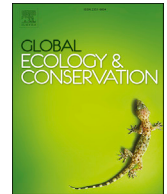




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# Predicting the potential hybridization zones between native and invasive marmosets within Neotropical biodiversity hotspots



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## ABSTRACT

The human-induced introductions of marmoset species (*Callithrix* genus) threaten the native species persistence within Brazilian biodiversity hotspots. Invasive marmosets can hybridize with native congeners reducing the genetic integrity on native populations. However, no study quantified the spatial extent of these invasions and which species can be impacted by a hybridization process. Here, we predicted the range expansion and hence the potential geographic overlap between *Callithrix* species, particularly in Atlantic Forest and Cerrado, to discuss management strategies. We hypothesized that marmosets endemic to the Atlantic Forest are more threatened by invasive congeners than other marmosets. We generated species distribution models for six *Callithrix* species using four algorithms, six environmental layers and 445 georeferenced localities extracted from literature published since 2000. Suitability maps for each species were binarized using a 20-percentile threshold and overlapped to predict invasion and quantify hybridization potential risks. All *Callithrix* species had potential to expand their range within the Atlantic Forest although suitable habitats for *C. flaviceps* and *C. kuhlii* were more limited. *C. jacchus* and *C. penicillata* have already expanded their range to different biomes and our model shows that they can spread even further. The potential hybridization zones were identified within

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the distribution range of all species, and more markedly within Atlantic Forest species ranges. For assuring the ecosystem equilibriums, we urge to prevent the biological invasions and to control the human-induced *Callithrix* introductions and expansions within Neotropical hotspots.

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## 1. Introduction

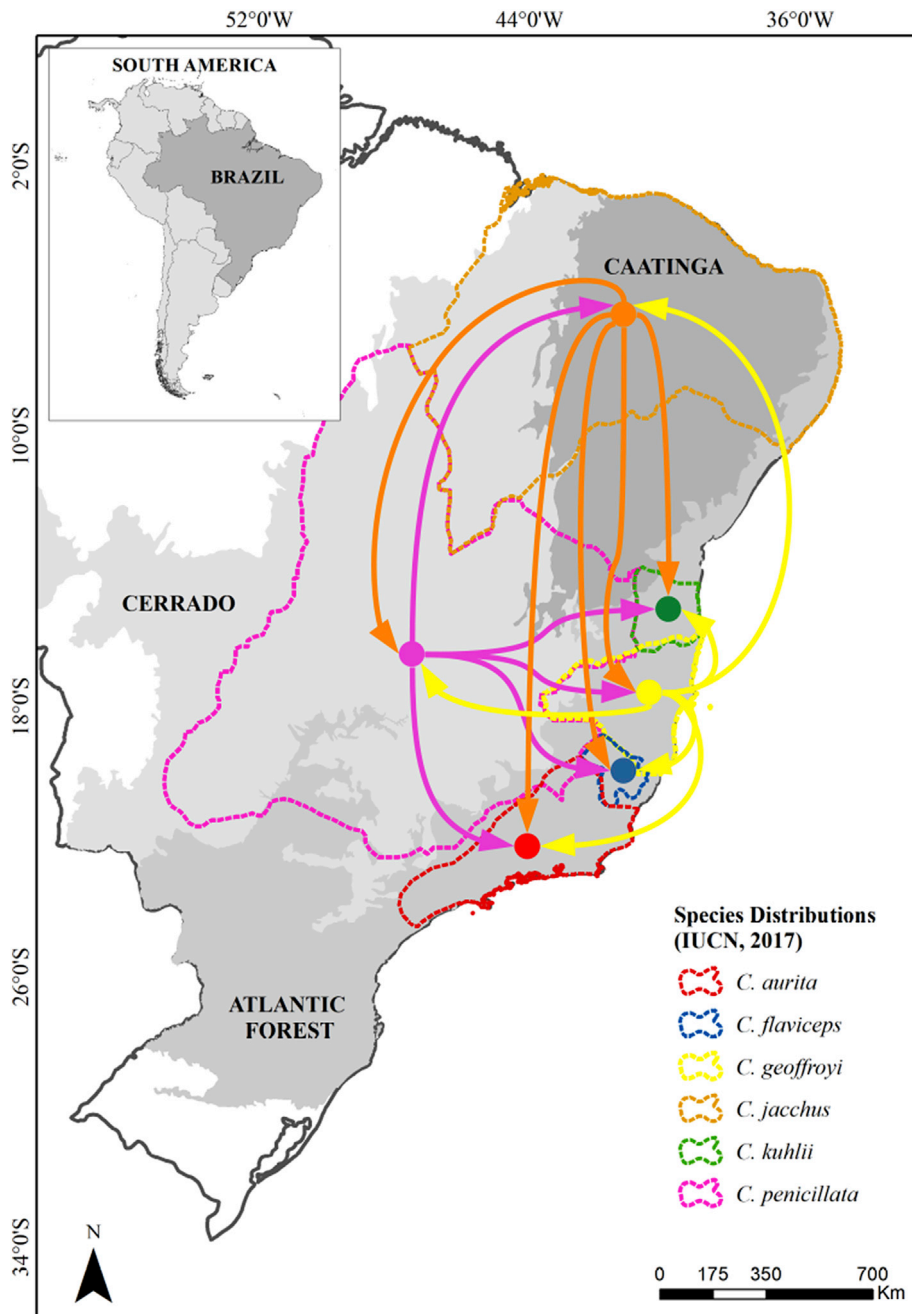
Predicting the potential expansion of invasive species distribution may help inferences on their ecological impacts in natural ecosystems and biodiversity (Peterson, 2003) and contribute to drawing more efficient management strategies. The identification of priority regions for native biodiversity conservation and potential areas of high invasion risk should be also contemplated in conservation plans (IUCN and Species Survival Commission, 2000). In general, broad-scale invasion control is very costly and rare worldwide (Kopf et al., 2017) and a correct understanding of (1) which species can be invasive, (2) what is the spatial extent of potential invasion risk, and (3) which species can be threatened by this invasion are essential knowledge to support suitable management interventions and policies (Kopf et al., 2017; Morais, 2010; Simberloff et al., 2005).

