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Habitat determinants of golden-headed lion tamarin (*Leontopithecus chrysomelas*) occupancy of cacao agroforests: Gloomy conservation prospects for management intensification

Juliana M. de Almeida-Rocha[1,2] | **Carlos A. Peres**[2,3] | **Julio A. B. Monsalvo**[4] | **Leonardo de C. Oliveira**[1,5,6]

[1]Departamento de Ecologia, Applied Ecology and Conservation Lab, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil

[2]Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich, Norfolk, UK

[3]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil

[4]Departamento de Ecologia, Laboratório de Ecologia e Conservação de Aves, Programa de Pós-graduação em Ecologia, Universidade de Brasília, Brasília, Distrito Federal, Brazil

[5]Departamento de Ciências, Faculdade de Formação de Professores, Universidade do Estado do Rio de Janeiro, São Gonçalo, Rio de Janeiro, Brazil

[6]Bicho do Mato Instituto de Pesquisa, Belo Horizonte, Minas Gerais, Brazil

Correspondence
Juliana M. de Almeida-Rocha, Departamento de Ecologia, Applied Ecology and Conservation Lab, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, 45662-900, Brazil.
Email: almeidarocha.jm@gmail.com

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Abstract

Organismal distributions in human-modified landscapes largely depend on the capacity of any given species to adapt to changes in habitat structure and quality. The golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*) is an Endangered primate from the Brazilian Atlantic Forest whose remaining populations occupy heterogeneous landscapes consisting primarily of shade cacao (*Theobroma cacao*) agroforestry, locally known as *cabrucas*. This cash crop can coexist with high densities of native tree species and holds a significant proportion of the native fauna, but its widely extolled wildlife-friendly status is increasingly threatened by management intensification. Although this potentially threatens to reduce the distribution of GHLTs, the main determinants of tamarin's occupancy of *cabrucas* remain unknown, thereby limiting our ability to design and implement appropriate conservation practices. We surveyed 16 *cabruca* patches in southern Bahia, Brazil, and used occupancy modeling to identify the best predictors of GHLT patch occupancy. Key explanatory variables included vegetation structure, critical resources, landscape context, human disturbance, and predation pressure. We found a negative relationship between GHLT occupancy and the prevalence of jackfruit trees (*Artocarpus heterophylus*), which is likely associated with the low representation of other key food species for GHLTs. Conversely, *cabrucas* retaining large-diameter canopy

trees have a higher probability of GHLT occupancy, likely because these trees provide preferred sleeping sites. Thus, key large tree resources (food and shelter) are currently the main drivers of GHLT occupancy within *cabruca* agroecosystems. Since both factors can be directly affected by crop management practices, intensification of *cabrucas* may induce significant habitat impacts on GHLT populations over much of their remaining range-wide distribution.

KEYWORDS

agriculture, Atlantic forest, *Callitrichidae*, land-sharing, predators

1 | INTRODUCTION

As a result of burgeoning human demands on Earth's natural resources, human-modified landscapes have expanded relentlessly, particularly in species-rich biomes (Watson et al., 2016). The long-term persistence of many taxa is therefore strongly contingent on their capacity to survive in such novel habitat mosaics (Tabarelli, Peres, & Melo, 2012). Species capacity to deal flexibly with habitat change—such as those related to microclimate, vertical stratification, and availability and quality of food resources—will determine their ability to occupy and persist in many anthropogenic habitats (Purvis, Gittleman, Cowlishaw, & Mace, 2000).

A pantropical meta-analysis has shown that primate assemblages in human-modified habitats, such as those resultant of logging and agriculture practices, can present declines of 17–43% in biodiversity metrics (e.g., abundance, density, and species richness), with more detrimental effects when the forest is converted to agricultural land (Almeida-Rocha, Peres, & Oliveira, 2017). However, agro-mosaics and agroforests can support or subsidize populations of many primate species due to the more heterogeneous nature of vegetation at these sites (Almeida-Rocha et al., 2017; Estrada, Raboy, & Oliveira, 2012), representing a viable "win-win" solution in reconciling human economic demands with biodiversity conservation (Perfecto & Vandermeer, 2008). The capacity of these agro-systems to retain native forest biodiversity depends on the amount of residual forest cover in the landscape and the type and intensity of management practices (Cassano, Barlow, & Pardini, 2014; Steffan-Dewenter et al., 2007).

