Primate conservation in the Arc of Deforestation: a case study of Vieira's titi monkey *Plecturocebus vieirai*

RODRIGO COSTA-ARAÚJO, LUCAS GONÇALVES DA SILVA
FABIANO RODRIGUES DE MELO, ROGÉRIO VIEIRA ROSSI, JOÃO PEDRO BOTTAN
DIEGO AFONSO SILVA, FABIO OLIVEIRA DO NASCIMENTO, FELIPE PESSOA DA SILVA
GERSON BUSS, LUAN GABRIEL LIMA-SILVA, LUCIANO FERREIRA DA SILVA
MARCOS FIALHO, PATRICK RICARDO DE LÁZARI, RAFAEL SUERTEGARAY ROSSATO
RAFAELA LUMI VENDRAMEL, RAVENA FERNANDA BRAGA DE MENDONÇA
RICARDO SAMPAIO, TOMAS HRBEK, RAONY MACEDO DE ALENCAR
JOSÉ DE SOUSA E SILVA JUNIOR and GUSTAVO RODRIGUES CANALE

Abstract Fifty years of deforestation in the Arc of Deforestation have put at risk species survival, ecosystem services and the stability of biogeochemical cycles in Amazonia, with global repercussions. In response, we need to understand the diversity, distribution and abundance of flagship species groups, such as primates, which can serve as umbrella species for broad biodiversity conservation strategies and help mitigate climate change. Here we identify the range, suitable habitat areas and population size of Vieira's titi monkey *Plecturocebus vieirai* and use it as an emblematic example to discuss biodiversity conservation and climate change mitigation in one of the largest deforestation frontiers. Our findings show that deforestation for agriculture and cattle-ranching expansion is the major threat to *P. vieirai* and is responsible for present (56%) and projected (14%) reductions in habitat area and population size. We also found that human-driven climate change affects the *P. vieirai* niche negatively, triggering habitat degradation and further population decline even inside protected areas. Primate watching can be a profitable alternative to forest exploitation on private, public or Indigenous lands in the Arc of Deforestation and is a way to shift the traditional, predatory extraction of natural resources from Amazonia towards sustainable land use based on biodiversity conservation at local, regional and global scales, local people's welfare and climate change mitigation. New models of land use and income generation are required to protect the unique natural and human heritages of the Arc of Deforestation and the life-supporting ecosystem services and products provided by Amazonia.

Keywords Amazonia, cattle ranching, climate change, Critically Endangered, Data Deficient, deforestation, *Plecturocebus vieirai*, primate watching

Supplementary material for this article is available at doi.org/10.1017/S003060532100171X

RODRIGO COSTA-ARAÚJO (Corresponding author, orcid.org/0000-0002-6092-4892, rcostaaraujo@dpz.eu) Primate Genetics Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37075 Göttingen, Germany

LUCAS GONÇALVES DA SILVA (orcid.org/0000-0002-7993-9015) Universidade de Brasília, Brasília, Brazil

FABIANO RODRIGUES DE MELO Universidade Federal de Viçosa, Viçosa, Brazil

ROGÉRIO VIEIRA ROSSI, LUAN GABRIEL LIMA-SILVA and RAVENA FERNANDA BRAGA DE MENDONÇA Universidade Federal de Mato Grosso, Cuiabá, Brazil

JOÃO PEDRO BOTTAN, GUSTAVO RODRIGUES CANALE, LUCIANO FERREIRA DA SILVA and PATRICK RICARDO DE LÁZARI Universidade Federal de Mato Grosso, Sinop, Brazil

DIEGO AFONSO SILVA and RAONY MACEDO DE ALENCAR Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil

FABIO OLIVEIRA DO NASCIMENTO (orcid.org/0000-0003-0557-7581) and RAFAELA LUMI VENDRAMEL (orcid.org/0000-0003-3333-6160) Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil

FELIPE PESSOA DA SILVA (orcid.org/0000-0003-1411-1249) Universidade Federal de Goiás, Goiânia, Brazil

GERSON BUSS, MARCOS FIALHO, RAFAEL SUERTEGARAY ROSSATO and RICARDO SAMPAIO Instituto Chico Mendes de Conservação da Biodiversidade, João Pessoa, Brazil

TOMAS HRBEK* (orcid.org/0000-0003-3239-7068) Universidade Federal do Amazonas, Manaus, Brazil

JOSÉ DE SOUSA E SILVA JUNIOR Coleção Mastozoológica, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil

*Also at: Trinity University, San Antonio, USA

Received 8 December 2020. Revision requested 1 April 2021.
Accepted 18 November 2021. First published online 15 September 2022.

Introduction

Amazonia, the largest tropical forest, is paramount as a functioning ecosystem for human welfare. It covers 5.3 million km^2 across nine South American countries and provides life-supporting resources such as food, water and medicines, regulates weather and rainfall, and stores carbon (Fearnside, 2003, 2017; Soares-Filho et al., 2006; Malhi et al., 2008; Hubau et al., 2020; Harris et al., 2021). Nonetheless, 5 decades of continuous and unregulated

PLATE 1 Vieira's titi monkey *Plecturocebus vieirai*. Photo: F. Reis.

expansion of agriculture and settlements have transformed southern Amazonia, adjacent ecotonal forests and the northern Cerrado into the largest global deforestation frontier (Kirby et al., 2006; FAO, 2016; Silva et al., 2019; Montibeller et al., 2020), known as the Arc of Deforestation, significantly affecting the functioning of the Amazonian ecosystem (Nobre et al., 2016; Gatti et al., 2021).

There are 52 primate species in the Arc of Deforestation. The majority are endemic to this region and approximately half are threatened or near threatened with extinction (Costa-Araújo et al., 2021b). At the same time, there is a scarcity of baseline data on these primates, including a significant taxonomic deficit (Costa-Araújo et al., 2019; Byrne et al., 2021), which hampers the protection of these species (Rylands & Mittermeier, 2014). An understanding of species diversity, distribution and abundance is therefore necessary to clarify and quantify extinction risks and to provide a scientific foundation for the conservation of the poorly studied primates endemic to the Arc of Deforestation.

Investment in research into and the conservation of primates is especially important as they play a vital role in ecosystem functioning (Peres et al., 2016; Trolliet et al., 2016; Heymann et al., 2017), and they are the most vulnerable vertebrate group globally (Arroyo-Rodríguez et al., 2013, 2017), with c. 60% of all primate species threatened to some degree (Estrada et al., 2017). Moreover, primates are valuable as flagship species (Dietz et al., 1994; Chapman et al., 2020), and so the protection of their habitats in the Arc of Deforestation will not only contribute to their conservation but also provide protection to other species endemic to this region, contributing to biodiversity conservation with impacts at local, regional and global scales.