Biological invasions (Davis and Thompson, 2000) are one of the greatest threats to biodiversity (IUCN and Species Survival Commission, 2000). The intentional or no-intentional species introductions in different ecosystems have been facilitated by the intense trade worldwide (Levine and D'Antonio, 2007; Lövei, 1997; Meyerson and Mooney, 2007). Alien or exotic species (i.e. that occurs outside of its natural distribution range) are considered invasive when it modifies and threatens the biodiversity of invaded natural ecosystems (IUCN and Species Survival Commission, 2000). Ecological and evolutionary effects of invasive species on biodiversity include introductions of diseases, niche displacement due to competitive exclusion, hybridization and introgression, predation, decreasing of natural population size, and even extinction of native species (e.g., Gurevitch and Padilla, 2004; Mooney and Cleland, 2001; Sales et al., 2010). However, few studies quantified the potential range of invasive species and the associated potential hybridization risk in a broad-scale perspective (Jiménez-Valverde et al., 2011; Kopf et al., 2017).

Marmosets (genus *Callithrix*, subgenus *Callithrix*) are Neotropical primates that have been introduced outside their natural distribution range (e.g., Culot et al., 2018; Oliveira and Grelle, 2012; Ruiz-Miranda et al., 2006; Silva et al., 2018). They consist of a group of six species with different threat levels widely distributed in eastern portion of Brazil (Fig. 1): *C. aurita* (Vulnerable), *C. flaviceps* (Endangered), *C. geoffroyi* (Least Concern), *C. jacchus* (Least Concern), *C. kuhlii* (Near Threatened) and *C. penicillata* (Least Concern) (IUCN, 2017; Rylands et al., 2009, 1993). Barriers such as rivers, mountains, climate, relief and vegetation type are important determinants of marmoset geographic ranges (Ferrari et al., 1996; Grelle and Cerqueira, 2006; Malukiewicz, 2019; Malukiewicz et al., 2014; Rylands et al., 2009). *C. penicillata* and *C. jacchus* occur in more seasonal environments, such as Cerrado (savanna) and Caatinga (dry forest/scrubland), respectively (Rylands et al., 2009, 1993). *C. jacchus* may also occur in Atlantic Forest of northeastern Brazil (Rylands et al., 2009, 2008d, 1993). *C. aurita*, *C. flaviceps*, *C. geoffroyi*, and *C. kuhlii* are endemic to the Atlantic Forest, originally occurring in eastern Brazil (IUCN, 2017; Ferrari et al., 1996; Rylands et al., 2009, 1993). *C. geoffroyi* is restricted to lowland forests ( $\leq 500$  m of elevation), *C. flaviceps* to montane forests ( $\geq 500$  m), and *C. aurita* to a wider range of elevations (100–1200 m) (Brandão and Develey, 1998; Coimbra-Filho et al., 1981; Rylands et al., 2009, 2008a, 2008c, 1993). However, there are exceptions to these geographic distribution patterns. Natural hybridization zones between *C. flaviceps* and *C. geoffroyi* or *C. aurita* (Grelle and Cerqueira, 2006; Mendes, 1993), and between *C. jacchus* and *C. penicillata* (Malukiewicz et al., 2015, 2014) were reported. In addition, human-induced introduction of *C. geoffroyi*, *C. jacchus*, and *C. penicillata* outside of their original geographic range lead to hybridizations between them and native marmosets. These introduced species are likely to threaten the local persistence of native marmosets (particularly *C. flaviceps* and *C. aurita*) due to competition for territory, food and sexual competition (Aximoff et al., 2016; Braz et al., 2016; Malukiewicz, 2019; Malukiewicz et al., 2015, 2014; Oliveira and Grelle, 2012; Ruiz-Miranda et al., 2006; Silva et al., 2018; Vivo et al., 2011).

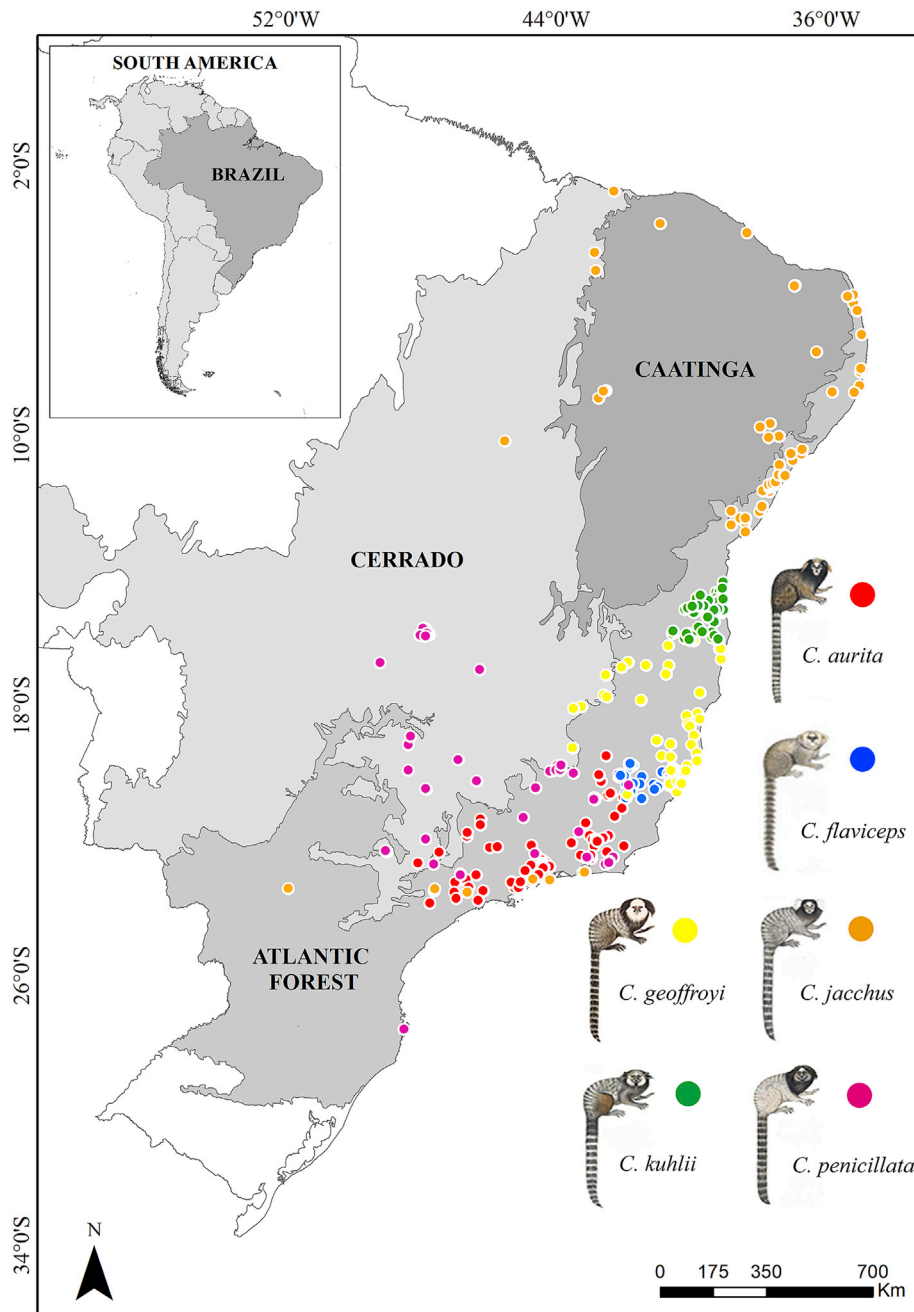
The human-induced contact zones among marmoset congeners and the emergence of hybrids are considered a threat to native species conservation (Cezar et al., 2017; Coimbra-Filho, 1971; Malukiewicz, 2019; Malukiewicz et al., 2015, 2014; Oliveira and Grelle, 2012; Pereira, 2006; Ruiz-Miranda et al., 2006; Silva et al., 2018). All *Callithrix* species occur within the Atlantic Forest of southeastern Brazil, and some them can be found in Santa Catarina and Rio Grande do Sul states (Culot et al., 2018) where no species of *Callithrix* occurs naturally (Fig. 2). Consequently, endangered and endemic marmoset species may become extinct due to the reduction of their genetic integrity, i.e., ability of a population to preserve its genotypes over generations (Aximoff et al., 2016; Malukiewicz, 2019; Silva et al., 2018). Rare taxa can have their growth rate reduced and be replaced over time by maladaptive hybrids (Todesco et al., 2016). Furthermore, introduced marmosets compete with and threaten other endangered primates with similar ecological requirements, such as the golden lion tamarin, *Leontopithecus rosalia* (Morais, 2010; Oliveira and Grelle, 2012; Ruiz-Miranda et al., 2006; Sales et al., 2010). Predation on nests by invasive marmosets (e.g., Alexandrino et al., 2012; De Almeida et al., 2013) also threatens the viability of native avifauna community (Oliveira and Grelle, 2012). Therefore, the human-introduced marmosets, *C. geoffroyi*, *C. jacchus*, and *C. penicillata*, were here considered potentially invasive when occurring outside their original geographic range.