Deforestation of the Atlantic Forest of Bahia, northeastern Brazil, has been so severe that only ~11% of the original forest remains (SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais, 2018). Much of forest conversion occurred due to cacao (*Theobroma cacao*) cultivation that began in 1,746 and expanded rapidly in the late 19th century, particularly in southern Bahia (Piasentin & Saito, 2014). Since the cacao expansion period, much of the original forest of southern Bahia has been converted to shade-cacao agroforestry systems, locally known as *cabrucas* (Piasentin & Saito, 2014). Traditional *cabrucas* are established by replacing the native forest understory with cacao trees that grow underneath the canopy of predominantly native tree species that are retained for their shade, in addition to trees that were subsequently either planted or regenerated (Alves, 1990). Consequently, the vertical structure of *cabrucas* is very simplified compared with intact forests, but much more complex than monoculture systems, such as "sun-cacao" and other annual or perennial crops (Alves, 1990). According to the Executive Committee of the Cacao Cropland Plan (CEPLAC), *cabrucas* should retain between 25 and 30 shade trees/ha (Mandarino, 1981), but traditional *cabrucas* of this region usually retain a much higher tree density: an average of 197 (70–480) shade trees/ha of which ~63% (18–100%) are native species (Schroth et al., 2015). These *cabrucas* maintain a vegetation complexity that enables a significant proportion of native fauna to use them as habitat, supplementary resources, and/or dispersal corridors between forest patches (Faria, Paciencia, Dixo, Laps, & Baumgarten, 2007).

Due to their compatibility with both biodiversity conservation and forest carbon storage (Schroth et al., 2011, 2015), *cabrucas* are considered a wildlife-friendly production system. Unfortunately, this status is now threatened by land-use intensification (Schroth et al., 2011). Former Brazilian environmental legislation banned native tree felling within *cabrucas* (Federal Decree no 6.660 of 21 November 2008, chapter VIII, article 28), but the State Decree no. 15.180 (Chapter 2, Section IV) published by the Bahia Government in 2014 (hereafter referred to as the *management decree*) sanctioned the legal removal of shade trees in high-density *cabrucas* to increase cacao yields, allowing landowners to retain a minimum native tree density of 40 stems/ha. This tree density threshold is far below that observed in traditional *cabrucas* of southern Bahia (Schroth et al., 2015), and will undoubtedly make this agroecosystem far more structurally simplified than it has been until now (Figure 1), potentially diminishing their wildlife-friendly status (Cassano et al., 2014; Schroth et al., 2015) and negatively affecting many endangered species.

The golden-headed lion tamarin (GHLT, *Leontopithecus chrysomelas*) is an endangered small-bodied (~620 g) callitrichid primate endemic to the Brazilian Atlantic Forest whose geographic range has been severely reduced by deforestation and is currently dominated by *cabrucas* (Raboy et al., 2010). The most recent assessment of vegetation cover within the GHLT range indicates that approximately 60% is currently covered by *cabrucas*, with greater dominance in the eastern range—the region containing the most viable populations (Zeigler, Fagan, DeFries, & Raboy, 2010)—where *cabrucas* represent about 47% (± 33% SD) of the landscape (Raboy et al., 2010). The GHLT diet consists mainly of ripe fruits, arthropods and small vertebrates (Rylands, 1989), and in *cabrucas* is largely comprised of the exotic

