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1 Habitat Puzzles: Linking Primate Invasions and Declines to 2 Landscape Connectivity

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9 **Abstract**

10 The distribution of primate species in Brazil is currently heavily impacted by the exploitation and
11 fragmentation of the Atlantic Forest. This forest is one of the world's biodiversity hotspots, and its
12 ecosystems are home to an extremely rich fauna. Fragmentation can lead to the decline of certain
13 species, such as *Sapajus nigritus* (*S. nigritus*). Conversely, the proximity of roads and built-up areas
14 can lead to the accidental introduction of species with invasive potential that compete with endemic
15 species, including *Callithrix jacchus*, *Callithrix penicillata*, and their hybrids. Anticipating and
16 estimating the invasive threat of marmosets and its amplification over time is an important issue for
17 the conservation of declining primate populations. Similarly, knowing which environments are
18 favorable for the spread of capuchins would make it easier to anticipate their dispersal and
19 maintenance.

20 Using data on climate, human density, vegetation cover, and vegetation types, as well as
21 coordinates indicating the presence and absence of these primates, a comparison of generalized
22 linear models and random forest models enabled us to estimate the conditions for their presence.
23 The study took place in the Atlantic forest fragments of the S o Jo o river basin in the state of Rio
24 de Janeiro. By extrapolating the probability of the presence of individuals throughout this territory,
25 these models predicted the most suitable habitats. Based on these predictions, and assuming that the
26 resistance to movement of these animals is linked to the suitability of the environment for these
27 species, we were able to model the connectivity between different habitats.

28 Our results show that the probability of marmoset presence increases with decreasing humidity,
29 non-vegetation, and tree cover. The presence of *S. nigritus* is explained by an increase in the
30 distance to the nearest road. While marmosets now occupy vegetation types under anthropogenic

1 influence, *S. nigritus* prefers predominantly natural vegetation. *Callithrix*'s tolerance of anthropized
2 habitats explains its dispersal potential. Comparisons between models showed that random forest
3 models performed better than GLM models.

4 The territory occupied by the species corresponds to a 0.5-fold increase in the area already occupied
5 by marmosets. This dispersal could primarily occur around territories close to their current
6 presence. The possibilities for the dispersal of *S. nigritus* are quite significant and are not limited to
7 forest fragments, contrary to our hypotheses. We can expect the existing distribution to multiply by
8 7.5. These results provide important information that will be used by local associations to manage
9 the populations, habitats, and dispersal paths identified. This is all the more important as marmosets
10 compete with the endangered golden lion tamarin.

11 **Keywords:** *animal dispersal, Atlantic forest, habitat, invasion, modeling, primate.*

12

13 **Introduction**

14 The spatial distribution of an animal species can change according to the seasons, the availability of
15 resources, and other abiotic and biotic factors, such as climate, the surface area of the available
16 habitat (Arroyo-Rodríguez & Dias, 2010) and inter- and intra-specific competition (Reyna-Hurtado
17 et al., 2018). These ecological characteristics must then be considered when estimating a species
18 distribution. Differences in habitat occupancy are, therefore, linked to the degree to which sites
19 match a species' ecology. However, while the importance of habitat size and quality in predicting
20 the persistence of individuals is undeniable, it is not sufficient to maintain stable population
21 numbers over time. Studies have shown that a species' presence is also dependent on its
22 geographical isolation (Benchimol & Peres, 2013). In fragmented habitats, the structure and
23 characteristics of the landscape play a vital role (Arroyo-Rodríguez & Mandujano, 2009) in
24 determining the movement and colonization of suitable habitats for the species (Boyle & Smith,
25 2010; L. G. da Silva et al., 2015). Therefore, populations require corridors to connect landscapes
26 and their inhabitants (Galindo-Leal & Câmara, 2003), or else they risk seeing their populations
27 disappear in the long term due to the pressure of inbreeding depression (Farias et al., 2015; W.
28 Wang et al., 2017).

29 Understanding the unique ecologies of various species can be harnessed to map their distribution
30 and assess habitat connectivity (Beier et al., 2008). This information is crucial for guiding
31 conservation efforts and enhancing the management of both animal populations and their habitats.

1 However, it's essential to acknowledge that anthropogenic factors wield a significant influence on
2 species distribution. Climate change, alterations in land use, exploitation, pollution, and the
3 introduction of invasive species all exert substantial impacts on species distribution (Pyšek &
4 Richardson, 2010; Schwitzer et al., 2011; Yackulic et al., 2014).

5 In this context, the Atlantic Forest, despite being one of the world's biodiversity hotspots has now
6 been largely reduced to forest fragments of less than 50 hectares, primarily due to over-exploitation
7 (e.g., logging and poaching) and the expansion of agricultural land (grazing, and forestry)
8 (Magnago et al., 2015; Morellato & Haddad, 2000) However, there is a decree in place aimed at
9 advancing the protection, conservation, and sustainable use of the Atlantic Forest. The Brazilian
10 Forest Code of 1965 mandates that 20% of the area of any rural property within the Atlantic Forest
11 must be designated as a legal forest reserve, and gallery forests and forests on steep slopes should
12 be regarded as permanently protected areas. Furthermore, Federal Decree 750 of 1993 stipulates
13 that all logging and any potential disturbances to the Atlantic Forest must undergo prior
14 authorization (Ditt et al., 2008; Tabarelli et al., 2005).

15 Despite legal protection, numerous threats persist (Hirakuri, 2003). Forest fragmentation resulting
16 from urban expansion, land use changes, and livestock farming has a significant impact on species
17 distribution. On the one hand, it reduces the available habitat area and hinders the dispersal of
18 individuals, ultimately leading to a decline in the population numbers of affected species over time.
19 On the other hand, the proximity of roads and urban areas can facilitate the introduction of new
20 species with invasive potential (Pyšek et al., 2020). Non-human primates are among the species
21 affected by these anthropogenic threats (Almeida-Rocha et al., 2017). The Brazilian Atlantic Forest
22 hosts a rich diversity of primates. However, this study focuses on the distribution and habitat
23 connectivity of three primate species under different themes: the black-horned capuchin (*Sapajus*
24 *nigritus*) and the marmosets (*Callithrix jacchus*, *Callithrix penicillata*, and their hybrids). While
25 some species are experiencing population declines, others appear to thrive in disturbed habitats (N.
26 Pinto et al., 2009; With, 2004). Primate responses to changes in land use vary (Strier, 2000).
27 Generalist species, with their flexible diets and greater habitat tolerance, are more likely to persist in
28 forest remnants (Marvier et al., 2004; Ramiadantsoa et al., 2018).

29 The capuchin monkey is classified as 'near threatened' on the IUCN Red List and has experienced a
30 significant population decline in recent decades (Alfaro et al., 2015; González-Solís et al., 2001;
31 Lynch Alfaro et al., 2014). Their decline serves as a prominent example of the consequences of
32 habitat fragmentation and exploitation in a primate species (Aguiar et al., 2011; Alfaro et al., 2015;
33 Galán-Acedo et al., 2021; Lynch Alfaro et al., 2014). Furthermore, researchers have shown that
34 with climate change (including higher temperatures and changes in precipitation), by the year 2100,

1 their distribution areas could be further altered, resulting in changes such as the distribution loss of
2 half of the area for 14 species and 75% for 9 species (M. P. Pinto et al., 2023; Sales et al., 2020).

3 Human impact on primate populations due to fragmentation can also be indirect, primarily through
4 the introduction of invasive species. In the case of marmosets, urbanization appears to result in a
5 decrease in predator numbers and an increase in the availability of their food resources (De Andrade
6 et al., 2020). In fact, both the common marmoset (*C. jacchus*) and the black-brushed marmoset (*C.*
7 *penicillata*) have populations that are continuously growing in certain areas (Detogne et al., 2017).
8 The total population size of these two species has become quite large. Another significant aspect is
9 that these two species are capable of hybridization, resulting in fertile offspring (Malukiewicz et al.,
10 2015; Miranda et al., 2015; Rímoli et al., 2015). Studies indicate that marmosets pose a risk for the
11 conservation of endangered and endemic species (i.e., golden lion tamarins – *Leontopithecus*
12 *rosalia*), as they exploit their resources and lead to changes in other primate behaviours (making
13 their territoriality behavior). This increased competition, especially during the scarce resource
14 conditions of winter, can threaten the survival of endemic primates by reducing their access to
15 essential resources. It is important to understand the distribution of this species to develop effective
16 conservation strategies aimed at protecting endemic primate populations in the forest fragments
17 (Ruiz-Miranda et al., 2006).

18 Identifying the parameters important to the distribution of capuchins, a species currently in decline,
19 and to the distribution of *C. jacchus*, *C. penicillata* and their hybrids, a population with increasing
20 numbers but invasive, can help manage their habitats and connectivity. This study will enable us to
21 better assess the risks and consequences of the colonization of *Callithrix* species, and to clarify the
22 issues at stake for endemic primate populations. To this end, predictive species distribution models
23 such as generalized linear models (GLM) (Dobson & Barnett, 2018; Gestich et al., 2023; Guisan et
24 al., 2002) or random forest models (RF) (De'ath & Fabricius, 2000; Magness et al., 2008) can be
25 used to estimate the conditions favorable to the presence of a species by relating points of absence
26 and presence to ecological variables likely to influence the distribution of individuals (Elith &
27 Leathwick, 2009; Miller, 2010; Molnár et al., 2011; Srivastava et al., 2019). Thus, we predict that
28 primate distribution should be dependent on climatic data such as temperature and hygrometry, but
29 also on vegetation type, Atlantic Forest cover and human presence. By looking at the effects of
30 these variables, we will be able to investigate the potential for colonization of an invasive species
31 (i.e., marmosets) while assessing the vulnerability of an endemic primate species (i.e., capuchins).
32 By building a resistance matrix that represents a species' ability to move through an environment,
33 based in part on the probability of presence, it will be possible to analyze the connectivity between
34 current and potential habitats. The models should indicate good habitat tolerance and potential

1 dispersal routes. This study is used to predict the invasive potential of marmosets, as well as the
2 possible expansion of capuchins. This analysis thus help guide the management of these species and
3 conservation strategies.

4

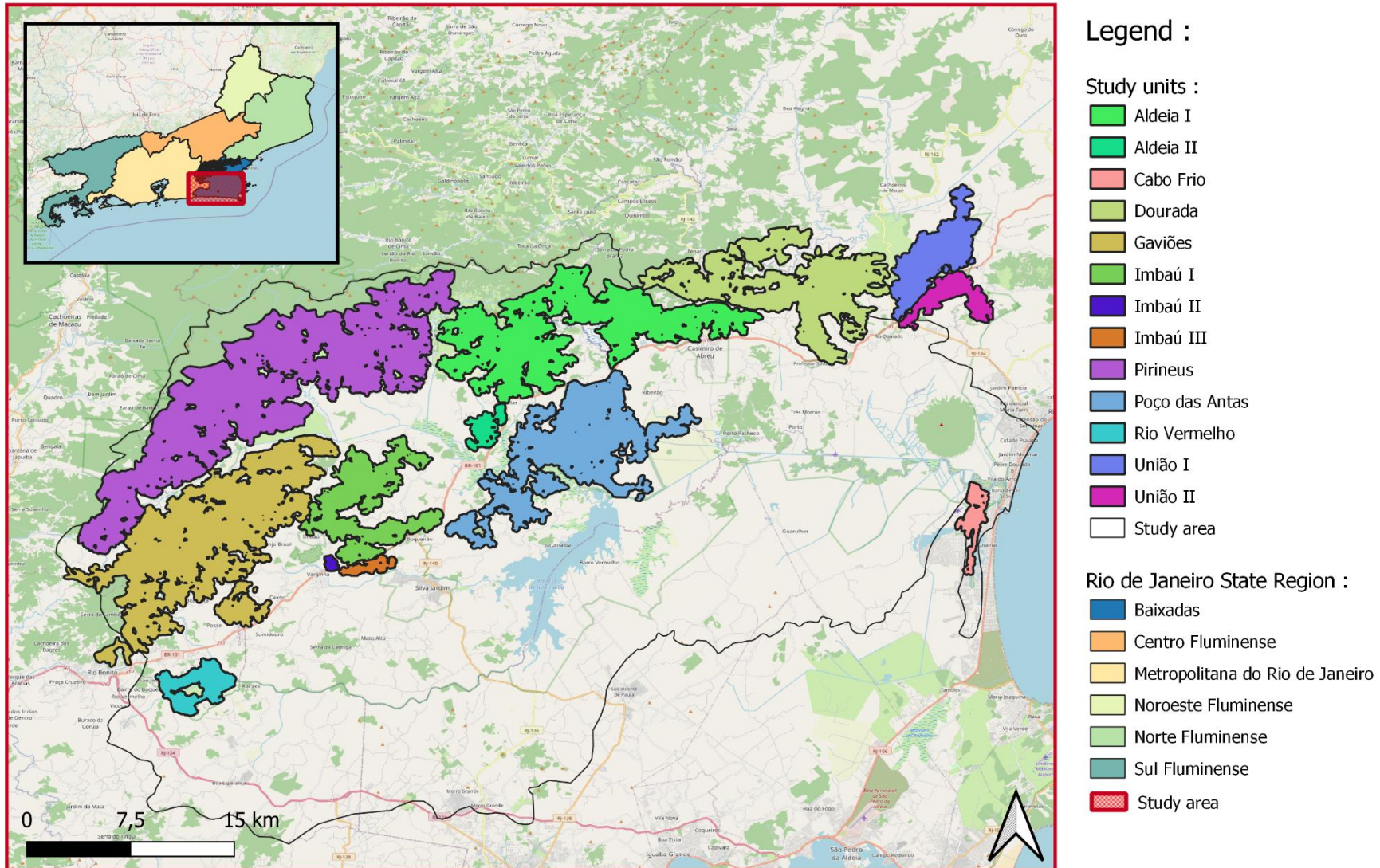


Fig.1: Map of the study area and the various fragments of Atlantic Forest located in the São João river basin in the state of Rio de Janeiro, Brazil. Areas of the same color are connected to each other. This study area is used by the *Associação Mico-Leão-Dourado* for the conservation of the golden lion tamarin (*Leontopithecus rosalia*).

1 **Material and method**

2 **Study site**

3 Our study sites are located in the State of Rio de Janeiro, Brazil, in the São João river basin (**fig.1**).
4 The site is characterized by the Atlantic forest, whose forest ranges from rainforest to semi-
5 deciduous forest, including marginal vegetation (Marques et al., 2011). We worked on 13
6 management units that are being studied by a local NGO (*Associação Mico-Leão-Dourado*) and are
7 priority areas for the protection of the golden lion tamarin, a flagship species used for the
8 conservation of the area. These management units are relatively connected forest fragments,
9 enabling the movement and exchange of primate populations (Moraes et al., 2018). Some of these
10 sites are more isolated than others, such as Aldeia II and Imbau I, while others are completely
11 isolated, such as Rio Vermelho and Cabo Frio (**fig.1**).

12 **Species studied**

13 **Common marmoset (*Callithrix jacchus*), black-brushed marmoset (*Callithrix* 14 *penicillata*) and their hybrids**

15 Although they are now widely distributed across the study site, the *C. penicillata* and *C. jacchus*
16 species are mainly different because of their geographical area of origin (Bouchardet da Fonseca &
17 Lacher, 1984; Malukiewicz et al., 2015; Miranda et al., 2015; Rímoli et al., 2015). The common
18 marmoset is native to the northern states of Brazil while the black-brushed marmoset is native to the
19 southeast states of Brazil. In our study site, marmoset is an inhabitant of the gallery forests, semi-
20 deciduous and deciduous forests of Brazil's Atlantic rainforest (Miranda et al., 2015; Rímoli et al.,
21 2015; Schiel & Souto, 2017). It is also capable of living in gardens, parks, and rural villages where
22 it has sufficient food (Bouchardet da Fonseca & Lacher, 1984; Goulart et al., 2010; Lacher et al.,
23 1984; Teixeira et al., 2015). Environmental factors such as altitude, climate and phytophysiognomy
24 may play a role in determining suitable habitats for them (Norris et al., 2011). Both species are
25 frequently found in secondary forests, where resources such as fruit, insects, small vertebrates and
26 plant exudates are abundant (M. A. F. Silva et al., 2018; Souza-Alves et al., 2022). In fact, these are
27 often degraded environments where the canopy provides better light penetration for feeding
28 (Cerqueira et al., 1998). They also have morphological adaptations that enable them to dig into tree
29 trunks and branches to stimulate the flow of gum, which they eat and which is an important part of
30 their diet (Scanlon et al., 1989; Thompson et al., 2013). This enables them to live in highly seasonal
31 habitats (Miranda et al., 2015). Disturbed habitats and orchards are also used extensively by

32 marmosets, who consume fruit and nectar. *C. jacchus* and *C. penicillata* generally have small home
33 ranges: 1.25 ha to 18.5 ha (Miranda et al., 2015).

34 **Black-horned capuchin (*Sapajus nigritus*)**

35 The black-horned capuchin is found in several states in Southeastern Brazil, and it inhabits a wide
36 range of habitats (Fragaszy & Visalberghi, 2004). It has been considered that its ability to exploit
37 resources not accessible to other primate species is one of the reasons for its wide geographic
38 distribution and widespread existence in many ecosystems (Brown & Zunino, 1990; Izawa &
39 Mizuno, 1977; Mittermeier, 2013; Panger, 1998). The black-horned capuchin lives in the forests of
40 the mountainous zone of Rio de Janeiro state, in a humid climate with high rainfall, but rather low
41 temperatures (Lima, 2016). It can live in deciduous and semi-deciduous forests, but can also inhabit
42 drier tropical forests. It is present in secondary forests, uses pine and eucalyptus plantations and also
43 inhabits fragments close to corn, bananas, manioc and sugarcane fields (Alfaro et al., 2015). They
44 appear to be sensitive to anthropogenic disturbances (Agostini et al., 2015; Aguiar et al., 2011). The
45 home range of *S. nigritus*, spans between 56 and 465.3 hectares (Alfaro et al., 2015).

46 **Collection of covariates**

47 Predictive modeling of animal presence using GLM enables us to study the linear relationship
48 between a dependent variable Y and a set of explanatory variables. This modeling involves locating
49 both the presence and absence points of the primate species considered in this study (dependent
50 variable) (Guisan et al., 2002). The model is then based on layers of environmental variables to
51 study the conditions of presence of a species (explanatory variables). RF models are machine-
52 learning algorithms that combine several decision trees to make predictions about the presence or
53 absence of a species as a function of different environmental variables (Liu et al., 2010). These
54 models are particularly effective at identifying non-linear relationships between these explanatory
55 variables and the presence/absence variable. Species occurrence predictions from GLM and RF are
56 then projected over an entire region of interest based on the mathematical relationships they have
57 identified between the presence/absence variable and ecological conditions (Syphard & Franklin,
58 2009).

59 The following covariates were chosen according to their apparent importance for the distribution of
60 these species, according to the existing literature. All the rasters, i.e. images containing the
61 spatialized information for each variable, were adjusted to a resolution of 1 km², corresponding to
62 the lowest resolution possible given to the data available.

63 **Vegetation and land use data**

64 Data on vegetation type and land cover were downloaded from the Instituto Brasileiro de Geografia
65 e Estatística (*Vegetação 1:250.000 | IBGE, 2021; Land Use and Cover in Brazil | IBGE, 2018,*
66 respectively) for the State of Rio de Janeiro, Brazil.

67 Variables on vegetation cover variable were extracted from NASA's EROS Visible Infrared
68 Imaging Radiometer Suite (eVIIRS) collection, from which we downloaded the available granules
69 from January 2022 to January 2023 covering the State of Rio de Janeiro in our entire study area
70 (U.S. Geological Survey – USGS – Earth Resources Observation And Science – EROS – Center,
71 2021). The NDVI or Normalized Difference Vegetative Index was then averaged. It is characterized
72 by a physical quantity, reflectance, which determines the ability of vegetation to reflect light. This
73 vegetation index is used to measure the rate of plant cover and the vigor of vegetation present on a
74 plot. The higher the values, the denser the vegetation.

75 MOD44B Version 6 Vegetation Continuous Fields, provided the average fractional vegetation
76 cover (VCF) from 2000 to 2021 (DiMiceli et al., 2015). This is the ratio of the area of the vertical
77 projection of green vegetation above the ground to the total area, which captures the horizontal
78 distribution and density of vegetation on the Earth's surface. It is a global representation of surface
79 vegetation cover in the form of gradations of three ground cover components: percentage of tree
80 cover, percentage of non-tree cover and percentage of non-vegetated surface.

81 Finally, to study the impact of human proximity on primate population, human population density
82 data were collected on Nasa search observations (*Population Density | NASA, 2000*). Distance to
83 roads was calculated using OpenStreetMap road network data (Gestich et al., 2023). Only freeways,
84 tertiary roads, secondary roads, primary roads and national roads representing the busiest roads
85 were retained (*Key:Highway – OpenStreetMap Wiki, 2023*). For each presence and absence point,
86 the distance to the nearest road was then calculated (Detogne et al., 2017). Topographical data were
87 not considered in our study. During the field season where we collected data on species
88 presence/absence (see section 'Occurrence point collection'), we followed a local safety protocol
89 and filtered accessible areas by the degree of the slope.

90 **Climate data**

91 Monthly climate data from WorldClim version 2.1 for the period 1970–2000 were used for averages
92 of precipitation (mm), water vapor pressure (kPa) representing humidity, solar irradiance (kJ m⁻²
93 day⁻¹) and temperature (in °C). Annual averages were calculated for each variable (*Historical*
94 *Climate Data – WorldClim 1 Documentation, 2020*).

95 Occurrence point collection

96 This study was conducted in collaboration with the Associação Mico-Leão-Dourado (AMLD), a
97 Brazilian non-governmental organization focused on the monitoring of golden lion tamarins in the
98 São João river basin. We used historical occurrence data spanning from 2013 to 2022, which
99 focused on the observation of golden lion tamarins during transect protocols but that also recorded
100 ad-libitum the presence of other primate species, including marmosets and capuchins. Data on the
101 presence and absence was collected via random sampling protocols using playback transects – a
102 well-established methodology in our field site (Ruiz-Miranda et al., 2019). The selection of
103 transects involved a preliminary filtering process to exclude those that intersected watercourses or
104 major roads and had a slope exceeding 15° (due to safety reasons to field activities). For each
105 quadrat, we selected transects measuring 800 meters in length for fragments larger than 10 km²,
106 while 400-meter-long transects were chosen for fragments smaller than 10 km². This approach
107 ensured that the sampling effort was proportionate to the size of the management unit. Transects
108 were surveyed between 7 a.m. and 3 p.m. At intervals of 200 meters along the transects, we
109 conducted playbacks of 'long calls' vocalizations of golden lion tamarins (Ruiz-Miranda et al.,
110 2019). These vocalizations included eight 'long calls' which are long-distance alarm or
111 coordination calls. Following these playbacks, the presence of the species was monitored for the
112 subsequent five minutes. The purpose of these playbacks was to enhance species detection, as using
113 the tamarin's long call increases the likelihood of detecting this species, as well as marmosets. In
114 cases where no individuals of a species were observed, we recorded the species as absent. In such
115 instances, the playback emission points served as reference. Transects were surveyed until the
116 presence of each species was confirmed or until there were four points of absence in smaller
117 fragments under 10 square kilometers and six points of absence in larger fragments exceeding 10
118 square kilometers (Ruiz-Miranda et al., 2019). Additionally, data available on GBIF from 2000 to
119 2023 were integrated into the dataset (GBIF, 2023).

120 Data processing

121 All presence and absence data were imported into R (*version 4.2.3*). Around each presence point,
122 buffers of the home range size of each species were created to eliminate overlapping points and
123 avoid spatial duplication. In the case of marmosets, given the low resolution of the maps and the
124 high volume of points, a threshold was applied. The number of points within each pixel was
125 reduced to enhance the model's generalization and prevent overfitting, allowing the model to better
126 adapt to new data. In doing so, we retained a maximum of 250 data points per pixel to strike a
127 balance between model performance and the available data quantity, which ensures the creation of a

128 quality model. Through the model's performance on the subset of data and with cross-validation,
129 we subsequently ensured that the model was not overfit. The number of presences and absences was
130 equalized. Thus, 600 presence and absence data were used to build the model. The remaining 120
131 presence/absence points were retained for model testing. For capuchins, due to the limited number
132 of points, all presence points (78) were used to construct the model. At each point of absence and
133 presence, buffer surfaces were again formed. An average of 9.875 hectares is used for setting up
134 buffers for this species. The average of 261 ha is retained for buffer formation. For each buffer
135 zone, the average of each covariate was extracted.

136 **Data analysis**

137 The variables extracted from the global and national database were grouped in a multi-layer raster
138 of 1 km² resolution, then they were subjected to a correlation test (Petrie, 2020) ('cor' function in
139 the 'stats' package). All variables correlated with each other by more than 90% were removed, and
140 a VIF (variance inflation factor) collinearity test was performed to retain only those variables with a
141 VIF of less than 10 (Sureiman & Mangera, 2020; Franke, 2010; Tu et al., 2005; Naimi & Araújo,
142 2016). Finally, principal component analyses (PCA) were used to eliminate other potential
143 correlations between the variables extracted from the buffers. We removed the variables
144 precipitation, which correlated positively with humidity, percentage tree cover, which correlated
145 negatively with percentage non-tree cover, and land use, which correlated positively with vegetation
146 type.

147 The variables thus retained for each species were temperature, humidity, solar irradiance, NDVI:
148 primary productivity, human population density, vegetation type, VCF: percentage of non-
149 vegetation cover, and VCF: percentage of tree cover.

150 **Models**

151 Generalized Linear Models (GLM) and Random Forests (RF) are two commonly used approaches
152 to build species distribution models. GLMs are generally easy to interpret as they provide
153 coefficients for each explanatory variable and assume a linear relationship between the explanatory
154 variables and the presence of a species. However, in some cases, this may be limiting as the
155 relationship can be more complex. RF models can capture complex non-linear relationships
156 between explanatory variables and the response, potentially making them more accurate and robust
157 in certain situations. Consequently, they may exhibit better performance in explaining species
158 presence, but the contribution of different variables to species presence can be challenging to

159 interpret. For these reasons, we will use both types of models, providing complementary insights
160 into our dataset.

161 Generalized linear models and random forest models were then compared in order to most
162 accurately predict the presence or absence of species as a function of different climatic,
163 topographical and vegetation data. Because species presence was recorded on a binary scale
164 (Presence/Absence), we used logistic regression for the GLM models. The data structure involved
165 both quantitative and qualitative variables, written as such: Species presence \sim T°C + humidity +
166 radiation + NDVI + human density + vegetation type + VCF tree + VCF non-vegetation. We
167 applied the Akaike's information criterion (AIC), via a bottom-up approach, to select the model
168 that is best fit for the data. At each step, the 'stepAIC' function selects the variable that will have
169 the highest score once introduced into the model (Ripley et al., 2023). Once the best model has been
170 selected, the model coefficients and confidence intervals were extracted using the 'stats' package.
171 The McFadden R² and root mean square error were calculated (Jackman et al., 2023), and the
172 eigeneffects of the variables were analyzed using ANOVAs and odds ratios (Barnier et al., 2023).

173 RF models are composed of multiple trees. Each tree is trained on a subset of the dataset and
174 produces a result. The results from all decision trees are then combined to provide a final answer.
175 This way, a robust model is built from multiple models. For the RF model, the number of trees and
176 the number of variables to be taken into account for each tree node were adjusted (Cutler & Wiener,
177 2022). The model was built using the following variables: Species presence \sim T°C + humidity +
178 radiation + NDVI + human density + vegetation type + VCF tree + VCF non-vegetation. Similarly,
179 for the GLM and RF models, we calculated the Area Under the Curve (AUC) based on the
180 predicted values (Fielding & Bell, 1997; Pearce & Ferrier, 2000). The AUC serves as an indicator
181 of the overall quality of the model's classification rule for both absences and attendances (Hirzel et
182 al., 2006; Kuhn et al., 2023; Robin et al., 2023). The closer the AUC is to 1, the better the model's
183 performance. We also verified the model fit using the additional marmoset dataset (N = 120). For
184 both marmosets and capuchins, we employed cross-validation to assess model accuracy. All
185 datasets were divided into five groups, and the AUC and root-mean-square error were calculated for
186 each. Additionally, we computed sensitivity, which measures the model's ability to correctly
187 identify true positives; specificity, which measures the model's ability to correctly identify true
188 negatives; and F1-score, which combines accuracy and sensitivity into a single metric to gauge the
189 balance between false positives and false negatives. These indices range from 0 to 1, with values
190 closer to 1 indicating better model performance (Liu et al., 2010). We then calculated the kappa
191 coefficient, which measures the concordance between model predictions and actual values,
192 accounting for the agreement that could be attributed to chance. Kappa values range from -1 to 1,

193 and values closer to 1 indicate better model fit (Hirzel et al., 2006; Liu et al., 2009). Finally, we
194 computed the Matthews Correlation Coefficient (MCC), which evaluates the quality of predictions
195 by considering true positives, true negatives, false positives, and false negatives. This index also
196 ranges from -1 to 1, with a score of 1 indicating excellent model performance. For RF models, we
197 assessed the importance of variables, which reflects the contribution of each variable to reducing
198 the model's prediction error relative to the other variables.

199 The model with the best performance was selected for further study. In order to spatially visualize
200 and map the probability of occurrence of each species over the entire study area, occurrence
201 predictions can be generated (Hijmans et al., 2023; Pebesma, Bivand, Racine, et al., 2023; Pebesma,
202 Bivand, Rowlingson, et al., 2023). These predictions were made using the most parsimonious
203 models. Only the variables that are part of the model with the lowest AIC are used to make
204 predictions. The 'predict' function (Bolar, 2019) was used to geographically project the probability
205 of occurrence of each species over the entire study site (Benavides et al., 2022; Cutler & Wiener,
206 2022; Fox et al., 2023). The standard deviation was also represented at each pixel of the raster
207 containing the spatial information on the probability of presence, to ensure that the variability of
208 this probability was not too great. A Pearson correlation test was then carried out on the presence
209 probabilities of marmosets and capuchins, at each pixel, in order to observe any potential
210 similarities between the habitats of these primates. The maps were created using the QGIS software
211 (*version* 3.28.5).

Table 1A: Models tested using the ‘stepAIC’ bottom-up approach for *Callithrix* (*jacchus*, *penicillata* and their hybrids). The AIC of each model is provided, along with the Δ AIC, which represents the difference between the smallest AIC and the AIC of the models.

Models	AIC	Δ AIC
Presence of <i>Callithrix</i> ~ type of vegetation + water vapour pressure + percentage of non-vegetation cover + percentage of tree cover	667.33	/
Presence of <i>Callithrix</i> ~ type of vegetation + pressure + water vapour pressure + percentage of non-vegetation cover	681.05	13.72
Presence of <i>Callithrix</i> ~ type of vegetation + water vapour pressure	686.73	19.4
Presence of <i>Callithrix</i> ~ type of vegetation	760.73	93.4
Presence of <i>Callithrix</i> ~ 1	833.78	166.45

Table 1B: Models tested using the ‘stepAIC’ bottom-up approach for *S. nigrurus*. The AIC of each model is provided, along with the Δ AIC, which represents the difference between the smallest AIC and the AIC of the models.

Models	AIC	Δ AIC
Presence of <i>Sapajus</i> ~ distance from roads + NDVI	202.25	/
Presence of <i>Sapajus</i> ~ distance from roads	202.5	0.25
Presence of <i>Sapajus</i> ~ 1	218.26	16.01

Table 2A: Comparison of the performance indices of the GLM and RF models for *Callithrix* (*jacchus*, *penicillata* and their hybrids). The results are those obtained under the second dataset. The AUC was calculated through cross-validation.

Performance index	GLM model	RF model
AUC	0.83	0.97
MCC	0.55	0.85
Kappa	0.55	0.85
Accuracy	0.78	0.93
Sensitivity	0.88	0.97
Specificity	0.68	0.88
F1score	0.80	0.93
R ² of McFadden	0.74	/

Table 2B: Comparison of the performance indices of the GLM and RF models for *Sapajus nigrurus*. The AUC was calculated through cross-validation.

Performance index	GLM model	RF model
AUC	0.72	1
MCC	0.31	1
Kappa	0.31	1
Accuracy	0.65	1
Sensitivity	0.60	1
Specificity	0.71	0.99
F1score	0.64	0.99

R² of McFadden	0.92	/
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Connectivity analyses

Once the prediction maps for each species had been obtained, the matrices of resistance to species movement was created using graph theory, which provides a representation of the structure and functionality of a landscape. The graph is made up of nodes. These nodes, i.e. the possible habitats of the species, has links through which the species can disperse. The links represent values of the resistance matrix, which is made up of habitats that are permeable to species movement, but in which they cannot subsist (Y.-H. Wang et al., 2008). These maps are derived from the spatial distribution models (Duflot et al., 2018) after a linear transformation (Keeley et al., 2021; Zeller et al., 2018; Ziółkowska et al., 2012). The probability of presence of a species at each point on the map ranged from 0 to 1, and these values were rescaled from 0 to 100. Favorable habitats with a high probability of species presence offer low resistance to movement, while habitats with a low probability offer high resistance to movement (Beier et al., 2008; Zeller et al., 2018). It is assumed that such resistance is linked to the suitability of the habitat for the species. To make the model more accurate, we added the presence and location of roads to the resistance maps. Given the low resolution of the raster, a sorting was carried out to increase the resistance only of roads presenting a real danger to primate movements, i.e. freeways, tertiary roads, secondary roads, primary roads and national roads. When a road crossed a pixel of the movement matrix, the resistance value was increased to the maximum, and when it partially cut through a habitat, it was represented by a white line on the maps.

Potential habitats for the species were defined as those where individuals were already present. This was determined by adding surfaces with a probability of presence greater than 0.5 on Graphab (*version 2.8.5*) (Clauzel et al., 2022). This threshold was selected to retain only habitats classified as favorable. The links between each node were then established, considering the resistance matrix and the distance between each habitat. The ‘complete’ link topology was employed to consider all links between habitats, while removing links crossing spots. A study on the reintroduction of *Callithrix melanura*, a marmoset of the genus *Mico*, indicated that this species could travel more than 7 km from its release point before settling in its living area (Marques et al., 2011). This value was used as reference in our models as, to our knowledge, limited work has been done about the dispersal distance of the two marmosets species studied here. Nevertheless, these species are highly adaptable. So, to address the scenario in which they are most invasive, a generous dispersal distance threshold of 7 km was employed, using the cost-to-distance conversion tool. Least-cost paths with a

maximum distance corresponding to the marmosets' daily movements were also plotted (mean = 1200 m)

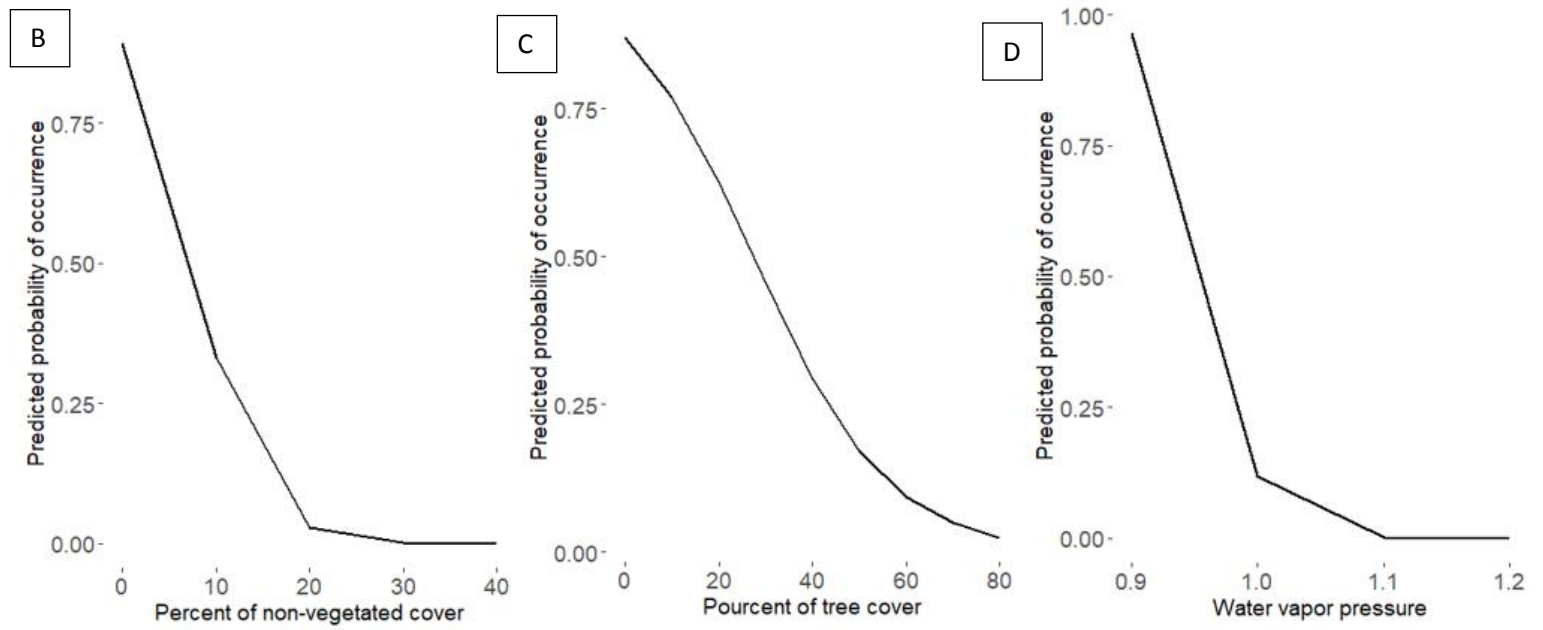
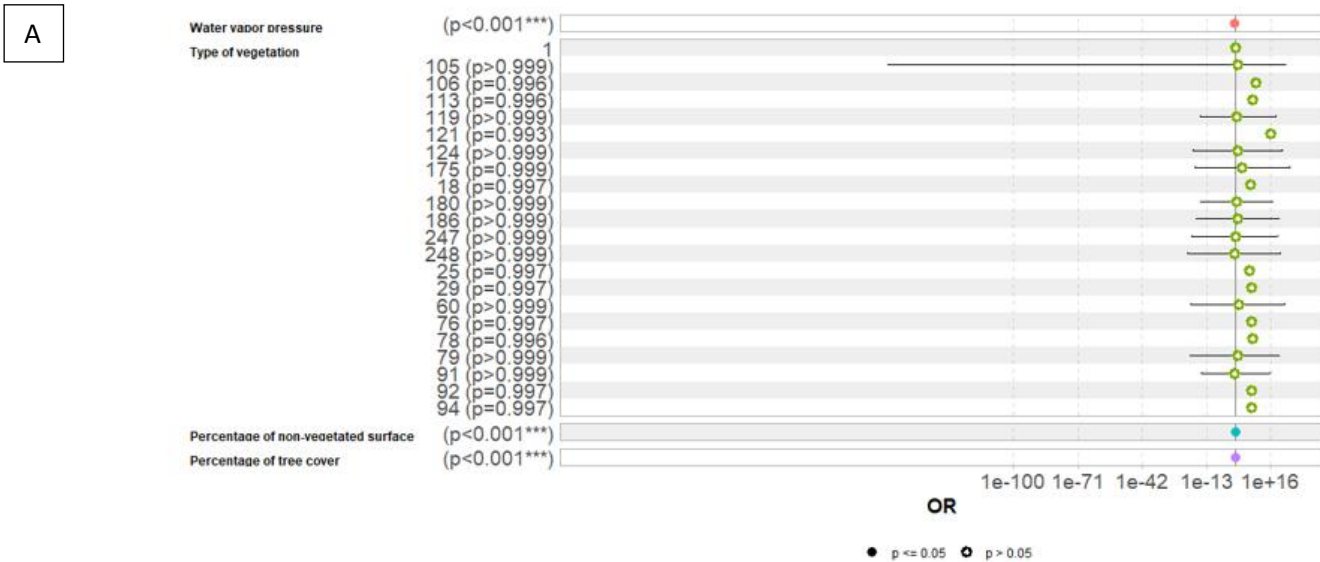


Fig.2: Odds ratios for each model variable: vegetation type, percentage of tree cover, non-vegetated area and humidity (A); and probabilities of species presence predicted by the model when there is an increase in the percentage of non-vegetated cover (B), tree cover (C) and water vapour pressure (D).

(Cawthon Lang, 2005; B. Raboy et al., 2008), along with paths with a cumulative cost of less than 90 to avoid road crossings. For capuchins, links with a length of less than 4500 m, corresponding to the maximum daily distance observed in *Sapajus*, were generated (Mittermeier et al., 2013). Metrics were then calculated: the probability of connectivity, representing the likelihood that two individuals drawn at random from the study area would manage to make contact; the diameter, which measures the maximum cost between two habitat patches in the study area; and the flux, which is the sum of habitat capacities (surface area) different from the habitat patch under consideration and weighted according to their minimum distance from this patch. This sum is an indicator of potential dispersal from, or conversely to, the habitat patch under consideration; the sum of flows, which is the sum of potential dispersal from all habitat patches; Harary index, which measures the sum of the inverse of the number of links separating all habitat pairs; intermediate centrality, which is the sum of the shortest paths passing through the focal spot, each path being weighted by the product of the capacities of the connected (surface) patches and their probability of interaction; proximity centrality, which is the average cumulative cost from one habitat spot to all the others accessible to it; node degree, which represents the number of neighboring nodes. To calculate these metrics, a dispersion probability between two habitat patches of maximum distance of 7 km for marmosets (Marques et al., 2011) and 4.5 km for capuchins (Alfaro et al., 2015) of 0.05 was used; and a beta value of 1, meaning that patch capacity plays a linear role in the weighting (Clauzel et al., 2022).

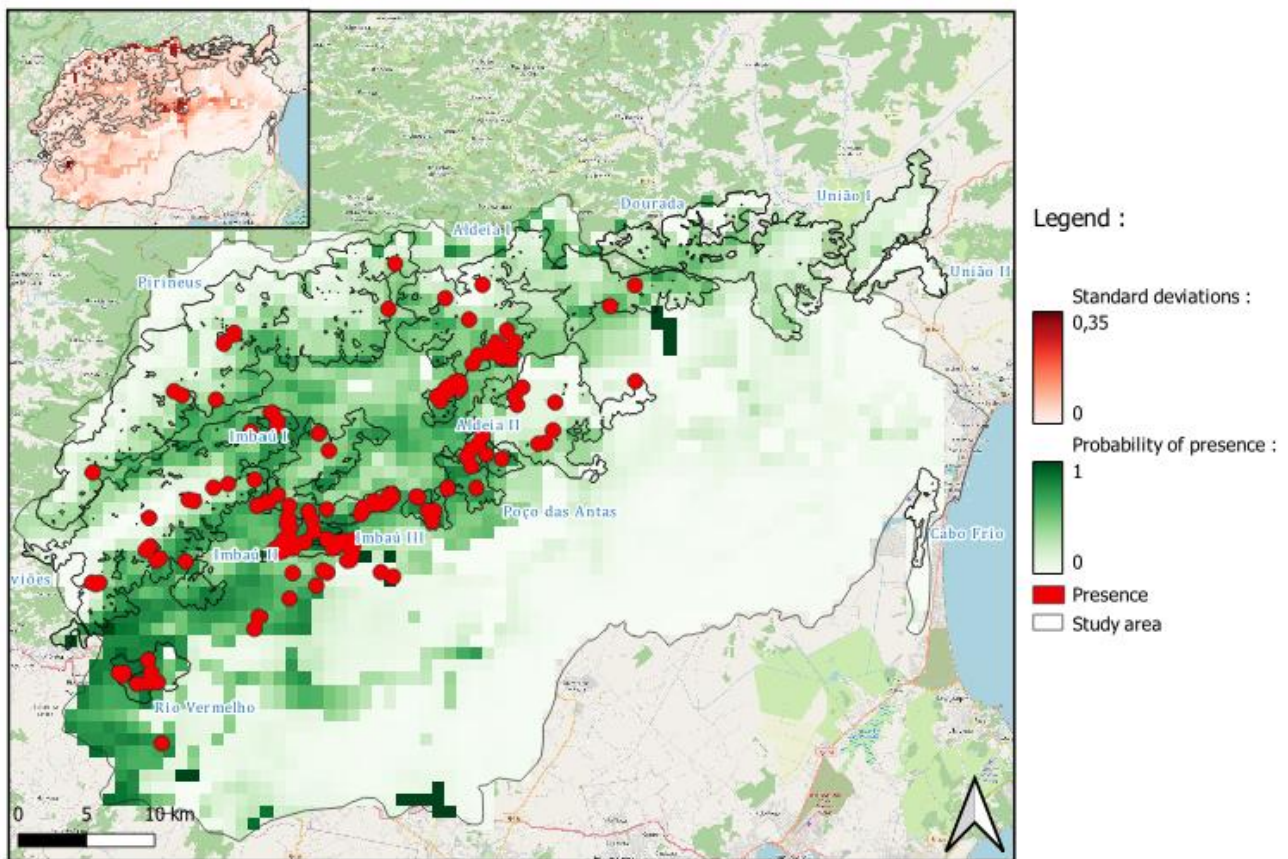
Results

Common marmoset (*Callithrix jacchus*) and black-brushed marmoset (*Callithrix penicillata*) and their hybrids

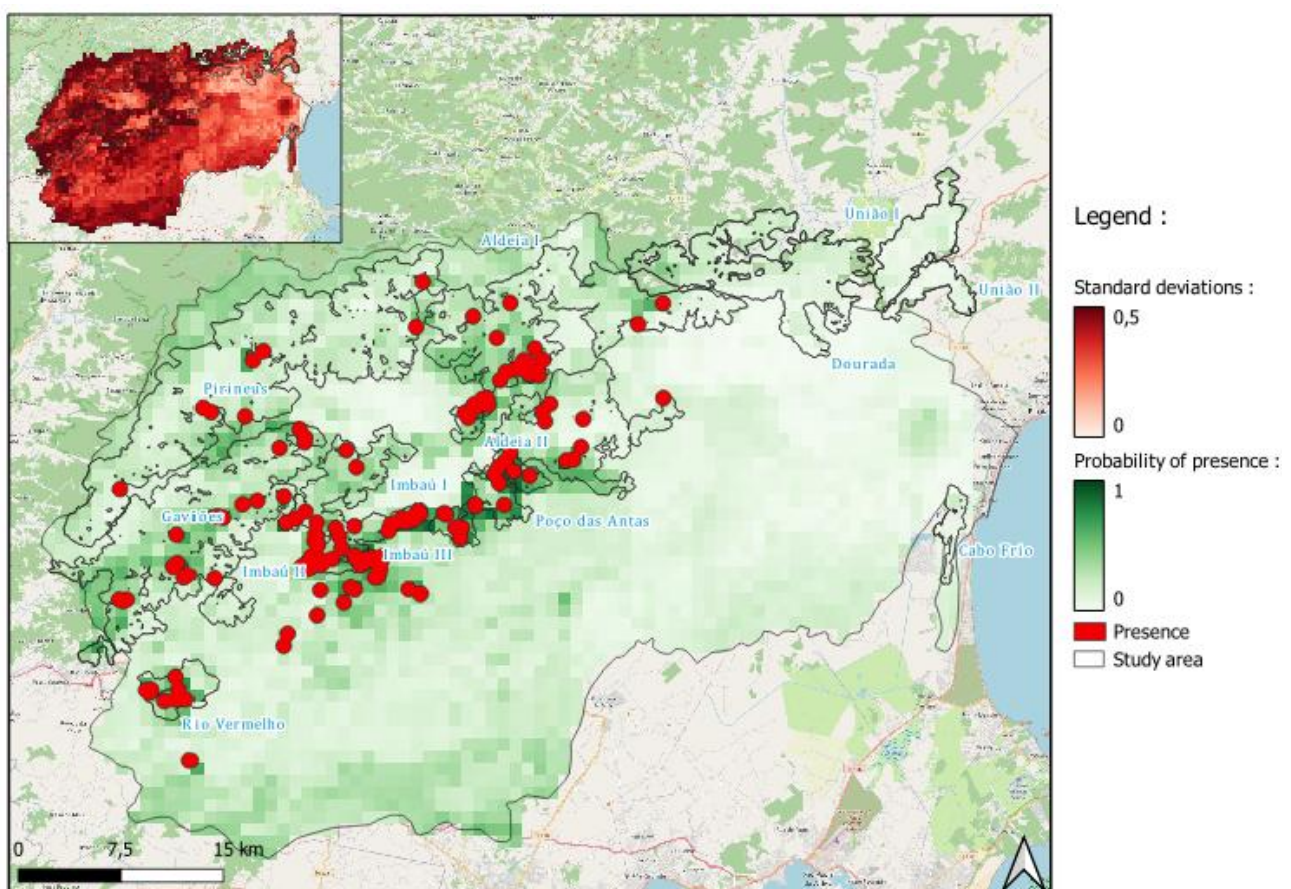
Model comparison

The GLM model with the lowest AIC (667.3) includes both the percentage of non-vegetation cover (p-value < 0.001) and tree cover (p-value < 0.001), vegetation type and water vapour pressure (p-value < 0.001) (**Tab.1.A**). The model indicates that if the percentage of tree cover increases, then the probability of encountering a marmoset decreases (OR = 0.93) (**fig.2A**, **fig.2C**). If the percentage of non-vegetation cover increases, the probability of encountering a marmoset decreases (OR = 0.76) (**fig.2B**). When humidity increases, the probability of *Callithrix* presence decreases (OR = 0.59) (**fig.2C**). The model indicates the importance of vegetation type in predicting the presence of marmosets, but indicate a non-significant positive association between the vegetation

type and the presence of marmosets (**fig.2**). Even if its effect is not significant, this variable can nevertheless



A: GLM model: *Callithrix* presence ~ type of vegetation + percentage of wooded area + percentage of non-vegetated area + water vapour.



B: RF model: *Callithrix* presence ~ vegetation type + percentage of tree-cover area + percentage of non-vegetated area + water vapour pressure + solar radiation + temperature + NDVI + human population density + distance to roads.

Fig.3: Map of predicted presence probabilities with associated standard deviations of the two *Callithrix* species and their hybrids, in the São João river basin in the state of Rio de Janeiro, Brazil. These maps were produced by the GLM model (A) and RF model (B).

improve the quality of the model and its fit to the data, as well as its predictive capacity. The exact proportion of variance explained by each variable is 16.6% for the type of vegetation (ANOVA; p-value < 0.001), 6.4% for water vapour pressure (ANOVA; p-value < 0.001), 1.9% for the percentage of wooded area (ANOVA; p-value < 0.001) and 0.9% for the percentage of non-vegetated area (ANOVA; p-value < 0.01). Finally, chi2 indicates that there is a significant difference between the occupancy of the different types of vegetation (see supplementary material). Today, marmosets are more present in areas dominated by human activity than in areas with natural vegetation (Pearson's Chi-squared test, p-value < 0.001, Haberman residues > |1.96|).

The estimated OOB error is 15.5%. The RF model shows that the most influential variable for prediction is water vapour pressure (72), followed by the percentage of non-vegetation cover (34.31), distance to roads (31.69), solar radiation (31.59), vegetation type (30.83), human population density (27), percentage of tree cover (25.97), temperature (25.34) and finally NDVI (18.17).

The best GLM model performed less well than the RF models (**Tab.2A**). Indeed, the AUC, accuracy, the MCC, kappa, sensitivity, specificity and F1score values are lower than those of the RF models. Given the better performance of the RF model, we retain it for the remainder of the connectivity analysis.

Presence prediction map

We observed that the species is present in all the fragments of the study area under consideration, with the exception of União I, União II, Dourada and Cabo Frio. The model's predictions produce a map (**Fig. 3B**) with presence probabilities over the entire study area ranging from 0 to 1 and standard deviations from 0 to 0.5 (**Fig. 3B**). The highest probability of presence is concentrated in the southern fragments: Imbau II (mean probability = 0.99), Imbau III (mean probability = 0.75), Aldeia II (mean probability = 0.50) and on the edges of the forest fragments. A low probability of presence is found within the fragments of União II (mean probability = 0.07), União I (mean probability = 0.10) and Cabo Frio (mean probability = 0.10), where the probability of marmosets being present is practically zero.

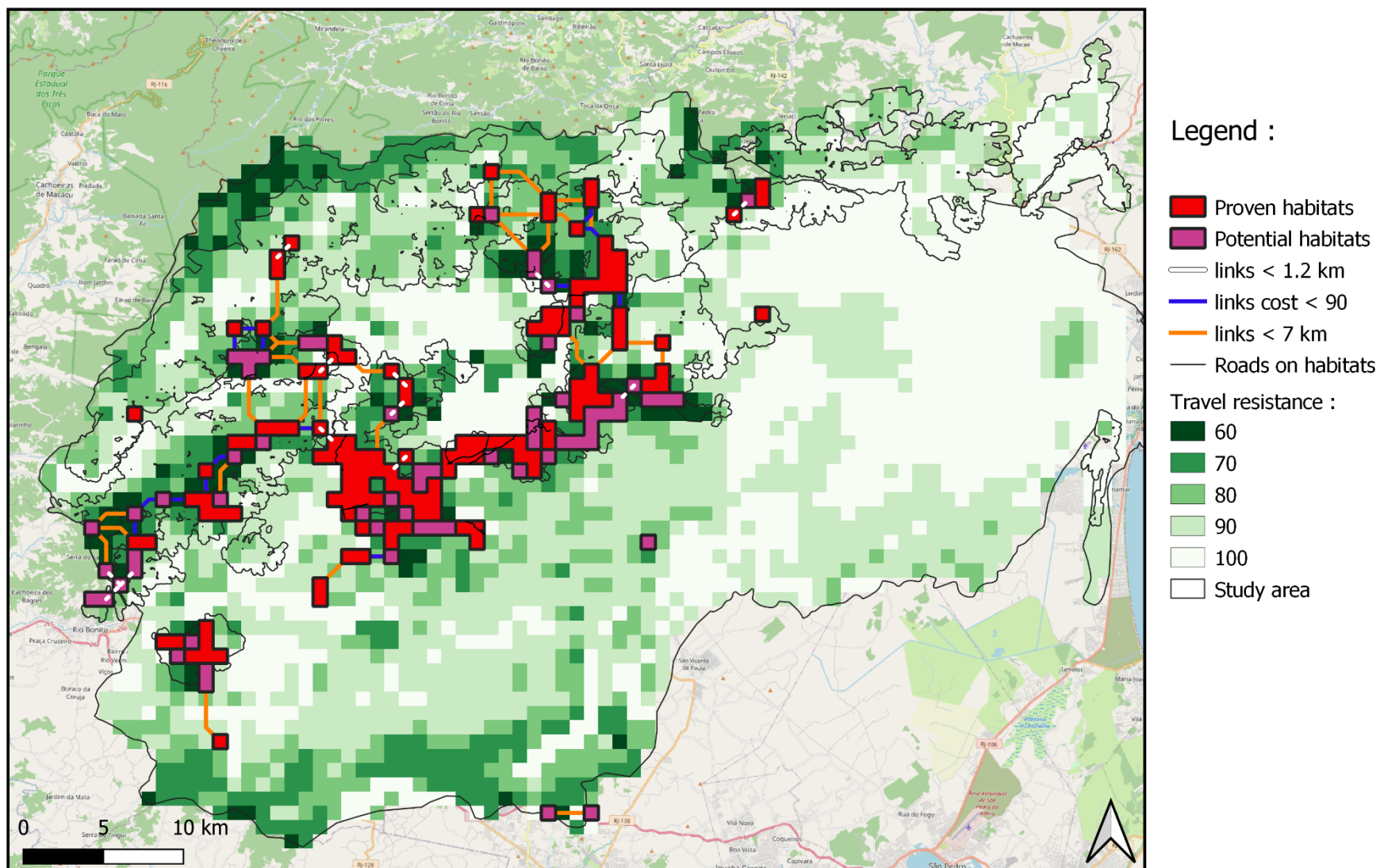


Fig.4: Map of habitat connectivity for the two *Callithrix* species (*jacchus*, *penicillata* and their hybrids) in the São João river basin in the state of Rio de Janeiro, Brazil. The orange links represent least-cost paths of less than 7 km, the blue overlapping links are paths of less than 90 that do not cross roads and the white dotted links are least-cost paths of less than 1200 m (daily dispersal distance). The thin white solid lines represent the passage of primary, secondary and tertiary roads and motorways through habitats. Areas where the species is present are shown in red, and favourable habitats, i.e. those with a probability of hosting the species of greater than 0.5, are shown in purple. The habitat patches represent the surface area of the habitat available at the scale of the map.

Habitat connectivity

The connectivity map shows that the total surface area of marmoset habitats, at the 0.5 probability of presence threshold, is 15 203.48 ha. The surface area currently inhabited by the species is 10 188.72 ha, while the total surface area of habitats favourable to the species, yet to be colonized, is 5 014.76 ha (**fig.4**). In the northern forest fragments, the habitats have a smaller surface area than in the southern fragments. The habitats are spread throughout all the forest fragments except Uniao I/II, Dourada and Cabo Frio, which remain unsuitable territories for the species according to the model. Only patches 14, 25 and 36 are completely disconnected from other habitat patches for a dispersal distance of 7 km (**fig.5A**). There are seven components, i.e. seven unconnected networks, three of which consist of a single habitat patch.

The probability of connectivity, i.e. that two individuals will cross paths within the network, is 0.0006. The degree of node varies from 0 to 7. The most connected habitat patches are found in the southern fragments: Aldeia I (57), Gavioes (9) and Imbau I (22) (**fig.5A**). The average cost between habitat patches varies from 0 to 800.79 (**fig.5B**). The maximum distance between two connected patches is 4.3 km. The maximum cumulative cost between two directly connected patches is 290.

Intermediate centrality varies from a transit weight of $2.56e+11$ to $7.03e+15$ for links, and from 0 to $6.41e+14$ for nodes (**fig.5C**). Patch 22, which has the largest surface area in the network, helps to increase the intermediate centrality of its neighbouring patches (28, 27), which are themselves highly connected in the network (**fig.5C**). The links starting from Rio Vermelho, crossing patches 27, 26, 22, 9 and 23 and going up to Aldeia I, therefore have a high intermediate centrality (**fig.5C**).

The Harary index is 195.31. The flux varies from 0 to $8.62e+7$ (**fig.5D**) and the sum of the fluxes is $1.12e+9$. Because of the larger surface area of the habitats in Rio Vermelho and Imbau, and the short distance between them and neighbouring habitats, the southern part of the network benefits from a large flux, particularly for habitats 23, 28 and 29 (**fig. 5D**).

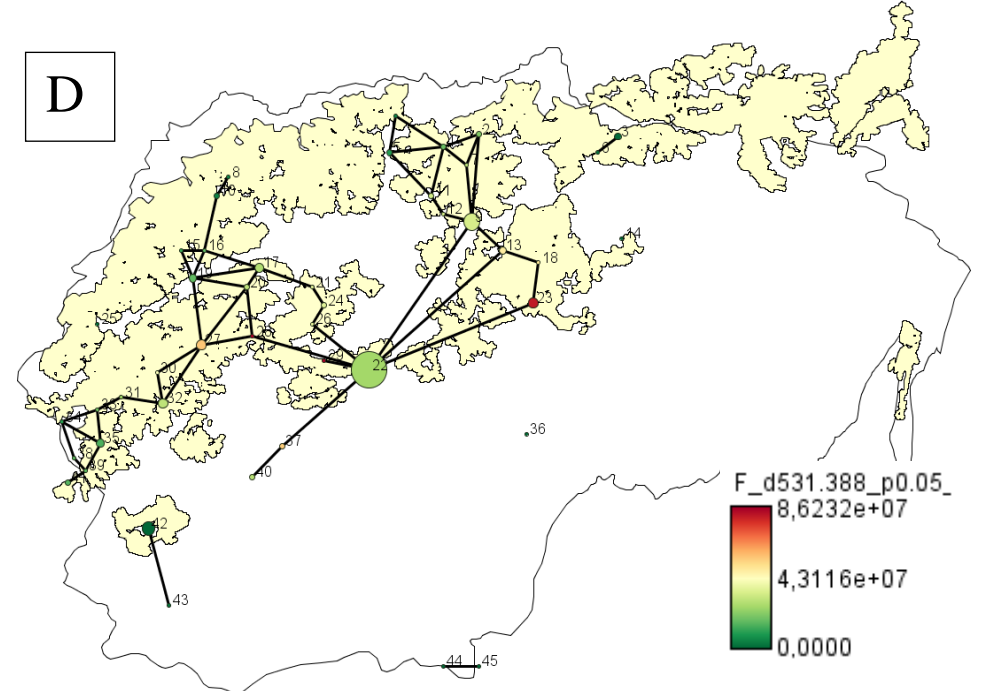
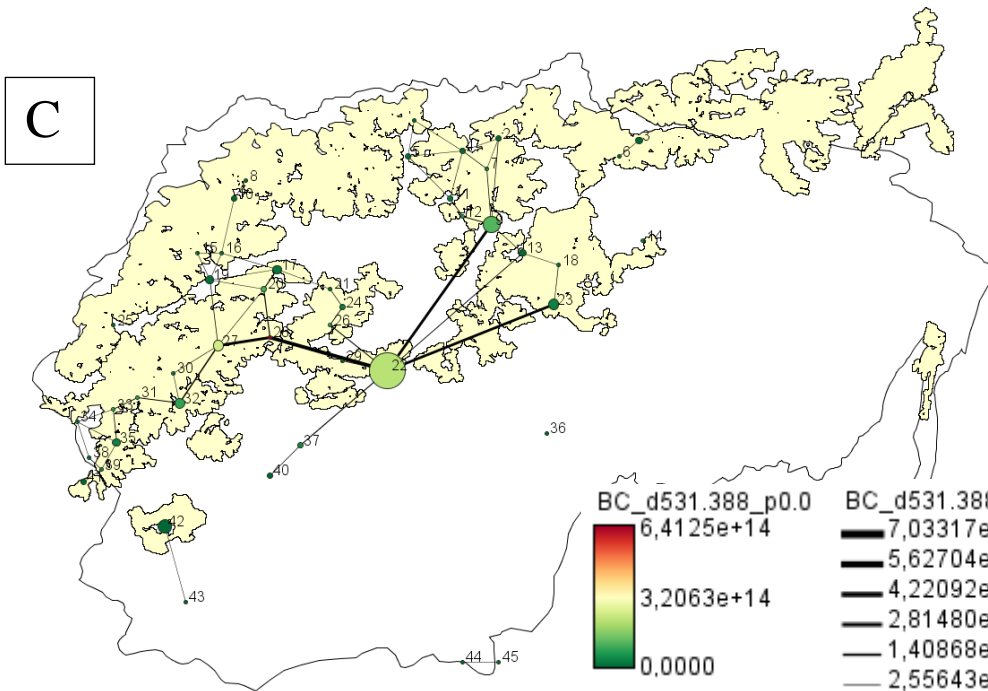
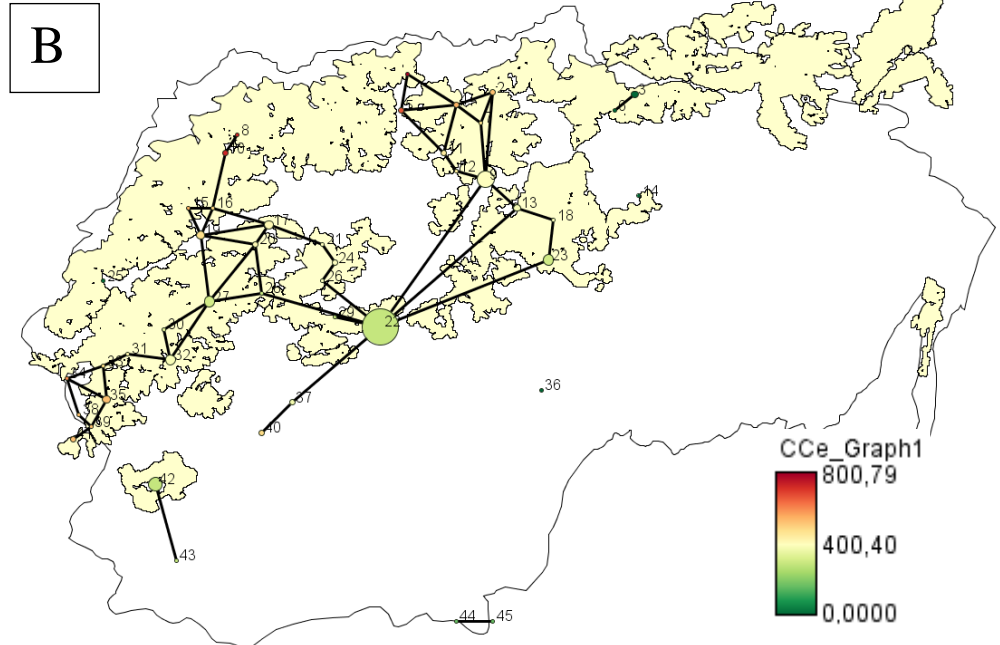
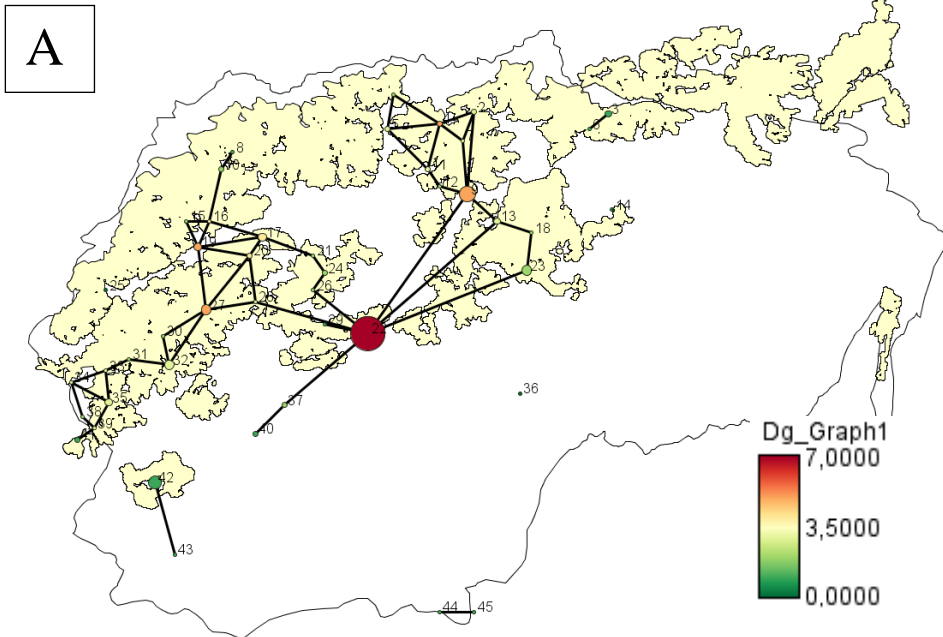


Fig.5: Simplified view of the degree of nodes (A), the proximity centrality (B), the intermediate centrality (C) and the flow of marmoset habitats (D). The potential transit weights of the intermediate centrality are indicated proportionally by the thickness of the links and the colour of the nodes (C). The values of the flows, proximity centrality and degree are indicated by the colour of the nodes. The numbers represent the patches identifiers. The diameter of the circles represents the surface area of the habitat patch (and therefore its carrying capacity).

Black-horned Capuchin (*Sapajus nigritus*)

Distribution model

The most parsimonious GLM model, with the lowest AIC value of 202,25, incorporated the variables of distance to roads (p-value < 0.001) and NDVI (**Tab.1.B**). Since the AIC values of the models ‘Presence of *Sapajus* ~ distance from roads + NDVI’ and ‘Presence of *Sapajus* ~ distance from roads’, are very close ($\Delta AIC < 7$), we can consider them equivalent and we choose the most parsimonious model, meaning the one with the fewest variables, as the best model. The Chi2 test indicates that there is a significant difference between the occupancy of the different vegetation types (see supplementary material). Capuchins are more present in areas with natural vegetation than in areas with dominant anthropogenic areas (Pearson’s Chi-squared test, p-value > 0.001, Haberman’s adjusted residuals > |1.96|). The model coefficients and odds ratios (**fig.6A**) indicate that as distance from roads increases, the probability of the species’ presence increases (OR = 1.00) (**fig.6B**). The exact proportion of variance explained by each variable is 8.2% for distance to roads (ANOVA; p-value < 0.001). McFadden’s R^2 was 0.92.

The estimated OOB error is 35.9%. The variable distance to roads is the most influential in the random forest model (21.29). This was followed by solar irradiance (8.99), vegetation type (8.41), human population density (7.73), NDVI, the percentage of non-vegetated area (5.82) and, finally, the percentage of wooded area (5.62).

Because all the indexes indicate that the RF model performs better than the GLM models (**Tab.2.B**), it was this model selected for the following connectivity analyses.

Presence prediction map

The species is absent from the Gavioes, Imbau II/III, Rio Vermelho and Dourada fragments (**fig.7**). The probabilities of presence predicted by the model over the entire study area range from 0 to 1 and the standard deviations from 0 to 0.5 (**fig.7B**).

The highest probabilities of presence are concentrated mainly within the forest fragments, in Poço das Antas (mean of probabilities = 0.61), União I (mean of probabilities = 0.46), União II (mean of probabilities = 0.43). There is a lower probability of presence in Imbau II (mean probability = 0.15), Rio Vermelho (mean probability = 0.20) and, in Cabo Frio (close to 0), even though there are several records of presence there, because in this last forest fragment, presence probability predictions could not be generated (**fig.7**). However, it should be noted that the standard deviation is also highest in this same zone. As we move away from the forest fragments towards the south of the basin, we also see a higher probability of presence. This increase in the probability of the species’

presence in these parts of the basin is correlated with a decrease in the standard deviations in these forest-free zones. The Pearson correlation test showed a negative correlation between the potential habitats predicted by the RF models between marmosets and capuchins (Pearson correlation, p-value < 0.001, cor = -0.22).

Habitat connectivity

The total surface area of *S. nigritus* habitats is 74 318.67 ha. The surface area currently inhabited by the species is 8 762 ha, while the total surface area of habitats favourable to the species, yet to be colonized, is 65 556.67 ha (**fig.8**). The habitats are spread over all the forest fragments except ImbauII/III, which remain unsuitable territories for the species according to the model. There are 9 different components.

The probability of connectivity is 0.025. The degree of node varies from 0 to 10 (**fig.9.A**). The average cost between habitat patches varies from 0 to 725.39 (**fig.9.B**) and the largest cumulative cost between two directly connected habitats is 241. The maximum distance between two connected patches is 4.3 km, but the smallest distance frequently found is 1.27 km.

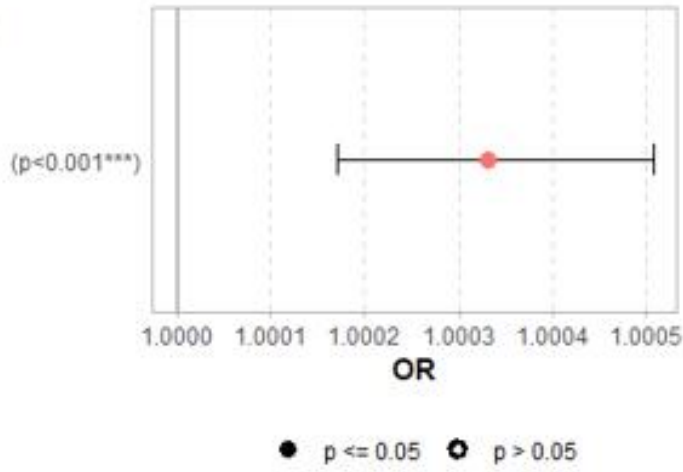
As these indices show, the most connected habitat patches are found in and around Poço das Antas (25) and Dourada (9). These habitats form the largest network in the study area. The habitats at the southern ends of the basin, on the other hand, are much more isolated and form much less connected networks (61, 64, 65, 68, 70), as does Cabo Frio (63) (**fig.9**).

Intermediate centrality varies from a transit of 3.93e+11 to 2.44e+16 for links, and from 0 to 2.36e+16 for nodes (**fig.9.C**). As this index shows, the habitat on and around the Poço das Antas fragment influences the communication of the patches in the surrounding network. It is particularly noteworthy because of its very large surface area, which offers interesting migration opportunities for individuals found in other neighbouring patches (35, 29) (**fig.9.C**).

These patches therefore have a large flow, as do the patches located at Dourada, which are directly connected to patch 25 at Poço das Antas. Over the whole area, the flux varies from 0 to 5.01e+8 (**fig.9.D**) and the sum of the fluxes is 1.61e+10. The Harary index is 393.68, which confirms that this graph is much more complex than that of the marmosets when we consider the connections and the number of nodes.

A

Distance to roads



B

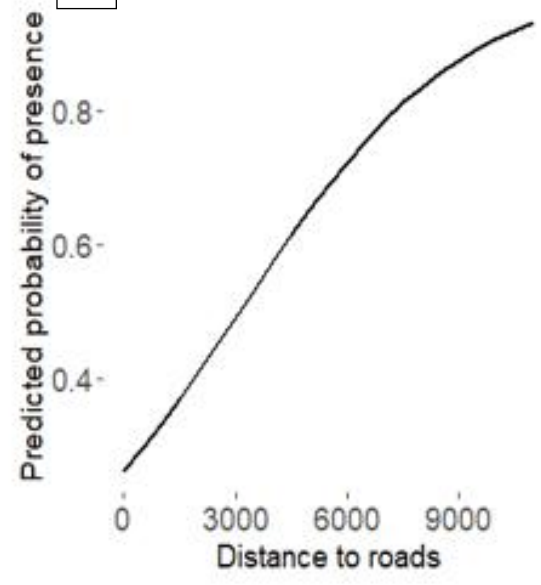
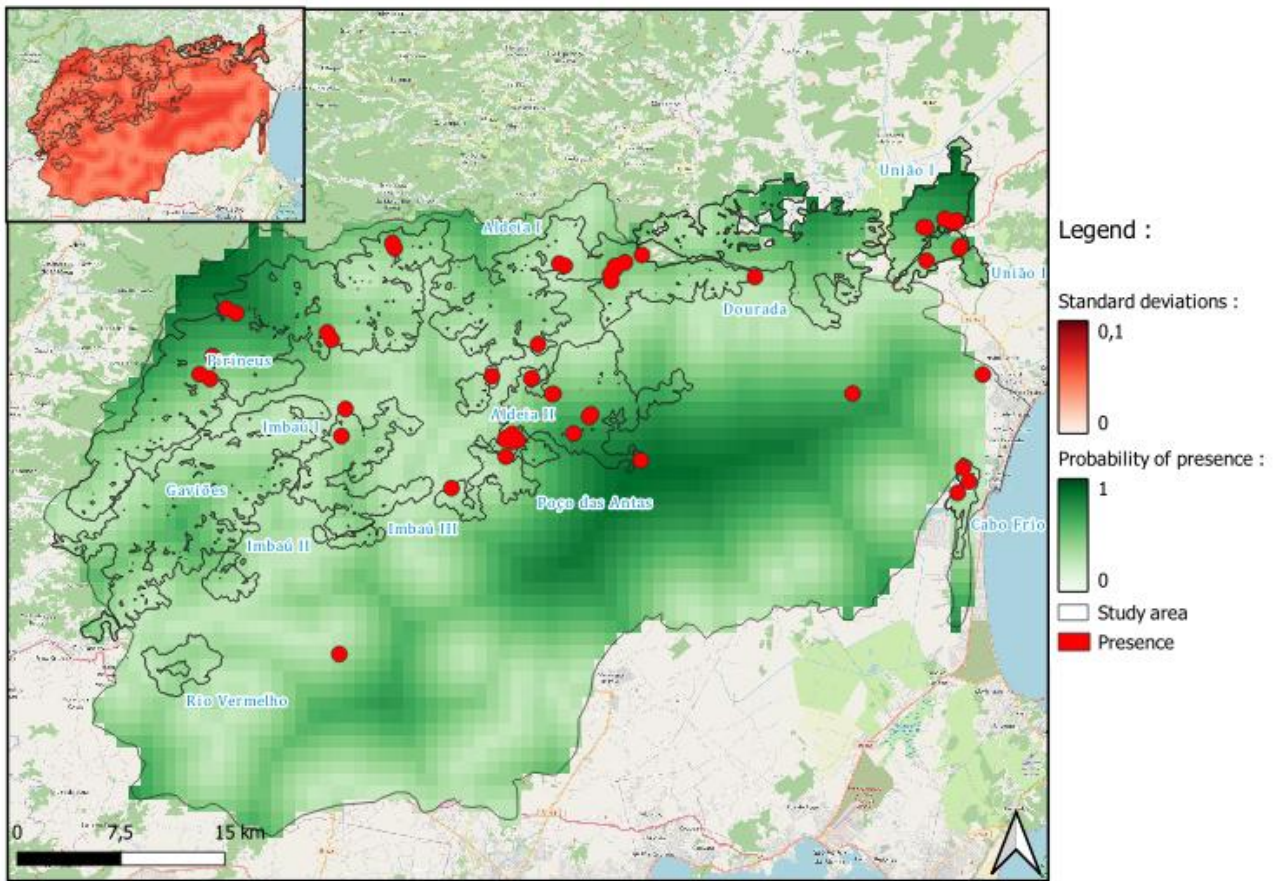
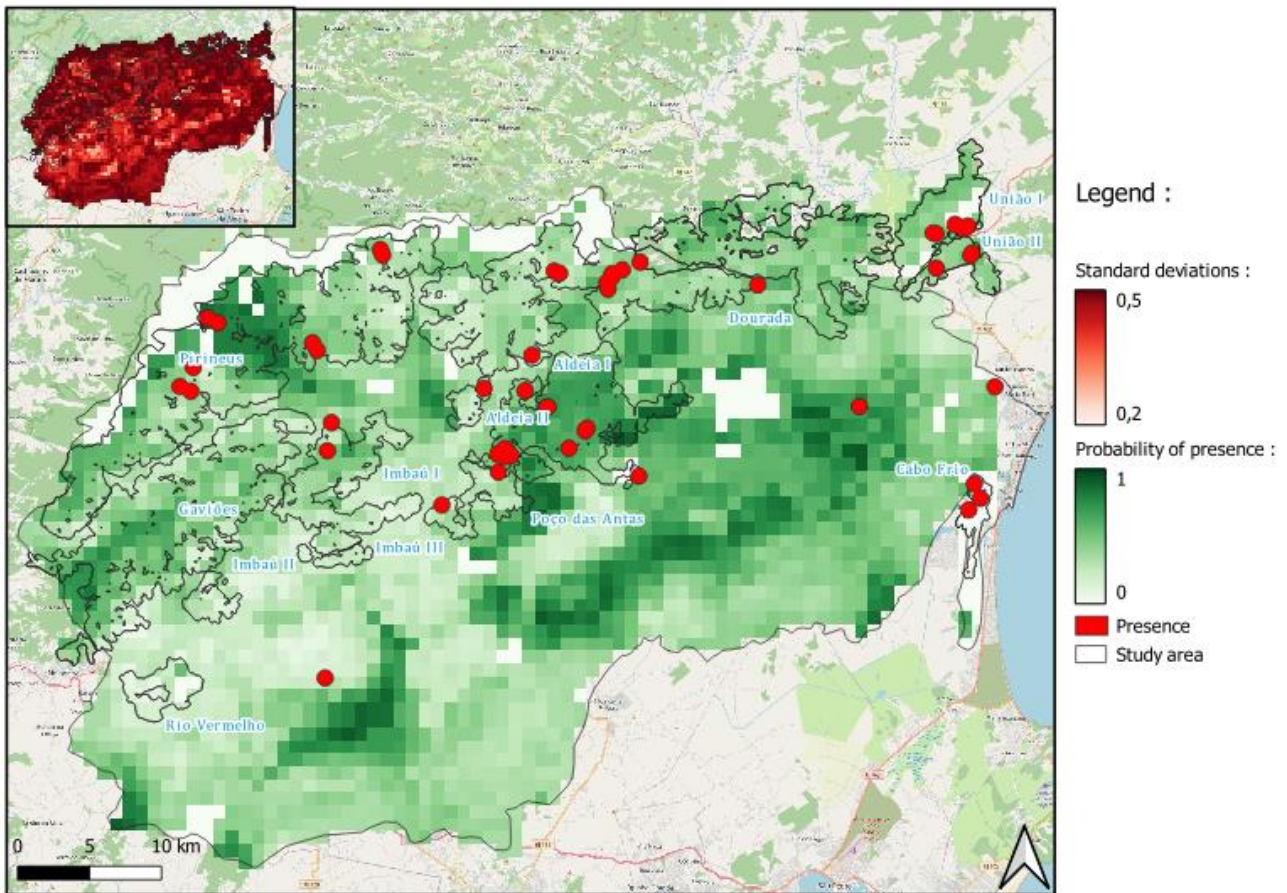


Fig.6: Odds ratios for each variable in the GLM model: distance to roads, NDVI (A); and probabilities of presence of the species predicted by the model when there is an increase in distance to roads (B).



A: GLM model: *S. nigritus* presence ~ distance to roads.



B: RF model: *S. nigritus* presence ~ vegetation type + percentage of tree-cover area + percentage of non-vegetated area + water vapour pressure + solar radiation + temperature + NDVI + human population density + distance to roads.

Fig.7: Map of predicted probabilities of presence with associated standard deviations of *S. nigritus*, in the São João river basin in the state of Rio de Janeiro, Brazil. These maps were produced by the GLM model (A) and RF model (B).

Discussion

Primates distribution

This study aims to identify ecological factors affecting the distribution and prospects of marmosets and capuchins, two primate species encountering contrasting management and conservation challenges in SE Brazil. While GLM models reveal linear relationships between primate presence and specific environmental conditions, the superior performance of RF models suggests that certain connections between environmental variables and primate presence are more intricate than linear causality. For instance, in the case of marmosets, RF models rank the distance from roads as the 3rd most important variable, with vegetation type coming in 5th place after solar radiation. It's worth noting that RF models don't readily allow for the interpretation of the individual influence of each characteristic on the presence variable. Consequently, this part of the discussion primarily pertains to the interpretation of relationships between variables obtained through GLM models.

The presence, condition, and type of vegetation emerge as critical determinants in the choice of habitat for these primates. This is particularly pronounced for marmosets, which have exhibited their adaptability by increasingly inhabiting anthropized areas. These marmoset species now demonstrate their capacity to thrive in various habitats. Presently, they can be found not only in forests but predominantly in anthropized environments near plantations and livestock pastures. Hence, their presence extends beyond the boundaries of the Atlantic forest, encompassing regions with more significant urban or anthropogenic influences.

Additionally, GLM models underscore that the presence of both *Callithrix* species is influenced by a single climatic parameter: water vapor pressure. The reduction in the likelihood of their presence with increasing water vapor pressure can be attributed to the absence of the forest. Notably, the Atlantic Forest is characterized by high moisture levels. As these species move towards the edges of forest fragments and urban areas, this humidity decrease. It has also been shown that during the rainy season, when humidity is at its highest, resting time is increased (Passamani, 1998), that humidity is correlated with a cessation of activity in *C. jacchus* (Suchi & Rothe, 1999) and that an increase in this variable would help explain stereotyped behavior in certain captive primates (de la Barrera Cardozo et al., 2021).

What's more, although marmosets' presence decreases when tree cover is high, the species still seems to need a minimum of vegetation to persist, since its presence decreases when non-vegetation cover

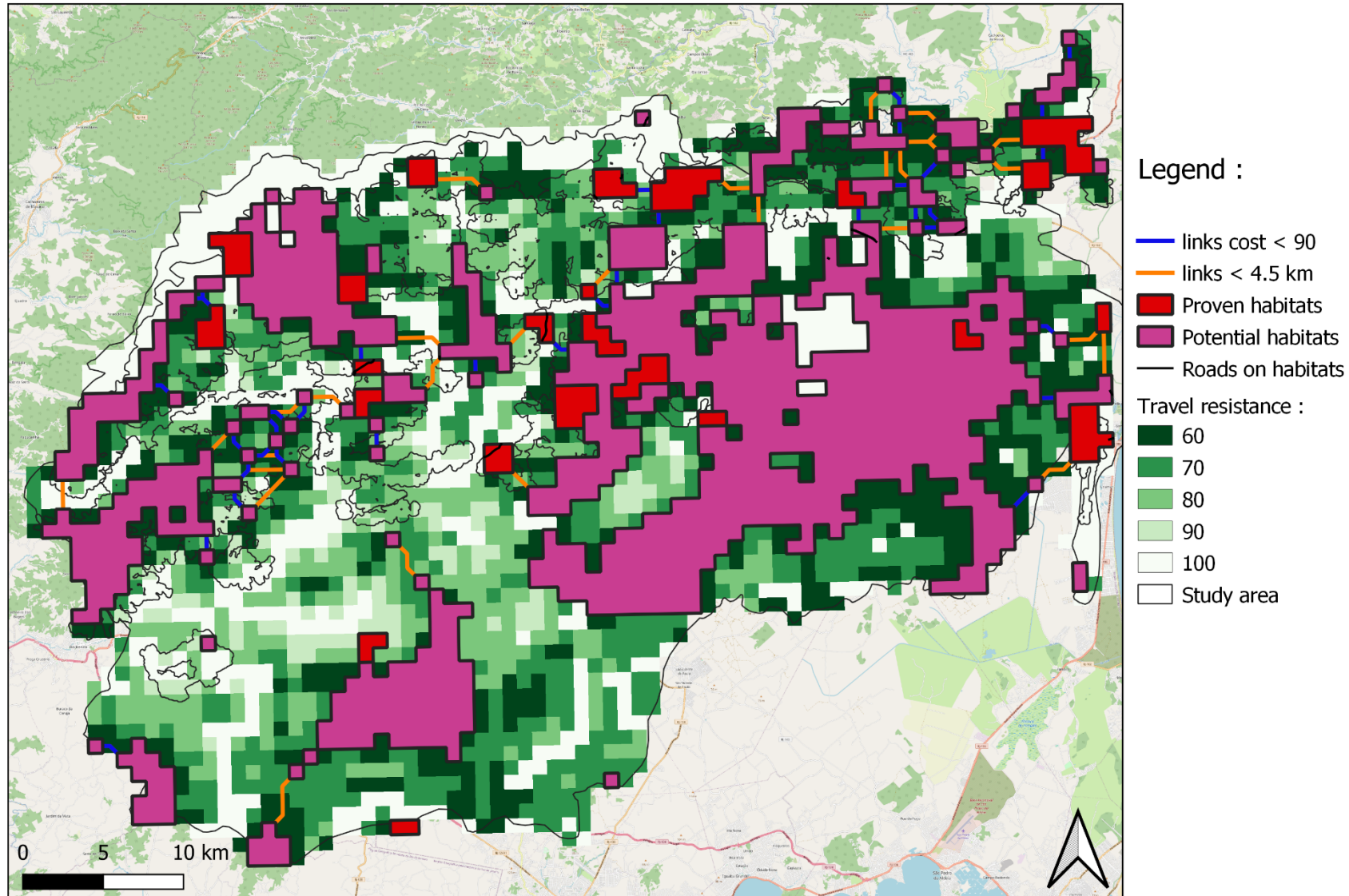


Fig.8: Connectivity map of *S. nigritus* habitats, in the São João river basin in the state of Rio de Janeiro, Brazil. The orange links represent paths of least cost of less than 4.5 km, the blue dotted links superimposed are paths of cost of less than 90 that do not cross a road. The thin white lines represent primary, secondary and tertiary roads and motorways that cross habitats. Areas where the species is present are shown in red, and favourable habitats are shown in purple, i.e. habitats with a probability of hosting the species of greater than 0.8. The habitat patches represent the surface area of the habitat available at the scale of the map.

increases. So, while the species can live in towns and villages, it must mainly occupy gardens or planted public spaces such as parks.

In the past, it is likely that the two *Callithrix* species were introduced at different points in the Sao Joao river basin, as supported by the presence of *C. jacchus* and *C. penicillata* (Márcio-de-Morais-Jr, 2010). Multiple introductions may have facilitated the widespread distribution of these species throughout the area, accounting for their relatively uniform presence in the fragments of the São João river basin. The complete absence of both species in the northern fragments, Uniao I and II, can be attributed to the strict protection status of this biological reserve by the State of Rio de Janeiro. The primary objective of establishing this reserve is to shield the environment and its resident species from direct human interference. Consequently, the area has remained largely untouched by human activities, with access limited to guards and authorized personnel. Given these stringent restrictions, it is unlikely that the two *Callithrix* species were introduced by humans in this region. Furthermore, *Callithrix* species are often fed by humans in urban areas, possibly leading to their establishment in proximity to cities. The Uniao I and II reserves, being almost devoid of human presence, are more likely to maintain the absence of marmosets. Nonetheless, the Poço das Antas fragment, also under protection, is now experiencing colonization by these species, despite models not predicting a high probability of habitat suitability in this area. Thus, a crucial consideration is that these individuals possess the capability to disperse, albeit potentially limited by the high degree of naturalness in these forest fragments. Additionally, their absence from the Cabo Frio fragment could be attributed to the fact that they have yet to be introduced to this fragment, which remains largely isolated from the others.

As evidenced by the 30% decline in the *S. nigritus* population over the last three generations, the species' distribution has declined (Alfaro et al., 2015). It is possible that *S. nigritus* occupied a wider distribution in the past and that, as a result of global changes, its range has shrunk.

The GLM model shows that the distribution of *S. nigritus* can be explained by distance from roads. Although marmosets today prefer to live in anthropized environments with less tree cover, the data on the current presence of *S. nigritus* shows that it is currently evolving in environments with predominantly natural vegetation. Furthermore, the model shows that as distance from the nearest road increases, so does the probability of encountering a capuchin, which corroborates the previous results.

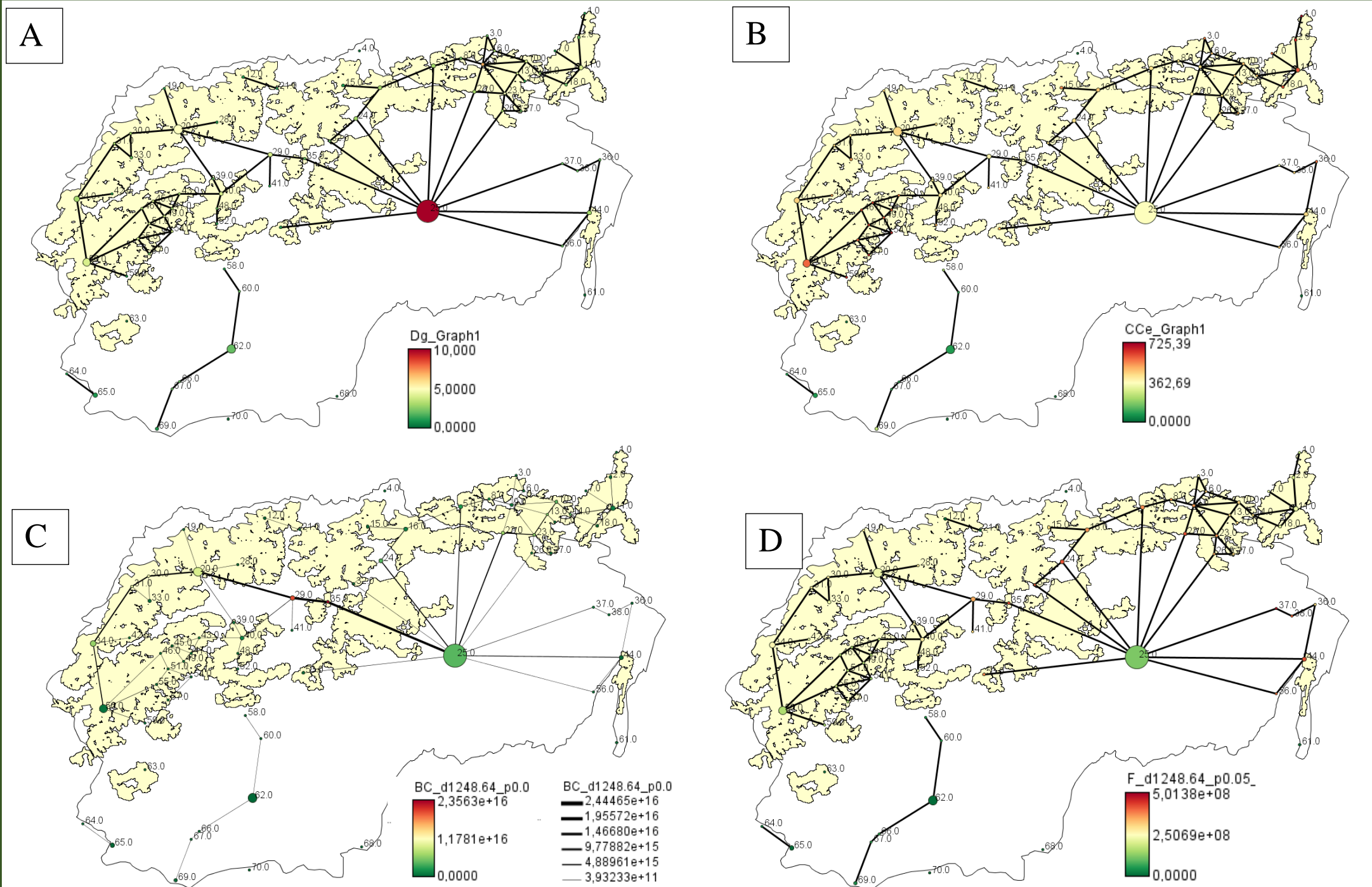


Fig.9: Simplified view of the degree of nodes [A], the proximity centrality (B), the intermediate centrality (C) and the flow of *S. nigritus* habitats. The potential transit weights of the intermediate centrality are indicated proportionally by the thickness of the links and the colour of the nodes. The values of flux, proximity centrality and degree are indicated by the colour of the nodes. The numbers represent the habitats identifiers. The diameter of the circles represents the surface area of the habitat.

However, even if this species shows an interest in patches of preserved vegetation, the latter seems to be sufficiently flexible to overcome forest fragmentation. Indeed, capuchins are found in some fairly isolated forest fragments. These observations can be explained by work showing that the species is able to survive at a good density in environments with intermediate fragmentation. As some studies suggest, the distribution of this species depends on the availability of food. Thus, certain non-vegetated territories could be used as complementary foraging sites, which could counterbalance the low forest cover (Hendges et al., 2017). By occupying pastures and farms, these animals could feed on the fruit grown there, as reported in previous studies (Flesher, 2015). These explanations could help to explain the presence of favourable habitats in some non-forested areas in the south-east of the basin. However, usually, dense, semi-deciduous rainforests are areas that support capuchin populations (N. Pinto et al., 2009), as they host a wide range of plant species, a wide variety of fruits, seeds and a significant proportion of arthropods and frogs, on which the capuchin feeds. Favorable habitats can be found in the forest fragments of Poço das Antas, Gavioes and Pirineus.

Habitat connectivity

We relied on graph theory to create a connectivity map between different areas classified as suitable for the presence of different species. We used RF species distribution models based on habitat suitability for the species and also integrated elements that could impact the dispersion of individuals: roads. The RF models showed better performance indices than the GLM models and were thus selected. They demonstrate a more qualitative accuracy of presence and extrapolation. The analysis of the connectivity of the different habitats thus identified can provide more robust information. However, as the dispersion distances are poorly known in these primates and especially in marmosets, additional studies could complement this research.

We were able to model the connectivity between the habitats currently occupied by the species and the areas classified as suitable for their establishment. Some areas seem to be more important in terms of ease of dispersion and establishment of these animals. In marmosets, the most important areas are located near the forest fragments in the southern basin: Imbau I, II, and III. This area is already colonized, but an extension of the population could occur rapidly. Indeed, the areas identified as favorable in these basin zones are contiguous. Some paths could play a significant role in the dispersion of marmosets. The particularly important paths connecting Gavioes, Imbau I, II, and III, Poço das Antas, and Adeia I traverse the first part of the study area lengthwise. The second half of the study area has much less habitat. Today, these forest fragments are not considered by the

RF model as favorable for the establishment of marmosets. Connectivity is very undeveloped, and the presence of marmosets is sporadic. According to the ecological and climatic characteristics of the environment, no potential habitat is detected there. In the northwest of the basin, at the Pirineus and Aldeia I forest fragments, habitats do not seem to be fundamental for the spread of marmosets but appear to be at the end of the dispersion chain.

For capuchins, the possibility of extension is very important and oriented towards the east of the basin. It is interesting to note that many paths between habitats pass through the large patch to the east of the network (patch 25, **fig.10**), forming a kind of spiderweb, with this patch as the center. Today, this patch has a very large surface, but this surface is largely uncolonized. Dispersion could thus occur especially in non-forest areas. This contrasts today with habitats where the presence of the species is confirmed. A dispersion path crosses the entire length of the basin. It passes through the northwest: Pirineus, the center: Aldeia II, and then the northeast: Dourada and Uniao I. The southwest has the most isolated or poorly connected habitats, and most are still uninhabited, suggesting a slower colonization than in the northwest of the network where the presence of capuchins is confirmed.

This connectivity analysis allows us to assess the overall habitat network but also to consider each patch individually, although for greater precision, it would be necessary to work with a finer resolution. These maps can be used for conservation planning by helping to identify the most important paths or areas to consider and prioritize.

The dispersal potential of capuchins is particularly great, and remains more extensive than that of marmosets, which are more restricted to the areas surrounding their current presence. Capuchins thus seem to show a certain flexibility in exploiting the resources of their environment. Indeed, these animals are known for their ability to use tools to access a food source. Some articles report an increase in the amount of damage caused by *S. nigritus* in agricultural and forestry plantations, which would not coincide with an increase in their population density, but rather with a lack of food resources (Mikich & Liebsch, 2014). Thus, their cognitive abilities combined with forest fragmentation that favors resource scarcity and intraspecific competition could help explain their movement into more urbanized areas.

In the case of marmosets, the expansion of the species into habitats classified as favorable occurs mainly in the vicinity of areas already inhabited by individuals. Moreover, expansion is impossible in certain areas that are inaccessible to dispersal. Because of this adaptability to sparsely treed environments, marmoset species could also proliferate around forest fragments, even if there has

been an extension into certain forest patches in the southern fragments of the basin. This proximity suggests that these habitats will soon be colonized.

Considerations and limitations

Certain biases may exist during data collection. The transects were designed to be found only in forests. However, primates can live in anthropized areas such as crops, gardens or trees close to dwellings, which is specially the case for marmosets. Thus, it is possible that the importance of certain factors (such as human population density) is minimized in the models due to a lack of sampling in towns and villages. In addition, sampling outside forest fragments would also reduce the variance in the probability of species presence by consolidating the model. On the other hand, the difficulty of the terrain makes it impossible to collect data in submontane or montane forests, whereas altitude would potentially be a factor to be taken into account in the models to characterize the habitat of these species (Gestich et al., 2023). As the resolution of the rasters available for each variable covering the entire study area is low (1 km²), the location of potential habitats for each species would still need to be improved. Working with higher resolution rasters would enable us to pinpoint environmental factors, the position of different populations, but also elements that could impact connectivity, such as roads.

In addition, no inter-species interaction was incorporated into our models, although this might be necessary. As the presence of marmosets could be conditioned by the presence of capuchins, their inclusion in the models would be interesting, as would the inclusion of other species such as golden lion tamarins, which share the same food resources as marmosets (Elith & Leathwick, 2009).

What's more, today's environmental conditions are changing. Temperatures, precipitation and humidity are gradually changing. It would be necessary to take this phenomenon into account to more accurately describe future habitats for each species (Braz et al., 2019; da Silva et al., 2022; Hellmann et al., 2008). Using current and future weather predictions would be necessary to adjust the position of habitats. Even if averages can be used to smooth out extreme climatic events, current climate change remains poorly integrated. However, climate change is yet another threat to species and is likely to have major consequences for the range of primates and their long-term survival (Sales et al., 2020).

Furthermore, being able to compare data for each species over time and observe changes in their spatial distribution would provide information about the invasive dynamics of marmosets and the regression of *S. nigritus* populations. By establishing long-term monitoring and using rasters corresponding to the years of presence of the species observed, it would be possible to better

pinpoint the causes of the decline in capuchin populations, as well as the introduction sites and dispersal paths used by marmosets.

Finally, connectivity maps were produced using maps derived from species distribution models, based on the environmental conditions that are most favourable to them. These connectivity maps were therefore produced based on the habitat suitability predicted by our models and weighted according to the road network. Models based on GPS collar data, or genetic data could be compared in the future (Zeller et al., 2018).

Conclusion

In this study, we used GLM and RF species distribution models to gain insights into the key parameters governing the spatial distribution of three primate species: *S. nigritus*, a species currently facing a decline in its native range, and *Callithrix* (*jacchus*, *penicillata*, and their hybrids), which are considered invasive species. These models were successful in effectively predicting the potential habitats for these primates across the Atlantic forest fragments in the São João river basin. They highlighted the significance of various factors, including the nature, type, and presence of vegetation, as well as the broader influence of human activities on these species' distribution.

Connectivity modeling confirmed, as predicted, that marmosets still have opportunities for dispersal. To curb their expansion, preventive measures could be communicated to local populations in areas where these species are present and where they might potentially spread. For instance, measures like prohibiting the feeding of marmosets and restricting access to resources by installing nets around fruit trees could help mitigate marmoset proliferation. Similarly, targeted contraceptive interventions could be considered in priority habitats. Another approach would be to study the impact of capuchins on the presence of marmosets. Some authors have noted a negative correlation between the presence of capuchins and the proliferation of marmosets (Hilário & Ferrari, 2015). Similarly, a case of predation was observed (Albuquerque et al., 2014), as well as avoidance mechanisms (Bastos et al., 2018). Although our models suggest that marmosets and capuchins primarily inhabit different types of habitats, extending the distribution of capuchins might serve to limit the range of marmosets in these areas.

Contrary to our initial hypotheses, a significant portion of the basin appears to be capable of accommodating capuchins. While capuchins are currently found mainly in forest fragments, our models indicate that they can also inhabit more anthropized areas. Importantly, there is minimal overlap between the habitats of capuchins and marmosets in the study area, allowing these two species to occupy distinct territories. By focusing on these habitats, it becomes possible to create

corridors that would facilitate capuchin movements. Additionally, capuchins exhibit more versatile modes of locomotion compared to marmosets, which are more specialized in jumping and climbing. Corridors with fewer trees would impede marmoset movements while facilitating those of capuchins. Lastly, constraining marmoset dispersal is particularly important, as they may compete with endangered primates, such as the golden lion tamarin (Ruiz-Miranda et al., 2006).

To mitigate conflicts between humans and capuchins in cultivated or urban areas, it is vital to preserve and reforest areas that can support capuchin populations. Access to an adequate food supply is crucial to prevent the need for these primates to migrate to anthropized areas. In addition, informing locals about conservation and protection strategies remains well perceived (Rocha & Fortes, 2015) and fundamental to fostering understanding between our species. This study has the potential to contribute to primate management by guiding conservation efforts through the mapping of various suitable habitats and the corridors connecting them.

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Conflict of interest

The authors declare that they have no conflicts of interest.

Data availability

Scripts, supplementary information and anonymised data are available at Zenodo: <https://doi.org/10.5281/zenodo.10652985>

The geographical coordinates of animal groups or individuals have been omitted from the tables for security reasons.

Ethical approval

All applicable international, national, and organizational guidelines for the care and use of animals were followed. The Brazilian Environmental Ministry approved the ethics for this study (SISBIO protocols#47964-2 and #28075-2).

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