The distribution range expansion of *C. geoffroyi*, *C. jacchus* and *C. penicillata* outside of their natural habitat due to the deforestation process and illegal captures are known (e.g., Malukiewicz, 2019; Rylands et al., 2009, 1993; Silva et al., 2018).



**Fig. 1.** Interactions between marmoset species, *C. aurita*, *C. flaviceps*, *C. kuhlii*, *C. geoffroyi*, *C. jacchus* and *C. penicillata*, used in this study to predict invasion and hybridization risks within suitable habitats of all marmoset species. The interactions evaluated are indicated by arrows. The species distribution ranges (based on IUCN, 2017) are indicated by polygons in yellow (invasive marmosets) and red (threatened marmosets). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

However, the potential hybridization risks including all marmoset species in a broad-scale perspective are still unknown. Here, we used the six marmoset species to determine which species are more prone to be negatively affected by the invasion of congeners and infer where hybrid zones are more likely to occur in a broad-scale perspective. We evaluated the invasion risks by marmoset species in Brazil using Species Distribution Models (SDM) based on bioclimatic and local landscape variables. We quantified the spatial extent of potential invasion of six marmoset species and overlapped them to identify the regions where native and non-invasive species are prone to be threatened by hybridization. Based on records of published literature (e.g., Malukiewicz, 2019; Oliveira and Grelle, 2012; Ruiz-Miranda et al., 2006; Rylands et al., 2009, 1993; Silva et al., 2018), we hypothesized that marmosets endemic to the Atlantic Forest (*C. aurita*, *C. flaviceps*, *C. kuhlii*, and occasional *C. geoffroyi*) are more



**Fig. 2.** Study area including the Brazilian Atlantic Forest, Cerrado and Caatinga biomes, and the occurrence records of *C. aurita*, *C. flaviceps*, *C. kuhlii*, *C. geoffroyi*, *C. jacchus* and *C. penicillata* used for modeling. Primates illustrated by Stephen Nash.

highly threatened by potential biological invasions given their restricted geographic range and the high suitability of their forest habitats to invasive congeners occurring in dry forests and savannas (*C. jacchus* and *C. penicillata*) (Fig. 1).

## 2. Material and methods

### 2.1. Study area and occurrence data

The studied area embraced three Brazilian morphoclimatic domains (referred as to biomes; Olson et al., 2001) within the Neotropical region: Atlantic Forest, Cerrado, and Caatinga (MMA, 2007a) (Fig. 2). The Atlantic Forest and Cerrado are two global biodiversity hotspots, with high biological diversity, endemism and a large proportion of human-modified habitats (Myers

et al., 2000). The Atlantic Forest extends through Brazil, reaching Argentina and Paraguay through the coastal zone and is mainly composed by forest vegetation interspersed with seasonally dry forests, mangroves, resting as, savannas and rocky grasslands (Muylaert et al., 2018; Ribeiro et al., 2009). The Cerrado comprises several types of tropical savanna vegetation in the Central Brazil, from grasslands to open tree formations with low shrubland grassy undergrowth – interspersed with isolated forest formations (riparian and seasonally dry forests) (MMA, 2007b; IBGE, 2012). The Caatinga is the New World's largest and most diverse seasonally dry tropical forest, with a semi-arid climate and located in Northeastern Brazil (Silva et al., 2017).

We defined the Atlantic Forest, Cerrado and Caatinga geographic delimitations as background to SDMs building, as they comprise (1) all known *Callithrix* occurrence data and (2) species ranges over time (based on Barve et al., 2011) (Fig. 2). For each species, we searched for known-occurrence records in both peer-reviewed and gray literature, and in the Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org)) and SpeciesLink ([splink.cria.org.br](http://splink.cria.org.br)) databases (Fig. 2 and Supplementary Material, Table A1). Based on reports of expansion of exotic marmosets within the occurrence area of endangered and endemic Atlantic Forest marmosets (Malukiewicz, 2019; Rylands et al., 2009, 1993; Silva et al., 2018), we considered three species as threatened by invasion – *C. aurita*, *C. flaviceps* and *C. kuhlii* – and three as potential invasive congeners – *C. geoffroyi*, *C. jacchus* and *C. penicillata* (Fig. 1). When an occurrence record was labeled as 'hybrid marmoset', we registered the geographic coordinate as belonging to both maternal and paternal species. Our search strategy was limited to articles published on or after the year 2000, since articles published prior to this date often lack georeferenced data and may introduce location uncertainties on the occurrence records. We used two criteria to select occurrence points: (1) points located within the same pixel (with 1 km<sup>2</sup> cell size – resolution) were considered as a single occurrence, and (2) points located in pixels with biomass and canopy height (two environmental layers used in the SDM, see below) equal to zero were excluded.