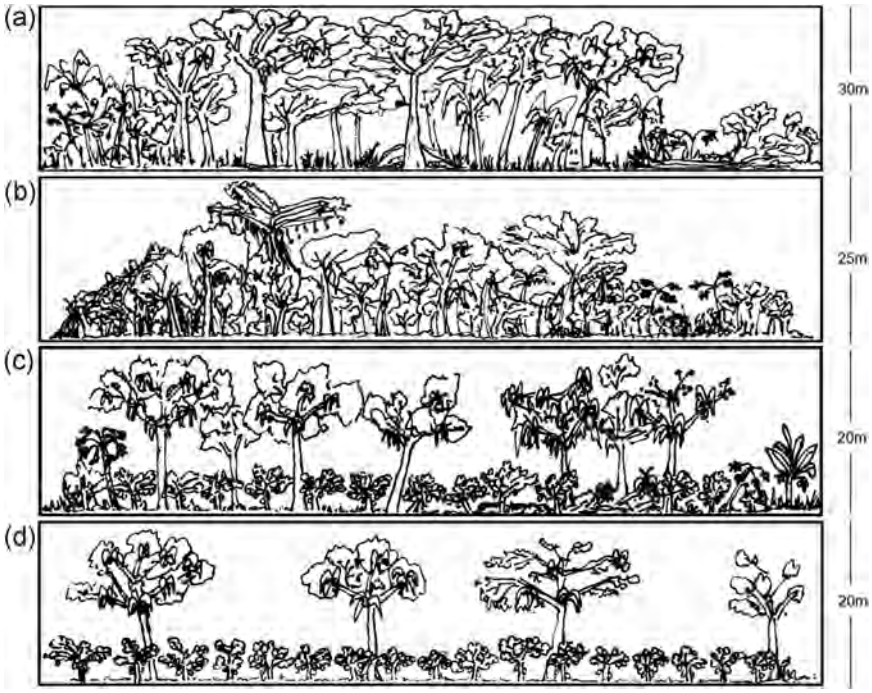

FIGURE 1 Profiles of the vertical structure and diversity of trees in (a) mature (old-growth) forests, (b) secondary forests, (c) traditional *cabrucas*, and (d) intensified *cabrucas*. Bars on the right of the panels indicate mean canopy height. Illustration by Gastón Giné

jackfruit (*Artocarpus heterophylus*), which is widely available almost all year-round (Oliveira, Neves, Raboy, & Dietz, 2011). Other key resources for this species are bromeliads, the main microhabitat used for arthropod foraging (Rylands, 1989). In *cabrucas*, GHLTs typically occur at a mean density of 0.12 (0.04-0.21) ind./ha (Oliveira et al., 2011) and live in groups of 2–15 individuals, usually with one breeding female (Baker, Bales, & Dietz, 2002). All group members sleep together preferentially in large tree cavities (Rylands, 1989), which may be a constraint on group size. GHLTs usually repeat the use of individual trees in *cabrucas* more than in forests (Oliveira, Hankerson, Dietz, & Raboy, 2010), which may increase predation risk since some predators can learn the location of the sleeping sites (Franklin, Hankerson, Baker, & Dietz, 2007). Also, GHLTs usually prefer the lower levels of the vertical strata in forests, but they increase the use of the upper levels in *cabrucas*—probably due to the distribution of food resources and travel routes—being even more exposed to aerial predators (Almeida-Rocha, De Vleeschouwer, Reis, Grelle, & Oliveira, 2015).

Despite their ability to use *cabrucas* (Oliveira et al., 2011), GHLTs do not occupy all *cabruca* patches within its range (Raboy et al., 2010). Therefore, identifying *cabruca* features that favor GHLT occupancy is critical to effectively advocate for management practices that will best protect this species and maintain the wildlife-friendly status of *cabrucas*, particularly given the current policy context that encourages widespread management intensification. Here, we investigate which habitat and landscape characteristics facilitate the occupation of *cabrucas* by GHLTs, as well as the role of natural and domesticated predators in this process. GHLTs experience a higher predation risk in *cabrucas*—mainly from raptors—compared to relatively undisturbed forests (Oliveira & Dietz, 2011). Domestic dogs (*Canis familiaris*) are highly abundant at *cabrucas*, and attacks on GHLTs have been reported (Oliveira & Dietz, 2011). Since habitat alteration can lead to unbalanced trophic interactions (Irwin, Raharison, & Wright, 2009), predation pressure may exert a strong influence on GHLT *cabruca* occupancy.