Here we identify the areas of suitable habitat, delimit the geographical distribution, estimate the population size and assess the conservation status of Vieira's titi monkey *Plecturocebus vieirai* (Plate 1). This species was recently discovered in the Arc of Deforestation (Gualda-Barros et al., 2012) but is known only from its pelage colour and occurrence in three localities and is therefore considered Data Deficient (Alonso et al., 2018; IUCN, 2021). Using our findings, we discuss the threats to primates and the opportunities for biodiversity conservation coupled with climate change mitigation and income generation in the Arc of Deforestation using *P. vieirai* as an emblematic example, a species that we assess to be Critically Endangered based on the IUCN Red List criteria (IUCN, 2019).

Study area

The study area is located in the Tapajós–Xingu interfluve, a region within the Arc of Deforestation that is especially susceptible to land-use change (Laurance et al., 2002; Fig. 1). The Arc of Deforestation extends across southern Amazonia, ecotonal forests and the northern Cerrado from its eastern edge in the states of Pará and Maranhão to the state of Acre in the west (Fearnside et al., 2009; Silva et al., 2019). This region accounts for almost half of the total global land-use changes during 1990–2015 (FAO, 2016). Although sustainable development was expected for the Tapajós–Xingu region 2 decades ago (Nepstad et al., 2002), it became an epicentre of deforestation as a result of logging and slash-and-burn clearance for agriculture and cattle ranching as well as legal and illegal gold mining, affecting even protected areas and Indigenous lands (Printes, 2017; Montibeller et al., 2020).

Methods

Data collection

We collected new occurrence records in field expeditions within the Tapajós–Xingu interfluve during 2015–2019 to model areas of suitable habitat and to delimit the geographical distribution of *P. vieirai*. We reviewed the literature and examined specimens housed in museum collections in Brazil, the USA and Europe for additional occurrence records. To estimate the size and density of the *P. vieirai* population, we surveyed four areas during 2016–2018 using the linear transect method (Buckland et al., 1993). In each area we established a transect of 5 km covering mature and secondary forests. Each transect was surveyed at a constant speed of c. 1.25 km/h twice daily, at 07.00–11.00 and 14.00–18.00 by DAS, LFS and RMA. We noted the number of individuals and the perpendicular distance between the group and the transect using a GPS and a measuring tape; we considered each of the two daily surveys to be independent (Peres & Cunha, 2011). The four forest areas surveyed are on the east bank of the middle Teles Pires River in the

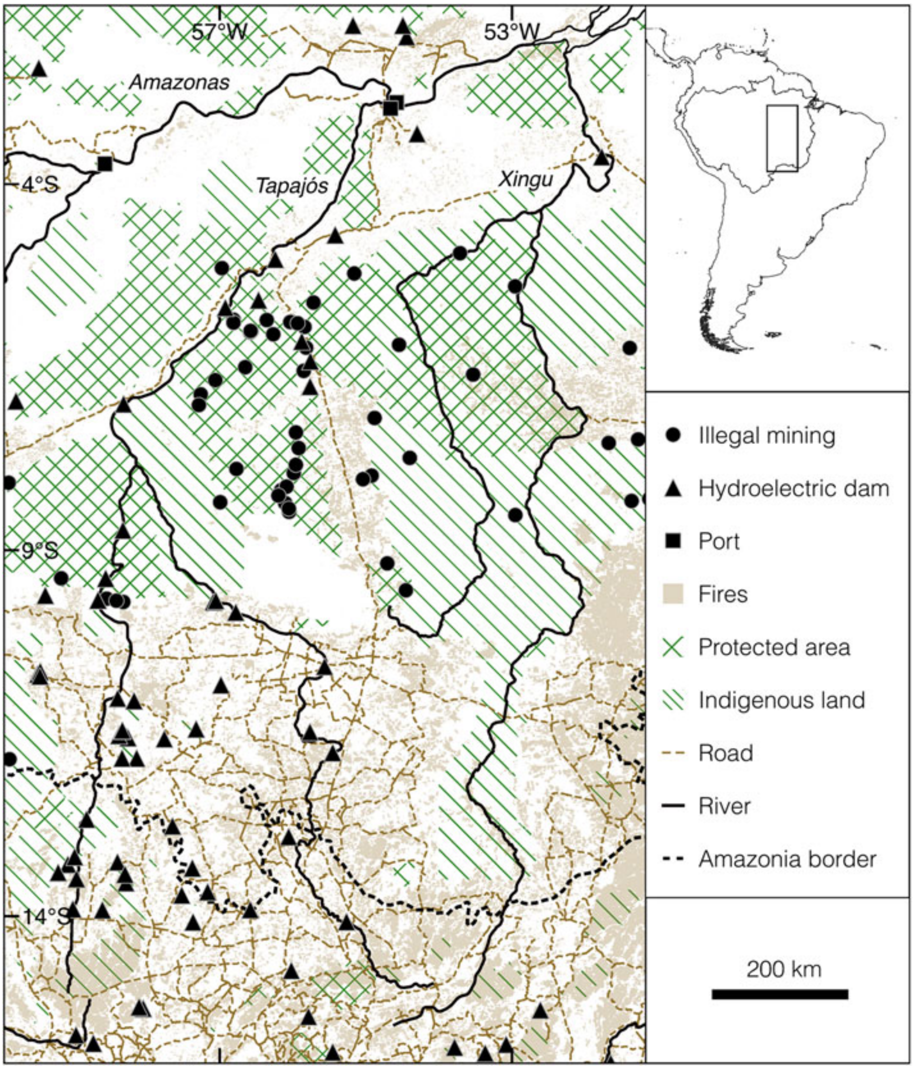

FIG. 1 The Tapajós–Xingu interfluve, southern Amazonia, Brazil, showing the location of fires, illegal mining, hydroelectric dams as of 2020 (RAISG, 2020), protected areas and Indigenous lands (MMA, 2018).

municipalities of Cláudia and Sinop, Mato Grosso State, Brazil, c. 50 km from the the type locality of *P. vieirai*.

