SCIENTIA PLENA VOL. 16, NUM. 5 2020
www.scientiaplena.org.br doi: 10.14808/sci.plena.2020.052401

Distribution and invasive potential of the black-tufted marmoset *Callithrix penicillata* in the Brazilian territory

Distribuição e potencial de invasão do mico estrela *Callithrix penicillata* no território brasileiro

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(Recebido em 07 de setembro de 2019; aceito em 18 de abril de 2020)

Biological invasions are one of the greatest existing threats to biodiversity. Invasive species can cause economic and environmental damage. *Callithrix penicillata* is naturally found in the Brazilian savanna and Caatinga. Its introduced populations have become a conservation problem due to its high occupancy potential, native fauna predation, competition with native primates, congeners and hybridization. We used Species Distribution Modeling (SDM) through the Maxent software in this study in order to identify areas with a higher probability of *C. penicillata* occurrence. The AUC value was close to 1 (AUC=0.966), with a curve value close to 1. Through the Jackknife test we observed that temperature seasonality was the variable most related to distribution (AUC=0.86), which agrees with other studies that show climatic variables influencing primate distribution. The Atlantic Forest in the Southeast and South regions of Brazil was indicated as susceptible to invasion by *C. penicillata*. The marmoset *C. penicillata* has become a successful invader of Atlantic Forest areas, causing depreciation in many native species and other problems. However, biological invasions might be mitigated or even extinguished through successful interventions and management.
Keywords: Ecosystem impact, Species Distribution Modeling, Primates.

Invasões biológicas são uma das maiores ameaças a biodiversidade, espécies invasoras podem causar prejuízos econômicos e ambientais. *Callithrix penicillata* é naturalmente encontrado no cerrado brasileiro e caatinga. Suas populações introduzidas tornaram-se um problema de conservação devido ao seu alto potencial de ocupação, predação da fauna nativa, competição com congêneres nativos e hibridação. Neste estudo utilizamos a Modelagem de Distribuição de Espécies (MDE) através do software Maxent para identificar áreas com maior probabilidade de ocorrência de *C. penicillata*. O valore encontrado foi de AUC = 0,966, com valor da curva próximo a 1. Por meio do teste Jackknife, observamos que a sazonalidade da temperatura foi a variável mais relacionada à distribuição (AUC = 0,86), indo de acordo com outros estudos que demonstram que variáveis climáticas influenciam a distribuição de primatas. A Floresta Atlântica nas regiões Sudeste e Sul do Brasil foram as suscetíveis à invasão por *C. penicillata*. O sagui *C. penicillata* se tornou um invasor bem sucedido na Floresta Atlântica, onde vem causando vários danos e prejuízos para a fauna nativa desse bioma. No entanto invasões biológicas podem ser mitigadas ou mesmo quantidades quando são realizadas intervenções e manejo adequado.
Palavras-chave: Impacto nos ecossitemas, modelagem de Distribuição de Espécies, Primatas.

1. INTRODUCTION

Biological invasions are responsible for significant environmental alterations and are one of the greatest existing threats to biodiversity [1]. Once settled in a new habitat, the invasive species threatens the native biodiversity, being able to cause potentially irreparable economic and environmental losses [1]. In order to mitigate this global problem, tools have developed that enable us to predict invasion events [2]. Among these, Species Distribution Modeling (SDM) has become increasingly important for predict biological invasions [3, 4]. Species distribution models have been used in biogeography, conservation, ecological and paleontological studies [5].

Species Distribution Modeling can be designed promptly and with a low budget, helping to identify areas in which a species has a higher probability of occurring [6]. Precisely identifying areas that may be successfully occupied by invasive species is one of the greatest challenges when studying biological invasions [1]. Data used to determine the distribution of a species in a given geographical area is usually scarce and incomplete, which hinders conservation and management projects [7]. These projects are only made possible by knowing which areas have already been invaded and which ones are more susceptible to invasion. In this way, management strategies can be focused on areas of high-risk areas of invasion [1, 2].

The *Callithrix penicillata* (É Geoffroy 1812) is a well-known invasive species for some areas in Brazil [8]. The species is a small-sized arboreal primate that inhabits many vegetal physiognomies and may occur in secondary or disturbed vegetation, typical in Cerrado (Brazilian savannas) and Caatinga areas in the states of Bahia (reaching the southern borders of the Grande and São Francisco rivers in its northern distribution), Minas Gerais, Goiás, southwestern Piauí, Maranhão and northern São Paulo (north to the Tietê and Piracicaba rivers) [9].

This species was introduced in the states of Rio de Janeiro, Espírito Santo, São Paulo, Paraná and Santa Catarina, and also in some areas in eastern Minas Gerais, mainly in the Atlantic forest [9]. The Atlantic Forest is a world hotspot, with some of the highest rates of endemism and biodiversity in the entire planet. It originally spread approximately 1,300,000 km^2, but currently, only 22% of the original coverage exists [10, 11]. Most of its territory is found in the Southeast and South regions, which have the greatest demographic densities in Brazil. The forest is therefore threatened by urbanization, industrialization, deforestation, fragmentation, anthropic occupation, and recently biological invasions [10, 12].

Such sites include Conservation Units which function is to ensure the representativeness of significant and ecologically viable samples of different populations, habitats and ecosystems by preserving the existing biological patrimony [13]. Introduced *C. penicillata* populations have become a concerning issue for environmental conservation due to their general diet, tolerance for fragmentation and tendency to increase their density, especially in defaunated areas [14, 15] where they impact the native fauna, transmit diseases and hybridize with native congeners of the Atlantic Forest [16].

Negative impacts on avifauna by invasive marmosets have mainly been reported for birds and eggs predation [14, 17, 18, 19, 20]. Studies on the decline of bird populations, especially on islands, have pointed to the introduced marmosets as one of those responsible [20, 21, 22]. Conversely, invasive marmosets can play important ecological roles in outdated areas where there are no native primates, such as dispersers or maintaining important ecological relationships [23, 24]

Callithrix penicillata was chosen due to its relevance in the conservation scenario and the need for further investigations, since the existing studies [see 16, 20, 25] are limited to report on their local damage, such as predation record on native fauna and recorded hybridization with native congeners, but with no in-depth approach to the problem. Our goals were to discriminate the actual distribution of the *C. penicillata* and through the SDM modelling Maxent (Maximum Entropy) software to predict which areas are more probable to invasions by this species and to discuss the ecological relevance of invaded areas, as well as the losses caused by the marmoset in such sites. Finally, to provide data about the biological invasion and demonstrate the importance of predictive modelling in management and conservation actions for invasive species.

2. MATERIAL AND METHODS

We used the Maxent software (www.cs.princeton.edu/~schapire/maxent/) in order to estimate the potential species distributions. This algorithm requires the entry of a set of layers or environmental variables (e.g., precipitation rates, altitude, etc.) and a set of georeferenced occurrence locations in order to generate a SDM of a given species [7, 26], as used bellow.

The marmoset occurrence locations (302 occurrence points) (Figure 1) were attained through an extensive literature review in the Web of Science (apps-webofknowledge.ez25.periodicos.capes.gov.br), Scielo – Scientific Electronic Library Online (www.scielo.org/php/index.php), and Academic Google (scholar.google.com.br) databases, as well as consultations to biological collections (Appendix I) and in the Global Biodiversity Information Facility (gbif.sibbr.gov.br), Mammal Networked Information System (https://ecologicaldata.org/wiki/mammal-networked-information-system), SpeciesLink (splink.cria.org.br) and Táxeus (taxeus.com.br) databases. Unreferenced data was georeferenced through the Geoloc tool (splink.cria.org.br/geoloc) and Google Earth. Records with inaccurate information about the locality were discarded.