We, therefore, expected to find that patch occupancy is positively related to (a) vegetation structural complexity (e.g., density and height of shade trees, vertical stratification, canopy connectivity and abundance of lianas); (b) availability of key trophic resources (e.g., key tree species for feeding, sleeping, and foraging); and (c) total amount of vegetation cover at the local and landscape scales. In contrast, patch occupancy should be negatively related to (d) predation risk (i.e., an abundance of potential predators); and (e) management intensification of shade-cacao plantations (i.e. high frequency of weeding, high density of cacao trees, and low shade cover).

2 | METHODS

Our research adhered to the American Society of Primatologists' Principles for Ethical Treatment of Primates. Since we did not use any invasive field technique, it was not necessary to obtain approval from any Brazilian committee for this study.

2.1 | Study area

From May 2014 to May 2015, we surveyed 16 *cabruca* sites located within the GHLT geographic range, covering 12 municipal counties (encompassing an area of ~4,000 km^2) of southern Bahia, Brazil (Figure 2). The *cabruca* sites were at least 11 km apart (mean

distance: 52 km; range: 11–114 km), ensuring an appropriate level of spatial independence. The study region is characterized by a high level of deforestation and fragmentation, especially in the western portion of species range where the dominant vegetation is tropical seasonal semi-deciduous forest (Zeigler et al., 2010). The eastern portion retains the largest and most intact forest fragments, with the coastal evergreen tropical rainforest as the dominant vegetation type (Zeigler et al., 2010). The mean annual temperature and rainfall are 24°C and 2,500 mm, respectively, with no marked seasonality (Mori, Boom, de Carvalho, & dos Santos, 1983).

2.2 | Golden-headed lion tamarin survey

All sampling was performed by Almeida-Rocha JM with the help of a field assistant. Playback was used to systematically search for GHLTs in each study area over three nonconsecutive days. The number of visits was defined a priori based on the GHLT detection history of a previous study developed within *cabrucas* using the same techniques (L. G. Neves [personal communication, November, 2013]). Visits to the same *cabruca* site were separated by at least 1 week to avoid animals habituating to playbacks (Dong & Clayton, 2009), but all surveys within the same site were completed within 30 days.

Using Landsat images from Google Earth (Google, 2016), we deployed a pre-selected sampling grid within each *cabruca* site, so playbacks could be performed at the intersection points of this grid (Figure 3). The methodology consisted of playing an adult male GHLT long-call—which in this genus typically attracts neighboring groups before territorial encounters (Peres, 1989)—to stimulate intraspecific responses by attracting counter-calls. To do this, we used a Sony ICD-PX470 digital voice recorder and a portable Anchor Audio AN-MINI Speaker (frequency response: 100 Hz–15 kHz ± 3 dB).

