



WHO LET THEM OUT? INVASION OF ALIEN MARMOSET SPECIES IN THE *Callithrix aurita* NATURAL RANGE

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ABSTRACT

The microregion of Viçosa, southeastern Brazil, is part of the range of *Callithrix aurita*, an endangered marmoset, which suffers several ecological problems caused by the introduction of alien congeners species. We sampled 39 forest fragments and combined playback census and occupancy models to evaluate whether the city of Viçosa may act as a dispersal center of alien species and their hybrids (i.e., *Callithrix* sp.). Likewise, we explored whether landscape features (i.e., native forest, native forest in the regeneration stage, and eucalyptus fields) may favor the occupancy probability of *Callithrix* sp. in sampled fragments. We detected *Callithrix* sp. in 17 (out of 39) fragments. A group formed only by individuals of the *C. aurita* was not found in any fragment, even though we found individuals of the native species in a group formed by hybrids. The probabilities of occupancy and detection of *Callithrix* sp. were 0.93 and 0.12 respectively. None of the analyzed variables showed greater support than the null model, showing no direct relationship with the distribution of *Callithrix* sp. in the sampled fragments, indicating their ecological plasticity. The absence of groups of *C. aurita* may be not simply due to the occurrence of the *Callithrix* sp., but also due to the defaunation process originated from the human activities that fragmented the continuum forest before the invasion process started. However, the human alterations may have also facilitated the invasion process of *Callithrix* sp., putting the native species at a significant risk of genetic erosion and local extinction.

Keywords: Conservation; Invasive species; Landscape analysis

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POR QUE SUMIRAM? INVASÃO DE ESPÉCIES EXÓTICAS DE SAGUIS NA DISTRIBUIÇÃO NATURAL DE *Callithrix aurita*

RESUMO A microrregião de Viçosa, no sudeste brasileiro, faz parte da extensão de ocorrência do *Callithrix aurita*, uma espécie de sagui endêmica da Mata Atlântica que sofre com sérios problemas ecológicos causados pela introdução de saguis alóctones. Amostramos 39 fragmentos florestais combinando censo de playback e modelos de ocupação a fim de avaliar se a cidade de Viçosa age como um centro dispersor de espécies de saguis invasoras e de suas formas híbridas (i.e., *Callithrix* sp.). Além disso, avaliamos se características da paisagem (i.e., floresta nativa, floresta nativa em estado de regeneração, e campos de eucalipto) poderia favorecer a probabilidade de ocupação de *Callithrix* sp. nos fragmentos amostrados. Detectamos espécies invasoras e formas híbridas em 17 fragmentos. Não encontramos grupos da espécie nativa em nenhum dos fragmentos, apenas um indivíduo em um grupo formado por híbridos. A probabilidade de ocupação e detecção de *Callithrix* sp. foi de 0.93 e 0.12, respectivamente. Nenhuma das variáveis analisadas demonstrou influência sobre a ocupação e detecção de *Callithrix* sp. A ausência de grupos de *Callithrix aurita* pode não estar relacionada somente com a invasão e hibridação de espécies invasoras, mas também pelo processo de defaunação ocorrido pelas atividades antrópicas, que fragmentaram e destruíram contínuos florestais ao longo da região de estudo, muito antes do processo de invasão ocorrer. De qualquer modo, as atividades antrópicas na região podem ter facilitado processo de invasão de espécies invasoras, colocando a espécie nativa sob um grande risco de erosão genética e extinção local.

Palavras-Chave: Conservação; Espécies invasoras; Análise de paisagem

1. INTRODUCTION

One of the more threatened phytogeographical domain in the world is the Atlantic Forest, which originally covered ~150 million hectares in the east of the South American continent. After centuries of exploration, it was reduced to ~12% of its original coverage, being divided into more than 250,000 fragments, among which the vast majority (83.4%) have less than 50 hectares (Dean, 1996; Ribeiro et al., 2009; Fundação SOS Mata Atlântica, 2019). Moreover, 73% of the remaining Atlantic Forest is located less than 250m from any forest edge, exposing it towards edge-effects, which can modify fragments in many aspects, such as their forest structure, microclimate, and animal species composition (Murcia, 1995; Ribeiro et al., 2009).

In the context of Atlantic Forest, the capacity of extant fragments to preserve biodiversity is inherently associated with the nature of human land around them (i.e., matrix) (Lira, Portela & Tambosi, 2021), which underscores the necessity to evaluate biodiversity within a designated area by considering both the fragment and matrix components collectively (i.e., landscape). A landscape may be defined as a human-defined portion of territory which is delimited according to specific processes or species of interest (Arroyo-Rodríguez & Mandujano, 2009). Understanding how landscape influences species' habitat occupancy is essential to develop conservation projects, especially for endangered species which inhabit highly anthropized areas (Marsh, 2003; Silva et al. 2015; Umetsu & Pardini, 2007; Umetsu et al., 2008).