Figure 1 - Comparison between the Brazilian phytogeographical biomes and the spatial distribution area listed for Callithrix penicillata by IUCN (in blue), ICMBIO (black) and the occurrence records found in this study (red dots).

The environmental variables used in this study were the 19 listed by Hijmans et al. (2005) [27], attained from consulting the WordClim database (www.worldclim.org). Additionally, data on the altitude and vegetation of biomes were attained from the *Instituto Nacional de Pesquisas Espaciais – INPE* (www.dpi.inpe.br/Ambdata/index.php). In order to reduce overfitting, which tends to be larger with larger number of dimensions, through principal component analysis (PCA), we used six variables that together explained 99% of the data variation, BIO 4 (temperature seasonality), BIO 5 (Max Temperature of Warmest Month), BIO 10 (Mean Temperature of Warmest Quarter), BIO 11 (temperature mean of the coldest quarter), BIO 12 (Annual Precipitation) and BIO 15 (Precipitation Seasonality).

An independent dataset was then built and divided into training data and testing data in order to assess the quality and reliability of the model. The testing dataset was created by using a 25% randomization of the presence points (totaling 227 training points and 75 test points). The adjustment measure in the model was a random prediction with an AUC value = 0.5.

Two other statistical parameters were taken into account, the omission rate and the binomial proportion [28]. These parameters help us understand how much the model failed to predict the occurrence of test points and how statistically significant it is. Complementary analysis of data overlay in the marmoset occurrence in Conservation Units, phytogeographic domains and priority conservation areas (www.mapas.mma.gov.br/i3geo/datadownload.htm) were carried out using the DIVA-GIS software (www.diva-gis.org/download).

3. RESULTS AND DISCUSSION

Our results show that the sites which are more susceptible to *C. penicillata* invasion outside their likely occurrence area are in the Southeast of the Atlantic Forest (Figure 2).

The calculated values regarding the model's reliability were AUC=0.923. Pearce & Ferrier (2000) [29] consider that values over 0.75 are indicators of good model performance, and therefore the closer the area under the curve is to 1, the smaller the probability of the model being a result from a random prediction. The model presented low values for both the omission rate (0.000) and the binomial test (0), indicating that the generated models are significantly different from those generated at random.

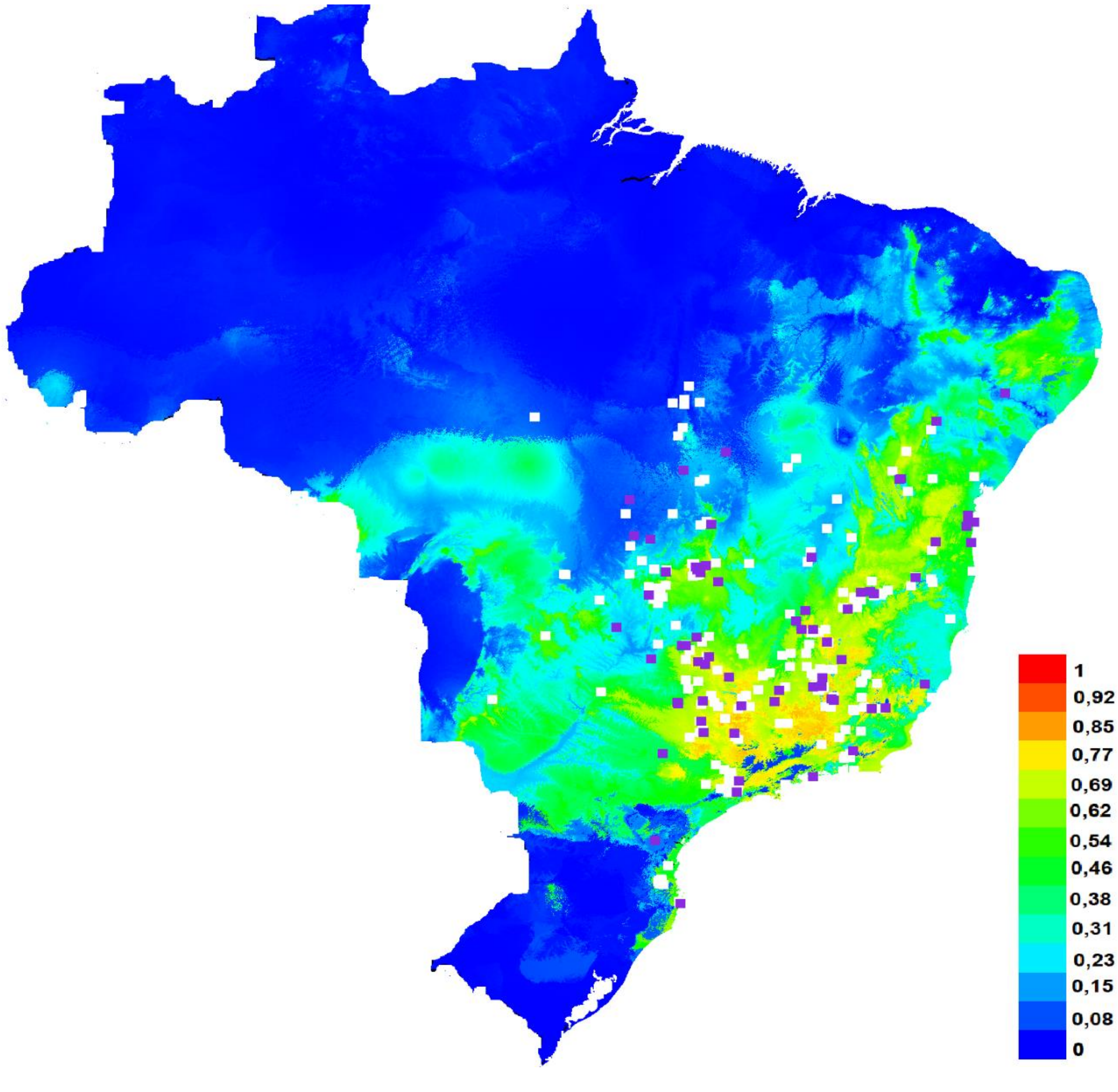

Figure 2 - Geographical representation of the potential distribution for Callithrix penicillata in the Brazilian territory; white dots represent locations used to generate the model (training) and purple dots represent the locations used to test the model.

Regarding the environmental variables that most influenced the model prediction, the Jackknife test showed that the species distribution is closely related with the variables: Max Temperature of Warmest Month (BIO 5) AUC=0.84, and Temperature Seasonality (BIO4) AUC=0.83, followed by Annual Precipitation (BIO 12) AUC= 0.82. The influence of these variables on the species distribution is due to its natural habitat being the Cerrado, which has differences in the temperature seasonality throughout the year. Two distinct seasons are markedly present: the hot and rainy season (from October to April), in which 75% of the precipitation takes place and temperatures range from 20°C to 28°C, and the cold and dry season (from May to September), with temperatures going as low as 16°C and relative air humidity getting close to 20% during droughts [30]. The Atlantic forest presents the highest potential for invasion, where the predominant climate is the humid tropical climate, which is marked by medium to high temperatures and high air humidity throughout the year and regular and well distributed rainfall [31]. The characteristics of this biome favor the occupation of *C. penicillata* in these areas. Climatic and environmental factors may interfere in the marmoset distribution in the Brazilian territory, thus creating areas with higher or lower invasion probability. However, it is necessary to consider that results are limited to the data currently available on locations of occurrence of the species who are mainly from the southeastern region of Brazil.