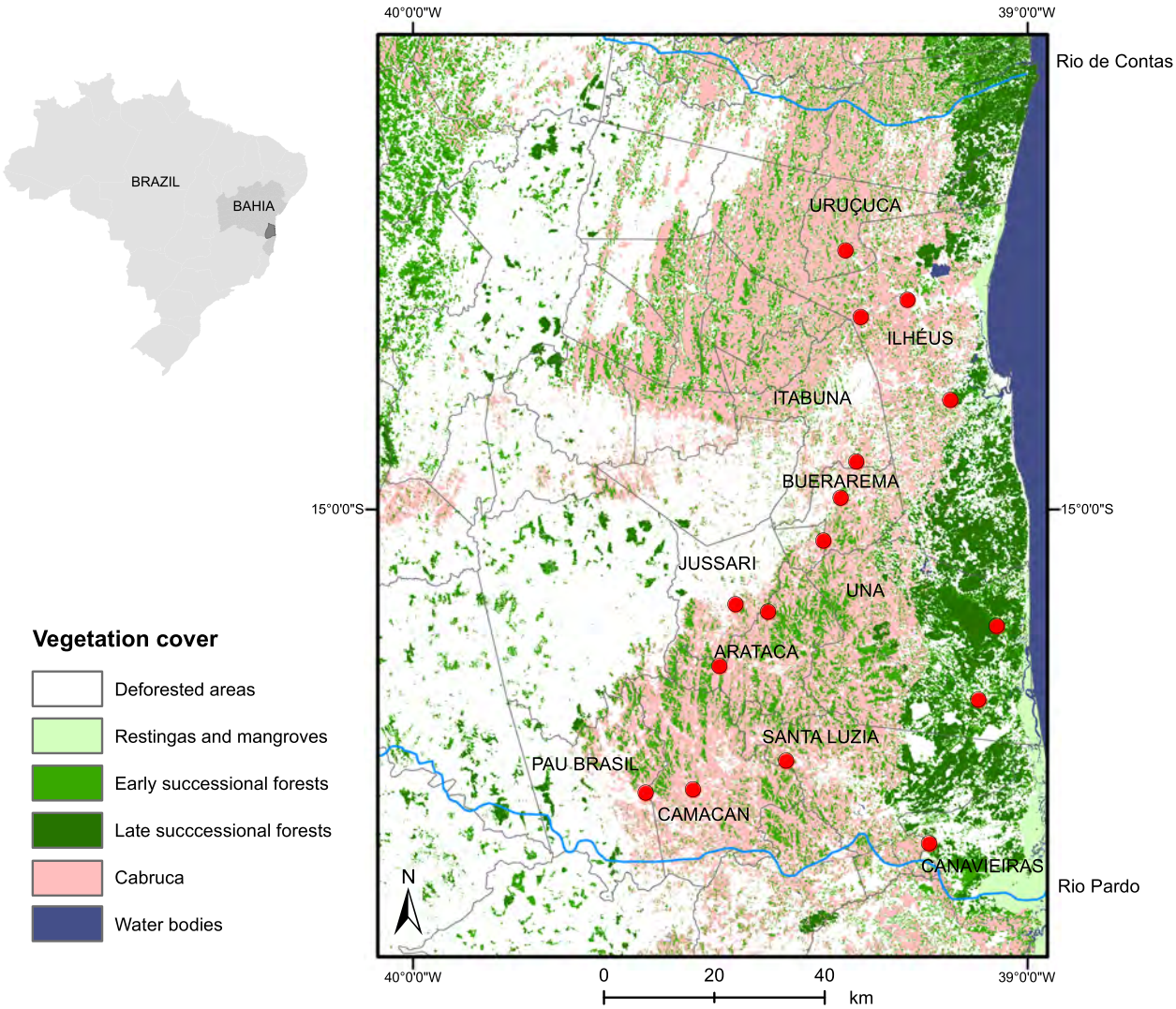

FIGURE 2 Natural vegetation cover within the geographic range (the dark gray region on the map of Brazil) of the golden-headed lion tamarin (*Leontopithecus chrysomelas*), and the location of the 16 *cabruca* sites surveyed in this study (red circles). Classification of vegetation cover is based on Landau, Hirsch, and Musinsky (2008)