Data analysis

We used the occurrence records, and environmental variables from *WorldClim 2.1* (Fick & Hijmans, 2017) and *CliMond* (Kriticos et al., 2012), to model habitat suitability and delimit the geographical distribution of *P. vieirai*. We selected only spatially independent records (n = 33) from our dataset (n = 99 records), applying a threshold of 10 km between records. We eliminated autocorrelated environmental variables to avoid model overfitting (Pearson's correlation test $r > 0.80$, $P < 0.05$; Supplementary Table 1; Callegari-Jacques, 2003; Mateo et al., 2013). We converted the 11 environmental variables selected to a 2.5-min scale using the *raster* package (Hijmans & Etten, 2012) in *R 4.1* (R Core Team, 2018). We modelled habitat suitability using four algorithms adequate for the type of data available (presence and pseudo-absence records), using the *Biomod2* package (Thuiller et al., 2016) in *R*: artificial neural networks (Ripley, 1996), generalized boosted models (Friedman, 2001), random forest (Breiman, 2001) and maximum entropy (Phillips et al., 2006). We selected these four algorithms to avoid model overfitting that could result from the use of algorithms suitable for presence-only and presence and true absence records from long-term surveys (Andrade et al., 2020; Silva et al., 2020). For each algorithm we established five datasets, each composed of 10,000 background records randomly distributed throughout the study area. We then used 70% of the records for training and 30% for evaluating model fitting. In total we performed 200 runs (four algorithms, 10 runs of cross-validation, five sets of random background points), with 1,000 iterations each. To check the accuracy of models we used true skill statistical (TSS) analysis (Allouche et al., 2006) and the area under the curve value (AUC) of the receiver operating characteristic curve, incorporating a binomial probability as a null model (Phillips et al., 2006). The AUC and TSS values

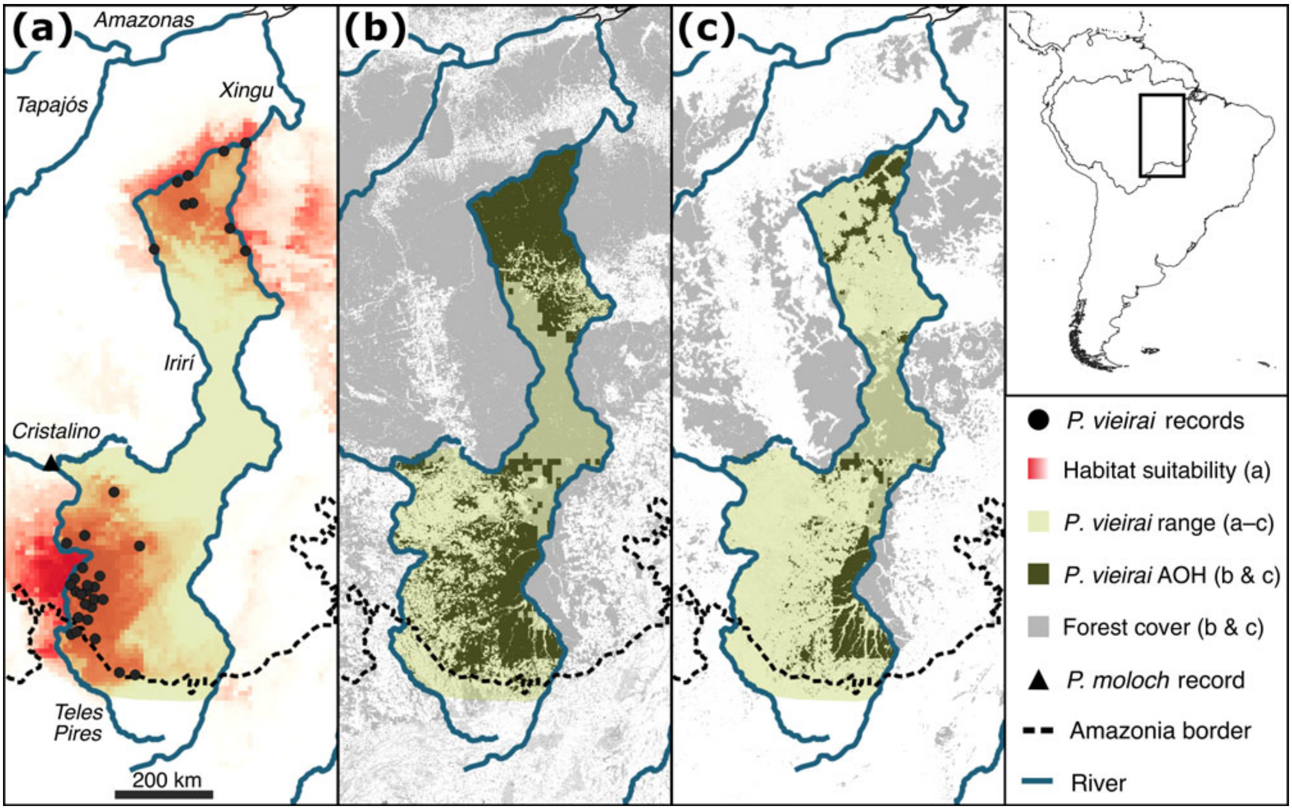

FIG. 2 Geographical distribution and potential habitat of *Plecturocebus vieirai* in the Tapajós–Xingu interfluve: (a) records of *P. vieirai* and *Plecturocebus moloch*, and habitat suitability modelled using environmental variables; (b) suitable forest habitat area in 2020; (c) modelled potentially suitable habitat area in 2044. AOH, area of habitat (based on environmental suitability and forest availability).

vary from 0 to 1 based on the specificity and sensitivity of the species' response to environmental variables. We selected models with AUC > 0.7 and TSS > 0.4 (Buisson et al., 2010) using the mean suitability value of each grid (2.5-min scale) and the minimum omission method (Silva et al., 2017, 2020). To identify the environmental variables that best explain the occurrence of the species we used the jackknife test (Phillips et al., 2006).

Using *ArcGIS 10.1* (Esri, Redlands, USA), we delimited the geographical distribution of *P. vieirai* from the occurrence records, the ensemble model, knowledge of the distribution of congeneric, neighbouring species and considering that rivers restrict the occurrence of primate species in Amazonia (Mourthé et al., 2022). Finally, we overlaid the species distribution with raster layers of vegetation classes (Souza et al., 2020), elevation (which is a constraint for species occurrence; Jarvis et al., 2008) and forest cover (Soares-Filho et al., 2006), to extract the area of suitable habitat available for *P. vieirai* in the present (2020) and in the future (2044). We used a threshold of 24 years, representing three *P. vieirai* generations (Veiga et al., 2011; Defler & García, 2012), as a baseline to estimate the availability of suitable habitat in the future and to assess the species' conservation status. We calculated the extent of occurrence and the area of suitable habitat (Brooks et al., 2019) in 2020 and in 2044 using the *R* package *red* (Cardoso, 2017, 2018). We validated the area of suitable habitat using our dataset of location records overlain on a binary map of presence or absence predicted from the environmental variables.