Other primate studies have shown the existence of an influence between environmental variables and the distribution limits, as well as the use of space [see 25, 32, 33]. For instance, the distribution limits for *Brachyteles arachnoides* (É. Geoffroy, 1806) are influenced by climatic factors (AUC=0.994) such as temperature and precipitation [34]. The environmental variables that most influenced the *B. arachnoides* distribution were temperature seasonality (AUC=0.96), followed by annual temperature mean (AUC=0.93) and maximum temperature of the hottest month (AUC=0.93). As found in our study, temperature seasonality was the variable most correlated to distribution. For *Callithrix flaviceps* (Thomas 1903), study with model attained through logistic regression (with a 95.6% concordance value) showed that climatic factors seem to limit its distribution, suggesting that there are areas with higher probabilities (> 40%) of species occurrence [25]. The occurrence of *C. flaviceps* was positively related to relative humidity (0.8057, sd ± 0.0229), and it seemed to show a preference for Ombrophilous forest areas (more than 50% of the occurrence was in Ombrophilous Forests).

In order to understand the impact of *C. penicillata* invasion, we analyze its distribution area throughout the country along with the Protected Areas (PA, Conservation Units – CU in Brazil) (Figure 3), Priority Conservation Areas and the Atlantic Forest domain itself (Figure 4). When *C. penicillata* occurrence is overlaid with Brazilian Conservation Units, it is evident that the species has invaded Conservation Units belonging to the Atlantic Forest (Appendix I).

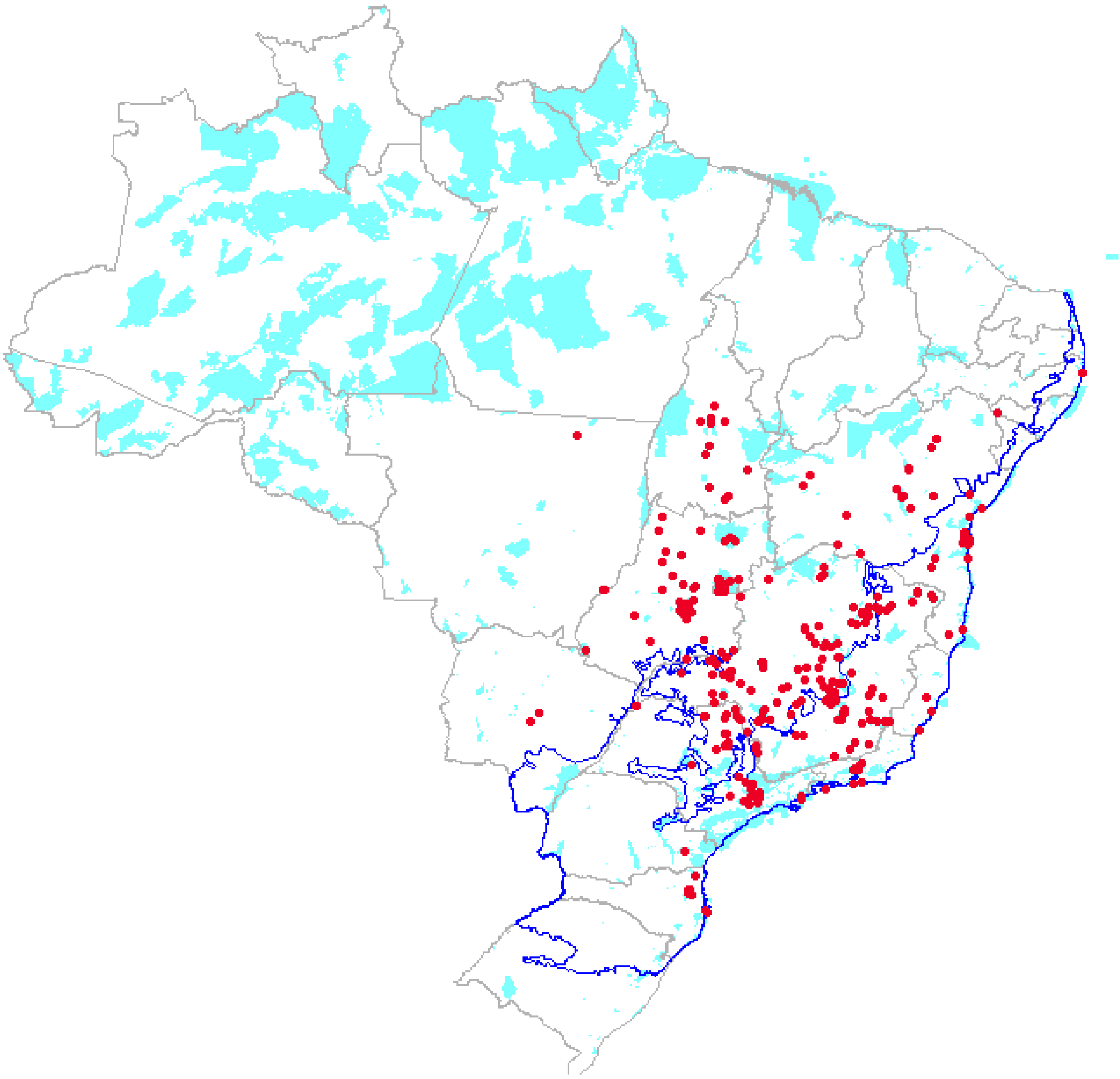

Figure 3 - Protected Areas (blue): Federal, state and Municipal, Atlantic Rain Forest (dark blue) versus Callithrix penicillata occurrence (red dots) (Appendix I). This figure was generated in the DIVA-GIS 7.5.0 software [35].