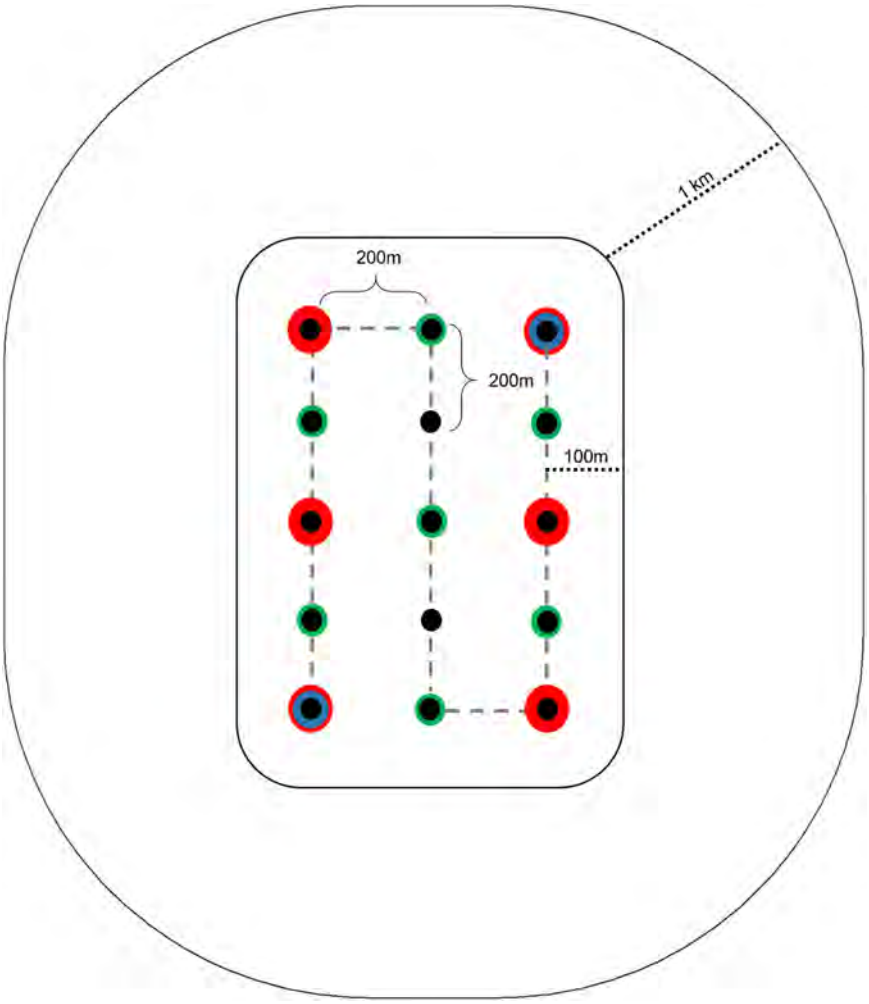

FIGURE 3 Schematic representation of the study design showing the sampling grid (delimited by the transects represented here as dashed gray lines), the survey area (delimited by a 100-m radius of playback hearing range), and the surrounding area (delimited by a 1-km radius from the boundaries of the survey area) of a *cabruca* site. The sampling grid shows the location of the playback points for both golden-headed lion tamarins (black circles) and diurnal raptors (blue circles), as well as the camera-trapping stations (red circles), and the vegetation plots (green circles). Active searches for diurnal raptors were conducted in the external transects (spaced by 400 m), and landscape metrics were calculated within the surrounding area

At each playback point, a complete long-call was directed towards the four cardinal points, holding the speaker ~2 m above ground, followed by a 5-min on-site wait-and-listen interval. When responses were detected, we recorded their location, time, direction, and the number of vocalizations. These parameters helped us to assess whether more than one group responded to the playbacks. To reduce the chance of detecting the same group more than once on the same day, playback points were spaced 200 m apart to prevent overlap in their auditory range (~100 m), which had been previously tested experimentally using a radio-collared GHLT group from another study. Previous studies used the same distance (Kierulff & Rylands, 2003; Raboy et al., 2010).

Each sampling grid had at most 15 playback points (equivalent to a sampling area of 60 ha, considering the playback range) to enable sampling of all points in the morning (06:00 hr–11:00 hr) when GHLTs are most active in *cabrucas* (Reis, 2012). Total sampling effort amounted to 612 playbacks (24–48 per site). At each visit, we started from a different playback point to increase detection probability by considering any possible variation in the use of space by the groups throughout the day. We used a thermo-hygrometer to record mean air temperature and humidity levels during each visit so we could model the effect of these parameters on species detectability (Waser & Waser, 1977). Playback surveys were never performed during rainy weather or strongly windy conditions.

2.3 | Predator surveys

Based on points of occurrence and distribution maps, we identified 15 mammalian carnivores and 46 diurnal raptor species that can occur in the study region (Tables S1 and S2). We classified them as potential predators of GHLTs based on (a) records of predation on primates, (b) records of attacks on primates, (c) body mass, (d) typical prey size, (e) records of mammals in the diet, (f) degree of dietary specialization, and (g) foraging strategy. To make this classification more systematic, each criterion received a categorical value, with high values attributed to characters that favor GHLT predation (Table S3). These values were then summed to create a Potential Predation Index (PPI) which was used to rank all species according to their probability of preying on GHLTs, attributing greater weights to categories (a), (b), and (g), which were considered most important. Details on this classification are presented in Tables S1–S3.

We included the yellow-breasted capuchin monkey (*Sapajus xanthosternos*) and domestic dogs among the potential predators based on records of predation on primates (capuchin monkeys: Lawrance, 2003; Sampaio & Ferrari, 2004; domestic dogs: Galetti & Sazima, 2006; Oliveira, Linares, Corrêa, & Chiarello, 2008) and attacks on GHLTs in *cabruca* sites (domestic dogs: Oliveira & Dietz, 2011). Thus, our final checklist of potential predators comprised 30 species: eight nonaerial (species with primarily terrestrial, scansorial or arboreal habits) and 22 aerial species (Tables S1 and S2). Logistic limitations prevented us from surveying serpents and nocturnal raptors (i.e., owls), which may have led to an underestimated number of potential predators in *cabrucas*. Some serpent species that inhabit *cabrucas* such as the jararaca (*Bothrops jararaca*), the whitetail lancehead (*B. leucurus*), and the common boa (*Boa constrictor*), can prey on primates (Corrêa & Coutinho, 1997; Ferrari & Beltrão-Mendes, 2011; Teixeira et al., 2016). Regarding owls, most species exhibit the opposite activity period to GHLTs, but we occasionally recorded active owls in *cabrucas* during the daytime, such as the tawny-browed-owl (*Pulsatrix koeniswaldiana*), the ferruginous pygmy-owl (*Glaucidium brasilianum*), and the screech owl (*Megascops* sp.). Although there is a predation record of a burrowing owl (*Athene cunicularia*) on a young marmoset (*Callithrix jacchus*) (Stafford & Ferreira, 1995), this seems very rare so we believe that extant owls do not exert significant predation pressure on GHLTs.

2.3.1 | Nonaerial predators

We sampled nonaerial predators simultaneously with GHLT surveys using four to six digital camera-traps (Tigrinus® 6.0D) per site, depending on the size of the sampling grid. Camera-trap stations were spaced at least 300 m apart and positioned near playback points (Figure 3). At each station, one camera was fixed to a tree at ~50 cm above the ground and baited with a banana lure (10 ml), carnivore essence (Bobcat urine; 10 ml) and sardine oil (10 ml), specifically selected to attract potential GHLT predators such as felids and mustelids (Schlexer, 2008). Baits and lures were placed separately into perforated pots protected from rain and animal consumption that were attached to wooden sticks at ~50 cm above the ground and 2 m perpendicular to the camera. In all *cabruca* sites, the cameras were operated simultaneously for 24 hr during consecutive days for an overall total sampling effort of 128 ± 28 camera-trap/days per site (which is following the recommendations of Espartosa, Pinotti, & Pardini, 2011).

Camera-trap stations were checked weekly to replace baits, lures, batteries, memory cards, or the cameras themselves in case of occasional malfunction. Malfunctioning cameras were replaced and kept operating longer to compensate for any losses in sampling effort. Photographs of conspecifics recorded within a 24-hr period were considered as a single record (i.e., the same individual), unless individual recognition was possible through natural marks, as in the case of domestic dogs. In the case of social species, such as coatis (*Nasua nasua*), we used "group" rather than "individual" records. Finally, we used camera-trap records to estimate the total abundance of nonaerial predators at each *cabruca* site.

2.3.2 | Aerial predators

A combination of active search, playback, and point count was used to survey for diurnal raptors, which were sampled during two nonconsecutive days at each site. These surveys were carried out after GHLT surveys were completed to avoid interference in the behavior and detectability of the tamarins. Sampling was carried out between 06:00 and 12:00 hr, the peak period of activity for most diurnal raptors (Mañosa, Mateos, & Pedrocchi, 2003; Thiollay, 1989), avoiding rainy and windy days (Granzinolli & