

RESEARCH ARTICLE

Effect of landscape attributes on the occurrence of the endangered golden-headed lion tamarin in southern Bahia, Brazil

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Abstract

The golden-headed lion tamarin (*Leontopithecus chrysomelas*) is an endangered primate that occurs exclusively in the Atlantic Forest of southern Bahia, Brazil. Its geographic range has been severely reduced by deforestation and its populations are restricted to a human-modified landscape consisting primarily of Atlantic forest fragments and shade cacao (*Theobroma cacao*) agroforestry, locally known as *cabruças*. In the last 30 years, there has been a 42% reduction in the geographic range and a 60% reduction in the population size of *L. chrysomelas*, with only 8% of its habitat represented by protected areas. Thus, we investigated the occurrence of *L. chrysomelas* in forest fragments and *cabruças* based on interviews and using playback census, and evaluated the influence of landscape attributes on its occurrence. The occurrence was measured using a Generalized Linear Model using a set of 12 predictor variables, including fragment size and elevation. *L. chrysomelas* inhabited 186 (38%) of the 495 forest fragments and *cabruças*. Most inhabited habitat patches ($n = 169$, 91%) are in the eastern portion (ca. 70 km wide region from the Atlantic coast to inland) of its geographic range. The remaining ($n = 17$, 9%) are in the western portion of the distribution, between 70 and 150 km from the Atlantic coast. Our models indicate a higher occurrence of *L. chrysomelas* in the eastern portion of its geographic range, where the landscape exhibits lower land cover diversity, greater functional connectivity, lower altitudes (<400 m), and is primarily composed of forest fragments and *cabruças* with a higher core percentage. In contrast, we observed a lower occurrence of *L. chrysomelas* in the western portion,

where the landscape is more diverse and heterogeneous due to anthropogenic activities, such as agriculture and livestock. We urge the establishment of ecological corridors via reforestation of degraded areas in the western portion of the range. This increase in habitat availability and suitability in the west together with the protection of the forests and *cabruças* in the east would increase our chances of saving *L. chrysomelas* from extinction.

KEYWORDS

Atlantic forest, habitat degradation, landscape variables, *Leontopithecus chrysomelas*, occupation

1 | INTRODUCTION

The continuous conversion of natural forests to anthropogenic use, such as rapid urbanization and intense land use for agriculture and livestock, is one of the greatest threats to global biodiversity (Ellis et al., 2010; Fonseca et al., 2009). As a consequence of this anthropogenic impact, habitat loss and fragmentation intensifies (Fahrig, 2003, 2013), and species that are highly dependent on forests, such as South American primates, are greatly affected (Chapman & Peres, 2001; Gilbert & Setz, 2001; Marsh et al., 2013). In the last decades, research has demonstrated the negative effects of habitat loss and fragmentation on primates (e.g., Arroyo-Rodríguez & Mandujano, 2006; Arroyo-Rodríguez et al., 2013; Bicca-Marques et al., 2020; Chiarello & de Melo, 2001; Costa-Araújo et al., 2021; Gestich et al., 2019), such as gradual declines in their populations and alterations in their geographic distributions (Isabirye-Basuta & Lwanga, 2008; Strier, 2009), changes in behavioral responses (Cristóbal-Azkarate et al., 2005; Pozo-Montuy & Serio-Silva, 2006), and reductions in home range size (Chiarello, 2000; Chiarello & de Melo, 2001). Due to the greater intensity of anthropogenic activities in the tropics, the consequences of anthropogenic disturbances may be more critical for primates that occur in tropical forests (Culot et al., 2019; Estrada et al., 2017; Galán-Acedo et al., 2019).

Studies with primates living in tropical forests have shown that the characteristics of the surrounding landscape can affect the structure of the vegetation and, in turn, the availability of food resources in forest fragments (Arroyo-Rodríguez & Mandujano, 2006; Gestich et al., 2021; Hilário et al., 2022). The reduction in size and greater isolation of forest fragments results in reduced seed dispersal for many plant species, because fewer fruits are removed from trees by primates and seed dispersal distances are truncated due to disperser absence (McConkey et al., 2012; Pereira et al., 2022). There is a lower diversity of primates in small degraded forest fragments (Chapman & Onderdonk, 1998), which may also affect the occurrence of these species in fragmented landscapes. In this context, primates that occur in disturbed tropical forests, such as the target species of this study, the golden-headed lion tamarin (*Leontopithecus chrysomelas*), are representative study models to understand the

impacts of anthropogenic habitat disturbances on the occurrence of primates.

L. chrysomelas is an Endangered callitrichid primate found in a restricted and fragmented region of the Atlantic Forest in southern Bahia state, Brazil (Oliveira et al., 2021; MMA/Ordinance No. 444/2022). Its geographic range has been severely reduced by deforestation and currently its populations are restricted to a highly human-modified landscape (Raboy et al., 2010; Teixeira, 2022), in which the attributes of this landscape may affect its occurrence. Primate surveys performed between 1991 and 1993 estimated the population size of *L. chrysomelas* between 6187 and 15,429 individuals and its geographic range at 19,426 km² (Pinto & Rylands, 1997); however, these estimates are outdated (Raboy et al., 2010; Teixeira, 2022). Between 1987 and 2007, *L. chrysomelas* lost approximately 13% of its viable habitat (Zeigler et al., 2010). There was a reduction in the number of occurrences of the species in areas sampled by Pinto and Rylands (1997) between 1991 and 1993 (Raboy et al., 2010). Compared to the estimates by Pinto and Rylands (1997), there was a reduction of 42% and 60%, respectively, in the geographic range and population size of *L. chrysomelas* (Teixeira, 2022).

In the eastern portion of the geographic range of *L. chrysomelas* (region close to the Bahian coast and about 70 km wide starting on the Atlantic coast), forest cover is predominantly composed of shade cacao (*Theobroma cacao*) agroforestry, locally known as “cabruças” (Araujo et al., 1998; Faria et al., 2007; Zeigler et al., 2010). As in forests, *cabruças* provide resources (food and shelter) to maintain populations of *L. chrysomelas* (Oliveira et al., 2010, 2011). In the western portion (most interior region in the state of Bahia, between 70 and 150 km from the Atlantic coast), forest fragments have been suffering the consequences of habitat loss and fragmentation at a greater rate and scale compared to the eastern portion (Azevedo et al., 2021; Raboy et al., 2010). The western forest fragments are constituted by degraded secondary vegetation and are isolated by large areas of pasture (Guidorizzi, 2008; Zeigler et al., 2010, 2013), potentially limiting the movement of *L. chrysomelas* between forest fragments. Western forest fragments are also more prone to edge effects (Guidorizzi, 2008; Zeigler et al., 2010), such as increased mortality of large trees and reduced availability of food resources

consumed by forest-dependent species (Laurance et al., 2000; Lindenmayer & Laurance, 2016).

In addition to *cabrucas*, *L. chrysomelas* occurs in other anthropogenically modified habitats, such as secondary forests in distinct stages of regeneration (Oliveira et al., 2010; Raboy et al., 2004) and survives in forest fragments and *cabrucas* of different sizes (Teixeira, 2022). The demographic and ecological parameters of the species vary between these habitats (De Vleeschouwer & Raboy, 2013; Oliveira et al., 2010; Raboy et al., 2004). In *cabrucas*, *L. chrysomelas* occur at a mean density of 0.12 ind./ha [range: 0.04–0.21 ind./ha], whereas in primary forest, its mean density is 0.06 ind./ha [range: 0.04–0.11 ind./ha], perhaps due to greater availability of food resources in *cabrucas* (Oliveira et al., 2011). In forest, the species tends to use lower levels of the vertical strata, but uses upper levels more in *cabrucas*, perhaps due to the greater availability of food resources and greater canopy connectivity in *cabrucas* compared to forests (Almeida-Rocha et al., 2015). Therefore, evaluating the effect of landscape attributes on the occurrence of *L. chrysomelas*, considering all these habitats and their characteristics, is a way to make more refined predictions about which areas should be prioritized for conservation.

Although some studies have indicated that landscape characteristics affect the occurrence of *L. chrysomelas* (Almeida-Rocha, et al., 2020; Raboy et al., 2010), it is not entirely clear which landscape attributes affect its occurrence. According to Raboy et al. (2010), some limitations of their study, including an inability to document forest loss in the 1990s, difficulty in sampling and identifying the occurrence of *L. chrysomelas* in larger forest fragments, and limited sample size (52 locations), prevented more definitive results for predicting the occurrence of *L. chrysomelas*, potentially impacting the accuracy of the model's prediction. Although Almeida-Rocha et al. (2020) achieved promising results regarding habitat attributes favoring *L. chrysomelas* occupancy, such as the greater probability of occurrence of the species in *cabrucas* retaining large-diameter shade trees (likely related to the availability of suitable sleeping sites [Hankerson et al., 2007]), the study was limited to *cabrucas*. This means that the study did not consider other habitats in which *L. chrysomelas* survives, such as primary and secondary forests. Therefore, due to the scarcity of data on attributes that potentially affect the occurrence of *L. chrysomelas*, and the importance of knowing these attributes for conservation planning, we investigated which landscape attributes affect the occurrence of *L. chrysomelas* in its current geographic range.

2 | METHODS

2.1 | Study area

This study was conducted in forest fragments and *cabrucas* located in the geographic range of *L. chrysomelas* in the Atlantic Forest in southern Bahia and a small stretch in northern Minas Gerais, encompassing an area of approximately 45,000 km² (Figure 1). This

area is characterized by a high level of deforestation and fragmentation, especially in the western portion of the species range where the dominant vegetation is tropical seasonal semideciduous forest (Azevedo et al., 2021; Guidorizzi, 2008; Zeigler et al., 2010). The forest fragments of the western portion have been mostly converted to large areas of pasture and currently the landscape is composed of small and isolated degraded forest fragments (Zeigler et al., 2010). The eastern portion retains the largest and most continuous forest fragments, with the coastal evergreen tropical rainforest as the dominant vegetation type (Guidorizzi, 2008; Zeigler et al., 2010). *Cabrucas* cover ca. 60% of *L. chrysomelas* geographic range, with greater dominance in the eastern portion, the region containing the most viable populations (Zeigler et al., 2010).

Using a combination of satellite images (MapBiomas) and published data on the size of the forest fragments and *cabrucas* in the region (Azevedo et al., 2021; Guy et al., 2016; Raboy et al., 2010; Zeigler et al., 2010), we identified sites for field sampling to assess the presence/absence of *L. chrysomelas*. We thus selected 425 forest fragments and *cabrucas* equal to or larger than 40 and 22 ha, respectively, which are the sizes of the smallest documented home range for *L. chrysomelas* in these two habitat types (Oliveira et al., 2010; Rylands, 1989). This sample includes 122 locations where *L. chrysomelas* had been recorded in previous studies (Pinto & Rylands, 1997; Raboy et al., 2010). The vegetation cover within the geographic range of *L. chrysomelas* (except in the western portion) consists of a relatively continuous complex of forest, *cabrucas*, pasture and other agricultural crops (Azevedo et al., 2021; Teixeira, 2022; Zeigler et al., 2010), and it is not possible to distinguish between forest fragment and *cabrucas*. MapBiomas satellite images also do not distinguish between forest fragment and *cabrucas* (Azevedo et al., 2021). Therefore, we did not separately quantify these two habitats.

2.2 | Golden-headed lion tamarin survey

Between June 2018 and March 2022, we performed survey of *L. chrysomelas* in 425 forest fragments and *cabrucas* (323 located in the eastern portion and 102 in the western portion of the geographic range of *L. chrysomelas*) based on interviews with the local community and using playback census (following Pinto & Rylands, 1997; Raboy et al., 2010). The interviews with the local community aimed to assess the occurrence of *L. chrysomelas* and request authorization to inspect forest fragments and *cabrucas* using playback on their rural properties (Supporting Information S1: Table 1). Playback consists of emitting an *L. chrysomelas* long call vocalization in the field to stimulate intraspecific responses and to attract counter-calls (Kierulff & Rylands, 2003; Peres, 1986). The four lion tamarin species (genus *Leontopithecus*) are territorial and use long call vocalizations to warn against the presence of other individuals or groups in their territory (Ruiz-Miranda & Kleiman, 2002). *L. chrysomelas* groups frequently respond with long call vocalizations and move closer to the site of the first playback

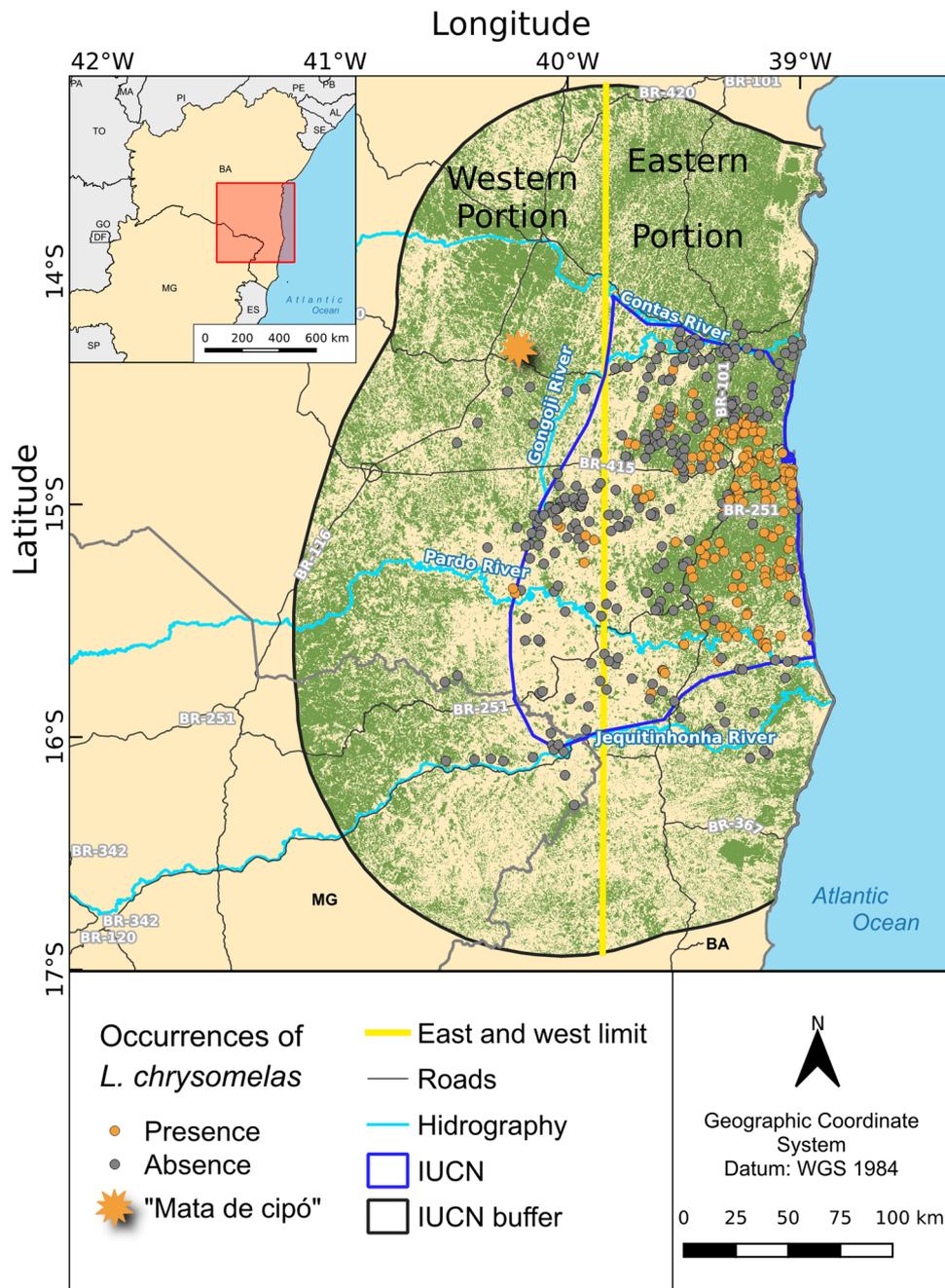


FIGURE 1 Map indicating the distribution of forest fragments and *cabruças* inspected in the study area. The blue line indicates the limit of the geographic range of *Leontopithecus chrysomelas*. The black line indicates the area where the landscape variables were calculated, as well as the spatial prediction areas of the distribution of *L. chrysomelas*. The yellow line indicates the border between the eastern and western portions of the geographic range of *L. chrysomelas*.

(Pinto & Rylands, 1997; Raboy et al., 2010), which ensures the efficiency of this technique for detecting groups in the field.

We traversed pre-existing trails or roads in forest fragments and *cabruças* and established a playback point every 200 m. We set this distance to avoid the overlapping of the species' auditory range (~100 m) and to reduce the chance of detecting the same group more than once on the same day (Almeida-Rocha et al., 2020; Kierulff & Rylands, 2003). Previous studies used the same distance (Almeida-Rocha et al., 2020; Kierulff & Rylands, 2003; Raboy et al., 2010).

Previously, we also tested this distance using a radio-collared *L. chrysomelas* group from another study. At each playback point, three complete long-calls (30 s each call) were directed toward the four cardinal points, holding the speaker ~2 m above ground, followed by a 5-min on-site wait-and-listen interval before performing a new playback. We reproduced male and female calls alternately because long call duets were observed in *Leontopithecus rosalia* for both sexes and sexual differences in the structure of three types of *L. rosalia* vocalizations, including the long call (Benz et al., 1990; Peres, 1986).

TABLE 1 Landscape and anthropic variables used to evaluate the effect of landscape attributes on the occurrence of *Leontopithecus chrysomelas* in the Atlantic Forest in southern Bahia and a small stretch in northern Minas Gerais, Brazil.

Variables	Explanation and calculation
<i>Fragment size</i>	Summed area, in hectares, of one or more fragments connected by structural corridors (identified as parts of fragments with a width smaller than two times the specified edge depth), excluding the area of the corridors and branches connecting them. Specified edge depth to identify structural corridors of 30 m.
<i>Patch size</i>	Summed area, in hectares, of one or more fragments connected by structural corridors (identified as parts of fragments with a width smaller than two times the specified edge depth), including the area of the corridors and branches connecting them. Specified edge depth to identify structural corridors of 30 m.
<i>Structural connectivity</i>	Habitat area, in hectares, structurally connected to a forest fragment or <i>cabruca</i> . This variable considers only connecting structures (other fragments, corridors and/or branches) structurally connected to a forest fragment or <i>cabruca</i> . The greater the number of connecting structures, the greater the structural connectivity. If there are no connection structures attached to the forest fragment or <i>cabruca</i> , its structure connectivity is zero. This variable indicates the amount of area structurally connected to a forest fragment or <i>cabruca</i> . Specified edge depth to identify structural corridors and branches was 30 m.
<i>Functional connectivity area</i>	Amount of functionally connected habitat area, in hectares, taking into account the distance that any focal species are able to cross (e.g., Jorge et al., 2013; Martensen et al., 2012; Ribeiro et al., 2009). This is calculated by generating a buffer of size equal to half of the gap-crossing capacity of the organism, around all patches, grouping all habitat patches close enough in the same clusters of patches, and summing up the area of all the grouped patches (Martensen et al., 2012). We considered the ability to gap-crossing of 60 and 120 m, based on the study by Zeigler et al. (2011), which considers a distance of 100 meters for <i>L. chrysomelas</i> to cross a matrix. Higher values imply greater mobility and consequently more available habitat.
<i>Habitat percentage</i>	Amount of habitat, in meters, available in the landscape. It was calculated as the percentage of habitat, based on the sum of the areas of all forest fragments and <i>cabruca</i> s covered by the buffers of 250, 500, 750, 1000, 1500, 2000, 2500, 3000, 3500, 4000, 5000, 6000, 7000, 8000, 9000, 10,000 m, in relation to the total area covered by each buffer.
<i>Core percentage</i>	The core percentage was calculated as a percentage of the area, in meters, of the forest fragments and <i>cabruca</i> s not subjected to the edge effect (Ribeiro et al., 2009), considering an edge width of 30 m and calculated by several radii (250, 500, 750, 1000, 1500, 2000, 2500, 3000, 3500, 4000, 5000, 6000, 7000, 8000, 9000, 10,000 m)
<i>Edge percentage</i>	Edge percentage (30 m of edge depth) calculated for several radii in meters (250, 500, 750, 1000, 1500, 2000, 2500, 3000, 3500, 4000, 5000, 6000, 7000, 8000, 9000, 10,000 m)
<i>Landscape diversity (Simpson's diversity)</i>	Simpson's diversity index calculated for several radii in meters (250, 500, 750, 1000, 1500, 2000, 2500, 3000, 3500, 4000, 5000, 6000, 7000, 8000, 9000, 10,000 m). The Simpson's index values vary from 0 to 1. Equals 0 when only one patch is present in the analysis radius. Approaches 1 when the number of class types increases and the proportions are equal (Tonetti et al., 2023). Diversity indices work comparatively: An index by itself means nothing. The premise is that there is more than one place to compare the indices. Thus, values close to 0 are homogeneous landscapes and values close to 1 are heterogeneous (Tonetti et al., 2023). All classes available in the land cover and land use classification system for MapBiomias in Brazil were considered (Souza et al., 2020).
<i>Distance from urban areas</i>	Euclidean distance from urban areas in meters (Souza et al., 2020). The urban areas were defined using the urban class from MapBiomias, that includes areas with significant density of buildings and roads, including areas free of buildings and infrastructure (Souza et al., 2020).
<i>Distance from protected areas</i>	Euclidean distance from protected areas in meters (UNEP-WCMC & IUCN, 2021). We used a map of the spatial distribution of the cities of Brazil, obtained from the Brazilian Institute of Geography and Statistics (IBGE, https://www.ibge.gov.br/), to extract the distance from urban areas.
<i>Distance from roads and highways</i>	Euclidean distance from roads in meters (Meijer et al., 2018). We selected roads type (primary roads, secondary roads and tertiary roads), road existence (open), road availability (seasonal access and all year access), and road surface (paved and dirt/sand) (Meijer et al., 2018).
<i>Elevation</i>	Elevation values based on sea level from EarthEnv-DEM90 digital evaluation model in meters (Robinson et al., 2014).

We reproduced the calls using a Sony ICD–PX470 digital voice recorder and a portable Anchor Audio AN–MINI speaker (response frequency: 100–15 kHz \pm 3 dB).

We performed playbacks between 05:00 and 11:00 a.m., the period in which *L. chrysomelas* is most active and likely to be awake (Almeida-Rocha et al., 2020; Raboy & Dietz, 2004; Raboy et al., 2010). When *L. chrysomelas* groups were detected (vocal response or visualization), we recorded their geographic location using a handheld GPS (Model Garmin GPSMAP 65), the hour of detection and, when possible to visualize the groups in the field, the number of individuals and composition (number of adults, juveniles, and infants) (Supporting Information S1: Table 2). These parameters reduced the likelihood of tallying the same group more than once during the field survey.

The number of visits (three) to forest fragments and *cabruças* was defined a priori based on the detection history of *L. chrysomelas* from previous studies that used the same techniques. (Almeida-Rocha et al., 2020; Pinto & Rylands, 1997; Raboy et al., 2010). When we did not detect the species on the first day, we visited the same site twice more on different days. Visits to the same site were separated by at least 1 week to avoid animals habituating to playbacks (Dong & Clayton, 2009). When we did not detect *L. chrysomelas* after the third visit, we considered for this study the site to be absent for the species.

At each visit, we started from a different playback point to increase the detection probability by considering any possible variation in the use of space by the groups throughout the day. We do not play playbacks on rainy days or with strong wind, as these conditions compromised the detection of *L. chrysomelas*. In forest fragments and *cabruças* with difficult access to the interior due to dense vegetation, we established transects at least 1 day before the sampling period. All field sampling was performed by JVST with the aid of a field assistant.

2.2.1 | Landscape variables

Initially, we defined the area for calculating the landscape variables using the geographic range of *L. chrysomelas* from the International Union for Conservation of Nature (IUCN) (Oliveira et al., 2021), adding a buffer of 10 km (Figure 1). We chose this area to ensure that all functionally and structurally connected forest fragments and *cabruças* were considered in the analyses (Marjakangas et al., 2020), as well as all occurrences (presence/absence) of *L. chrysomelas*. We calculated 12 landscape variables for all geographic range of *L. chrysomelas*: (1) fragment size (ha), (2) patch size (ha), (3) structural connectivity (ha), (4) functional connectivity area (ha), (5) habitat percentage, (6) core percentage, (7) edge percentage, (8) landscape diversity (Simpson's diversity), (9) distance from urban areas (m), (10) distance from protected areas (m), (11) distance from roads and highways (m), and (12) elevation (m) (Table 1; Supporting Information S1: Figure 1).

We chose these variables because they are highly relevant to the responses of primates that occur in anthropogenically modified

landscapes (Arroyo-Rodríguez & Mandujano, 2009), such as *L. chrysomelas* (Rezende et al., 2020), *L. chrysomelas* (Raboy et al., 2010), *Callicebus melanochir* (Costa-Araújo et al., 2021), *Callicebus nigrifrons* (Gestich et al., 2019), *Callicebus coimbrai* (Hilário et al., 2022) *Callicebus nigrifrons*, *Callithrix aurita*, and *Sapajus nigritus* (Silva et al., 2015). For the landscape variables, we used categorical land cover classification rasters, reclassified as habitat/non-habitat (habitat for classes: 3–Forest Formation and 4–Savanna Formation) with a resolution of 30 m, derived from Landsat 8, freely available on the MapBiomass version 5 platform for the year 2019 (Souza et al., 2020). We included class 4 (Savanna Formation) after verifying that 31% ($n = 32$) forest fragments situated in the western portion of the geographic range of *L. chrysomelas* were included in this category.

To evaluate the landscape size (scale effect) that best predicted the occurrence of *L. chrysomelas*, we calculated landscape variables that depend on different scales (habitat percentage, core percentage, edge percentage, landscape diversity—these variables can suffer alteration of their value depending on the scale used) in 13 windows of different sizes through moving window analysis (radii—250, 500, 750, 1000, 2000, 3000, 4000, 5000, 6000, 7000, 8000, 9,000, 10,000 m) (Jackson & Fahrig, 2015). The smallest radius (250 m) covers the smallest home range (22 ha) registered for *L. chrysomelas* (Oliveira et al., 2010), while the largest radius (10,000 m) was adopted after verifying, in preliminary analyses, that for some variables the occurrence of *L. chrysomelas* responded to broader scales.

We calculated the anthropic effect variables as Euclidean distance from roads and highways (Meijer et al., 2018), urban areas (Souza et al., 2020), and protected areas (UNEP-WCMC & IUCN, 2021) across the area. After calculating the landscape and anthropic variables, we extracted the values of these variables for the points where field sampling was carried out. We calculated the landscape variables using the application LandScape Metrics (Niebuhr et al., 2022) and the anthropic variables using the module “r.grow-distance,” both using the software GRASS-GIS (Neteler et al., 2012). We also accessed elevation data using the EarthEnv-DEM90 digital elevation model in meters (Robinson et al., 2014) also for each occurrence. We prepared all the maps variables using QGIS 2.0.1 (QGIS Development Team, 2013).

2.3 | Data analysis

Initially, we evaluated the scale effect that best predicted the occurrence of *L. chrysomelas* for the variables that depended on different scales (Table 1) (Jackson & Fahrig, 2015). For this, we defined a set of Generalized Linear Models (GLM with binomial distribution) using the presence (1) or absence (0) of the species (variable response) in relation to landscape variables (predictor variable) calculated at different analysis scales (as previously described). Through model selection by the Akaike Information Criterion (AIC), we checked the weight of evidence (wAICc) (Burnham & Anderson, 2002), selecting, as the best scale, the predictor variable whose model presented the highest Akaike

weight value (Supporting Information S1: Table 3). We then tested the correlation and multicollinearity between the predictor variables using the function “vifstep” in the *usdm* package (Naimi et al., 2014), setting a Pearson correlation coefficient threshold less than 0.75 and a Variance Inflation Factor (VIF) less than 10 as variables to be included in the models (Burnham & Anderson, 2002). Thus, we used the landscape variable that presented the greatest Akaike weight value for the variables measured at different scales and the other landscape variables measured at a single scale to test the correlation and multicollinearity of the models (Supporting Information S1: Table 3).

For the uncorrelated variables and those with low collinearity, we created other GLMs with binomial distributions, using the occurrence of *L. chrysomelas* as the response variable and the landscape variables as predictor variables, individually and in combinations of two predictor variables. Due to the difficulty of interpreting the models, we avoided creating models with more than two predictor variables. We used the function “AICctab” in the *bmle* R package (Bolker & Team, 2016) to find the models that best explained the occurrence of species. To achieve this, we included all the models with one and two variables and, with the results of the function, we considered the models with $\Delta\text{AICc} < 2.0$ as equally plausible to explain the occurrence of *L. chrysomelas* (Table 2).

Last, using the GLMs that best explained our data (presence/absence and landscape and anthropic variables), we used the “predict” function of the raster R package to make spatial predictions using the estimated parameters from models and the rasters of the landscape and anthropic variables (Hijmans, 2012). This resulted in maps with the predicted values, indicating the suitability to find the species in the field for areas that we not sampled, just considering the structure of the landscape (Figure 3)

(Supporting Information S1: Table 4). We performed all the analyses using R version 3.6.3 (R Core Team, 2020) and the R package *glmulti* (Calcagno & Mazancourt, 2010).

3 | RESULTS

We registered the occurrence of *L. chrysomelas* in 38% ($n = 186$) of the 425 investigated forest fragments and *cabrucas*. A total of 91% ($n = 169$) of the forest fragments and *cabrucas* in which *L. chrysomelas* was recorded are located in the eastern portion of its geographic range, and only 9% ($n = 17$) are located in the western portion. During field surveys, we registered *L. chrysomelas* for the first time in a transition area between the Caatinga and Atlantic Forest biomes, also known as “mata de cipó.” This record in *mata de cipó* was obtained at approximately 860 m above sea level, the highest elevation recorded for *L. chrysomelas* (Figure 1). Approximately 92% ($n = 171$) of the 186 forest fragments and *cabrucas* with occurrence of *L. chrysomelas* are located 400 m above sea level.

From the set of landscape variables, those that best explained the occurrence of *L. chrysomelas*, based on the models, were elevation, core percentage, functional connectivity area, and landscape diversity. The “scale of effect” for the variables core percentage and landscape diversity were more plausible for explaining the occurrence of the species, when considered at larger scales than 5000 and 1500 m, respectively. The models with two variables: (1) elevation + functional connectivity area, (2) elevation + core percentage, and (3) elevation + landscape diversity, with $\Delta\text{AICc} < 2$ and the sum of Akaike weight = 0.99, were the most plausible models to explain the occurrence of *L. chrysomelas* (Table 2, Figure 2). Model selection using the complete model and the models with two variables

TABLE 2 Model results for explaining the occurrence of *Leontopithecus chrysomelas* in its geographic range.

Model	Variables	Estimate	Standard error	p Value	ΔAICc	wAIC
1	Core percentage	0.0327	0.0053	<0.01	0	0.3612
	Elevation	-0.0040	0.0007	<0.01		
2	Functional connectivity area	0.5199	0.0908	<0.01	0	0.3526
	Elevation	-0.0032	0.0007	<0.01		
3	Landscape diversity	-3.5648	0.5835	<0.01	0.5	0.2845
	Elevation	-0.0045	0.0007	<0.01		
4	Functional connectivity area	0.5280	0.0953	<0.01	11.2	0.0013
	Landscape diversity	-2.2973	0.5920	<0.01		
1	Core percentage	0.0012	0.0093	>0.05	0	0.9957
	Elevation	-0.0034	0.0007	<0.01		
	Functional connectivity area	0.3687	0.1187	<0.01		
	Landscape diversity	-2.4677	0.8261	<0.01		
2	Core percentage	0.0327	0.0053	<0.01	12.9	0.0015
	Elevation	-0.0040	0.0007	<0.01		

Note: Plausible models ($\Delta\text{AICc} < 2$) were identified for the sets of models with one or two variables.

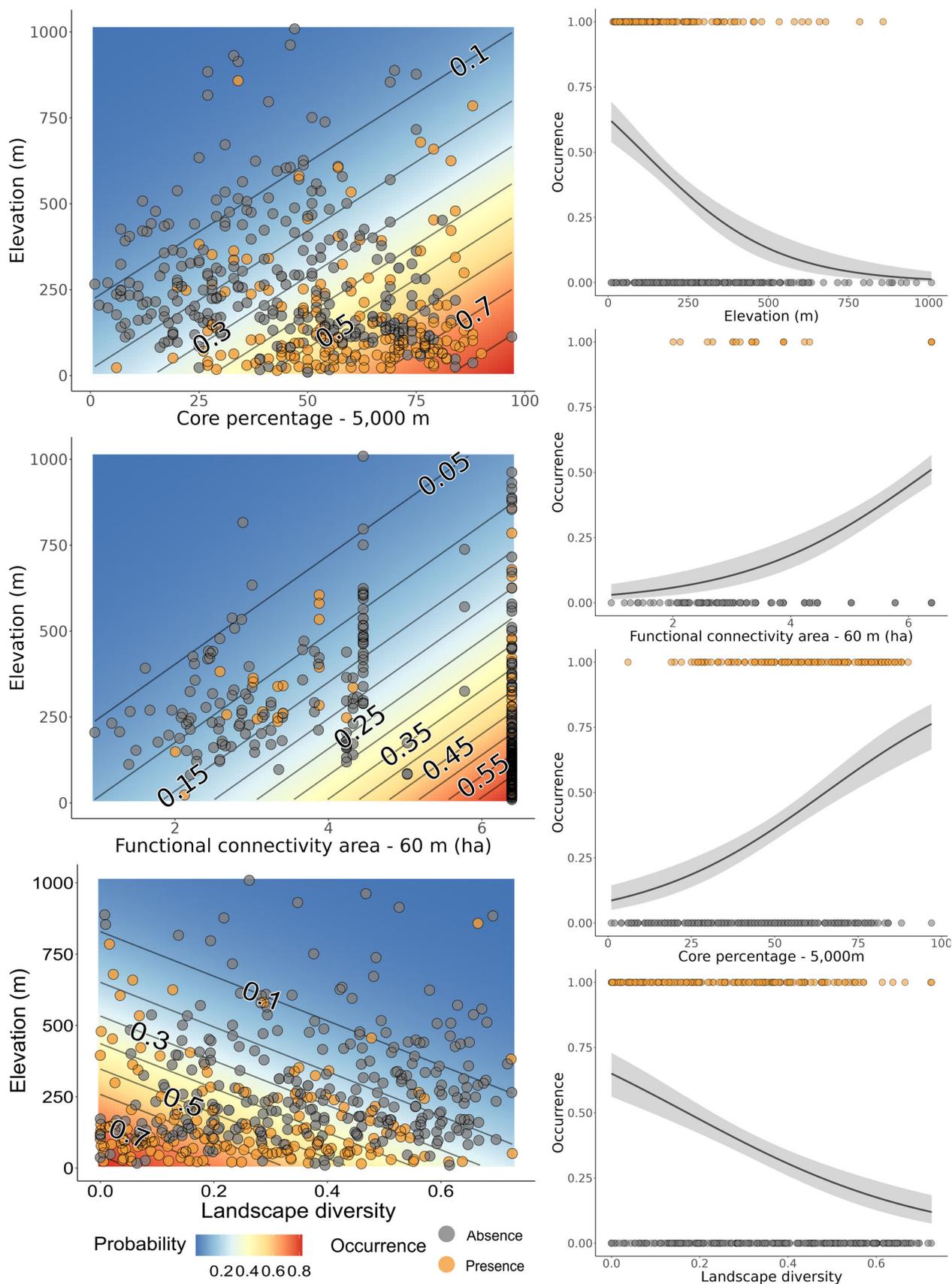


FIGURE 2 Occurrence of *Leontopithecus chrysomelas* in its geographic range, according to landscape variables in univariate and bivariate models. Plausible models: $\Delta AIC_c < 2$ and $wAIC = 0.99$.

showed that the complete model (elevation + functional connectivity area + core percentage + landscape diversity) with $wAIC = 0.99$, best explained the occurrence of *L. chrysomelas* (Table 2).

The occurrence of *L. chrysomelas* was positively associated with an increase in the percentage of core area of forest fragments and *cabruças* and was also higher in landscapes with greater functional connectivity. On the other hand, the occurrence of the species was negatively associated with increases in altitude and landscape diversity (Figure 2).

The predictive maps indicated areas with the highest probability of occurrence for *L. chrysomelas*, based on the landscape variables

that best explained the occurrence of the species in the models (Figure 3). We observed a strong weight of functional connectivity in predicting areas with greater probability of occurrence of the species (Figure 3, maps A and C). There is a greater probability of *L. chrysomelas* occurring in landscapes composed of forest fragments and *cabruças* with greater percentage of core area, with less land cover diversity, and located at low altitudes (<400 m) (Figure 3, map B); low altitude landscapes (<400 m) and comprised of forest fragments and *cabruças* with greater levels of functional connectivity (Figure 3, map C); landscapes comprised of forest fragments and *cabruças* located at low altitudes (<400 m) and with greater core

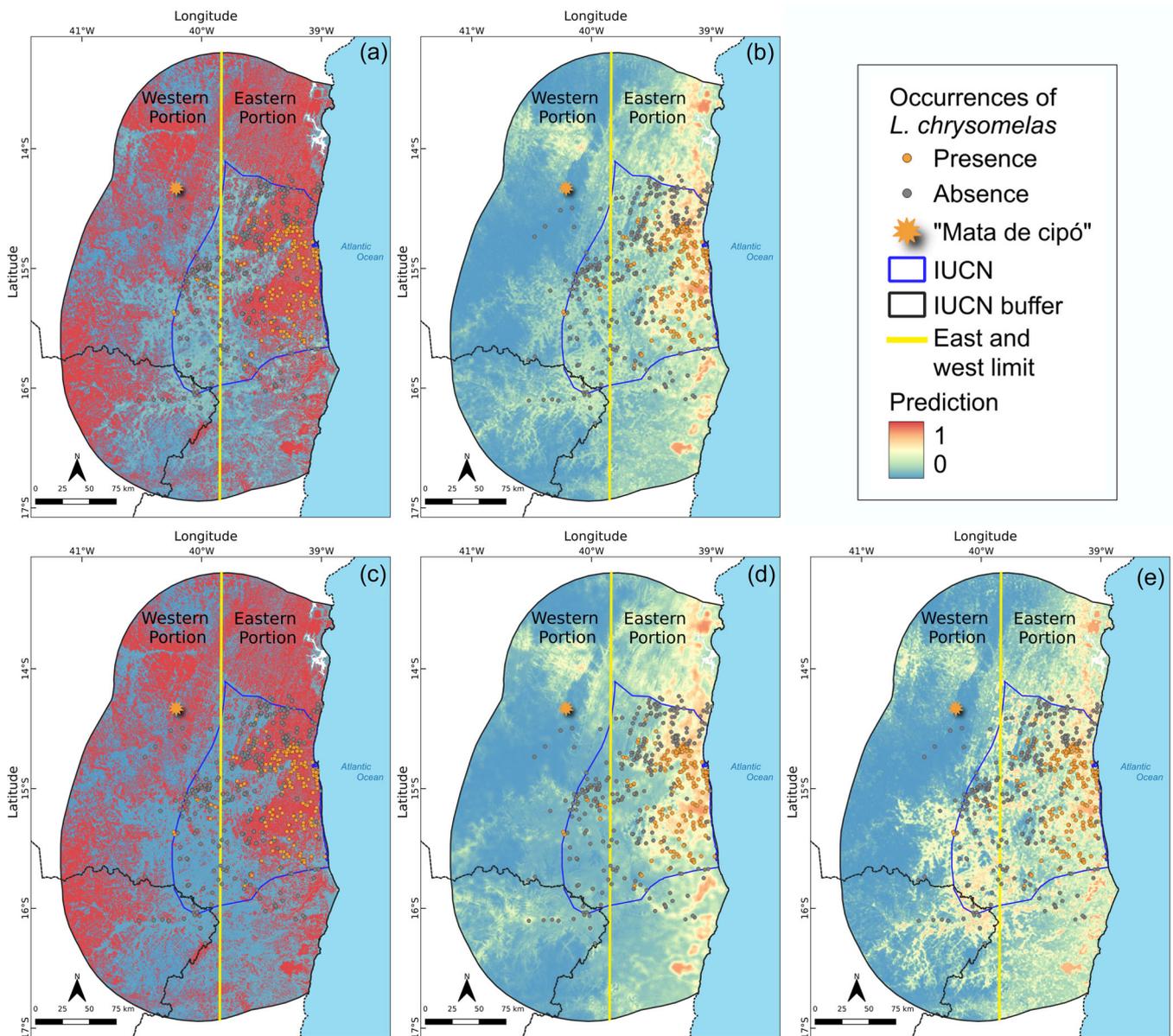


FIGURE 3 Predictive maps indicating the areas with the highest probability of occurrence of *Leontopithecus chrysomelas* in its geographic range, according to the landscape variables that best explained the occurrence of the species in the models. Plausible models: $\Delta AIC_c < 2$ and $wAIC = 0.99$. Interactive effect of landscape variables core percentage, functional connectivity area, landscape diversity, and elevation (a). Interactive effect of landscape variables core percentage, landscape diversity, and elevation (b). Interactive effect of landscape variables functional connectivity area and elevation (c). Interactive effect of landscape variables core percentage and elevation (d). Interactive effect of landscape variables landscape diversity and elevation (e).

percentage (Figure 3, map D), as well as a greater probability of occurrence of *L. chrysomelas* in landscapes with less land cover diversity and located at low altitudes (<400 m) (Figure 3, map E). These areas, in turn, are close to the Atlantic coast, that is, in the eastern portion of the geographic range of *L. chrysomelas* (Figure 3, maps A to E).

4 | DISCUSSION

Our findings indicate that elevation, core percentage, functional connectivity area, and landscape diversity best explained the occurrence of *L. chrysomelas* compared to fragment size, patch size, structural connectivity, habitat percentage, edge percentage, distance from urban areas, distance from protected areas and distance from roads and highways. Despite its ability to survive in human-modified habitats, such as degraded forests and *cabruças* (Oliveira et al., 2010; Raboy et al., 2004), *L. chrysomelas* has been shown to be sensitive to habitat degradation. We observed a reduction in its occurrence in landscapes situated at higher altitudes (>400 m), in areas composed of forest fragments and *cabruças* with smaller core area percentages and lower functional connectivity, and in landscapes with greater diversity of land cover classes.

Our results are useful for a better understanding of the conservation status of *L. chrysomelas* in each portion (eastern and western) of its geographic range and the landscape attributes that affect its occurrence. The eastern portion, where we recorded the highest occurrence of the species (91%), maintains the largest and most continuous forest fragments and *cabruças* (Azevedo et al., 2021; Zeigler et al., 2010), which provide a greater number of resources (food and shelter) and habitats to maintain greater populations (Zeigler et al., 2010). In contrast, the areas located in the western portion, where we recorded a lower occurrence of *L. chrysomelas* (9%), are highly disturbed, with the presence of extensive pastures and agricultural crops (Azevedo et al., 2021; Raboy et al., 2010), making the landscape more heterogeneous and reducing the habitat of the species.

Our models indicate a reduction in the occurrence of *L. chrysomelas* with increasing altitude; however, this does not imply a direct effect of altitude on the occurrence of the species. The larger and more preserved fragments of the Atlantic Forest contained in the geographic range of *L. chrysomelas* are situated near the Atlantic coast and at low altitudes (<400 m) (Zeigler et al., 2010, 2013) which increases the chances of the species occupying these areas. Due to the change in vegetation type, level of fragmentation and habitat composition, it was believed that the occurrence of *L. chrysomelas* at altitudes above 500–550 m was unlikely (Pinto & Rylands, 1997). As observed in our results, Raboy et al. (2013) also reported the occurrence of the species above 500 m.

There are no studies that indicate the effect of the altitudinal gradient on the potential resources of *L. chrysomelas*. In a study focusing on the avifauna of southern Bahia, it was reported that vegetation became markedly stunted from 800 m up, but the forests

still comprised tall trees and bromeliads (Silveira et al. 2005). In terms of vegetation composition, this ecological condition is favorable for the occurrence of *L. chrysomelas* (Oliveira et al., 2011; Raboy & Dietz, 2004). In a botanical inventory in southern Bahia, Amorim et al. (2009) recorded 1129 plant species at altitudes between 300 and 1080 meters. From this list, 17 species were present and classified as “extremely valuable” in a list of key resource species for *L. chrysomelas* in lower-lying forest (<100 m altitude) and another 25 species were listed as “key” (useful, but to a lesser degree than the “extremely valuable”) (Oliveira et al., 2010). Amorim et al. (2009) also recorded high bromeliad diversity above 400 m, one of the main resources used by *L. chrysomelas* to forage insects, arthropods and small vertebrates (Oliveira et al., 2010; Raboy et al., 2004). The results from Silveira et al. (2005) and Amorim et al. (2009), along with those of this study and that of Raboy et al. (2013), which documented the presence of *L. chrysomelas* above 400 m, suggest that the species might have adequate resources at these and higher elevations.

The landscape variable core percentage presented a positive effect on the occurrence of *L. chrysomelas*. Our results are consistent with Raboy et al. (2010), whose “core percentage” was the only variable that explained the occurrence of *L. chrysomelas* in the predictive models of their study. According to the authors, patches with lower core percentage showed a greater exposure to the interface between forest and agriculture or forest and urban areas, were narrower, and had interior areas of nonforest, which may represent suboptimal conditions for *L. chrysomelas*. Although the species uses the edges of forest fragments and *cabruças*, resources (food and shelter) are more abundant in mature forests and in the interior of these areas (Raboy et al., 2004). Forest edges present altered microclimatic conditions due to the edge effect (Tuff et al., 2016). This alteration may increase large tree mortality and reduce the diversity of resources used by forest-dependent species (Laurance et al., 2000; Lindenmayer & Laurance, 2016). At the edges, tamarins may also be more exposed to predation, mainly by birds of prey (Guidorizzi, 2008) and domestic dogs (*Canis familiaris*) (Chiarello, 2003), thus avoiding using this region to reduce the risk of predation. These arguments are also pertinent to explain the absence of effect of the edge percentage variable on the occurrence of *L. chrysomelas*. The broader scale that the species responded to for the variable core percentage (5000 m) may be related to diversity and resource availability. The higher the forest patch density in the landscape, the higher the availability of resources in it (Arroyo-Rodríguez et al., 2020; Fahrig et al., 2019). Larger scales have forest fragments and *cabruças* in greater size and quantity, and with a greater percentage of core area. This can increase the diversity and availability of resources (food and shelter) for *L. chrysomelas*.

Like other South American primates, *L. chrysomelas* depends on forested areas for its movement (Marsh et al., 2013; Raboy & Dietz, 2004; Rylands, 1989), which explains the positive effect of the functional connectivity variable on the occurrence of the species. Landscapes with greater connectivity enable the dispersion and persistence of primates (Costa-Araújo et al., 2021). The increase in functionally connected areas has an effect that “increases the size of

fragments,” as these fragments become accessible. It provides a greater amount of habitat and enables greater availability of resources for the occurrence of *L. chrysomelas*, in addition to maintaining larger populations in these areas. The dispersal of primates between closer fragments also reduces the risk of predation to which these species are exposed to (Bueno et al., 2013; Moraes et al., 2018). Therefore, we emphasize the importance of *cabruças* in contributing to the functional connectivity of the landscape in the eastern portion of the geographic range of *L. chrysomelas*, which can facilitate animals dispersal and reduce their risk of predation.

The occurrence of *L. chrysomelas* was higher in landscapes with lower diversity of land cover classes, which were found in greater proportions in the eastern portion. In addition to being predominantly composed of forest fragments and *cabruças*, the eastern portion maintains the largest populations of *L. chrysomelas* (Zeigler et al., 2010). The scale effect for landscape diversity was 1500 m, suggesting that *L. chrysomelas* also responds to land cover changes on a large scale. The occurrence of the species was lower in heterogeneous landscapes and landscapes with different land uses that are unfeasible for the survival of their populations, such as areas located in the western portion. In addition to the advance in livestock in the western portion, the expansion of other agricultural crops, such as rubber trees, coffee and eucalyptus, also contributed to the characterization of an anthropized and heterogeneous landscape (Guidorizzi, 2008; Raboy et al., 2010). Consequently, this anthropogenic alteration has been reducing the habitat and causing the continuous decline of western populations.

The variables fragment size, patch size, habitat percentage, and structural connectivity had no effect on the occurrence of *L. chrysomelas*, which may be related to the presence of populations in forest fragments of different sizes and in isolated forest fragments located in the western portion. However, these populations are highly vulnerable to local extinction and may not be viable in the long term (Raboy et al., 2010; Teixeira, 2022). The absence of the species in the northeast limit of its geographic range may also have contributed to the lack of significance in the predictive power of the fragment size and structural connectivity variables. Historically, the northeast region is known as an information empty regarding the occurrence of *L. chrysomelas* (Pinto & Rylands, 1997; Raboy et al., 2010; Rylands et al., 2002). Recent primate surveys have also not detected the species in the region (Teixeira, 2022). However, the forest cover of the northeast limit is connected to the eastern portion, forming a continuous block of vegetation consisting mainly of forests and *cabruças* (Azevedo et al., 2021; Zeigler et al., 2010), potentially allowing the occurrence and movement of the species to northeast region. Furthermore, we recorded *L. chrysomelas* in areas adjacent to the northeast region. The occurrence of the species was not influenced by the presence or proximity of protected areas, which can be explained by the low representation of the habitat of *L. chrysomelas* in protected areas (8%) (Teixeira, 2022). Although *L. chrysomelas* is a primate specialist in forests and *cabruças* (Oliveira et al., 2011; Raboy et al., 2004), its presence is common in urban areas (Teixeira, 2022), which may explain the absence of effect of the

variables distance from urban areas and distance from roads and highways in its occurrence.

5 | CONSERVATION IMPLICATIONS

We demonstrate the importance of functionally connected areas, consisting of forest fragments and *cabruças* with greater core percentages, situated at low altitudes (<400 m), and located in the eastern portion of the geographical range of *L. chrysomelas*, to guarantee the survival of its populations. We encourage the establishment of ecologically viable management practices in the *cabruças*, such as the maintenance and planting of shade trees used as food and shelter by the species. Considering that the largest number of occurrences of *L. chrysomelas* are located in the eastern portion, the establishment of new Full Protection Conservation Units and Private Natural Heritage Reserves are necessary to protect large populations (Magioli et al., 2021).

To guarantee the survival of the few and isolated populations in the western portion, more intense conservation measures are needed. Thus, in addition to preserving the remaining forest fragments, we incentivize the creation of ecological corridors and the passive and active restoration of habitat through the natural regeneration of forests and restoration to increase habitat and landscape connectivity and reduce the edge effects of forest fragments in the western portion. The establishment of effective ecological corridors will depend on negotiations with local landowners for the environmental regularization of properties. Brazilian environmental legislation determines that rural properties must maintain or restore vegetation located in Permanent Protection Areas (APPs) and preserve part of their area with native vegetation as Legal Reserve (LR) (Federal Law No. 12,651/2012). These legal requirements should support the establishment of ecological corridors and the restoration of forests in the western portion and throughout the geographic range of *L. chrysomelas*.

We must also better understand the survival ability of *L. chrysomelas* in isolated and degraded forest fragments located in the western portion. Future research must evaluate the occurrence of *L. chrysomelas* in terms of resources considered indispensable for the survival of the species in these forest fragments, such as the presence of tree hollows that serve as sleeping sites for groups, and the occurrence of bromeliads for foraging insects. Additionally, other resources that may limit the survival of *L. chrysomelas* in isolated and degraded western forest fragments need to be evaluated.

AUTHOR CONTRIBUTIONS

Joanison Vicente dos Santos Teixeira: Conceptualization (lead); data curation (equal); formal analysis (lead); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); software (equal); supervision (lead); validation (equal); visualization (lead); writing—original draft (lead); writing—review & editing (lead). **Fernando César Gonçalves Bonfim:** Data curation (lead); formal analysis (lead); methodology (equal); software

(equal); writing—original draft (equal); writing—review & editing (equal). **Maurício Humberto Vancine**: Data curation (lead); formal analysis (lead); software (lead); writing—original draft (equal); writing—review & editing (equal). **Milton Cezar Ribeiro**: Formal analysis (supporting); methodology (supporting). **Leonardo de Carvalho Oliveira**: Conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); supervision (lead); writing—original draft (equal); writing—review & editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available in “Supporting Information.”

ETHICS STATEMENT

Our research did not use any invasive field techniques and adhered to the American Society of Primatologists' Principles for Ethical Treatment of Primates. According to indications of ethics in research involving human beings, our research was submitted and approved by the Ethics Committee for Research with Human Beings (CEP) of the State University of Santa Cruz (Opinion number: 3,042,093/CAAE: 01508618,6,0000,5526). Before starting the interview, we explained the nature and objectives of the research, asking the informants for permission to record the information. Before being interviewed, we also presented the informants with a Free and Informed Consent Form (Supporting Information S1: Table 5) and an Image Use Authorization Term (Supporting Information S1: Table 6), according to the norms established by Resolution nº 196 of the National Health Council of 10/10 1996.

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