The callitrichids, the smallest neotropical primates, are distinguish from other primates by peculiarities such as twin pregnancy, a high fertility rate and adaptations for vertical locomotion in forest strata (Rylands et al., 2000; Sussman & Kinzey, 1984). The genus *Callithrix* comprises six species (*C. jacchus*, *C. geoffroyi*, *C. penicillata*, *C. kuhlii*, *C. aurita* and *C. flaviceps*), distributed parapatrically throughout eastern Brazil, creating narrow bands of natural hybridization between some



species (Malukiewicz, 2019; Rylands et al., 2000, 2009).

All taxa within *Callithrix* genus are recognized as species, but interspecific crosses can produce fertile hybrid forms (i.e., *Callithrix* sp.) (Coimbra-Filho & Mittermeier, 1973; Rylands et al., 2000). Over the last few centuries, anthropogenic interventions such as deforestation and illegal trafficking have led to the introduction of some *Callithrix* species into the natural distribution area of others (Carvalho et al., 2018; Silva et al., 2018). Reproduction among individuals of native species, alien species, and their hybrids presents a significant ecological challenge.

Hybridization has been demonstrated to promote a series of deleterious events in native populations, including: 1) Hybridization depression, which occurs when the crossing favours the gene expression of the invading species, thereby decreasing the gene expression of local alleles and altering the fitness of the hybrids formed (Rhymer & Simberloff, 1996); 2) Introgression, which occurs when invaders mate with natives and their descendants continue to reproduce with natives, thereby masking the gene expression of the invading species but maintaining its genetic stock (Rhymer & Simberloff, 1996); 3) Genetic innovation and adaptation, which occurs when hybridization forms individuals with characteristics that favor them compared to the parental species, both native and invasive (Malukiewicz, 2019). All of the aforementioned processes have the capacity to diminish the native population, either through the process of genetic erosion, which is precipitated by the crossbreeding of natives with allochthonous species, or through competition for resources in the medium and long term. This issue is further exacerbated by their high fertility rate, with healthy populations producing up to four offspring per year. (Carvalho et al., 2018; Mittermeier et al., 1982).

The city of Viçosa, located in southeastern Brazil, is included within the *Callithrix aurita* range; however, it has a long history of invasion by *Callithrix* alien species (i.e., *Callithrix geoffroyi*, *C. jacchus* and *C. penicillata*). As a university town,

Viçosa attracts a diverse community of students and professors from across Brazil and around the world. During the 1970s and 1980s, many marmosets were captured in rural and economically disadvantaged areas, especially in northeast Brazil (i.e., *C. penicillata* and *C. jacchus* natural range). These captured marmosets were then sold in public markets in cities in southeast Brazil (Mittermeier et al., 1982). During this time, it was a common practice for students and Professors to buy marmosets during travels to their hometowns or for academic purposes and bring them to Viçosa as pets. That practice resulted in the reckless release of countless alien marmosets into fragments within the city and its vicinity (Fuzessy et al., 2014; Silva et al., 2018). Consequently, these alien species and their hybrids have now dispersed and occupied numerous fragments, significantly reducing the presence of *C. aurita* groups (Vital et al., 2020).

Considering the history of successive invasions and subsequent hybridization of non-native marmosets in Viçosa, we used active surveys (i.e., linear transect + playback points) and occupancy models to access factors influencing the occupancy and detection probabilities of *Callithrix* sp. (i.e., non-native species, including hybrids) in forest fragments. We believe that Viçosa acts as a source of dispersion for *Callithrix* sp., given that over the decades, due to their high fertility rate, these animals have reached high densities in urban fragments, dispersing into the rural area. Therefore, we hypothesize that the occupancy of *Callithrix* sp. will be positively correlated with the proximity to the center of Viçosa.

Likewise, we hypothesized a positive correlation between *Callithrix* sp. occupancy probability and landscapes with a high percentage of native forests or with a high connectivity with areas containing forest structures (i.e., not only native and regenerating forests, but also eucalyptus fields). The main reason is that marmosets are arboreal primates and use these structures either as natural habitats (i.e., native forests) or for dispersal purposes (i.e., eucalyptus fields) (Rylands et al., 2009; Sussman & Kinzey, 1984). Finally, we hypothesized a negative correlation between detection

probability and fragment size, as the probability of detecting a group of marmosets in smaller than in larger fragments being higher, as the sound of the playback may propagate better in the former than in the latter; and because we have a better probability to sample within an area used by a marmoset group in small fragments rather than bigger ones.

2. MATERIAL AND METHODS

2.1 Study Area

The study was conducted in the microregion of Viçosa, southeastern Minas Gerais state, Brazil (Fig. 1). The region is part of Atlantic Forest biome and had experienced significant deforestation, leaving thousands of small forest patches surrounded by a heterogenous matrix composed by small cities, eucalyptus fields, pasture and croplands (Melo, 2006; Valverde, 1958). Altitude varies between 510 to 1950m, with an average of 840m (SISEMA, 2021). The climate, according to the Köppen classification, is Subtropical Humid (Cwa), with hot summers, averaging 23°C; and dry winters, averaging 16°C (Alvares et al., 2013).

2.2 Sampling Protocol

We employed a standard protocol for selecting forest fragments to be sampled. Using ArcGIS 10.5 (ESRI, 2019), we created three buffers at different distances (i.e., 10 km, 20 km, and 30 km) from downtown Viçosa. Each buffer was divided into four quadrants, resulting in 12 semi-circular buffers areas, with three areas for each quadrant (Fig. 1). Within each semi-circular buffer area, we randomly select fragments from four size categories: 1) < 50 ha; 2) ≥ 50 ha and < 100 ha; 3) ≥ 100 ha and < 200 ha and 4) ≥ 200 ha. These fragments were identified and extracted from a shapefile representing the Atlantic Forest remnants of the state of Minas Gerais (in Portuguese, “Remanescentes de Mata Atlântica do Estado de Minas Gerais”) (Fundação SOS Mata Atlântica, 2016).

The total area covered by the buffers was 3,019 km², encompassing 23

municipalities, of which 14, including Viçosa, had fragments selected by our sampling protocol. Initially, we aimed to select 48 fragments, as our sampling protocol accounted for four size categories for 12 semicircular buffer areas, however, some buffer areas lacked fragments in some size categories, leading us to select a total of 40 fragments.

Data collection was performed at fragments' borders, employing transect with playback methods, to enhance the detection of *Callithrix* species. The use of these techniques combined is widely adopted in surveys targeting marmosets, yielding significant results for endangered species (i.e., *Callithrix aurita*). This species exhibits elusive behavior, making it challenging to detect using traditional survey methods (Brasileiro, 2022; Massardi et al., 2022; Pacheco et al., 2022; Vital et al., 2020).

The sample points for playback were randomly generated by the 'Random Points' tool, available in ArcGIS 10.5 (ESRI, 2019). We respected a minimum distance of 300 meters between sampled points to minimize chances of a potential lack of independence between playback records, assuming after pre-testing that it could be listened in a distance < 300 m. To decide how many points should be sampled in each fragment, we divided its perimeter by 300 m (i.e., the minimum distance between points) and then dividing the result by 2, getting more space between sampled points. The number of points varied according to the perimeter length of each fragment, being larger fragments more sampled than smaller ones.

We utilized a multifunctional Bluetooth speaker HF-Q3 (frequency range: 150 hz – 20 khz) to broadcast a two-minute sequence of long calls (i.e., ‘phee’ calls) of *C. aurita*, which were previously obtained from a local group. It is known that marmosets, regardless of species, respond to interspecific long calls. In addition, average vocalization frequencies for the genus range between 6 and 7 kHz (Mendes, 1997). Thus, we assumed that the utilization of long calls from native species would not interfere with the playback response rate.

Marmosets employ long calls for various purposes, such as territorial defense (Mendes,



1997). When this vocalization is broadcast, it emulates a territorial contest, inducing nearby groups to vocalize in response and approach the sound origin. Once sighted, they can be photographed and identified (Mendes, 1997; Mendes & Melo, 2007). At each point, we performed three playback sessions spacing by two minutes. The first playback sessions started between 6:00 - 8:00 a.m. and finalized around 12:00 p.m. No points were sampled inside the fragments due to logistical constraints, especially difficulties to access the interior of most of them. All sampled points within each fragment were visited only once, and campaigns were conducted in August - September 2018 and May - September 2019 for sampling all fragments, where each fragment was sampled for a short period (mean time (days) = 1,87; minimum = 1; maximum = 23).

2.3 Modeling *Callithrix* sp. occupancy and detection as a function of covariates

The non-detection of *Callithrix* sp. in sampled fragments does not necessarily mean a true absence, as it might be related to an imperfect detection (i.e., detection is < 1) or false absence, which is common in many biological and ecological studies (MacKenzie et al., 2002). To address the potential issue of false absences and have unbiased estimates of factors influencing *Callithrix* sp. occurrence in these fragments, we used an single-season occupancy modeling approach (MacKenzie et al., 2002). In this approach, the occupancy probability (ψ) is defined as the probability that a site i (in our case, the fragment) is occupied by the target taxa (i.e., *Callithrix* sp.), while the detection probability (p) is defined as the probability of detecting the target taxa at a site i at time (or sampling occasion) t , given that the site is occupied. Both parameters can be modeled as function of relevant covariates. It is worth noting that sampling occasions are usually established as different visits to the same sampling unit but can also be established in a single visit with different observers or with different collection methods, or even as different sampling points within the large sampling unit (MacKenzie et al., 2002). In

our case, due to field logistics, we were unable to carry out different visits to each fragment and, therefore, we established the playback points as our sampling occasions.

