilot study prior to the survey, to detect *C. melanochir* and to record the species' calls, as these were not formerly available. In the absence of standard protocols for playback surveys of titi monkeys in fragmented landscapes, we developed an approach to avoid any potential detection bias from differential propagation of sound as a result of the variable vegetation structure of forest fragments. We modulated the distance between playbacks (50–150 m) in each fragment to allow sound overlap between adjacent sampling points and improve our detection rates, controlling for sound overlap with the aid of a field assistant. At each sampling point one long-call (2 minutes 45 seconds) was played; when titi monkeys responded with vocalization only, the same long-call was played up to three subsequent times to stimulate their approach. Informal interviews were conducted with local people in the vicinity of forest fragments and with citizens in nearby communities, to collect additional data on the species' occurrence. The long-call of *C. melanochir* is distinctive from any other primate in the region, can be heard at a distance of several kilometres from the source. Recent reports (< 5 years) of the species' vocalization were therefore considered as accurate and included in our data.

Patch and landscape metrics We adopted a patch–landscape perspective to investigate the responses of our model species to forest loss, degradation and fragmentation (following Arroyo-Rodríguez & Mandujano, 2009; Arroyo-Rodríguez & Fahrig, 2014), considering that the spatial scale within which populations are affected in a fragment relates to the dispersal ability of individuals (Jackson & Fahrig, 2015). We delimited forest fragments by interpreting high-resolution (< 1 m) images from the online World Imagery available through *ArcGIS 10.2* (Esri, Redlands, USA) and the Open Layer plugin of *QGIS 2.14* (QGIS, 2014). Fragments within 100 m of each other were considered a unique patch, assuming that titi monkeys can move across this

distance in pastures (Souza-Alves et al., 2019). We defined the scale of the effect of forest loss and fragmentation by setting a buffer of 500 m around the edges of study fragments, assuming a conservative estimate of the maximum dispersal recorded for titi monkeys in open areas (400 m; Mason, 1968), thus ensuring independence of the landscapes analysed. We calculated three patch-level metrics and one landscape-level metric (Supplementary Fig. 1) using the packages *raster*, *rgeo* and *gtools* in *R 3.5.0* (Hijmans & Eten, 2012; Warnes et al., 2015; Bivand et al., 2017). The forest fragments surveyed vary in area, quality and connectivity (Supplementary Table 1), and therefore our study area is representative of landscapes in the Atlantic Forest and other tropical forest hotspots. All four metrics (Table 1) were first tested for autocorrelation (Pearson $r < 0.7$; Supplementary Fig. 2).

Data analysis We first defined a set of univariate models considering species occurrence as a response variable and each patch–landscape metric (patch area, quality and visibility, and landscape connectivity) as a predictor variable, using linear generalized models with a binomial distribution. Because we hypothesized that patch area would have a major, but not ubiquitous, influence on the occurrence of arboreal mammals, we also defined a set of compound models combining patch area plus each of the other metrics, again with species occurrence as the response variable. We avoided models with more than two predictors because of potential difficulties with interpretation. We compared the performance of competing models within univariate and within univariate plus compound models, including also a null model representing random occurrence, using the Akaike information criterion corrected for small sample size (AICc), using the *bbmle* package in *R*. We considered univariate and compound models with $\Delta\text{AICc} \leq 2.0$ as equally plausible for explaining titi monkey occurrence; additionally we verified model weights to identify the best model among equally plausible models (Burnham & Anderson, 2002). To identify which predictor variables are more informative within each plausible compound model, we estimated the beta coefficients of the predictor variables using the *confint* function of the *bbmle* package. Absence of zero within the estimated 95% confidence interval of a predictor variable indicates a strong effect of that variable (Gelman & Hill, 2007).

Results

Considering the data from playback surveys and interviews, we recorded *C. melanochir* in 15 of the 38 study fragments. During playback censuses we recorded groups of 2–3 individuals in areas of native forest and, for the first time, in areas of shaded cocoa crops embedded in the forest fragments.

TABLE 1 Patch and landscape metrics used as predictor variables in univariate and compound models of occurrence of the arboreal black-handed titi monkey *Callicebus melanochir* in a fragmented landscape of Atlantic Forest, Bahia State, Brazil (Fig. 2).

Metric	Description & calculation
Patch area	Area (ha) of the study fragment.
Patch quality	Mean enhanced vegetation index of the study fragment, as a proxy of habitat quality. We overlaid a 90 × 90 m grid on each study fragment & extracted one value of the index for each grid cell, using 10-m resolution Sentinel satellite images, to obtain the mean index. The number of values obtained per fragment (1–3,309) depended on the area of the fragment. The index is a measure of vegetation reflectance developed for tropical forests; it performs well under heavy aerosol & burning biomass conditions (Miura et al., 1998), is sensitive to gross primary production & plant biomass (Ogaya et al., 2015), which in turn are higher in old growth forests (or high quality habitats) than in early successional forests (or low-quality habitats) (Gatti et al., 2015; Nyirambangutse et al., 2017), & is positively related to canopy structure (Huete et al., 2002).
Patch visibility	Sum of the area (ha) of visible neighbouring forest fragments within a 500-m buffer of the focal fragment, excluding the area of the latter. This is a measure of connectivity of forest fragments within the dispersal ability of the species. A 3-dimensional raster of relief, generated using a 30-m resolution digital elevation model in ArcGIS, overlaid on the 90 × 90 m grid (see patch quality, above), with visibility of surrounding fragments assessed following Silva et al. (2015). A neighbouring fragment was visible if it could be seen from at least one of the grid cells in the focal fragment.
Landscape connectivity	Sum of the total area (ha) of forest within the 500-m buffer, excluding that of the focal fragment (Martensen et al., 2008, 2012; Ribeiro et al., 2009).

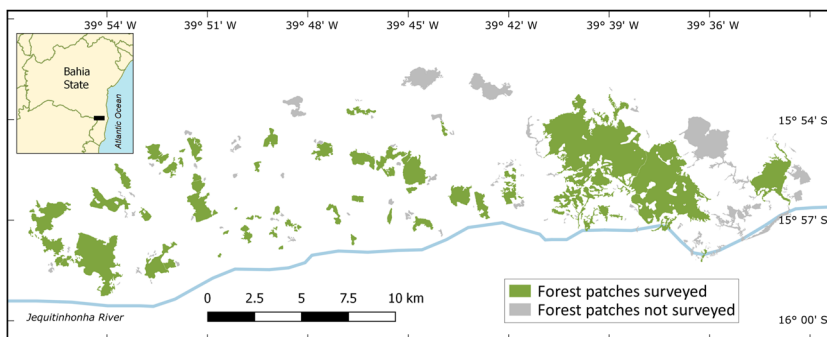


FIG. 2 Fragmented landscapes of the study area on the north margin of the Jequitinhonha River in Itapebi and Itarantim municipalities, Bahia, Brazil.

All four patch–landscape metrics showed a positive relationship with the occurrence of our model species in generalized linear models, as we expected. The best-supported univariate model was patch area, demonstrating that occurrence of our model species is primarily driven by the area of forest (Fig. 3a, Table 2, Supplementary Table 2).

The results from compound model selection (Table 2, Supplementary Table 2) showed an additive effect of other variables beyond the effect of patch area, demonstrating that species occurrence is also influenced by patch quality and visibility, and landscape connectivity. However, the additive variables had a weak contribution in the compound models. In Fig. 3b–d we present the response surface for the predicted occurrence of titi monkeys as a function of the compound models.

Discussion

Our findings confirm that patch area has a major effect on the occurrence of our arboreal model species *C. melanochir*: the larger the forest fragment, the higher is the probability of

occurrence. The relationship between the area of forest fragments and the occurrence of arboreal mammals is well documented (Harcourt & Doherty, 2005; Magioli et al., 2015), with evidence from studies on primates (Arroyo-Rodríguez et al., 2008; Sharma et al., 2013; Silva et al., 2015; Carretero-Pinzón et al., 2016), carnivores (Michalski & Peres, 2005; Nagy-Reis et al., 2017), marsupials and rodents (Nupp & Swihart, 2000; Linnell et al., 2017), bats (Muylaert et al., 2016), and ungulates and shrews (Lawes et al., 2000).

Additionally, forest quality has a positive effect on the occurrence of our model species, suggesting that forest quality is an important trait of forest fragments, balancing the effect of reduced area. Therefore, patch quality could be useful for predicting occurrence of arboreal mammals and for managing their conservation, especially in fragments of < 100 ha, which are common in tropical forest hotspots (Turner & Corlett, 1996; Ribeiro et al., 2009).

To measure habitat quality from the perspective of a single forest-dependent species is challenging, and species-specific measurements of habitat quality can rarely be extrapolated to other taxa (Mortelliti et al., 2010). To overcome

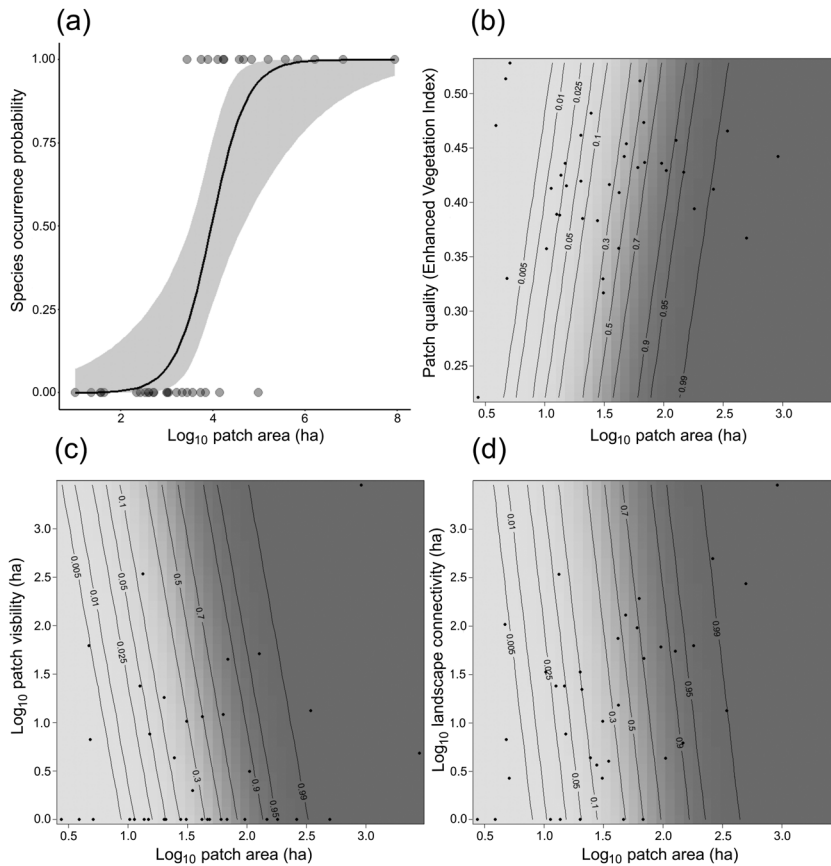


FIG. 3 Probability of occurrence of *C. melanochir* in fragmented landscapes in the Atlantic Forest (Fig. 2) according to predictor variables in univariate (a) and in compound models (b–d). The black lines represent the probability of species occurrence and the grey shaded area the 95% CI (a), and the response surface for the predicted species occurrence as a function of patch area and the additive variables (b–d).

TABLE 2 Values of the Akaike information criterion corrected for small sample size (AICc) for the relative contribution of univariate and compound models in explaining the occurrence of the arboreal *C. melanochir* in a fragmented landscape in the Atlantic Forest. Plausible models were identified within the set of univariate models and within the set of univariate plus compound models.

	$\Delta AICc^1$	df	Model weight
Univariate models			
Species occurrence ~ Patch area	0	2	1
Species occurrence ~ Patch quality	28.5	2	< 0.0001
Species occurrence ~ Patch visibility	27.6	2	< 0.0001
Species occurrence ~ Landscape connectivity	20.1	2	< 0.0001
Species occurrence ~ Null	26.6	1	< 0.0001
Univariate & compound models			
Species occurrence ~ Patch area	0	2	0.38
Species occurrence ~ Patch quality	28.5	2	< 0.001
Species occurrence ~ Patch visibility	27.6	2	< 0.001
Species occurrence ~ Landscape connectivity	20.1	2	< 0.001
Species occurrence ~ Patch area + Patch quality	1.4	3	0.19
Species occurrence ~ Patch area + Patch visibility	0.9	3	0.24
Species occurrence ~ Patch area + Landscape connectivity	1.4	3	< 0.001
Species occurrence ~ Null	26.6	1	< 0.001

¹ $\Delta AICc$, difference between the AICc value of a given model and the model with the lowest AICc in each set.

this, we suggest the use of remotely sensed vegetation indices as proxies of forest quality for arboreal taxa in investigations of occupancy patterns and in selection of priority fragments for conservation across tropical forest hotspots. There are three advantages of this approach: (1) the

enhanced and normalized difference vegetation indices are sensitive to gross primary production and plant biomass (Ogaya et al., 2015), which are higher in old-growth forests (or high quality habitats) than in early successional forests (or low quality habitats) (Gatti et al., 2015; Nyirambangutse

et al., 2017); (2) as our results show, there is a positive relationship between the enhanced vegetation index and the model species occurrence; and (3) such indices can be obtained from freely available satellite images.

Connectivity of arboreal mammal populations in fragmented landscapes may be maintained by dispersal events based on opportunities for visualization of surrounding habitat patches, as indicated by the positive effect of patch visibility on the occurrence of our model species and of *C. personatus* (see Silva et al., 2015). Patch visibility offers a new way to evaluate connectivity between populations of arboreal mammals in fragmented landscapes and its importance in explaining species occurrence should be further explored using other taxa and landscapes. The use of spatial memory can also play a role in dispersal events between forest fragments but, to our knowledge, this issue has not yet been investigated.

Considering the positive effect of patch visibility, which incorporates visibility modulated by landscape relief and linear distance, on the occurrence of our model species, it is likely that such arboreal mammals disperse across pastures between visible forest fragments that are close to each other (see also Moraes et al., 2018). Traveling over short distances between visible forest fragments, rather than dispersing over long distances may be a result of the high predation pressure arboreal mammals are exposed to during dispersal across open areas (Vuren & Armitage, 1994; Sakai & Noon, 1997).

Callicebus melanochir may be persisting in the study area as a result of metapopulation dynamics, with the large fragments being sources and the nearby smaller fragments that are visible being sinks. As arboreal mammals, we expect that isolated populations of *C. melanochir* have gone extinct in the study area as a result of the Allee effect (Stephens et al., 1999), genetic factors and stochastic events, considering that three titi monkey generations (Veiga et al., 2011) have passed since the stabilization of forest conversion into pastures in this region in the 1990s (Coimbra-Filho & Câmara, 1996).

Our study shows that forest area is the strongest predictor of the occurrence of our model species, *C. melanochir*. We also found positive effects of forest quality, visibility and landscape connectivity on the species. We recommend that further research should consider the effect of forest quality on the occurrence of arboreal mammals in tropical forest hotspots and we encourage the use of remotely sensed vegetation indices as proxies of habitat quality. The adoption of the visibility metric may offer insights on the occurrence of arboreal mammals and on the connectivity of populations. In addition to forest area, the use of forest quality and visibility, and landscape connectivity, can improve detection of arboreal mammal populations and also aid in the selection of fragments and the types of actions for species conservation at local and regional scales in fragmented

landscapes in tropical forest hotspots. Large remnants of tropical forest hotspots are scarce and therefore we require baseline data to support alternative conservation actions and management in small fragments.

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Author contributions Conception: RC-A, ALR, MCR; data collection design, fieldwork: RC-A; mapping and quantification of landscape structure indices: ALR, FM; data analysis: ALR, MCR, FM; writing: RC-A, with input from ALR, JPS-A, TH, MCR.

Conflicts of interest None.

Ethical standards Fieldwork followed the code of best practice of the International Society of Primatologists, and otherwise abided by the *Oryx* guidelines on ethical standards.

References

- ARROYO-RODRÍGUEZ, V. & FAHRIG, L. (2014) Why is a landscape perspective important in studies of primates? *American Journal of Primatology*, 76, 901–909.
- ARROYO-RODRÍGUEZ, V. & MANDUJANO, S. (2009) Conceptualization and measurement of habitat fragmentation from primates' perspective. *International Journal of Primatology*, 30, 497–514.
- ARROYO-RODRÍGUEZ, V., MANDUJANO, S. & BENÍTEZ-MALVIDO, J. (2008) Landscape attributes affecting patch occupancy by Howler monkeys (*Alouatta palliata mexicana*) at Los Tuxtlas, Mexico. *American Journal of Primatology*, 70, 69–77.
- BISSELEUA, D.H.B., MISSOUP, A.D. & VIDAL, S. (2009) Biodiversity conservation, ecosystem functioning, and economic incentives under cocoa agroforestry intensification. *Conservation Biology*, 5, 1176–1184.
- BIVAND, R., RUNDEL, C., PEBESMA, E., STUETZ, R. & HUFTHAMMER, K.O. (2017) *rgeos*: Interface to geometric engine—Open Source ('GEOS'). R package version 0.3–26. rdrr.io/cran/rgeos [accessed 24 March 2020].
- BURNHAM, K.P. & ANDERSON, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, USA.
- CARRTERO-PINZÓN, X., DEFLER, T.R., MCALPINE, C.A. & RHODES, J.R. (2016) What do we know about the effect of patch size on primate species across life history traits? *Biodiversity Conservation*, 25, 37–66.
- CASSANO, C.R., BARLOW, J. & PARDINI, R. (2012) Large mammals in an agroforestry mosaic in the Brazilian Atlantic Forest. *Biotropica*, 44, 818–825.

- COIMBRA-FILHO, A.F. & CÂMARA, I.G. (1996) *Os Limites Originais do Bioma Mata Atlântica na Região Nordeste do Brasil*. Fundação Brasileira para Conservação da Natureza, Rio de Janeiro, Brazil.
- COWLISHAW, G. & DUNBAR, R.I. (2000) *Primate Conservation Biology*. University of Chicago Press, Chicago, USA.
- CULOT, L., PEREIRA, L.A., AGOSTINI, I., ALMEIDA, M.A.B., ALVES, R.S.C., AXIMOFF, I. et al. (2019) ATLANTIC-PRIMATES: A dataset of communities and occurrences of primates in the Atlantic Forests of South America. *Ecology*, 100, e02525.
- ESTRADA, A., GARBER, P.A., RYLANDS, A.B., ROOS, C., FERNANDEZ-DUQUE, E., DI FIORE, A. et al. (2017) Impending extinction crisis of the world's primates: why primates matter. *Science Advances*, 3, e1600946.
- FAHRIG, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* 34, 487–515.
- GATTI, R.C., CASTALDI, S., LINDSELL, J.A., COOMES, D.A., MARCHETTI, M., MAESANO, M. et al. (2015) The impact of selective logging and clearcutting on forest structure, tree diversity and above-ground biomass of African tropical forests. *Ecological Research*, 30, 119–132.
- GELMAN, A. & HILL, J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York, USA.
- GESTICH, C.C., ARROYO-RODRIGUEZ, V., RIBEIRO, M.C., CUNHA, R.G.T. & SETZ, E.Z.F. (2019) Unraveling the scales of effect of landscape structure on primate species richness and density of titi monkeys (*Callicebus nigrifrons*). *Ecological Research*, 34, 150–159.
- HARCOURT, A.H. & DOHERTY, D.A. (2005) Species–area relationships of primates in tropical forest fragments: a global analysis. *Journal of Applied Ecology*, 42, 630–637.
- HEIDUCK, S. (2002) The use of disturbed and undisturbed forest by masked titi monkey *Callicebus personatus melanochir* is proportional to food availability. *Oryx*, 36, 133–139.
- HENLE, K., DAVIES, K.F., KLEYER, M., MARGULES, C. & SETTELE, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, 13, 207–251.
- HIJMANS, R.J. & ETTEEN, J.V. (2012) *raster*: Geographic analysis and modeling with raster data. R package version 2.0–12. rdrr.io/cran/raster [accessed 24 March 2020].
- HUETE, A., DIDAN, K., MIURA, T., RODRIGUES, E.P., GAO, X. & FERREIRA, L.G. (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, 83, 195–213.
- IUCN (2019) *The IUCN Red List of Threatened Species*. Version 2019-1. iucnredlist.org/initiatives/mammals/analysis/major-threats [accessed 20 October 2019].
- JACKSON, H.B. & FAHRIG, L. (2015) Are ecologists conducting research at the optimal scale? *Global Ecology and Biogeography*, 24, 52–63.
- JERUSALINSKY, L., OLIVEIRA, M.M., PEREIRA, R.F., SANTANA, V., BASTOS, P.C.R. & FERRARI, S.F. (2006) Preliminary evaluation of the conservation status of *Callicebus coimbrai* in the Brazilian State of Sergipe. *Primate Conservation*, 21, 25–32.
- LANDAU, E.C. (2003) Padrões de ocupação espacial da paisagem na Mata Atlântica do sudeste da Bahia, Brasil. In *Corredor de Biodiversidade da Mata Atlântica do Sul da Bahia* (organizers P.I. Prado, E.C. Landau, R.T. Moura, L.P.S. Pinto, G.A.B. Fonseca & K.N. Alger). CD-ROM. IESB/CI/CABS/UFMG/UNICAMP, Ilhéus, Brazil.
- LAWES, M.J., MEALIN, P.E. & PIPER, S.E. (2000) Patch occupancy and potential metapopulation dynamics of three forest mammals in fragmented afro-montane forest in South Africa. *Conservation Biology*, 14, 1088–1098.
- LINNELL, M.A., DAVIS, R.J., LESMEISTER, D.B. & SWINGLE, J.K. (2017) Conservation and relative habitat suitability for an arboreal mammal associated with old forest. *Forest Ecology and Management*, 402, 1–11.
- MACE, G.M., NORRIS, K. & FITTER, A.H. (2012) Biodiversity and ecosystem services: a multilayered relationship. *Trends in Ecology and Evolution*, 27, 19–26.
- MAGIOLI, M., RIBEIRO, M.C., FERRAZ, K.M.P.M.B. & RODRIGUES, M.G. (2015) Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest. *Animal Conservation*, 18, 499–511.
- MARTENSEN, A.C., PIMENTEL, R.G. & METZGER, J.P. (2008) Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: implications for conservation. *Biological Conservation*, 141, 2184–2192.
- MARTENSEN, A.C., RIBEIRO, M.C., BANKS-LEITE, C., PRADO, P.I. & METZGER, J.P. (2012) Associations of forest cover, fragment area, and connectivity with Neotropical understory bird species richness and abundance. *Conservation Biology*, 26, 1100–1111.
- MASON, W.A. (1968) Use of space by *Callicebus* groups. In *Primates: Studies in Adaptation and Variability* (ed. P.C. Jay), pp. 200–216. Holt, Rinehart and Winston, New York, USA.
- MICHALSKI, F. & PERES, C.A. (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, 124, 383–396.
- MIURA, T., HUETE, A.R., LEEUWEN, W.J.D. & DIDAN, K. (1998) Vegetation detection through smoke-filled AVIRIS images: an assessment using MODIS band passes. *Journal of Geophysical Research: Space Physics*, 103, 32001–32011.
- MORAES, A.M., RUIZ-MIRANDA, C.R., GALETTI-JR, P.M., NIEBUHR, B.B., ALEXANDRE, B.R., MUYLART, R.L. et al. (2018) Landscape resistance influences effective dispersal of endangered golden lion tamarins within the Atlantic Forest. *Biological Conservation*, 224, 178–187.
- MORTELLITI, A., AMORI, G. & BOITANI, L. (2010) The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia*, 165, 535–547.
- MUYLART, R.L., STEVENS, R.D. & RIBEIRO, M.C. (2016) Threshold effect of habitat loss on bat richness in Cerrado-forest landscapes. *Ecological Applications*, 26, 1854–1867.
- MÜLLER, K.H. (1995) Ranging in masked titi monkeys (*Callicebus personatus*) in Brazil. *Folia Primatologica*, 65, 224–228.
- MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., FONSECA, G.A.B. & KENT, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- NAGY-REIS, M.B., NICHOLS, J.D., CHIARELLO, A.G., RIBEIRO, M.C. & SETZ, E.Z.F. (2017) Landscape use and co-occurrence patterns of Neotropical spotted cats. *PLOS ONE*, 12, e0168441.
- NUPP, T.E. & SWIHART, R.K. (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy*, 81, 512–526.
- NYIRAMBANGUTSE, B., ZIBERA, E., UWIZEYE, F.K., NSABIMANA, D., BIZURU, E., PLEIJEL, H. et al. (2017) Carbon stocks and dynamics at different successional stages in an Afro-montane tropical forest. *Biogeosciences*, 14, 1285–1303.
- OGAYA, R., BARBETA, A., BASNOU, C. & PEÑUELAS, J. (2015) Satellite data as indicators of tree biomass growth and forest dieback in a Mediterranean holm oak forest. *Annals of Forest Science*, 72, 135–144.
- PRINTES, R.C., RYLANDS, A.B. & BICCA-MARQUES, J.C. (2011) Distribution and status of the Critically Endangered blond titi monkey *Callicebus barbarabrownae* of north-east Brazil. *Oryx*, 45, 439–443.
- QGIS (2014) *QGIS Development Team—Geographic Information System*. Open Source Geospatial Foundation. qgis.osgeo.org [accessed 24 March 2020].

- RIBEIRO, M.C., METGZER, J.P., MARTENSEN, A.C., PONZONI, F.J. & HIROTA, M.M. (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142, 1141–1153.
- RYLANDS, A.B. & MITTERMEIER, R.A. (2014) Primate taxonomy: species and conservation. *Evolutionary Anthropology*, 23, 8–10.
- SAKAI, H.F. & NOON, B.R. (1997) Between-habitat movement of dusky-footed woodrats and vulnerability to predation. *Journal of Wildlife Management*, 61, 343–350.
- SHARMA, N., MADHUSUDAN, M.D. & SINHA, A. (2013) Local and landscape correlates of primate distribution and persistence in the remnant lowland rainforests of the upper Brahmaputra Valley, northeastern India. *Conservation Biology*, 28, 95–106.
- SILVA, L.G., RIBEIRO, M.C., HASUI, E., COSTA, A.P. & CUNHA, R.G.T. (2015) Patch size, functional isolation, visibility and matrix permeability influences Neotropical primate occurrence within highly fragmented landscapes. *PLOS ONE*, 10, e0114025.
- SOULE, M.E. & SIMBERLOFF, D. (1986) What do genetics and ecology tell us about the design of nature reserves? *Biological Conservation*, 35, 19–40.
- SOUZA-ALVES, J.P., MOURTHÉ, Í., HILÁRIO, R., BICCA-MARQUES, J.C., REGH, J., GESTICH, C. et al. (2019) Terrestrial behavior in titi monkeys (*Callicebus*, *Cheracebus*, and *Plecturocebus*): potential correlates, patterns, and differences between genera. *International Journal of Primatology*, 40, 553–572.
- STEPHENS, P.A., SUTHERLAND, W.J. & FREECKLETON, R.P. (1999) What is the Allee effect? *Oikos*, 87, 185–190.
- THOMAS, W.W. (2003) Natural vegetation types in southern Bahia. In *Corredor de Biodiversidade da Mata Atlântica do Sul da Bahia* (organizers P.I. Prado, E.C. Landau, R.T. Moura, L.P.S. Pinto, G.A. B. Fonseca & K.N. Alger). CD-ROM. IESB/CI/CABS/UFMG/UNICAMP, Ilhéus, Brazil.
- TILMAN, D., ISBELL, F. & COWLES, J.M. (2014) Biodiversity and ecosystem functioning. *Annual Review in Ecology Evolution and Systematics*, 45, 471–93.
- TURNER, I.M. & CORLETT, R.T. (1996) The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology and Evolution*, 11, 330–333.
- VEIGA, L.M., BÓVEDA-PENALBA, A., VERMEER, J., TELLO-ALVARADO, J.C. & CORNEJO, F. (2011) *Plecturocebus oenanthe*. In *The IUCN Red List of Threatened Species 2011*: e.T3553A9939083. dx.doi.org/10.2305/IUCN.UK.2011-1.RLTS.T3553A9939083.en [accessed 12 September 2019].
- VEIGA, L.M., PRINTES, R.C., FERRARI, S.F., KIERULFF, C.M., DE OLIVEIRA, M.M. & MENDES, S.L. (2008) *Callicebus melanochir*. In *The IUCN Red List of Threatened Species 2008*: e.T39930A10292634. dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T39930A10292634.en [accessed 20 October 2019].
- VUREN, D.V. & ARMITAGE, K.B. (1994) Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? *Oikos*, 69, 179–181.
- WARNES, G.R., BOLKER, B. & LUMLEY, T. (2015) *gtools*: Various R programme tools. R package version 3.5.0 cran.r-project.org/web/packages/gtools/gtools.pdf [accessed 24 March 2020].