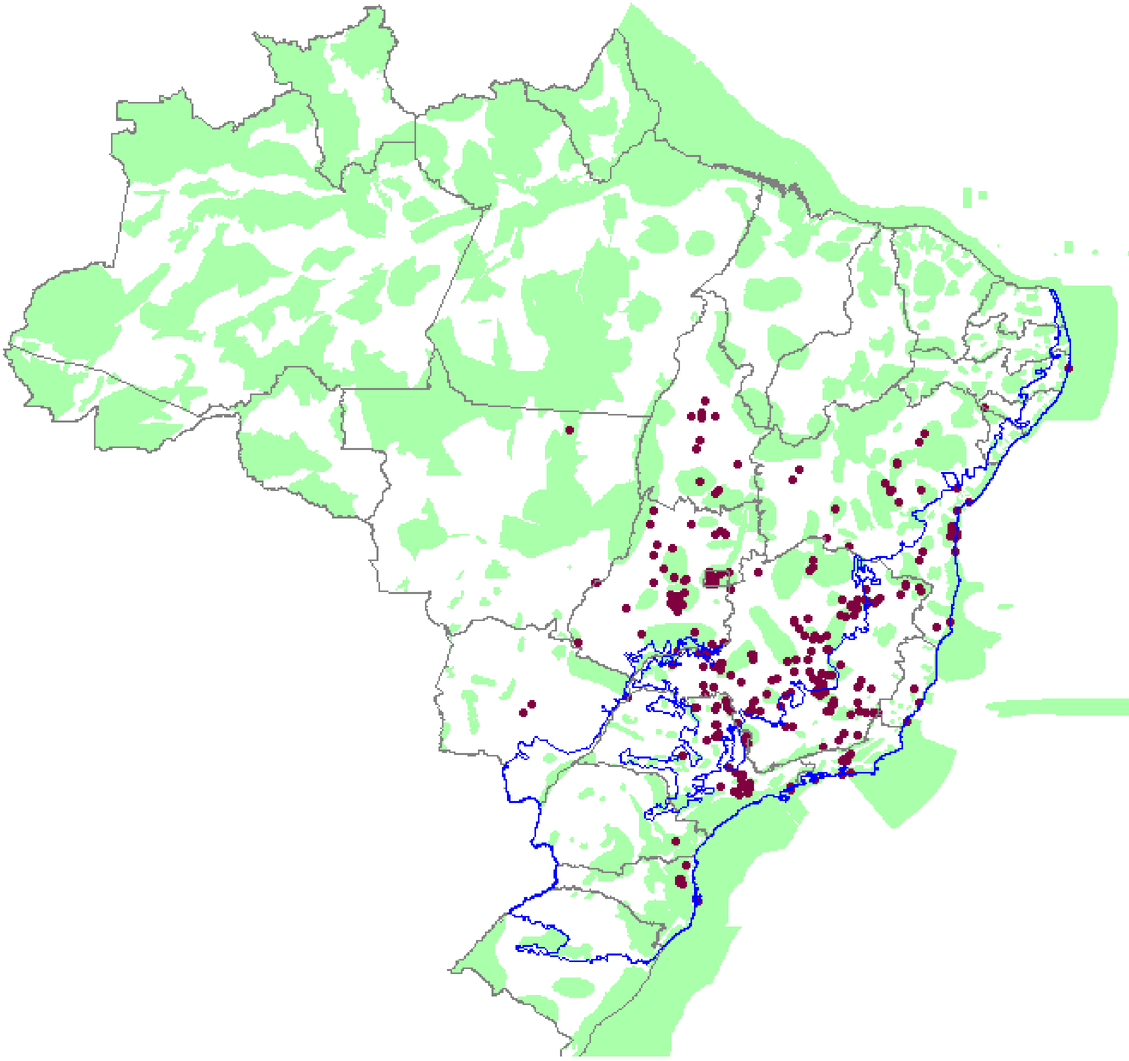

Figure 4 - Priority Conservation Areas (green), Atlantic Rain Forest (dark blue) versus Callithrix penicillata occurrence (red dots) (Appendix I). This figure was generated in the DIVA-GIS 7.5.0 software [35].

The black-tufted marmoset (*C. penicillata*) is a generalist invader [14], with a plastic diet, a high habitat occupation potential, and a capability of occurring in a widely variety of phytophysiognomies such as disturbed areas or secondary vegetation [36]. Additionally, *Callithrix* genus is also one of the most frequent in illegal trade, commonly commercialized as pet [37]. It has great potential on the predation of the native fauna (bird eggs and birds, amphibian and serpent hatchlings) [14, 20, 38]. Causing many problems in the Atlantic Forest areas where they were introduced [13], as direct competition with native primate species for habitat and resources [39] and hybridization (H) with the endemic *Callithrix* ssp. which may result in the loss of unique genotypes, endemism suppression and population depreciation [40], as well as the transmission of diseases to both native primates and human beings [41].

Primates of the *Callithrix* genus are reservoir for diseases that afflict primates, including humans, and are often potential transmitters. Marmosets are classified by the National Health Foundation (*Fundação Nacional de Saúde – FUNASA*) as a host species and/or a possible biological risk parasite reservoir, and therefore are monitored by the Surveillance and Control Coordination of Biological Risk Factors (*Coordenação de Vigilância e Controle dos Fatores de Risco Biológico*) in order to prevent and avoid any changes in key and conditional environmental factors related to human health [42]. Records dating back to 1930 describe diseases being transmitted from primates down to humans, with encephalomyelitis (from *Herpesvirus simiae*) being one of the first [43]. Still, diseases from fungal, viral, bacterial and helminthic origins are currently described as cycling between humans and other primates, such as rabies, herpes B, monkeypox, common cold, poliomyelitis, measles, yellow fever, dengue and others [42, 43].

Dozens of marmosets have been diagnosed with rabies, and human deaths have been caused by marmoset-transmitted rabies [44]. The *Callithrix* genus was the second most stricken by yellow fever among non-human primates [45] in the recent outbreaks of wild yellow fever that hit the southeast of the country between 2017-2018, the area most susceptible to invasion, caused high mortality of marmosets. The death of these animals mainly in urban areas with high population and occurrence of the *Aedes aegypti* mosquito increased the concern of health agencies about the risk of reurbanization of the disease in the country [46, 47]. Moreover, intestinal parasites may be transmitted by marmosets down to humans in urban areas frequented by marmosets and humans (such as parks or squares) [48].

While researching marmosets living in urban and forest areas, Verona (2008) [43] verified the presence of bacteria such as *Escherichia coli* (which may cause gastroenteritis, urinary infection, and meningitis in humans), *Klebisiela oxytoca* (causes infections in the urinary tract, and septicemia), *Klebsiela pneumoniae* (pneumonia), *Sphingomonas paucimobilis* (may cause peritonitis, cerebral abcesses, cervical adenopathy, respiratory infections, urinary infections, and meningitis) and *Salmonella enteriditis* (gastroenteritis). Aside from microfilaria, fungi, parasite eggs and nematode larva [43, 49].

Callithrix ssp. generally has the ability to survive in fragmented areas [5, 10]. Disturbed environments, especially when close to urban areas, are susceptible to colonization by generalist primates as the *Callithrix* genus [5, 9]. In southeast of the country, especially in the invaded areas, primates are living in environments near human settlements, they opportunistically interact with people aiming to supplement their diet [50]. This greater proximity then increases the risks of transmitting diseases for humans, and also increase the exposure of marmosets to parasites, risk attack by domestic animals, hunting for pets and susceptible to roadkill and electrocution when using power lines [19, 30, 31].

4. CONCLUSION

The Atlantic Forest is vulnerable to biological invasions since it is already under of pressure coming from urbanization, and degradation and environmental fragmentation. The marmoset *Callithrix penicillata* has become a successful invader of Atlantic Forest areas, causing depreciation in many native species, which already deal with various other pressures. Factors linked with urbanization and industrialization are harder to control since the human expansion process is not likely to be contained. However, biological invasions might be mitigated or even extinguished through successful interventions and management strategies when well applied can bring excellent results [see: 51, 52].

The generated model reached desirable reliability rates and may be used to help plan the control of *C. penicillata* invasions. Further studies are needed in order to design better control measurements. Our results provide data that may contribute to the conservation of the Atlantic Forest by helping and clarifying the potential biological invasion process by the *C. penicillata*, outlining the current invasion profile, based on environmental characteristics. Showing, therefore, which regions are more likely to be invaded, as well as which environmental conditions may contribute to or limit the invasion; data which may be used in future conservation and management projects.

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Appendix I

Records of the species *Callithrix penicillata* used in this study.

#	State	Provenance	Coordinates (WGS-84)	Source
1	ES	Linhares	-19.45671/-40.08198	MEL-M099
2	ES	Linhares	-19.45671/-40.08198	MEL-M100
3	ES	Vitória	-20.319444/-40.337778	MBML-Mamíferos 187
4	ES	Vitória	-20.319444/-40.33777	MBML-Mamíferos 367
5	ES	Santa Teresa	-19.86111/-40.56111	UFES-MAM -3291
6	ES	Itapemirim	-21.01667/-40.8	UFES-MAM 3292
7	ES	Rio Preto	-20.7000/-41.8333	MZUFV -1096
8	ES	Santa Leopoldina	-20.2333/-42.0333	Nicolaevsky, 2011
9	MG	Thomaz Gonzaga	-18.4333/-44.3000	manisnet.org
10	MG	Indianópolis, UHE Miranda	-19.03860/-47.916900	MCN-N -177
11	MG	Indianópolis	-19.03860/-47.916900	MCN-N -174
12	MG	Indianópolis	-19.0386/-47.9169	MCN-N -178
13	MG	Catas Altas	-20.07743/-43.41819	MCN-N -3099
14	MG	Salinas	-16.17029/-42.290298	MCN-N -038
15	MG	Rio Piracicaba	-19.9296/-43.1700	MCN-N -2470
16	MG	Santana do Riacho	-19.33/-43.73	MCN-N -1952
17	MG	Belo Horizonte	-19.94923/-43.904585	UFMG-BDT -000208
18	MG	Lagoa Santa	-19.633333/-43.883335	ZUEC-MAM 1840
19	MG	Lagoa Santa	-19.6272/-43.8894	ZUEC-MAM 1840
20	MG	Passos	-20.7191/-46.6094	ZUEC-MAM 1601
21	MG	Pirapora	-17.3449/-44.9418	FNJV- 7893
22	MG	Araponga	-20.6667/-42.5333	MZUFV -03032
23	MG	Fervedouro	-20.7258/-42.2789	MZUFV -687
24	MG	Viçosa	-20.7539/-42.8819	MZUFV -686
25	MG	Ponte Nova	-20.24583/-42.770833	Silva et al., 2018
26	MG	Rio Novo	-21.4833/-43.1333	MZUFV -487
27	MG	Viçosa	-20.7539/-42.8819	MZUFV -486
28	MG	Nova Ponte	-19.1528/-47.6744	MZUFV -484
29	MG	Viçosa	-20.745556/-43.014722	MZUFV -792
30	MG	Baldim	-19.288333/-43.956944	UFMG-BDT-958
31	MG	Clube de Caça e Pesca Itororó de Uberlândia	-18.46/-48.3	Vilela & Del Claro, 2011
32	MG	Muriaé, Horto Florestal	-21.12170/-42.369136	Fausto, 2009
33	MG	Lavras	-21.25/-45	Silva & Passamani, 2009
34	MG	Lavras	-21.3541/-44.8894	Silva et al., 2018
35	MG	Juiz de Fora, Fazenda Floresta	-21.7432/-43.3098	Neto et al., 2009
36	MG	Juiz de Fora, Jardim Botânico	-21.7378/-43.3716	Vale, 2013
37	MG	Juiz de Fora, Praça Jarbas de Lery Santos	-21.7716/-43.3522	Vale et al., 2018
38	MG	Juiz de Fora, Campus Universitário	-21.7754/-43.3711	Ribeiro et al., 2018
39	MG	Carangola	-20.7333/-42.0333	MZUFV -455
40	MG	Leopoldina	-21.5333/-42.6333	MZUFV -485
41	MG	Belo Horizonte, Horto Florestal	-19.887875/-43.917919	gbif.sibbr.gov.br
42	MG	Santa Rita do Ibitipoca	-21.700000/-43.900000	Nogueira et al., 2009
43	MG	Ouro Preto	-20.38698/-43.581354	gbif.sibbr.gov.br

44	MG	Ouro Preto, Parque Estadual do Itacolomi	-20.4159/-43.5196	Melo et al., 2009
45	MG	Belo Horizonte	-19.62722/-43.88972	Goulart et al., 2010
46	MG	Belo Horizonte, Parque das Mangabeiras	-19.94/-43.90	Câmara & Lessa, 1994
47	MG	Viçosa, Mata do Paraíso	-20.79516//-42.87782	Pereira, 2012
48	MG	Viçosa, Mata da Biologia	-20.7558/-42.8594	Pereira, 2012
49	MG	Viçosa, Mata da Dendrologia	-20.7688/-42.8775	Pereira, 2012
50	MG	Viçosa, Mata Funarbe	-20.7761/-42.8702	Pereira, 2012
51	MG	Viçosa, Barrinha II	-20.7469/-42.9166	Pereira, 2012
52	MG	Viçosa	-20.75486/-42.878579	gbif.sibbr.gov.br
53	MG	Augusto Lima	-18.000/-44.000	gbif.sibbr.gov.br
54	MG	Conceição de Alagoas	-20.02/-48.23	gbif.sibbr.gov.br
55	MG	Contagem	-19.900158/-44.110667	taxeus.com.br
56	MG	Lagoa Formosa	-18.784933/-46.441994	taxeus.com.br
57	MG	Perdigão	-19.944028/-45.081678	taxeus.com.br
58	MG	Santo Antônio do Monte	-20.075486/-45.279922	taxeus.com.br
59	MG	Buritis	-15.5540/-46.2720	Nicolaevsky, 2011
60	MG	Januária, Riacho da Cruz	-15.3355/-44.2461	Nicolaevsky, 2011
61	MG	Nepomuceno	-21.24467/-45.25070	taxeus.com.br
62	MG	Paraopeba	-19.23477/-44.38157	taxeus.com.br
63	MG	Nova Lima	-19.979031/-43.84304	taxeus.com.br
64	MG	Belo Horizonte	-19.78688/-43.95731	taxeus.com.br
65	MG	Maricá	-22.92651/-42.85205	taxeus.com.br
66	MG	Perdizes	-19.3500/-47.2917	Nicolaevsky, 2011
67	MG	Cristália	-16.8002/-42.8622	Nicolaevsky, 2011
68	MG	Almenara	-16.04963/-40.850902	Neves, 2008
69	MG	Bambuí	-20.042467/-45.953567	taxeus.com.br
70	MG	Conselheiro Lafaiete	-20.639417/-43.779158	Silva et al., 2018
71	MG	Capim Branco	-19.546414/-44.147528	taxeus.com.br
72	MG	Caratinga	-19.812689/-42.122158	taxeus.com.br
73	MG	Dores do Indaiá	-19.460771/-45.596489	gbif.sibbr.gov.br
74	MG	Formiga	-45.426389/-20.464444	UFMG-BDT-999
75	MG	Santo Antônio	-20.325067/-42.605606	taxeus.com.br
76	MG	Campus da Universidade de Belo Horizonte	-19.62722/-43.889722	UFMG-BDT-3823
77	MG	Itacarambi	-15.12142/-44.256669	gbif.sibbr.gov.br
78	MG	Mata entre Jacinto e Santo Antônio do Jacinto	-16.223243/-40.306451	Neves, 2008
79	MG	Santo Antônio do Jacinto	-16.102408/-40.350346	Neves, 2008
80	MG	Várzea da Palma, Serra da Onça	-17.2355/-44.4455	UFMG-BDT-1009
81	MG	Aparecida do Taboado	-20.1200/-51.0700	Nicolaevsky, 2011
82	MG	Lagoa Santa Rio das Velhas	-19.62719/-43.889701	splink.cria.org.br
83	MG	Lagoa Santa Rio das Velhas	-19.6300/-43.8800	splink.cria.org.br
84	MG	São João do Glória	-20.7200/-46.6200	manisnet.org
85	MG	Januária	-15.4833/-44.3667	manisnet.org
86	MG	Água suja	-18.88/-47.63	manisnet.org
87	MG	São João Del Rei	-21.143056/-44.285556	Silva et al., 2018
88	MG	Barbacena	-21.227125/-43.767894	Silva et al., 2018
89	MG	Araguari	-18.4833/-48.4333	manisnet.org

90	MG	São Roque, Fazenda Gameleira	-20.24527/-46.365833	UFMG-BDT -1040
91	MG	Araguari, Rio Jordão	-18.6509/-48.1854	Nicolaevsky, 2011
92	MG	Araguari	-18.6300/-48.1800	Nicolaevsky, 2011
93	MG	Verissímo	-19.7000/-48.3000	Nicolaevsky, 2011
94	MG	Romaria	-18.8837/-47.5637	Nicolaevsky, 2011
95	MG	Uberaba	-19.7500/-47.9200	Nicolaevsky, 2011
96	MG	São João Batista	-20.6300/-46.5000	Nicolaevsky, 2011
97	MG	Pedras de Maria	-15.5000/-44.3500	Nicolaevsky, 2011
98	MG	Pirapora	-17.3449/-44.9418	Nicolaevsky, 2011
99	MG	Lanssance	-17.9000/-44.5700	Nicolaevsky, 2011
100	MG	Curvelo	-18.7500/-44.4200	Nicolaevsky, 2011
101	MG	Morada Nova de Minas	-18.8300/-45.1800	Nicolaevsky, 2011
102	MG	Pompeu, Fazenda Bugio	-19.22444/-44.93527	UFMG-BDT -956
103	MG	Sete Lagoas	-19.28083/-44.07111	Silva et al., 2018
104	MG	Conceição do Mato Dentro	-18.814444/-43.447778	Silva et al., 2018
105	MG	Almenara, Fazenda Estância Betânia	-16.0167/-40.8500	Nicolaevsky, 2011
106	MG	José Gonçalves, Fazenda Irmãos Athachi	-16.5830/-42.6333	Nicolaevsky, 2011
107	MG	Pará de de Minas	-19.785278/-44.651667	Silva et al., 2018
108	MG	Fazenda Canabrana, Augusto Lima	-18.034722/-44.236667	Guedes et al., 2010
109	MG	Mata do Catingueiro, Patos de Minas	-18.58/-46.52	Reis et al., 2014
110	MG	Parque Nacional da Serra do Cipó	-19.3333/-43.5667	Leal et al., 2008
111	MG	Parque Nacional das Sempre Vivas	-17.9021/-43.7729	Leal et al., 2008
112	MG	Parque Estadual Serra do Rola Moça	-20.0769/-44.0267	Leal et al., 2008
113	MG	Aproveitamento Hidrelétrico de Queimado	-16.19/-47.27	Printes & Malta, 2007
114	MG	Acauá Reserve, Turmalina	-17.13/-42.77	Silva et al., 2018
115	MG	Botumirim	-17.13/-43.22	Silva et al., 2018
116	MG	Alfenas	-21.408056/-46.003333	Silva et al., 2018
117	MG	Parque Estadual Fernão Dias	-19.9333/-44.0667	De Melo Júnior & Fernando, 2007
118	MG	Córrego Contendas, Cristália	-16.75/-42.87	Silva, 2014
119	MG	Fazenda Mandasaia, Grão Mogol	-16.57/-43.2	Silva, 2014
120	MG	Ipatinga	-19.371389/-26.05556	Silva et al., 2018
121	MG	Virgem da Lapa	-16.67/-41.98	Silva, 2014
122	MG	Fazenda Santa Maria, Itinga	-16.6/-41.93	Silva, 2014
123	MG	Santana do Riacho	-19.33/-43.73	Silva, 2014
124	MG	Flelixlândia	-18.76/-44.9	UFMG-BDT -726
125	MG	Patos de Minas, Jadim Paraíso	-18.58379/-46.51038	UFMG-BDT -322
126	MG	Varginha	-21.346389/-45.522778	Silva et al., 2018
127	MG	Parque Municipal Américo Renné Giannetti, BH	-19.92079/-43.93780	Duarte et al., 2011
128	MG	Reserva Volta Grande, Conceição das Alagoas	-20.02/-48.23	Silva, 2014
129	MG	Verissimo	-19.7/-48.3	Silva, 2014
130	MG	Água Suja	-18.88/-47.63	Silva, 2014
131	MG	Uberaba	-19.75/-47.92	UFMG-BDT-531
132	MG	Buenopolis	-17.9000/-44.1833	Nicolaevsky, 2011

133	MG	Barra do Paraopeba	-18.83/-45.18	Silva, 2014
134	MG	Barão de Guaicuhy, Diamantina	-18.36/-43.74	Silva, 2014
135	MG	Fazenda do Geraldo, Diamantina	-18.38/-43.69	Silva, 2014
136	MG	Itamogi	-21.082107/-47.041427	gbif.sibbr.gov.br
137	MG	Estrela do Indaiá	-19.53922//-45.797581	Silva, 2014
138	MG	Itaverava	-20.677394/-43.617881	Silva, 2014
139	MG	Virgem da Lapa, Porto de Madacarú	-16.6220/-42.2194	Nicolaevsky, 2011
140	MG	Capitólio	-20.64808/-46.226199	gbif.sibbr.gov.br
141	MG	São Roque	-20.2437/-46.3652	UFMG-BDT-964
142	MG	Morro da Garça	-18.5469/-44.6027	Nicolaevsky, 2011
143	MG	São João Batista do Glória	-20.6300/-46.5000	Nicolaevsky, 2011
144	MG	Araxá	-19.611038/-46.915762	gbif.sibbr.gov.br
145	RJ	Guapimirim	-22.48134/-42.986369	gbif.sibbr.gov.br
146	RJ	Silva Jardim	-22.6130/-42.4036	De Morais Jr et al., 2008
147	RJ	Teresópolis	-22.333458/-42.983906	gbif.sibbr.gov.br
148	RJ	Parque Nacional da Serra dos Órgãos	-22.40044/-42.8300101	Carvalho et al., 2013
149	RJ	Angra dos Reis, Ilha Grande	-23.156786/-44.180866	Modesto & Bergallo, 2008
150	RJ	Reserva Biológica Poço das Antas	-22.52394/-42.3129	De Morais Jr et al., 2008
151	RJ	Parque Nacional do Itatiaia	-22.74360/-44.57241	Aximoff et al., 2016
152	RJ	Rio Bonito	-22.73333/-42.55875	De Morais Jr et al., 2008
153	RJ	Rio de Janeiro	-22.952269/-43.211761	gbif.sibbr.gov.br
154	RJ	Petrópolis, Cascata do Imbuí	-22.420793/-43.145759	gbif.sibbr.gov.br
155	RJ	Petrópolis	-22.503181/-43.172643	gbif.sibbr.gov.br
156	SP	Luís Antônio, Jataí	-21.5833/-47.799999	Nicolaevsky, 2011
157	SP	Barretos	-20.5500/-48.5500	Nicolaevsky, 2011
158	SP	São Paulo	-23.695907/-46.666731	gbif.sibbr.gov.br
159	SP	Campinas	-22.8999/-47.0600	FNJV -7911
160	SP	Campinas	-22.8999/-47.0600	FNJV- 7912
161	SP	Araçoibada Serra	-23.520265/-47.565766	gbif.sibbr.gov.br
162	SP	Iperó	-23.4344/-47.656575	gbif.sibbr.gov.br
163	SP	Jundiaí	-23.17169/-46.898639	gbif.sibbr.gov.br
164	SP	Bauru	-22.31445/-49.058695	gbif.sibbr.gov.br
165	SP	Parque Ecológico do Tietê	-23.4941/-46.5221	Pereira et al., 2001
166	SP	Ribeirão Preto	-21.170401/-47.810324	gbif.sibbr.gov.br
167	SP	Ubatuba	-23.42789/-45.082872	De Melo Júnior & Fernando, 2007
168	SP	Piracicaba, Campus da Esalq	-22.7132/-47.6313	Alexandrino et al., 2012
169	SP	Bosque de Campinas	-22.89999/-47.060001	splink.cria.org.br
170	SP	Araraquara	-21.742423/-48.17302	gbif.sibbr.gov.br
171	SP	Jandira	-23.550000/-46.866667	Begotti & Landesmann, 2008
172	SP	São José do Rio Preto, Campus Unesp	-20.786061/-49.35880	Gomes & Lima-Gomes, 2011
173	SP	Cotia	-23.7149/-46.9454	taxeus.com.br
174	SP	Bauru, APA Vargem Limpa	-22.33333/-49.016667	De Paula, 2005
175	SP	Ilha Anchieta	-23.53945/-45.06357	taxeus.com.br
176	SP	São Carlos	-21.9833/-47.8583	Nicolaevsky, 2011
177	SP	Divinolândia	-21.6/-46.733299	splink.cria.org.br

178	SP	Franca	-20.504575/-47.379647	taxeus.com.br
179	SP	Americana	-22.7299//-47.3300	FNJV- 7915
180	SP	Ribeirão Preto	-21.170389/-47.860519	taxeus.com.br
181	SP	Ituitaba	-18.957058/-49.431467	taxeus.com.br
182	SP	Patrocinio Paulista	-20.639061/-47.267758	taxeus.com.br
183	SP	Guará	-20.441036/-47.761714	taxeus.com.br
184	SP	São joaquim da Barra	-20.573431/-47.816872	taxeus.com.br
185	SP	Santana de Parnaíba	-23.434819/-46.915603	taxeus.com.br
186	SP	Tucuruvi	-23.483213/-46.61359	gbif.sibbr.gov.br
187	SP	Tapiratiba	-30.5167/-46.7833	splink.cria.org.br
188	SP	Ubatuba, Parque Estadual Ilha Anchieta	-45.016667/-23.533333	De Melo Júnior & Fernando, 2007
189	SP	Luís Antônio	-21.5833/-47.8	splink.cria.org.br
190	SP	Pedregulho	-20.256901/-47.4767	Nicolaevsky, 2011
191	SP	São Sebastião da Grama	-21.7167/-46.700001	splink.cria.org.br
192	SP	Divinolândia	-21.6/-46.7333	splink.cria.org.br
193	SP	Estação Ecológica de Jataí	-21.5000/-47.7500	Talamoni et al., 2000
194	SP	Estação Experimental de Luiz Antonio	-21.56972/-47.735000	Talamoni et al., 2000
195	SP	Mairiporã	-23.328245/-46.6843462	taxeus.com.br
196	SP	Campinas, Ribeirão das Cabras	-22.8855875/-46.9608089	Lima, 2008
197	SP	Joaquim Egídeo	-22.873183/-46.935008	Lima, 2008
198	SP	Souzas	-22.84836/-47.012925	Lima, 2008
199	SP	Jardim Botânico de São Paulo	-23.63877/-46.625038	gbif.sibbr.gov.br
200	DF	Reserva Ecológica do IBGE	-15.9597/-47.8764	Miranda & Faria, 2001
201	DF	Brasília	-15.72941/-47.858824	gbif.sibbr.gov.br
202	DF	Parque Nacional de Brasília	-15.74099/-47.923286	gbif.sibbr.gov.br
203	DF	Jardim Botânico de Brasília	-15.8667/-47.8333	Miranda & Faria, 2001
204	DF	Brasília, Reserva Ecológica do Roncador	-15.83/-47.83	Vilela & Faria, 2004
205	DF	Mata do Açudinho, Fazenda Sucupira	-15.92/-48.03	Vilela, 2007
206	GO	Santa Leopoldina	-20.2333/-42.0333	Nicolaevsky, 2011
207	GO	Santa Helena de Goiás	-17.834811/-50.568283	taxeus.com.br
208	GO	Aruana	-14.934817/-50.100306	taxeus.com.br
209	GO	Mundo Novo de Goias	-13.774975/-50.264947	taxeus.com.br
210	GO	São Miguel do Araguaia	-13.272800/-50.143919	taxeus.com.br
211	GO	Novo Crixas	-14.541153/-49.975594	taxeus.com.br
212	GO	Barro Alto		manisnet.org
213	GO	Inhumas	-16.3700/-49.5000	Nicolaevsky, 2011
214	GO	Goiânia	-16.6799/-49.2550	Nicolaevsky, 2011
215	GO	Itumbiara	-18.4200/-49.2200	Nicolaevsky, 2011
216	GO	Catalão	-18.1700/-47.9500	Nicolaevsky, 2011
217	GO	Anápolis	-16.3261/-48.9506	splink.cria.org.br
218	GO	Hidrolândia	-16.9700/-49.2200	Nicolaevsky, 2011
219	GO	Carmo do Rio Verde	-15.4500/-49.7300	Nicolaevsky, 2011
220	GO	Jaraguá	-15.7500/-49.3300	Nicolaevsky, 2011
221	GO	Goiânia, Fazenda São José, Campus II	-16.7339/-49.2161	Nicolaevsky, 2011
222	GO	Aragarças, Rio Araguia	-15.9583/-52.1981	Nicolaevsky, 2011
223	GO	Jaraguá	-15.7500/-49.3300	Nicolaevsky, 2011