## 2.2. Environmental data

Geographic ranges of arboreal primates such as marmosets are also sensitive to bioclimatic variables (Ferrari et al., 1996; Grelle and Cerqueira, 2006; Rylands et al., 2009) and local landscape conditions (Arroyo-Rodríguez and Fahrig, 2014; Estrada et al., 2017). Therefore, to predict the potential geographic distribution of marmoset species, we downloaded the 19 bioclimatic layers of the CHELSA database (available at [chelsa-climate.org](http://chelsa-climate.org)), that represent the climate for the time period 1979 to 2013. We also used the homogeneity index (a similarity measure of the Enhanced Vegetation Index between adjacent pixels; Tuanmu and Jetz, 2015), canopy height (Simard et al., 2011) and vegetation biomass (Avitabile et al., 2016) as landscape local variables. Initial analysis showed that the landscape local variables had low correlation among each other or with bioclimatic variables. Since bioclimatic variables are usually correlated among each other, we conducted a variable selection procedure based on Factorial Analysis with Varimax rotation to check for multicollinearity (similar to Sobral-Souza et al., 2015). We selected as final variables BIO02 (mean diurnal temperature range), BIO10 (mean temperature of the warmest quarter), and BIO18 (precipitation of warmest quarter) as bioclimatic predictors. We built the species distribution models to all marmoset species using both the selected bioclimatic and all landscape local variables together (Fig. 3).

## 2.3. Marmoset distribution models

We performed SDM analysis for each marmoset species using four different mathematical algorithms based on two classes of premises: presence-only algorithms, (1) Bioclim (Nix, 1986) and (2) Domain/Gower distance (Carpenter et al., 1993); and two presence/background algorithms, (3) support vector machines (SVM) (Tax and Duin, 2004) and (4) maximum entropy (MaxEnt v. 3.3.3k) (Phillips and Dudík, 2008). The combined use of different algorithm classes creates more reliable predictions (see Barry and Elith, 2006; Diniz-Filho et al., 2009). All models were generated for each species separately. After fitting, we evaluated the models by randomizing the occurrence points of each marmoset species into two subsets, training and testing, using k-fold sampling (k=2) with 75% and 25% of the occurrence points, respectively. We repeated the randomization process ten times for each algorithm to decrease the correlation between subsets, thus generating 40 models (10 replicates x 4 algorithms) for each marmoset species.

We then used ensemble forecasting (Araújo and New, 2007) to determine a consensus map for each marmoset species. We estimated "maximum sum of specificity and sensitivity" threshold values for each generated model, and then binarized the continuous suitability maps (presence or absence). This threshold value is recommended when using presence only algorithms (Liu et al., 2016). Also, we evaluated the models based on True Skill Statistic (TSS) values. The TSS values (Supplementary Material, Fig. A1) vary from –1 to 1, where negative and close-to-zero values indicate models that are not different from randomly generated models, while values close to 1 indicate good models, and values above 0.5 are assumed to indicate suitable models (Allouche et al., 2006). Prior to generating the suitability consensus map, all binarized maps were overlapped within the same algorithm and then between algorithms. The consensus maps (referred to as suitability map for each studied species) had suitability values varying from 0 to 40 and after divided by 40, indicating the frequency of models that predicted species presence in each cell (Fig. 3).

## 2.4. Predicting invasion and hybridization risks between marmoset species

We predicted invasion risk areas between threatened and invasive marmoset species based on the individual presence/absence species maps. Using known-occurrence sites for each species separately, we transformed each species suitability map

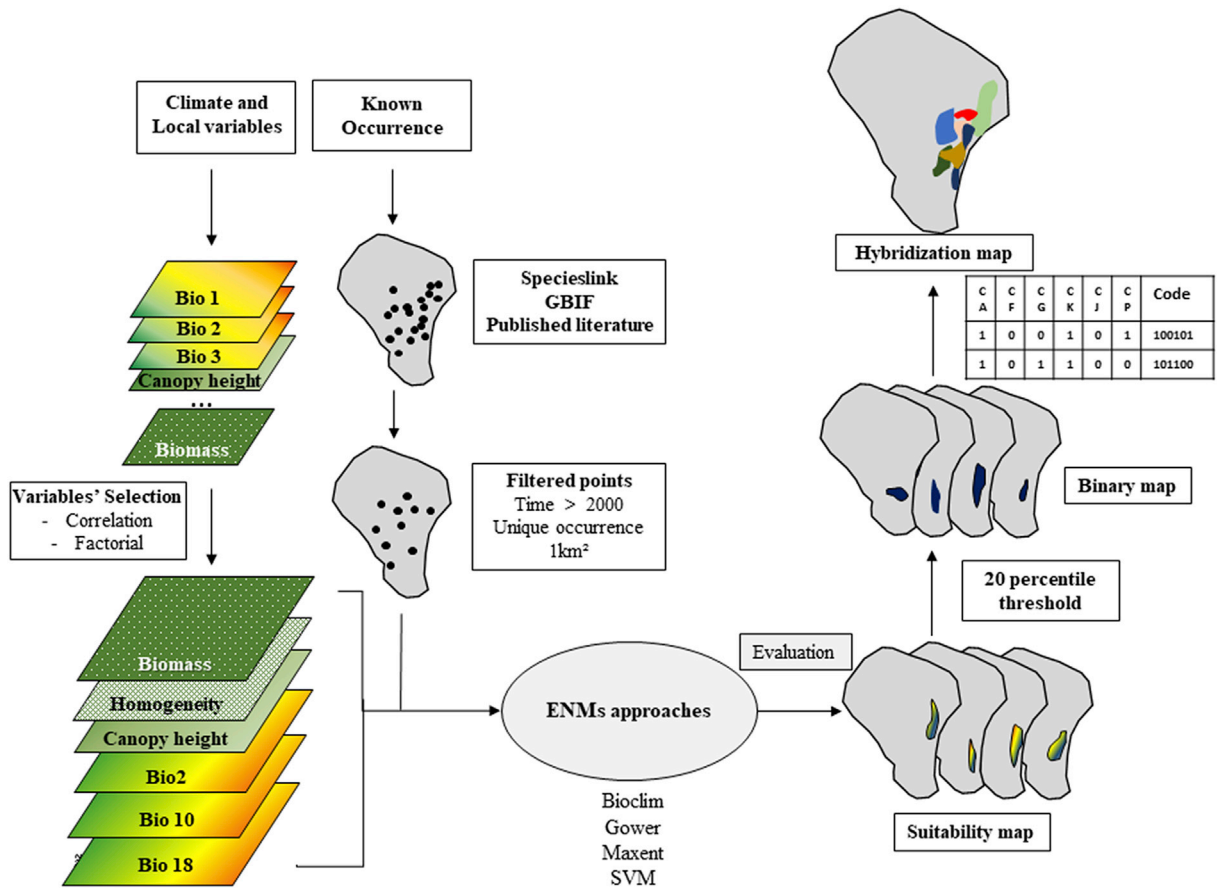


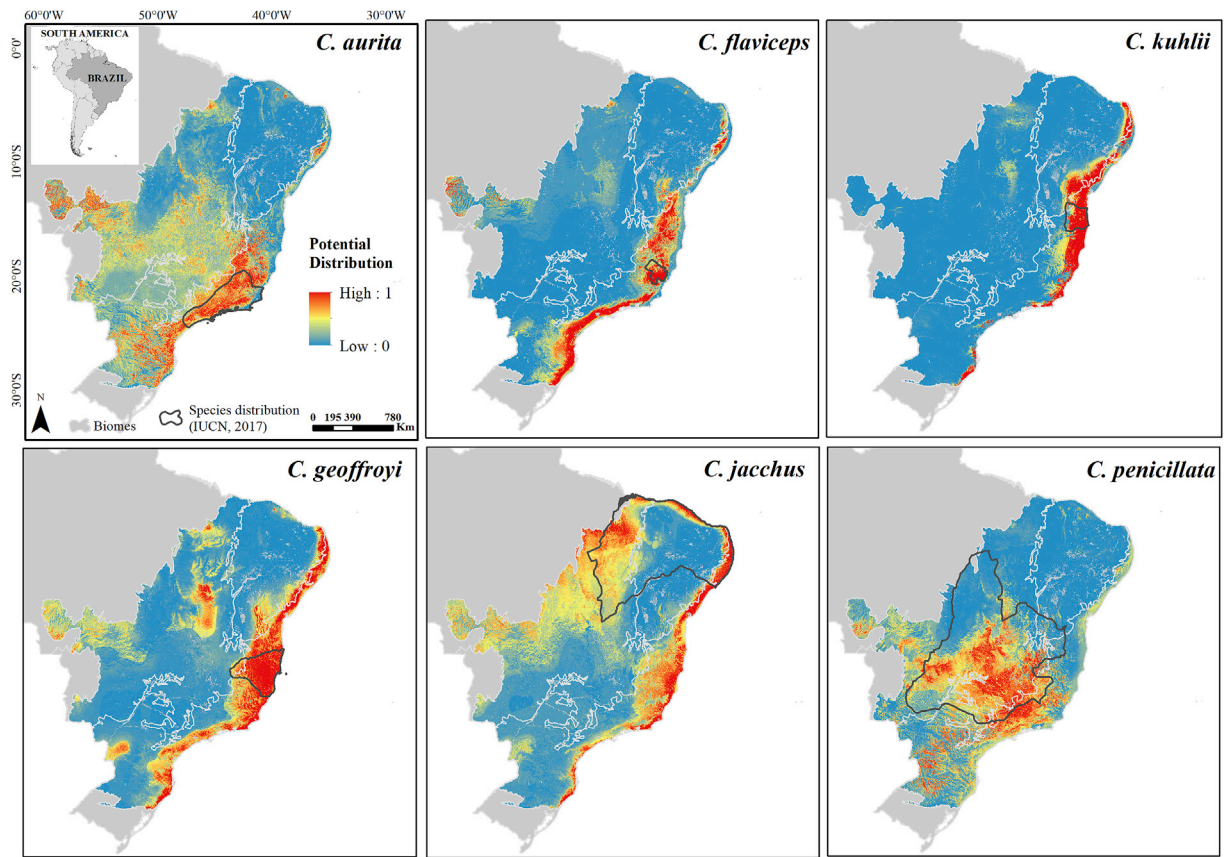
Fig. 3. Flowchart summarizing our methodological and analytical steps to predict invasion and hybridization risks among Brazilian marmoset species.

into a presence/absence map using the 20th percentile threshold (Fielding and Bell, 1997). Then, each value in the species map was recoded: an absence of all species was recoded to zero, presence of *C. aurita* was recoded as 1, and presences of *C. flaviceps*, *C. geoffroyi*, *C. jacchus*, *C. kuhlii* and *C. penicillata* were recoded as 10, 100, 1000, 10000 and 100000 on individual maps, respectively (Fig. 3). Finally, we overlapped all maps to generate the maps of hybridization risks among marmoset species, represented by six-digit binary sequences (Supplementary Material, Table A2). We clipped these maps of hybridization risks to areas inside natural vegetation using the 'forest', 'savanna' and 'mangrove' land use layers from the 2016 PPBIO land use map (Projeto MapBiomias, 2018) to refine the potential of hybridization of species and indicate priorities areas for conservation.

### 3. Results

#### 3.1. Potential expansion of marmoset geographic ranges

We inferred distribution pattern for each marmoset species using a broad-scale perspective combining climate and landscape conditions (Fig. 4). In total, we used 445 occurrence records to build distribution models (*C. aurita* = 89, *C. flaviceps* = 63, *C. geoffroyi* = 75, *C. jacchus* = 102, *C. kuhlii* = 50, *C. penicillata* = 66) (Supplementary Material, Table A1). The distribution models were evaluated as good with TSS values close to 0.5 (Supplementary Material, Fig. A1). *C. aurita* has high potential to occupy Atlantic Forest remnants and expand within the Cerrado as an exotic species. *C. flaviceps* and *C. kuhlii* showed high suitability in the Atlantic Forest coast. As expected, *C. geoffroyi*, *C. jacchus* and *C. penicillata* may occur in regions within the Atlantic Forest, Cerrado and Caatinga. Frequently, *C. geoffroyi* had higher suitability within the Atlantic Forest, including or not its original range. *C. jacchus* and *C. penicillata* had higher suitability within the Atlantic Forest and Cerrado and lower suitability in the Caatinga. Thus, the southeastern part of Atlantic Forest was highly suitable to invasion by *C. geoffroyi*, *C. jacchus* and *C. penicillata* (Fig. 4). Fig. 4 shows the potential for expansion or human-assisted invasion (followed by establishment) outside the original geographical range by each *Callithrix* species.



**Fig. 4.** Habitat suitability maps for marmoset species, *C. aurita*, *C. flaviceps*, *C. kuhlii*, *C. geoffroyi*, *C. jacchus* and *C. penicillata*, within the Atlantic Forest, Cerrado and Caatinga biomes. The potential distribution for each species is indicated by a color gradient varying from red (higher prevalence) to blue (lower prevalence). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

### 3.2. Predicting hybridization risk between marmoset species

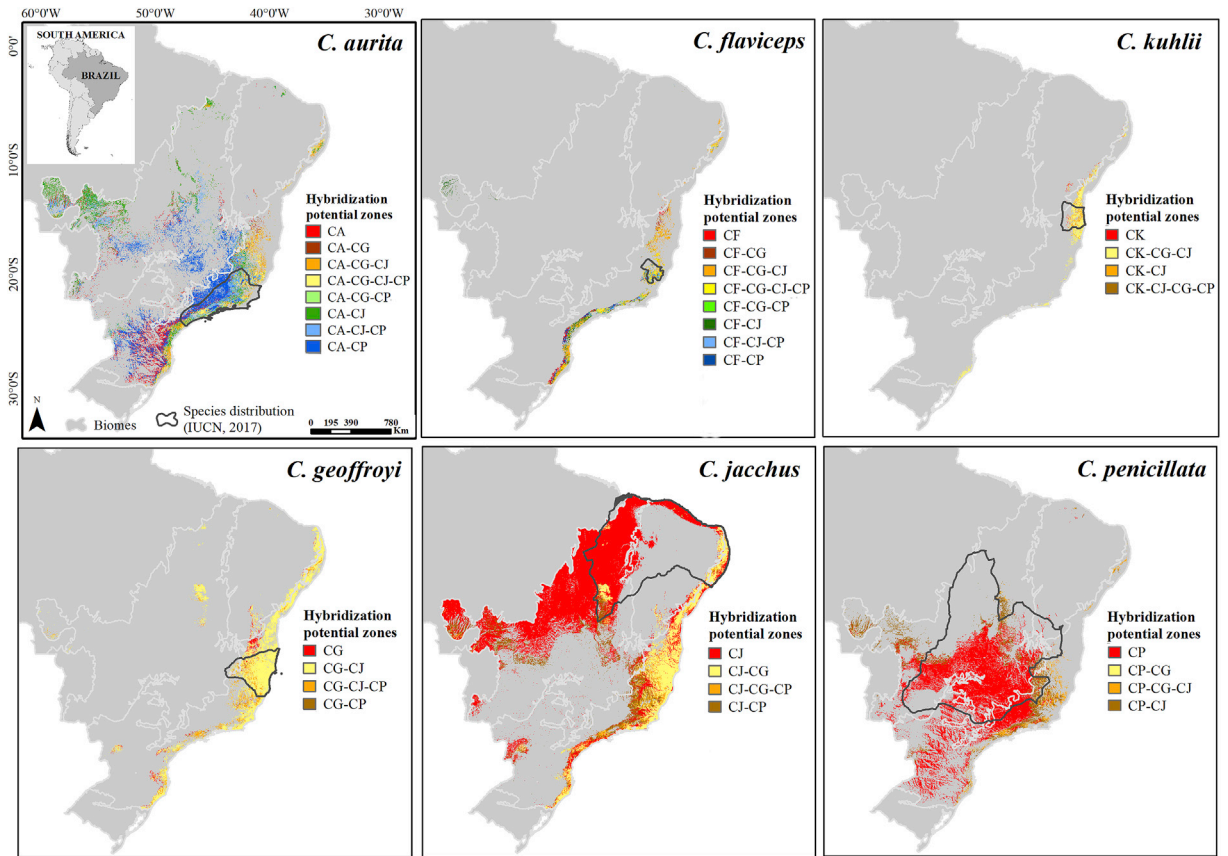
As we hypothesized, the invasion and hybridization risks were higher within the suitable habitats of *C. aurita*, *C. flaviceps* and *C. kuhlii* (native marmosets of the Atlantic Forest) than *C. jacchus* and *C. penicillata* (considered here as potentially invasive species) (Fig. 5), although all marmoset species may be threatened by invasion by congeners. The suitable habitats of *C. geoffroyi*, an endemic species of the Atlantic Forest, also showed a high susceptibility to invasion by *C. jacchus* and *C. penicillata* (Fig. 5). Moreover, we observed that *C. penicillata* and *C. jacchus* were the marmoset species with the highest potential to invade suitable congener habitats. In contrast, *C. kuhlii* may be threatened by the potential invasion of *C. geoffroyi* and *C. jacchus* (Fig. 6).

The area available for potential occurrence of threatened marmosets (*C. aurita*, *C. flaviceps* and *C. kuhlii*) without risk of hybridization and invasion by congener species decreased when we only considered natural vegetation areas (forests, savannas and mangroves). The threat level of *C. geoffroyi* also increased when we considered hybridization risk together with reduction of natural habitats (Fig. 6). When we considered only available natural vegetation under protected status and without invasion risk by exotic marmosets, the threat level for conservation of all marmosets endemic to the Atlantic Forest (*C. aurita*, *C. flaviceps*, *C. geoffroyi* and *C. kuhlii*) was even higher (Fig. 6 and Supplementary Material, Fig. A2). In contrast, *C. jacchus* and *C. penicillata* had large areas of natural vegetation available within and outside conservation areas where they were able to occur without hybridization risk (Fig. 6 and Supplementary Material, Fig. A2).

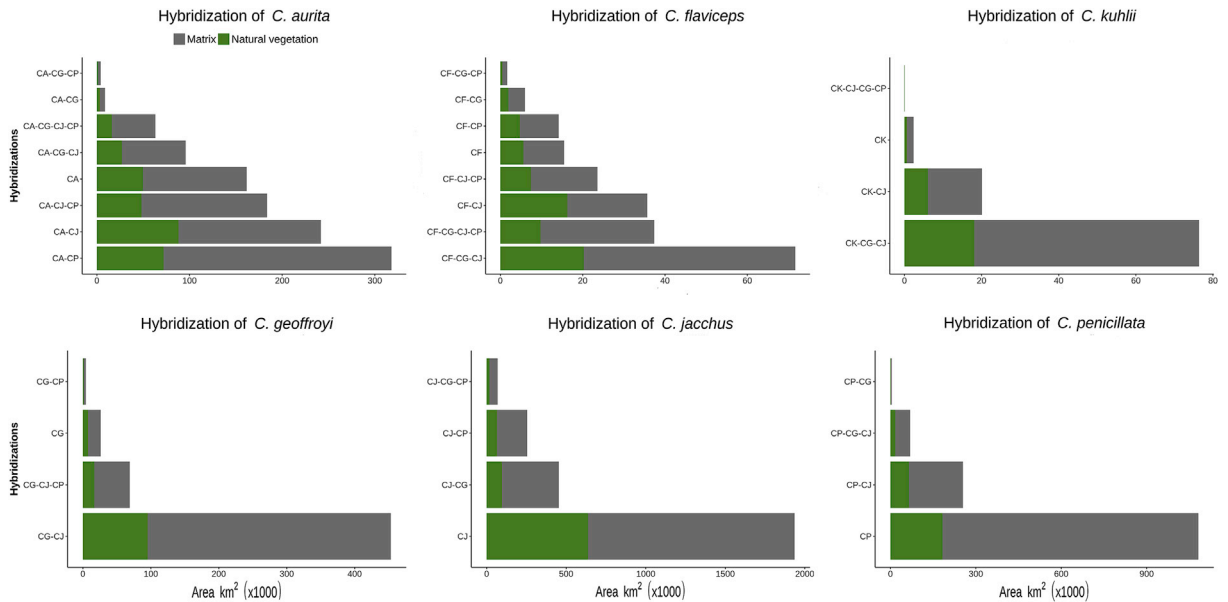
## 4. Discussion

### 4.1. Prediction of marmoset hybridization risks

We built a broad-scale map of marmoset species distribution and predicted the potential hybridization risk along species distribution. Our results showed that the original distribution ranges of all *Callithrix* species are suitable for the establishment of invasive congeners. Thus, population viability and persistence of all marmoset species may be threatened within their



**Fig. 5.** Potential hybridization zones among *C. aurita* (CA), *C. flaviceps* (CF) and *C. kuhlii* (CK) and invasive congeners – *C. geoffroyi* (CG), *C. jacchus* (C) and *C. penicillata* (CP) –, and among invasive marmosets themselves.



**Fig. 6.** Pixel numbers depicting potential hybridization among *C. aurita* (CA), *C. flaviceps* (CF) and *C. kuhlii* (CK) and invasive congeners – *C. geoffroyi* (CG), *C. jacchus* (C) and *C. penicillata* (CP) – and among invasive marmosets themselves, considering total area (Atlantic Forest, Cerrado and Caatinga biome limits) and areas of actual natural vegetation available.



natural habitats if human introductions of exotic marmosets are not controlled. The invasive marmoset species had high potential to distribution range expansion, increasing the probability of hybridization. Although marmoset hybridization has already been reported in the literature (e.g., Malukiewicz et al., 2015, 2014; Ruiz-Miranda et al., 2006), here we proposed a broad-scale view of hybridization risk inferring where hybridizations are more likely to occur and what species are more likely to invade. In [Supplementary Material, Figure A2](#) indicates some hybrid records obtained from the literature and the suitable and available forest habitats for the establishment of exotic marmosets. The control of the introduction of hybridization-prone exotics hybrids and restoring of habitats resistant to hybrid establishment should be the main management and conservation measures (Todesco et al., 2016).

Our model predicted the areas of range expansion already identified through empirical studies, which indicates that our model is valid. In line with previous results reported in the literature (Oliveira and Grelle, 2012; Ruiz-Miranda et al., 2006; Silva et al., 2018), our study showed that *C. jacchus* and *C. penicillata* can spread throughout the Atlantic Forest into the distribution range of other marmoset species. *C. jacchus* occurs originally in the Atlantic Forest and Caatinga of northeastern Brazil, and *C. penicillata* in the Cerrado (IUCN, 2017; Rylands et al., 2009, 1993). Still, our results showed that among all marmosets, *C. jacchus* and *C. penicillata* have the largest remaining area of natural vegetation available without potential hybridization risk. However, even native populations of *C. geoffroyi*, *C. jacchus* and *C. penicillata* may decline if natural habitat destruction and introduction of congeneric marmoset species within their geographic ranges are not contained (Rylands et al., 1993).

Endangered and endemic Atlantic Forest marmosets (*C. aurita*, *C. flaviceps* and *C. kuhlii*) are the species most threatened by biological invasion. Even *C. geoffroyi*, an Atlantic Forest species that has been reported as an invasive marmoset itself (e.g., Braz et al., 2016; Culot et al., 2018; Fuzessy et al., 2014; Vivo et al., 2011), may be threatened by human-assisted invasions of *C. jacchus* and *C. penicillata*. In addition, morphological analyses suggest that the pelage of hybrids between *C. geoffroyi* and *C. penicillata* and therefore gene flow/introgression may be biased towards *C. penicillata* (Fuzessy et al., 2014).

The entirety of habitats suitable to *C. aurita*, *C. flaviceps* and *C. kuhlii* can be potentially invaded by the invasive marmoset species - *C. geoffroyi*, *C. jacchus* and *C. penicillata*. Hybridizations between *C. aurita* and exotic marmosets have been frequently reported (e.g., Aximoff et al., 2016; Carvalho et al., 2013; Nogueira et al., 2011; Pereira, 2006), and the overlap between suitable areas for *C. aurita* and their exotic congeners may reduce its genetic diversity and population viability through hybridization (Mallet, 2005; Malukiewicz et al., 2014; Olmos and Martuscelli, 1995). Although there are few reports of exotic marmoset introductions within the occurrence area of *C. flaviceps* and *C. kuhlii* (Culot et al., 2018; Grelle and Cerqueira, 2006; Specieslink, 2017), these species may also be threatened if the factors responsible for invasive marmoset introductions are not prevented.

*Callithrix aurita*, *C. flaviceps* and *C. kuhlii* are even more threatened if we consider natural habitat destruction. Our results indicate that almost every area of natural vegetation available for the occurrence of these species is also suitable for invasive congeners. The recorded occurrences gathered from published literature confirm the potential of available habitats for Atlantic Forest marmosets (*C. aurita*, *C. flaviceps*, *C. geoffroyi* and *C. kuhlii*) to be invaded by exotic marmosets (see [Supplementary Material, Table A3](#)). In addition, genetic variation loss and introgression of *Callithrix* species due to inter-specific hybridizations should threaten mainly the conservation of small populations distributed within highly fragmented landscapes (Ballou et al., 1995; Malukiewicz et al., 2015, 2014; Woodroffe and Ginsberg, 1998). To preserve the genetic integrity of endangered and endemic marmoset species within the Atlantic Forest, one recommended conservation measure is the identification and establishment of protected areas (Silva et al., 2018).

#### 4.2. Potential expansion of marmoset geographic ranges

The habitat suitability maps of all marmoset species showed a larger potential distribution of marmosets than previously described (IUCN, 2017; Rylands et al., 2009, 1993). The IUCN list criteria are based on different methods than used by us. Here, we combined broad (climate) and narrow-scales (landscape) processes to predict the species distribution while IUCN maps use only polygon to infer species distribution. All marmosets, including *C. jacchus* and *C. penicillata*, were able to occupy humid forests such as the Atlantic Forest. As expected, *C. geoffroyi*, and mainly *C. jacchus* and *C. penicillata* (invasive species) can spread further their ranges within the Atlantic Forest, Cerrado and Caatinga biomes.

Our findings, based on a broad-scale distribution inference, indicate a highly complex potential hybridization zone. Marmosets with larger distributions, particularly *C. jacchus* and *C. penicillata*, overlapped the range of congeners with smaller distributions. These marmosets originally from savannas and dry forests (Cerrado and Caatinga) appear to be more susceptible to invade and establish in new habitats. The ability of *C. jacchus* and *C. penicillata* to become widespread among different vegetation types and more seasonal environments (Rylands et al., 2009, 1993) indicates that these species are more likely to invade the range of congeners, consequently increasing the hybridization risk. These marmosets have the ability to occupy and survive in extremely degraded habitats (Gonzales and Magalhães Jr, 2015; Pereira, 2012; Rylands et al., 2009, 1993; Teixeira et al., 2015), as they have a generalist diet, behavioral flexibility, high reproductive rates, and a cooperative social system that increases juvenile survival probability. These biological characteristics together with the absence of predators in the small forest fragments of southeastern Brazil (Morais, 2010; Morais et al., 2008) may favor the expansion and establishment of invasive marmosets.

Among the threatened marmosets from Atlantic Forest, *C. aurita* (Vulnerable; Rylands et al., 2008c) had a wide potential distribution in relation to distributions previously described for this species (Rylands et al., 2009), including the southern Brazil region and the Cerrado, beyond its original distribution range reported by IUCN (2017). Groups of *C. aurita* have already

been reported in patches of Cerrado (Olmos and Martuscelli, 1995). Also, Muskin (1984) proposed that the geographic distribution of *C. aurita* exceeded the reported limits, being able to extend to northward within the known ranges of *C. penicillata* and *C. flaviceps* in the states of São Paulo and Minas Gerais. Recently, Aximoff et al. (2016) recommended specific studies to inventory native populations considering the new records of *C. aurita* outside the known distribution range within the Brazilian territory.

Our results show that *C. flaviceps* and *C. kuhlii* had the smallest potential distribution within Brazilian eastern forests. In addition to be threatened by the restriction of their suitable habitats (Grelle and Cerqueira, 2006; Guy et al., 2016; Rylands et al., 2008a) and by the introduction of invasive congeners in their geographic distribution (see Culot et al., 2018), these species are also threatened by habitat loss and fragmentation (Chiarello, 2003; Mendes, 1993). *C. kuhlii* (Near Threatened; Rylands et al., 2008b) had a restricted geographic range in the southeastern portion of Bahia state, a region dominated by forest remnants characterized as mature forest, secondary forest or shaded-cocoa agroforest (Raboy et al., 2010). Shade-cocoa agroforests may contribute to the maintenance of relative landscape connectivity for native primate species such as *C. kuhlii* and *Leontopithecus chrysomelas* (Guy et al., 2016; Johns, 1999; Raboy et al., 2004). However, high rates of forest conversion into cattle pastures, including shaded-cacao agroforest, in southeastern Bahia, may reduce habitat suitability and limit dispersal between forest fragments, consequently affecting population viability for these primates (Guy et al., 2016; Johns, 1999; Moraes et al., 2018a; Raboy et al., 2004). Although arboreal primates have been recorded crossing open matrix, they are negatively affected by forest loss and fragmentation, therefore we urge conservation actions that increase habitat connectivity and landscape permeability (Arroyo-Rodríguez and Mandujano, 2009; Gestich et al., 2019; Moraes et al., 2018b, 2017).

#### 4.3. Implications for conservation

Our results showed the high potential for expansion and invasion by human-introduced marmosets of the natural habitats of native congeners. In addition, it has been reported that when exotic marmosets are introduced within congener natural habitats they have a high probability to hybridize (e.g., Aximoff et al., 2016; Carvalho et al., 2013; Nogueira et al., 2011). These results together indicate that *Callithrix* species have a great homogenizing risk by hybrid swarm formation in the Brazilian southeast due to human-assisted invasions (e.g., wild animal traffic; Ruiz-Miranda et al., 2006) decreasing biogeographic barriers. This homogenizing process may bring an irreversible loss of biological, ecological and genetic diversity (Lövei, 1997; Malukiewicz et al., 2014).

We reinforce that programs that control the introduction and range expansion of exotic marmosets are conservation emergencies and immediately necessary to conserve genetic integrity and species diversity within the genus *Callithrix* (Malukiewicz, 2019). Many marmoset introductions have occurred within the Atlantic Forest of Southeastern Brazil (e.g., Culot et al., 2018; Oliveira and Grelle, 2012; Ruiz-Miranda et al., 2006), a highly fragmented and urbanized region (Ribeiro et al., 2009). Generally, these introductions are carried at sites of local animal apprehensions by inspection institutions or by buyers from pet shops (RENTAS, 2001; Morais et al., 2008). Data on invasion dynamics (number of individuals, taxonomic and genetic diversity, etc.) and landscape structure should be both evaluated to identify possible dispersal routes and risks to biodiversity conservation (Morais et al., 2008). Genetic studies using adaptive markers should also be conducted to understand how marmoset species and their hybrids have adapted to the continuous introduction of exotic marmosets (RENTAS, 2001) and to habitat loss and fragmentation within the invaded landscapes.

Our study showed that marmosets are a good model to predict the potential invasion of congener species using SDMs. Therefore, SDMs can be indicated to predict species distribution ranges and propensity of habitats to be invaded by congener species. These predictive models are important to prevent the ecological impacts of invasive species on natural biodiversity and to support conservation strategies (Gaubert et al., 2006; Jiménez-Valverde et al., 2011; Peterson, 2003). Based on our results, we recommend actors and decision-makers involved in marmoset conservation to prioritize (1) training programs for the governmental agents responsible for monitoring wildlife traffic to avoid inappropriate animal releases; (2) agencies trained and equipped to receive and properly handle the seized animals; (3) programs to inform the population about the risks associated with the acquisition and release of wild animals and how to proceed; and (4) programs to monitor and control exotic animals, particularly inside within protected reserves and surroundings that have potential invasion risk by marmosets.

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## Appendix A. Supplementary data

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