We used the data from our linear transect surveys to estimate population density and sighting rates with *Distance 7.1* (Thomas et al., 2010). We carried out this analysis by pooling all sightings from the four survey areas using the hazard-rate model, a simple polynomial adjustment and 45 m as the effective sighting distance ($\chi^2 = 0.80$; df = 3; P = 0.84); the final model was selected using the Akaike information criterion. We used the oldest available satellite data of forest cover over the species range (1985; Souza et al., 2020) as a conservative baseline to extract an approximate estimate of the original habitat area of *P. vieirai*.

Results

We gathered 96 occurrence records of *P. vieirai* in addition to the three records available from the species description: 90 from fieldwork, four from the literature (Miranda et al., 2014; Vendramel, 2016) and two from specimens stored in the Museu Paraense Emílio Goeldi (MPEG 246, 21837; Supplementary Table 2). All records are from

TABLE 1 Survey effort, number of sightings, sighting rates and density estimates (per ha) for Vieira's titi monkey *Plecturocebus vieirai* obtained during 3 years (2016–2018) of systematic transect surveys in the southern part of the species range, Cláudia and Sinop municipalities, Mato Grosso State, Brazil.

		Groups			Individuals		
Locality[1]	Survey effort (km)	Number of sightings	Sighting rate/10 km	Density/ ha	Number of sightings	Sighting rate/10 km	Density/ ha
Fazenda da Madenorte	336	26	0.77	0.03	42	1.25	0.07
Fazenda do Balin	306	15	0.49		12	0.39	
Rio Roquete Pinto 02	237	15	0.63		6	0.25	
Tucunaré	313	22	0.70		26	0.83	
Total	1,192	78	0.65		86	0.72	

[1]Locality names as per Supplementary Table 2.

TABLE 2 Extent of occurrence, suitable habitat, suitable habitat in protected areas and forest cover for *P. vieirai* in 2020 and after three *P. vieirai* generations (2044), with actual (2020) or predicted habitat loss (2044).

Variable	2020	2044
Extent of occurrence (km^2)	226,054	
Suitable habitat (km^2)	113,765 (56%)[1]	29,381 (14%)[1]
Suitable habitat in protected areas (km^2)	66,142 (58%)[2]	25,763 (88%)[2]
Forest cover (km^2)	148,096 (73%)[1]	60,731 (30%)[1]

[1]Relative to original forest cover in 1985.
[2]Relative to suitable habitat.

150–410 m altitude and within the boundaries of Amazonian forests of the Tapajós domain, except for three records that fall within the boundaries of the Cerrado (Instituto Brasileiro de Geografia e Estatística, 2019) but were obtained in the Amazonia–Cerrado ecotonal forest (Silva et al., 2019). We also gathered a new record of *Plecturocebus moloch* on the north bank of the Cristalino River (9.552926° S, 55.928568° W; Fig. 2), which is the southernmost documented record of this species in the Tapajós–Xingu interfluve and helped us to delimit the geographical distribution of *P. vieirai*, which is expected to occur on the opposite bank of the river according to our modelling (see below).

Our combined results from habitat modelling and occurrence records show that *P. vieirai* occurs in an area of 226,054 km^2 and is limited in the east by the Xingu River, in the north by the Irirí River, in the west by the Irirí, Cristalino and Teles Pires rivers and extending southwards to the upper Teles Pires and Xingu rivers (Fig. 2). The linear transect surveys totalled 1,192 km of trails walked, with 78 group encounters and 86 individuals observed in the four areas, resulting in a mean density of 0.03 groups/ha and 0.07 individuals/ha (Table 1), with mean group sizes ranging from 1.5 (95% CI 1.0–4.2) to 2.62 (95% CI 2.13–3.23).

Considering the data on past and projected future forest cover (Soares-Filho et al., 2006; Souza et al., 2020) and our new range delimitation for *P. vieirai*, in 1985 forests covered 90% of the range of *P. vieirai* (204,191 km^2) but in 2044 only 30% (54,731 km^2) of these forests will remain. Our modelling shows that suitable habitat (Table 2) for *P. vieirai* is currently 56% of the original area and that 58% of this is within protected areas and Indigenous lands. By 2044, according to our model, only 14% of the original *P. vieirai* habitat will remain, 88% within protected areas and Indigenous lands.

We found that variables related to rainfall (specifically the wettest quarter and the driest month) explain 60% of the likelihood of *P. vieirai* occurrence (AUC = 0.999, TSS = 0.996) and therefore these variables are the best indicator of habitat suitability for this species (Supplementary Table 3).

Discussion

Our findings indicate that habitat loss as a result of conversion of forest into large-scale agricultural monocultures and pastures for cattle ranching is the main threat to *P. vieirai*. Our model showed that because of deforestation the habitat of *P. vieirai* has been reduced by 56% and only 14% will remain by 2044. We expect a concomitant decline in the population size of *P. vieirai*. We assess *P. vieirai* to be Critically Endangered (Costa-Araújo et al., 2022) based on IUCN criterion A3bc (IUCN, 2019), given that our estimates suggest a projected population size reduction of $\geq$ 80% within the next three *P. vieirai* generations (A3), and that these estimates are based on an index of abundance that is appropriate for the taxon (b) and a decline in the area of occupancy of > 80% (c).

Additionally, decreases in the suitability of any remaining habitat because of climate change compound the threats to the long-term survival of *P. vieirai*. Greenhouse gas emissions from human activities are causing extended dry seasons, increased frequencies of droughts and forest fires and reductions in rainfall, forest biomass and net primary production in southern Amazonia (Jiménez-Muñoz et al., 2016; Fearnside, 2017; Brando et al., 2020; Sales et al., 2020; IPCC, 2021). Conversely, we found that precipitation has a positive relationship with habitat suitability for *P. vieirai*, and forest biomass and primary production also have a positive relationship with titi monkey occurrence (Costa-Araújo et al., 2021a). Therefore, climate (IPCC, 2021) and forest (Soares-Filho et al., 2006) changes projected for southern Amazonia will negatively affect the biotic and abiotic dimensions of the *P. vieirai* niche in the next quarter of a century, further exacerbating the threats to the species' long-term survival.

Habitat loss from deforestation and degradation because of climate change have distinct implications for the conservation of *P. vieirai* populations at the northern and southern extents of the species' range. Deforestation and forest fires are and will remain high (Soares-Filho et al., 2006; Brando et al., 2020) in the southern portion of the range of *P. vieirai*, where most forests are on private lands and where there are few and only small protected areas. Although deforestation has been and is expected to continue to be low (Soares-Filho et al., 2006) in the northern portion of the range of *P. vieirai* because of the existence of an extensive system of protected areas and Indigenous lands, this habitat is not safe from degradation driven by climate change.

Therefore, the populations in the southern portion of the range of *P. vieirai* require immediate conservation efforts. Beyond protecting primate populations (Paim et al., 2019), the demarcation of Indigenous lands and establishment of public and private protected areas in the Tapajós–Xingu interfluve would safeguard other endemic species and protect representative tracts of Amazonia and the Amazonia–Cerrado ecotone, a unique and almost entirely unprotected ecosystem (Nepstad et al., 2006; Marques et al., 2019). These protected areas would also contribute to reducing the extent of land-use change and fire regimes in this region, maintain carbon stocks and sinks and generate income through REDD+ projects (Nogueira et al., 2018). For the same reasons, the effective protection of *reservas legais* (an area of 80% that legally must be preserved as forest in all private land holdings in Brazilian Amazonia) needs to be enforced and private landowners rewarded appropriately (Schielein & Börner, 2018).

Law enforcement, the establishment of public protected areas and the demarcation of Indigenous lands rely on governmental administration, but changes in policies and demonstrated inaction and a lack of regulation have resulted in increasing threats to Amazonian forests, biodiversity and traditional peoples in Brazil (Ferrante & Fearnside, 2019; Begotti & Peres, 2020). Moreover, the establishment of private protected areas and the protection of *reservas legais* are unattractive to landowners profiting from the conversion of forests into agricultural landscapes in the Tapajós–Xingu region (Crouzeilles et al., 2012; Printes, 2017). The model of income generation and the policies in Brazil that permit unsustainable extraction of natural resources in the Arc of Deforestation needs to shift towards the protection of the livelihoods of local people, biodiversity, climate change mitigation and the maintenance of the ecosystem services provided by Amazonia (Moutinho et al., 2016; Nobre et al., 2016; Carvalho et al., 2019).

In this context, private landowners are the key stakeholders (Nepstad et al., 2002; Soares-Filho et al., 2006, Fearnside, 2017) for biodiversity conservation and the protection of representative tracts of remaining forests in the Arc of Deforestation, which would contribute to climate change mitigation (Fearnside, 2003, 2009; Nogueira et al., 2018). The owners of large farms are responsible for 70% of deforestation in private areas in Amazonia (Fearnside, 2017) but could change their model of land use, which is currently putting at risk the ecosystem services and the resources provided by the biome (Lovejoy & Nobre, 2018). The official custodians of natural resources in protected areas (traditional and native peoples, local and federal governments) are also key conservation stakeholders (Nepstad et al., 2006).

As an important tool for the conservation of species and habitats (Russon & Wallis, 2014), we believe that primate-watching tourism could be a viable, sustainable alternative to monoculture agriculture and cattle-ranching expansion in the Arc of Deforestation. Firstly, there is a wealth of opportunities for primate watching in the Arc of Deforestation, with 52 species of primates (Costa-Araújo et al., 2021b). Secondly, primate-watching services on private lands, public protected areas and Indigenous lands are permitted under Brazilian environmental regulations. Thirdly, the logistics to facilitate ecotourism in the Arc of Deforestation are met by a network of roads, airports and lodging facilities. Additionally, regulations for the creation of private protected areas in Brazil are compatible with primate-watching tourism and biodiversity protection (Crouzeilles et al., 2012). This scenario would facilitate the establishment of primate-watching activities in protected areas, Indigenous lands and private areas within the Arc of Deforestation, a region where logistic capacity (one of the main constraints on ecotourism; Pegas & Castley, 2014) exists.

For example, a shift from agriculture to primate watching focused on *P. vieirai* in the private lands of the Tapajós–Xingu interfluve would contribute to reducing habitat loss in the southern portion of the range of *P. vieirai* and to mitigating climate change, in turn contributing to protecting *P. vieirai* populations in the northern part of its range. It is equally important to elect politicians committed to biodiversity conservation, the welfare of traditional peoples and climate change mitigation (Silva, 2005; Carvalho et al., 2019), so that all key stakeholders can work together to improve outcomes for natural areas in the largest global deforestation frontier (Moutinho et al., 2018).

Conclusion

Deforestation, mainly driven by expansion of monoculture agriculture and cattle ranching, is a ubiquitous threat to *P. vieirai*, responsible for the past, present and projected future habitat losses and consequent decreases in the populations of this species. These types of land use in the Arc of Deforestation have contributed directly to climate change, another major threat to *P. vieirai*, which we expect to cause habitat degradation and population declines even within protected areas.

Primate watching could be a profitable and sustainable alternative to the exploitation and overexploitation of natural resources on private, public and Indigenous lands and could be a way to shift from the current land-use model in the Arc of Deforestation towards biodiversity conservation. In the long term, the forests protected for and by tourism will serve as carbon stocks and sinks, contributing to the mitigation of climate change.

The traditional model of predatory extraction of natural resources in the Arc of Deforestation is pushing primate species to the brink of extinction and transforming Amazonia into a source, rather than a sink, of carbon emissions. An alternate model of land use and income generation is needed if we are to protect the unique natural and human heritages of Amazonia and its life-supporting ecosystem services and products.

Acknowledgements We thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (140039/2018-1; 316321/2020-6), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; 001; 88881.189052/2018-01) and Fundação de Amparo à Pesquisa do Estado do Amazonas for scholarships; the Conservation Leadership Programme, Global Wildlife Conservation's Margot Marsh Primate Action Fund and CAPES AUX/PE 3261/2013 for funding fieldwork; Idea Wild, Consórcio Usina Hidroelétrica Teles Pires and Consórcio Usina Hidroelétrica Sinop for supporting fieldwork; and Jessica dos Anjos for providing the record of *Plecturocebus moloch* at the Cristalino River. RC-A's field data were collected during his doctorate research at the Programa de pós-graduação em Ecologia of the Instituto Nacional de Pesquisas da Amazônia, and he led the writing while affiliated with the Mastozoology Collection of the Museu Paraense Emílio Goeldi.