224	GO	Parque Municipal Grande Retiro	-16.668889/-49.181111	Grande, 2012
225	GO	Morro do Macaco	-15.777222/-48.939444	Grande, 2012
226	GO	Morro do Medanha	-16.662222/-49.345000	Grande, 2012
227	GO	Jardim Madri	-16.745556/-49.346667	Grande, 2012
228	GO	Madre Germana	-16.833889/-49.361111	Grande, 2012
229	GO	Parque Estadual Altamiro de Moura Pacheco	-16.5237/-49.1416	Grande, 2012
230	GO	Pilar	-14.68/-49.45	Nicolaevsky, 2011
231	GO	Veadeiros, Rio Corumbá	-14.12/-47.52	Nicolaevsky, 2011
232	GO	Rio Uruhu	-15.45/-49.73	Nicolaevsky, 2011
233	GO	Planaltina	-15.62/-47.67	Nicolaevsky, 2011
234	GO	Goiânia, ECSJ da Universidade Católica de Goiás	-16.74/-49.05	Silva et al., 2008
235	GO	Inhumas	-16.37/-49.5	Nicolaevsky, 2011
236	GO	Itumbiara, Rio Paranaíba	-18.42/-49.22	Nicolaevsky, 2011
237	GO	Trindade	-16.6700/-49.5000	Nicolaevsky, 2011
238	GO	Caldas Novas	-17.7500/-48.6300	Nicolaevsky, 2011
239	GO	Neropólis	-16.4200/-49.2300	Nicolaevsky, 2011
240	GO	Alto Paraíso	-14.14349/-47.489616	gbif.sibbr.gov.br
241	GO	Pirenópolis	-15.84593/-48.957375	gbif.sibbr.gov.br
242	GO	Formosa, Fazenda São Manoel	-15.5372/-47.3344	Nicolaevsky, 2011
243	MS	Terenos	-20.73/-54.92	Nicolaevsky, 2011
244	MS	Campo Grande	-20.39/-54.59	Nicolaevsky, 2011
245	MT	Jarina, Peixoto de Azevedo	-10.333333/-53.2	MCN 164
246	BA	Malhada, Fazenda Belém	-9.4833/-37.9667	manisnet.org
247	BA	Castelo Novo	-14.64159/-39.20671	manisnet.org
248	BA	Ilhéus, Fazenda Pirataquisse	-14.8167/-39.0333	manisnet.org
249	BA	Pontal	-14.7892/-39.0492	splink.cria.org.br
250	BA	Itaeté, Macaco seco	-12.9800/-41.1200	Nicolaevsky, 2011
251	BA	Malhada, Faz. da Serra	-14.3000/-43.7333	Nicolaevsky, 2011
252	BA	São Gonçalo	-12.4500/-38.9500	Nicolaevsky, 2011
253	BA	Itinga, Fazenda Santana	-16.5000/-41.7719	Nicolaevsky, 2011
254	BA	Pindobaçu	-10.7694/-40.3528	Nicolaevsky, 2011
255	BA	San Salvador	-12.9833/-38.5167	manisnet.org
256	BA	Lamarão	-10.77/-40.35	manisnet.org
257	BA	Barreires	-12.1300/-45.0000	Nicolaevsky, 2011
258	BA	Rio Jucurucu	-17.35/-39.22	Nicolaevsky, 2011
259	BA	Sebastião Laranjeiras	-14.632778/-42.9425	manisnet.org
260	BA	Belmonte	-15.859796/-38.886904	manisnet.org
261	BA	Curral Velho	-9.9107303/-40.6583157	manisnet.org
262	BA	Itaberaba	-12.525806/-40.296151	manisnet.org
263	BA	Lençois	-12.553003/-41.39755	manisnet.org
264	BA	Ilhéus, Fazenda São Caetano	-14.7892/-39.0492	manisnet.org
265	BA	Guaibim, município de Valença	-13.269572/-38.945311	Neves, 2008
266	BA	Mata na estrada entre Itapetinga e Catiba	-15.08380/-40.340205	Neves, 2008
267	BA	Mata entre Nova Canaã e Poções,	-14.784812/-40.212699	Neves, 2008
268	BA	Riachão das Neves	-11.8000/-44.7300	Nicolaevsky, 2011
269	BA	Bom Jesus da Lapa	-13.2500/-43.4200	Nicolaevsky, 2011

270	BA	Reserva da Michelin, município de Ituberá	-13.819411/-39.158224	Neves, 2008
271	BA	Mata logo após a balsa do rio de Contas em Itacaré	-14.261560/-39.001363	Neves, 2008
272	BA	Mata na região do Piracanga, distrito de Maraú	-14.219353/-38.992872	Neves, 2008
273	BA	Mata na região do Piracanga, distrito de Maraú	-14.076325/-38.958686	Neves, 2008
274	BA	Mata na estrada entre Maraú e o distrito de Algodões	-14.12558/-38.991948	Neves, 2008
275	BA	Mata na estrada entre Maraú e Ubaitaba	-14.215853/-39.198629	Neves, 2008
276	BA	Mata na estrada entre Camamú e o distrito de Travesão	-13.988347/-39.165719	Neves, 2008
277	BA	REBIO Mata Escura, município de Jequitinhonha	-16.341856/-41.012016	Neves, 2008
278	BA	Iraquara	-12.24635/-41.622157	gbif.sibbr.gov.br
279	PE	Recife	-8.05389/-34.881099	splink.cria.org.br
280	TO	Canabrava, Rua Tocantins	-9.2300/-48.2000	Nicolaevsky, 2011
281	TO	Porto Nacional, Rio Tocantins	-10.7000/-48.4200	Nicolaevsky, 2011
282	TO	Barrolândia	-9.8300/-48.7300	Nicolaevsky, 2011
283	TO	BR 101	-9.800186/-47.867007	Santiago et al., 2019
284	TO	PONTE	-9.700184/-48.350361	Santiago et al., 2019
285	TO	LARES	-11.000202/-48.550371	Santiago et al., 2019
286	TO	LAMON	-9.883520/-48.350361	Santiago et al., 2019
287	TO	MANAL	-11.583546/-47.000306	Santiago et al., 2019
288	TO	ENERM	-12.233554/-48.383699	Santiago et al., 2019
289	TO	ENERR	-12.633560/-47.867011	Santiago et al., 2019
290	TO	Paranã	-12.5500/-47.7000	Nicolaevsky, 2011
291	SC	Florianópolis	- 27.583333/-48.50000	Silva et al., 2009
292	SC	Joinville	-26.323886/-48.895783	taxeus.com.br
293	SC	Florianópolis, Campeche	-27.676062/-48.486223	gbif.sibbr.gov.br
294	SC	Blumenau, Água Verde	-26.908782/-49.13484	gbif.sibbr.gov.br
295	SC	Florianópolis, Parque Ecológico do Córrego Grande	-27.5990/-48.5130	Nakamura, 2015
296	PR	Cianorte	-23.66333/-52.605000	Passos et al., 2006
297	PR	Curitiba	-25.425462/-49.3066	gbif.sibbr.gov.br
298	PR	Paranaguá, Floresta Estadual do Palmito	-25.520000/-48.509167	Passos et al., 2006
299	PR	São José dos Pinhais	-25.53472/-49.206389	Passos et al., 2006
300	PR	Maringá	-23.425278/-51.938611	MZEUM s/ nº
301	PR	Parque Barigüí, Curitiba	-25.427778/-49.273056	Passos et al., 2006
302	PR	Mercês, Curitiba	-25.417551/-49.30819	gbif.sibbr.gov.br

Abbreviations:
MEL-Museu Elias Lorenzutti
MZUFV-Museu de Zoologia João Moojen, Universidade Federal de Viçosa
MCN-Coleção de Mastozoologia do Museu de Ciências Naturais PUC- MINAS
UFMG-BDT Centro de coleções taxonômicas UFMG
ZUEC-MAM Museu de Zoologia da Universidade Estadual de Campinas
FNJV-Fonoteca Neotropical Jacques Vielliard e Museu de Zoologia Adão José Cardoso, Universidade Estadual de Campinas
MBML-Mamíferos Museu de Biologia Professor Mello Leitão
UFES-MAM Coleção de Mamíferos da Universidade Federal do Espírito Santo

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