To investigate the environmental factors influencing *Callithrix* sp. occupancy probability, we incorporated a 300-meter radius buffer around the perimeter of each fragment and extracted habitat feature covariates from both the total area encompassed by the buffer and the fragment area (i.e., landscape). We choose this buffer radius based on insights from Melo (pers. comm.), as it represents a distance that can be traversed by marmosets in areas of non-forest matrix.

Vegetation classes used in the study, including Native Forest, Native Forest in Regeneration, and *Eucalyptus* Field, were extracted from images provided by DigitalGlobe®, available through the Basemap option in ArcMap (ESRI, 2019). The following metrics were considered: 1) distance (meters) to the center of Viçosa (DV); 2) percentage of native forest (P_NF); 3) Connectance index (CONNECT) (McGarigal, 2015) for the class “Native Forest” (C_NF); 4) Connectance index for the class “Native Forest in Regeneration Stage” (C_RS) and; 5) Connectance index for the Class “*Eucalyptus* Field” (C_EF).

The connectance index calculates the percentage of functional connections between same class in a landscape (McGarigal, 2015). We considered not only the class of native forest, but also the classes of regenerating native forest and eucalyptus fields as potential connectors between the fragments. Finally, we used the fragment area (AS) to explore its influence on *Callithrix* sp. detection probability. We used Fragstats (McGarigal & Marks, 1995) and ArcGIS 10.5 (ESRI, 2019) to calculate these metrics. We evaluated for correlation among our selected variables, but none were highly correlated ($|r| \leq 0.70$ in all cases) (Table 1).

2.4 Data analysis

We compiled the playback records of *Callithrix* sp. to compose detection histories for each fragment. For each point within a fragment, we documented whether *Callithrix* sp. was detected (1) or not (0) during

Table 1. Covariates used to model the probabilities of occupancy and detection of *Callithrix* sp. in the microregion of Viçosa, southeastern Brazil. Mean and range (minimum-maximum) of each covariate are given considering each forest fragment plus a 300-m-radius buffer surrounding them. Data relating to each fragment is available in appendix 2

Tabela 1. Covariáveis utilizadas para modelar as probabilidades de ocupação e detecção de *Callithrix* sp. Na microrregião de Viçosa, sudeste do Brasil. Média e amplitude (mínimo-máximo) de cada covariável são listadas considerando cada fragmento somado ao buffer de 300 metros ao redor do mesmo. Dados relacionados a cada fragmento estão disponíveis no Apêndice 2

Variables	Mean (min – max)
For p	
AS – Fragment Area Size (ha)	174,88 (6,18 – 1111,00)
For Ψ	
DV – Distance to Viçosa (m)	15,829 (1,606 – 29,595)
P_NF – % of Native Forest	31,56 (15,35 – 50,38)
C_NF – Connectance Index of Native Forest (%)	34,97 (8,72 – 100,00)
C_RS – Connectance Index of Native Forest in Regeneration Stage (%)	15,84 (2,01 – 60,00)
C_EF – Connectance Index of <i>Eucalyptus</i> Field (%)	18,03 (0,00 – 100,00)

playback sessions. Additionally, apart from the records obtained through playbacks, any direct observations of *Callithrix* sp. individuals were also included as records if they were spotted at the playback points either after or during the interval of the playback samplings.

We adopted a ‘step down’ strategy (Lebreton et al., 1992) to construct single-season occupancy models in Program MARK (White & Burnham, 1999). Using a fix structure of a most parametrized model (containing all covariates) for Ψ , we built different model structures with only one covariate for p. Based on the best ranked models that contained the most explanatory covariates ($\Delta AICc \leq 2$; Burnham & Anderson, 2002) for p, we began to build different model structures with only one covariate for Ψ , fixing the most explanatory covariates for p in a single model structure. In the last step, we identified the models and covariates that provided the best support and that were most likely determinants of the occupancy and detection probabilities of *Callithrix* sp.

We used the maximum likelihood procedures available in Program MARK to estimate the occupancy and detection probabilities of *Callithrix* sp. Due to model selection uncertainty, we calculated model-averaged estimates of *Callithrix* sp. occupancy probability. Finally, using our most parametrized model, we performed a Goodness-of-fit (GOF) test to evaluate for

overdispersion (i.e., $\hat{c} \geq 1$), which might be interpreted as a lack of independence among our observations in the sampled fragments. This test was performed in Program Presence (Hines, 2006) using a Pearson’s GOF test, which was developed specifically for the single-season occupancy model (MacKenzie & Bailey, 2004).

3. RESULTS

Of the 40 forest fragments surveyed, 39 were visited (one was lost due to a forest fire), totaling 210 playback points. During these surveys, we recorded 27 direct and indirect observations (i.e., vocalizations) of *Callithrix* sp. at 24 playback points, distributed across 17 sampled fragments, resulting in a naïve occupancy of 17/39 (0.43). Among the 27 records, 26 were identified as *Callithrix* alien species or their hybrids. Only one group, found in a single fragment, included an individual displaying a phenotype consistent with *C. aurita* (i.e., exhibiting all known pelage patterns of *C. aurita*), suggesting a mixed group. No groups composed solely of *C. aurita* were detected in this study (Figure 1). Further information regarding each forest fragment is provided in Appendix 1 and 2.

The Goodness-of-fit test (GOF) indicated no significant overdispersion ($\chi^2 = 138676.6843$, $\hat{c} = 1.77$, $P = 0.06$). Model-averaged estimates of *Callithrix* sp. occupancy probability were 0.93 ($\Psi = 0.93$; 95% CI = 0.66 - 1.00) while the probability

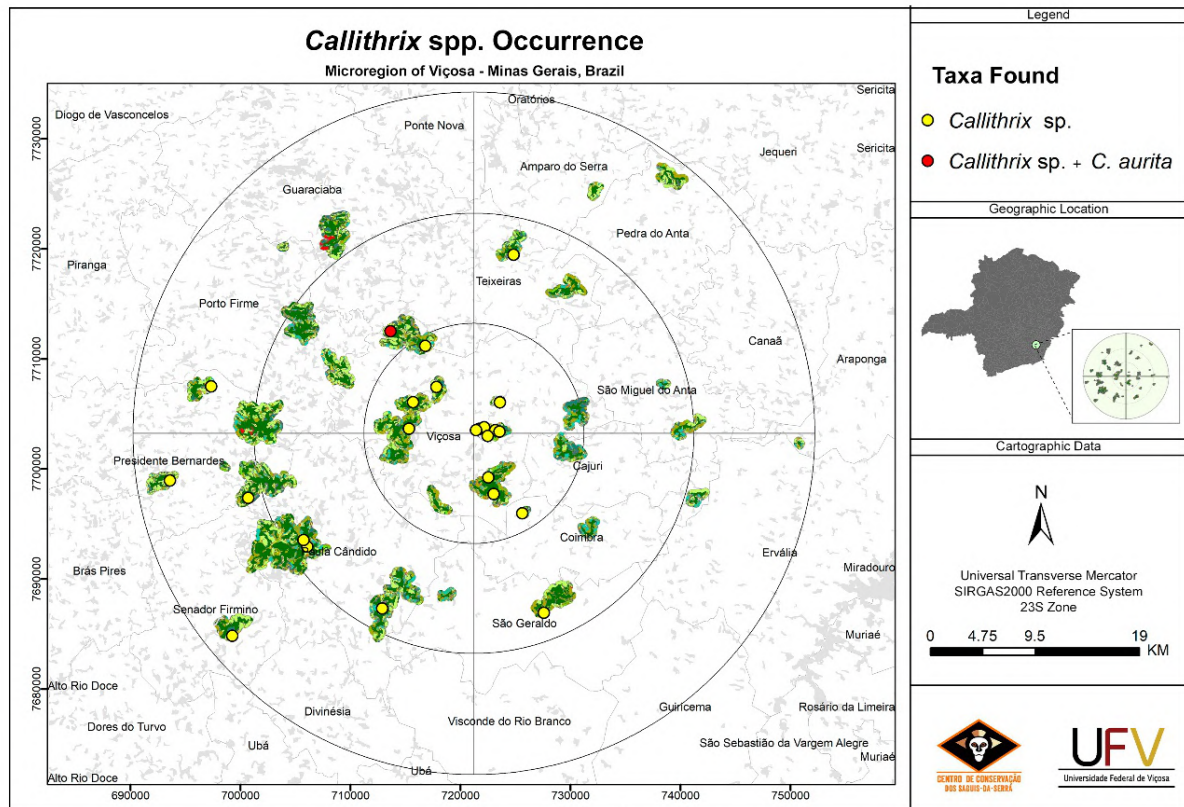


Figure 1. Buffers of 10, 20, and 30 km radius from the center of Viçosa divided into 12 semi-circular areas, which were used to randomize the fragments to be sampled for *Callithrix* sp. The 39 landscapes (fragment + buffer of 300 m) are also represented as well as the playback points where groups of either *Callithrix* sp. (in yellow) or mixed groups formed between *C. aurita* and *Callithrix* sp. (in red) were found

Figura 1. Buffers de 10, 20 e 30 km de raio, a partir do centro de Viçosa, divididos em 12 áreas semi-circulares. Cada área foi utilizada para escolher fragmentos de maneira aleatória a serem levantados. As 39 paisagens (fragmento + buffer de 300 metros) estão representadas no mapa, assim como os pontos de playback onde foram encontrados grupos de *Callithrix* sp. (em amarelo) e o grupo misto, formado por um indivíduo de *Callithrix aurita* e demais indivíduos de *Callithrix* sp. (em vermelho)

of detecting *Callithrix* sp. in the playback points was 0.12 ($p = 0.12$; 95% CI = 0.07 - 0.21). There were no detection differences among different size fragments. Although models with covariates were supported by our data ($\Delta AICc \leq 2$; Table 2), the null model (i.e., intercept-only) structure was ranked as the most parsimonious model, indicating a weak effect of these covariates on the *Callithrix* sp. occupancy probability.

4. DISCUSSION

The presence of non-native marmosets in Atlantic Forest fragments extends beyond the Viçosa region and is widespread across several areas in southeastern Brazil (Aximoff et al., 2016; Brasileiro, 2022; Carmo, 2023;

Carvalho et al., 2018; Detogne et al., 2017; Massardi et al., 2022; Pacheco et al., 2022; Pereira et al., 2008; Silva et al., 2018). This invasion poses a serious ecological problem for native species populations, such as *C. aurita* and *C. flaviceps*.

In our sampled area, only one individual, apparently *C. aurita*, was observed within a mixed group composed of hybrid individuals, likely resulting from mating between *Callithrix aurita* and *C. penicillata*. The presence of such mixed groups indicates the ongoing expansion of invasive species in the region (Fuzessy et al., 2014; Silva et al., 2018) exposing the remaining *C. aurita* populations to deleterious events such as hybridization depression, introgression and

Table 2. Model selection results of detection (p) and occupancy (Ψ) probabilities of *Callithrix* sp. in the microregion of Viçosa, southeastern Brazil using the “step-down” strategy. Ψ modeled as function of: Distance from the center of Viçosa (DV); Percentage of the class “Native Forest” in the landscape (P_NF); Connectance index for the Native Forest, “Native Forest in Regeneration Stage” and “Eucalyptus Field” classes (C_NF, C_RS and C_EF, respectively). p modeled as function of the “size of the sampled fragment area” (AS)

Tabela 2. Seleção de modelos resultante da probabilidade de detecção (p) e ocupação (Ψ) de *Callithrix* sp. Na microregião de Viçosa, usando a estratégia step-down. O Ψ foi modelado em função do somatório de todas as variáveis: Distância do centro de Viçosa (DV); Porcentagem de mata nativa (P_NF); Índice de conectância da Classe “Mata Nativa”, “Mata Nativa em Estado de Regeneração”, e “Campos de Eucalipto” (C_NF, C_RS and C_EF, respectivamente). E p foi modelado em função do tamanho da área do fragmento (AS)

Model	AICc	Δ AIC	AICc (weight)	Parameters	Deviance
Modelling p					
{ Ψ (DV+P_NF+C_NF+C_RS+C_EF)p(.)}	162.15	0.00	0.77	7	144.54
{ Ψ (DV+P_NF+C_NF+C_RS+C_EF)p(AS)}	164.59	2.44	0.22	8	143.79
Modelling Ψ					
{ Ψ (.)p(.)}	153.46	0.00	0.28	2	149.13
{ Ψ (P_NF)p(.)}	154.30	0.83	0.19	3	147.61
{ Ψ (C_NF)p(.)}	154.58	1.11	0.16	3	147.89
{ Ψ (DV)p(.)}	155.08	1.61	0.12	3	148.39
{ Ψ (C_RS)p(.)}	155.23	1.76	0.11	3	148.54
{ Ψ (C_EF)p(.)}	155.58	2.12	0.10	3	148.90
{ Ψ (DV+P_NF+C_NF+C_RS+C_EF)p(.)}	165.14	11.6	0.00	7	147.53

genetic innovation and adaptation of hybrids (Rhymer & Simberloff, 1996; Malukiewick, 2019). These events could cause a genetic erosion of native populations, leading it to local extinction in the mid and long term (Carvalho et al., 2018; Melo et al., 2021). A survey conducted in the same region in 2017 found a similar result, with 31 fragments sampled in Viçosa and its surroundings resulting in 21 groups of *Callithrix* spp., 1 mixed group, and only 1 group formed exclusively by *C. aurita* (Vital et al., 2020). The majority of records (63%, $n = 17$) consisted of *C. penicillata* and hybrids exhibiting a pelage pattern similar to this species.

The observed deforestation in the Atlantic Forest might be creating more favorable conditions for the persistence and proliferation of *C. penicillata* (Braz, Lorini & Vale, 2019). The species shows a more specialized dentition to gummivory, allowing it to survive in small and disturbed areas (Vilela & Del-Claro, 2011). Also, the species is native to the Cerrado biome (Rylands et al., 2009), characterized by open areas with sparse forest vegetation, resembling the rural

landscape of Viçosa. As the invaders continue to expand in the landscape, the probability of contact with the native species increases, consequently exposing them to competition for resources and hybridization (Carvalho et al. 2019).

The decline of *C. aurita* populations in the region could be also attributed to habitat reduction due to deforestation, which has led to a decrease in available resources and restricted the dispersal of remaining populations. This has consequently limited the species' capacity for population growth (Carvalho et al., 2018; Melo et al., 2020). Although *C. aurita* exhibits elusive behavior and occurs at low densities (Muskin, 1984; Melo et al., 2018), it is reasonable to infer that the deforestation process allied with invasion of non-native marmosets strongly contribute to the scarcity of registers for this species in this study.

We were surprised that none of the evaluated variables provided stronger support than the null model, leading to the conclusion that the occupancy probability of *Callithrix* sp. was not strongly influenced by the



proximity from the city of Viçosa, the connectivity of forest structures or the proportion of native forest within the sampled landscapes. However, it is important to highlight that the high occupancy probability (i.e., 0.93) underscores the severity of invasion by alien species and their hybrid forms in the sampled fragments. These findings suggest that other factors may create favorable conditions for marmosets to disperse, irrespective of whether there is a predominance of forest classes in the landscape. For example, the presence of marmosets in these areas could be facilitated by various landscape features and diverse human land use practices, extending beyond the proportion of native forest or patch connection and that perhaps need to be measured a finer scale.

The weak effect of the distance from the center of Viçosa on *Callithrix* sp. occupancy probability indicates that the city might not currently serve as a dispersal center for non-native marmosets. It is likely that the hybrid population, consisting of former invaders introduced to Viçosa decades ago, has experienced relevant growth and dispersion throughout the fragments. As a result, inputs generated by Viçosa may no longer play a relevant role in influencing the population dynamics of non-native marmosets. It is essential to acknowledge that despite the smaller size and predominantly rural economy of other sampled municipalities, which lack the same level of human traffic observed in a university town like Viçosa, there remains a possibility that they could also serve as dispersal centers for non-native marmosets. Thus, conducting historical surveys and accessing data from environmental police regarding marmoset releases in these areas are valuable measures that can help shed light on this matter and contribute to a better understanding of the situation.

It is also worth noting that primates which demonstrate the ability to utilize the matrix and its different components tend to have greater long-term viability of their populations in fragmented environments (Marsh, 2003). Additionally, a similar study conducted with *C. penicillata* and *Callicebus*

nigrifrons (Sales et al., 2016) showed that neither the amount of forest nor their connectivity was a reliable predictor of colonization and extinction of these species, thus reinforcing our own findings. The environmental plasticity and adaptability of *C. penicillata* to open and sparse vegetation areas, such as those found in the Cerrado biome and the anthropic matrix surrounding Viçosa, can present challenges in predicting the dispersal and occupancy patterns of these animals based solely on traditional forest variables. Therefore, future research should provide further insights into how exotic species are taking advantage of deforestation to disperse and populate fragments in the southeastern region of Brazil. By exploring this phenomenon, we can better understand the impact of deforestation on the distribution and dynamics of non-native marmoset species in the area.

We also did not observe an influence of fragment size on the detection probability of marmoset groups in the sampled areas, which might suggest that the sound of the playback propagated equally among our fragments of different sizes and thus, did not influence the marmoset detection. However, it is important to emphasize that the occupancy probability estimates we obtained from the sampled landscapes might be biased high due to the low detection probability (0.12) observed during our study. This low detection probability can introduce a potential bias, potentially resulting in an overestimation of the actual occupancy rate (Mackenzie et al., 2002). The low probability of detection observed in our study can be partly attributed to the sampling design, which specifically targeted the edges of fragments. However, conducting surveys along fragment borders comes with inherent limitations due to the study area's characteristics, which include secondary forest fragments of varying sizes and without accessible trails within a rural matrix, which is the scenario of Viçosa. Despite the inherent limitations, this approach has been successfully employed in marmoset species surveys for several years, consistently yielding satisfactory results. Notably, this method has led to important findings, including observations of threatened species like *C. aurita* in locations where the

species had never been recorded before (Brasileiro, 2022; Pacheco et al., 2022). Additionally, this approach has facilitated the rediscovery of marmoset populations (i.e., *C. aurita*) in areas where the species was previously considered regionally extinct (Vital et al., 2020).

Another factor that can explain the low detection probability is the deforestation process observed in our study area, which occurred mostly in the 19th century as a result of coffee plantation expansion (Lira et al., 2021; Valverde, 1958). Today, primary forest fragments were not observed, indicating that most of the native forest patches were removed at some point during exploration. With the forest clearing, the fauna that lived there had suffered some type of impact (i.e., population decrease), including arboreal species such *C. aurita* (i.e., native species). Deforestation has significantly reduced the local fauna by shrinking their habitat and isolating the remaining populations in fragments of the Atlantic Forest, especially for arboreal species such as *Callithrix aurita*.

Deforestation had consequences beyond its direct impact on the former *C. aurita* population. In the medium and long term, the remaining groups may have been subject to stochastic processes, such as population variations caused by environmental catastrophes like epidemics and forest fires (Pardini, Nichols & Puttker, 2017). Such variations tend to be more severe in populations isolated by fragmentation due to the small number of individuals and their difficulty or inability to disperse to more stable environments. Additionally, isolation increases homozygosity, resulting from the mating of closely related individuals. An increased frequency of homozygosity can fix recessive alleles, resulting in inbreeding depression and a subsequent loss of genetic variability and population reduction in small, isolated populations (Frankham et al., 2019).

From the mid-20th century, with the decline of coffee plantations and the beginning of rural exodus, fragments started to form in previously cleared areas. It's conceivable that these relatively new

fragments might not have been colonized by any remaining populations of *C. aurita* or by invasive species and their hybrids. This situation could explain the observed low detectability, even in the case of small fragments, as observed not only in this study but also in others conducted within the region (Massardi et al, 2022; Pacheco et al., 2021; Silvério, 2022; Vital et al., 2020).

In future research and monitoring efforts, enhancing detection techniques, and employing complementary survey methods such the use of thermal cameras allied with playback points (Massardi, in prep.), can help mitigate the detection probability issue, leading to more robust and reliable estimates of occupancy probabilities for the marmoset populations in the studied landscapes. By addressing these methodological considerations, we can obtain a more comprehensive and accurate assessment of marmoset occupancy and population dynamics, which is crucial for effective conservation and management strategies.

Our study offers valuable insights into the occupancy probabilities of invasive marmoset species in fragmented landscapes of southeastern Brazil. The ongoing deforestation, coupled with the invasion of non-native marmosets, exacerbates the threats to *C. aurita* populations, likely accelerating their decline both within the study area and across their entire distribution range. To gain a deeper understanding of the specific mechanisms driving the dispersal and successful establishment of marmoset invasive species in these anthropogenic landscapes, further research is essential. Investigating the interactions between invasive marmosets and the human-altered environment can provide valuable insights into their adaptability and resilience in such habitats. Also, genetic studies related to invasive and hybrid groups can provide information about their origins and possible assimilation of native populations. These findings will be crucial for developing effective conservation strategies and management plans to mitigate the potential positive influence of human activities on these non-native species and protect the native species.

Additionally, to advance our



understanding and conservation efforts, future research should focus on refining detection methods and incorporating complementary survey techniques. By addressing these limitations, we can work towards safeguarding this remarkable primate and its critical role in the ecosystems it inhabits. Such conservation endeavors are crucial to ensure the long-term viability and survival of native marmoset populations in the face of anthropogenic pressures and landscape fragmentation.

Relevant efforts are underway to preserve the genetic heritage of *C. aurita* populations, highlighted by the establishment of the Mountain Marmosets Conservation Center (CCSS – UFV) within the Federal University of Viçosa. This center's primary mission is to create captive colonies of *C. aurita* and *C. flaviceps*, aiming to counteract the increasing hybridization in the region. The CCSS – UFV is a component of the Mountain Marmoset Conservation Program (MMCP), an initiative created to integrate and direct proposals and projects for the conservation of the aforementioned species, involving researchers, NGOs, universities and companies. Additionally, extensive population surveys are being conducted in areas where *C. aurita* still persists, with the objective of understanding potential differences in habitat occupancy preferences between native and non-native marmoset species. Such initiatives are essential measures contributing to the conservation of *C. aurita* in the medium and long term.

5. CONCLUSION

While it is promising that these efforts may offer some hope for the survival of native populations where they still prevail, our current findings paint a concerning picture. No pure *C. aurita* groups were found, and instead, the invasive species and their hybrids exhibited a high occupancy probability in the studied landscapes. This unfortunate reality emphasizes the urgent need for intensified conservation actions. By continuing to monitor the success of *C. aurita* in modified landscapes and implementing targeted conservation measures, we can strive to ensure the persistence of this native species in its remaining habitats. The collaborative efforts

of research institutions, conservation organizations, and policymakers, as the MMCP, are crucial in safeguarding the future of *C. aurita* and preserving the rich biodiversity of the region.

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AUTHOR CONTRIBUTIONS

O.V.: Conceptualization, Data Curation, Methodology, Project Administration, Writing – Original Draft. R.M.: Conceptualization, Formal Analysis, Methodology, Software, Visualization. R.S.: Data Curation, Software, Visualization, Writing – Review & Editing. F.C.M.: Funding Acquisition, Resources, Supervision, Writing – Review & Editing. F.R.M.: Conceptualization, Funding Acquisition, Resources, Supervision, Writing – Review & Editing.

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