Author contributions Conception: RC-A, GRC; data collection design: RC-A, FRM, RVR, GRC; data collection: all authors; mapping and species distribution modelling: LGS, FPS, with inputs from RC-A; population density analysis: FRM; writing: RC-A, with inputs from all authors.

Conflicts of interest None.

Ethical standards Fieldwork followed the code of best practices for field primatology of the International Society of Primatologists and otherwise abided by the *Oryx* guidelines on ethical standards.

References

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43, 1223–1232.

Alonso, A.C., Boubli, J.P. & Miranda, J. (2018) *Plecturocebus vieirai*. In *The IUCN Red List of Threatened Species* 2018. dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T70330181A70616831.en.

Andrade, A.F.A., Velazco, S.J.E. & Júnior, P.M. (2020) *ENMTML*: an *R* package for a straightforward construction of complex ecological niche models. *Environmental Modelling & Software*, 125, 104615.

Arroyo-Rodríguez, V., Galán-Acedo, C. & Fahrig, L. (2017) Habitat fragmentation. In *The International Encyclopedia of Primatology*, vol. 2 (ed. A. Fuentes), pp. 516–523. Wiley, Chichester, UK.

Arroyo-Rodríguez, V., González-Perez, I.M., Garmendia, A., Solà, M. & Estrada, A. (2013) The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico. *Landscape Ecology*, 28, 1717–1727.

Begotti, B. & Peres, C.A. (2020) Rapidly escalating threats to the biodiversity and ethnocultural capital of Brazilian Indigenous lands. *Land Use Policy*, 96, 104694.

Brando, P.M., Soares-Filho, B., Rodrigues, L., Assunção, A., Morton, D., Tuchschneider, D. et al. (2020) The gathering firestorm in southern Amazonia. *Science Advances*, 6, eaay1632.

Breiman, L. (2001) Random forests. *Machine Learning*, 45, 5–32.

Brooks, T.M., Pimm, S.L., Akçakaya, H.R., Buchanan, G.M., Butchart, S.H.M., Foden, W. et al. (2019) Measuring terrestrial area of habitat (AOH) and its utility for the IUCN Red List. *Trends in Ecology & Evolution*, 34, 977–986.

Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman & Hall, New York, USA.

Buisson, L., Thuiler, W., Casajus, N., Lek, S. & Grenouillet, G. (2010) Uncertainty in ensemble forecasting of species distribution. *Global Change Biology*, 16, 1145–1157.

Byrne, H., Costa-Araújo, R., Farias, I., Silva, M.N.F., Messias, M., Hrbek, T. & Boubli, J.P. (2021) Uncertainty regarding species delimitation, geographic distribution, and the evolutionary history of south-central Amazonian titi monkey species (*Plecturocebus*, Pitheciidae). *International Journal of Primatology*, published online 4 November 2021.

Callegari-Jacques, J. (2003) *Bioestatística: Princípios e Aplicações*. Artmed, Porto Alegre, Brazil.

Cardoso, P. (2017) *Red* – an *R* package to facilitate species red list assessments according to the IUCN criteria. *Biodiversity Data Journal*, 5, e20530.

Cardoso, P. (2018) *red: IUCN Redlisting Tools*. *R* package version 1.4.0. cran.r-project.org/web/packages/red/red.pdf [accessed 10 November 2020].

Carvalho, W.D., Mustin, K., Hilário, R.C., Vasconcelos, I., Eilers, V. & Fearnside, P. (2019) Deforestation control in the Brazilian Amazon: a conservation struggle being lost as agreements and regulations are subverted and bypassed. *Perspectives in Ecology and Conservation*, 17, 122–130.

Chapman, C.A., Bicca-Marques, J.C., Dunham, A.E., Fan, P., Fashing, P.J. & Gogarten, J.F. et al. (2020) Primates can be a rallying symbol to promote tropical forest restoration. *Folia Primatologica*, 91, 669–687.

Costa-Araújo, R., Melo, F.R., Canale, G.R., Hernández-Rangel, S.M., Messias, M.R., Rossi, R.V. et al. (2019) The Munduruku marmoset: a new monkey species from southern Amazonia. *PeerJ*, 7, e7019.

Costa-Araújo, R., Melo, R., Silva Júnior, J.S., Buss, G., Boubli, J.P., Hrbek, T. & Canale, G.R. (2022) *Plecturocebus vieirai*. In *The IUCN Red List of Threatened Species* 2022. dx.doi.org/10.2305/IUCN.UK.2022-1.RLTS.T70330181A215349266.en.

Costa-Araújo, R., Regolin, A.L., Martello, F., Souza-Alves, J.P., Hrbek, T. & Ribeiro, M.C. (2021a) Occurrence and conservation of the Vulnerable titi monkey *Callicebus melanochir* in fragmented landscapes of the Atlantic forest hotspot. *Oryx*, 55, 916–923.

Costa-Araújo, R., Silva, J.S. Jr, Boubli, J.P., Rossi, R.V., Canale, G.R., Melo, F.R. et al. (2021b) An integrative analysis uncovers a new, pseudo-cryptic species of Amazonian marmoset (Primates: Callitrichidae: *Mico*) from the Arc of Deforestation. *Scientific Reports*, 11, 15665.

Crouzeilles, R., Valle, M.M., Cerqueira, R. & Grelle, C.E.V. (2012) Increasing strict protection through protected areas on Brazilian private lands. *Environmental Conservation*, 40, 209–210.

Defler, T.R. & García, J. (2012) *Plecturocebus caquetensis*. In *The IUCN Red List of Threatened Species* 2012. dx.doi.org/10.2305/IUCN.UK.2012-1.RLTS.T14699281A14699284.en.

Dietz, J.M., Dietz, L.A. & Nagagata, E.Y. (1994) The effective use of flagship species for conservation of biodiversity: the example of lion tamarins in Brazil. In *Creative Conservation: Interactive Management of Wild and Captive Animals* (eds P.J.S. Olney, G.M. Mace & A.T.C. Feistner), pp. 32–49. Chapman & Hall, London, UK.

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.

FAO (2016) *Global Forest Resources Assessment 2015* (2nd edition). Food and Agriculture Organization of the United Nations, Rome, Italy. fao.org/forest-resources-assessment/en [accessed 8 September 2020].

Fearnside, P.M. (2003) *A Floresta Amazônica nas Mudanças Globais*. INPA, Manaus, Brazil.

Fearnside, P.M. (2009) Global warming in Amazonia: impacts and mitigation. *Acta Amazonica*, 39, 1003–1012.

Fearnside, P.M. (2017) Deforestation of the Brazilian Amazon. In *Oxford Research Encyclopedia of Environmental Science* (ed. H. Shugart). Oxford University Press, Oxford, UK. oxfordre.com/environmentalscience/view/10.1093/acrefore/9780199389414.001.0001/acrefore-9780199389414-e-102 [accessed 10 November 2018].

Fearnside, P.M., Righi, C.A., Graça, P.M.L.A., Keizer, E.W.H., Cerri, C.C. & Nogueira, E.M. et al. (2009) Biomass and greenhouse-gas emissions from land-use change in Brazil's Amazonian 'Arc of Deforestation': the states of Mato Grosso and Rondônia. *Forest Ecology and Management*, 258, 1968–1978.

Ferrante, L. & Fearnside, P.M. (2019) Brazil's new president and 'ruralists' threaten Amazonia's environment, traditional peoples and the global climate. *Environmental Conservation*, 46, 261–263.

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.

Friedman, J.H. (2001) Greedy function approximation: a gradient boosting machine. *Annals of Statistics*, 29, 1189–1232.

Gatti, L.V., Basso, L.S., Miller, J.B., Gloor, M., Domingues, L.G., Cassol, H.L.G. et al. (2021) Amazonia as a carbon source linked to deforestation and climate change. *Nature*, 595, 388–393.

Gualda-Barros, J., Nascimento, F.O. & Amaral, M.K. (2012) A new species of *Callicebus* Thomas, 1903 (Primates, Pitheciidae) from the states of Mato Grosso and Pará, Brazil. *Papéis Avulsos de Zoologia*, 52, 261–279.

Harris, N.L., Gibbs, D.A., Baccini, A., Birdsey, R.A, Bruin, S., Farina, M. et al. (2021) Global maps of twenty-first century forest carbon fluxes. *Nature Climate Change*, 11, 234–240.

Heymann, E.W., Culot, L., Knogge, C., Tirado Herrera, E.R., Noriega Piña, T.E., Klapproth, M. et al. (2017) Long-term consistency in spatial patterns of primate seed dispersal. *Ecology and Evolution*, 7, 1435–1441.

Hijmans, R.J. & Etten, J.V. (2012) *raster: Geographic Analysis and Modelling with Raster Data*. *R* package version 2.0–12. rdrr.io/cran/raster [accessed 24 March 2020].

Hubau, W., Lewis, S.L., Phillips, O.L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A. et al. (2020) Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, 579, 80–87.

Instituto Brasileiro de Geografia e Estatística (2019) *Mapa de Biomas do Brasil*. ibge.gov.br/geociencias/informacoes-ambientais/estudos-ambientais/15842/biomas.html?=&t=acesso-ao-produto [accessed 8 September 2020].

IPCC (Intergovernmental Panel on Climate Change) (2021) *Sixth Assessment Report, Working Group I, Regional Fact Sheet—Central and South America*. ipcc.ch/report/ar6/wg1/downloads/factsheets/IPCC_AR6_WGI_Regional_Fact_Sheet_Central_and_South_America.pdf [accessed 30 August 2021].

IUCN (2019) *Guidelines for Using the IUCN Red List Categories and Criteria. Version 14*. IUCN Standards and Petitions Committee, Gland, Switzerland.

IUCN (2021) *The IUCN Red List of Threatened Species. Version 2021-2*. iucnredlist.org [accessed 26 October 2021].

Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008) Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM 90m *Database*. srtm.csi.cgiar.org [accessed 8 September 2020].

Jiménez-Muñoz, J.C., Mattar, C., Barichivich, J., Santamaría-Artigas, A., Takahashi, K., Malhi, Y. et al. (2016) Record-breaking warming and extreme drought in the Amazon rainforest during the course of El Niño 2015–2016. *Scientific Reports*, 6, 33130.

Kirby, K.R., Laurance, W.F., Albernaz, A.C., Götz, S., Fearnside, P.M., Bergen, S. et al. (2006) The future of deforestation in the Brazilian Amazon. *Futures*, 38, 432–453.

Kriticos, D.J., Webber, B.L., Leriche, A., Ota, N., Macadam, I., Bathold, J. et al. (2012) *CliMond:* global high resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, 3, 53–64.

Laurance, W.F., Albernaz, A.K.M., Schroth, G., Fearnside, P.M., Bergen, S., Venticinque, E.M. et al. (2002) Predictors of deforestation in the Brazilian Amazon. *Journal of Biogeography*, 29, 737–748.

Lovejoy, T.E. & Nobre, C. (2018) Amazon tipping point. *Science Advances*, 4, eaat2340.

Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W. & Nobre, C.A. (2008) Climate change, deforestation, and the fate of the Amazon. *Science*, 319, 169–173.

Marques, E.Q., Marimon-Junior, B.H., Marimon, B.S., Matricardi, E.A.T., Mews, H.A. & Colli, G.R. (2019) Redefining the Cerrado–Amazonia transition: implications for conservation. *Biodiversity and Conservation*, 29, 1501–1517.

Mateo, R.G., Vanderpoorten, A., Munoz, J., Laenen, B. & Desamore, A. (2013) Modelling species distributions from heterogenous data for the biogeographic regionalization of the European bryophyte flora. *PLOS ONE*, 8, e55648.

Miranda, J.M.D., Zago, L., Rubio, M.B.G., Santos, R.E.F.S. & Ludwig, G. (2014) Primatas da região do médio Rio Teles Pires, sul da Amazônia, Brasil. In *A Primatologia no Brasil* (eds F.C. Passos & J.M.D. Miranda), vol. 13, pp. 89–95. Sociedade Brasileira de Primatologia, Curitiba, Brazil.

MMA (2018) *Ministério de Meio Ambiente*. antigo.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs/dados-georreferenciados.html [accessed 26 August 2018].

Montibeller, B., Kmoch, A., Virro, H., Mander, Ü. & Uuemaa, E. (2020) Increasing fragmentation of forest cover in Brazil's legal Amazon from 2001 to 2017. *Scientific Reports*, 10, 5803.

Mourthé, Í., Hilário, R.R., Carvalho, W.D. & Boubli, J.P. (2022) Filtering effect of large rivers on primate distribution in the Brazilian Amazonia. *Frontiers in Ecology and Evolution*, 10, 857920.

Moutinho, P., Guerra, R. & Azevedo-Ramos, C. (2018) Achieving zero deforestation in the Brazilian Amazon: what is missing? *Elementa: Science of the Anthropocene*, 4, 000125.

Nepstad, D.C., McGrath, D., Alencar, A., Barros, A.C., Carvalho, G., Santilli, M. et al. (2002) Frontier governance in Amazonia. *Science*, 295, 629–631.

Nepstad, D.C., Schwartzman, S., Bamberger, B., Santilli, M., Ray, D., Schlesinger, P. et al. (2006) Inhibition of Amazon deforestation and fire by parks and Indigenous lands. *Conservation Biology*, 20, 65–73.

Nobre, C.A., Sampaio, G., Borma, L.S., Castilla-Rubio, J.C., Silva, J.S. & Cardoso, M. (2016) Land-use and climate change risks in the Amazon and the need of a novel sustainable development paradigm. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 10759–10768.

Nogueira, E.M., Yanai, A.M., Vasconcelos, S.S., Graça, P.M.L.A. & Fearnside, P.M. (2018) Brazil's Amazonian protected areas as a bulwark against regional climate change. *Regional Environmental Change*, 18, 573–579.

Paim, F.P., Bizri, H.R.E, Paglia, A.P. & Queiroz, H.L. (2019) Long-term population monitoring of the threatened and endemic black-headed squirrel monkey (*Saimiri vanzolinii*) shows the importance of protected areas for primate conservation in Amazonia. *American Journal of Primatology*, 81, e22988.

Pegas, F.V. & Castley, J.G. (2014) Ecotourism as a conservation tool and its adoption by private protected areas in Brazil. *Journal of Sustainable Tourism*, 22, 604–625.

Peres, C.A. & Cunha, A.A. (2011) *Manual para Censo e Monitoramento de Vertebrados de Médio e Grande Porte por Transeccção Linear em Florestas Tropicais*. Wildlife Technical Series. Wildlife Conservation Society, Manaus, Brazil.

Peres, C.A., Emilio, T., Schietti, J., Desmoulière, S.J. & Levi, T. (2016) Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 892–897.

Phillips, S.J., Anderson, R.P. & Shapire, R.E. (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, 190, 231–259.

Printes, R.C. (2017) *Adeus Amazônia: Conflitos Agrários e Socioambientais por Trás do Desmatamento no Sudoeste do Pará*. Editora Prismas, Curitiba, Brazil.

R Core Team (2018) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. R-project.org [accessed 9 February 2022].

RAISG (2020) *Amazon Geo-Referenced Socio-Environmental Information Network*. amazoniasocioambiental.org/en/maps [accessed 9 February 2021].

Ripley, B.D. (1996) *Pattern Recognition and Neural Networks*. Cambridge University Press, Cambridge, UK.

Russon, A.E. & Wallis, J. (2014) Primate tourism as a conservation tool: a review of the evidence, implications, and recommendations. In *Primate Tourism: A Tool for Conservation?* (eds A.E. Russon & J. Wallis), pp. 313–332. Cambridge University Press, Cambridge, UK.

Rylands, A.B. & Mittermeier, R.A. (2014) Primate taxonomy: species and conservation. *Evolutionary Anthropology*, 23, 8–10.

Sales, F., Santiago, T., Biggs, T.W., Mullan, K., Sills, E.O. & Monteverde, C. (2020) Impacts of protected area deforestation on dry-season regional climate in the Brazilian Amazon. *Journal of Geophysical Research: Atmospheres*, 125, e2020JD033048.

Schielein, J. & Börner, J. (2018) Recent transformations of land-use and land-cover dynamics across different deforestation frontiers in the Brazilian Amazon. *Land Use Policy*, 76, 81–94.

Silva, C.A. Jr, Costa, G.M., Rossi, F.S., Vale, J.C.E., Lima, R.B., Lima, M. et al. (2019) Remote sensing for updating the boundaries between the Brazilian Cerrado–Amazonia biomes. *Environmental Science and Policy*, 101, 383–392.

Silva, F.P., Fernandes-Ferreira, H., Montes, M.A. & Silva, L.G. (2020) Distribution modelling applied to deficient data species assessment: a case study with *Pithecopus nordestinus* (Anura, Phyllomedusidae). *Neotropical Biology and Conservation*, 15, 165–175.

Silva, L.G., Kawanishi, K., Henschel, P., Kittle, A., Sanei, A., Reebin, A. et al. (2017) Mapping black panthers: macroecological modelling of melanism in leopards (*Panthera pardus*). *PLOS ONE*, 12, e0170378.

Silva, M. (2005) The Brazilian protected areas program. *Conservation Biology*, 19, 608–611.

Soares-Filho, B.S., Nepstad, D.C., Curran, L.M., Cerqueira, G.C., Garcia, R.A., Ramos, C.A. et al. (2006) Modelling conservation in the Amazon basin. *Nature*, 440, 520–523.

Souza, C.M., Shimbo, J.Z., Rosa, M.R., Parente, L.L., Alencar, A.A., Rudorff, B.F.T. et al. (2020) Reconstructing three decades of land use and land cover changes in Brazilian biomes with Landsat archive and Earth Engine. *Remote Sensing*, 12, 2735.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L. et al. (2010) *Distance* software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, 5–14.

Thuiller, W., Georges, D., Engler, R. & Breiner, F. (2016) *biomod2: Ensemble Platform for Species Distribution Modelling. R* package version 3.3-7. cran.r-project.org/web/packages/biomod2/index.html [accessed 24 March 2020].

Trolliet, F., Serckxa, A., Forget, P.M., Jamar, R.C.B., Huynen, M.C. & Hambucker, A. (2016) Ecosystem services provided by a large endangered primate in a forest–savanna mosaic landscape. *Biological Conservation*, 203, 55–66.

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. doi.org/10.2305/IUCN.UK.2011-1.RLTS.T3553A9939083.en.

Vendramel, R.L. (2016) *Revisão taxonômica do grupo moloch, gênero Callicebus Thomas, 1903 (Primates, Pitheciidae, Callicebinae)*. MSc thesis. Universidade de São Paulo, São Paulo, Brazil.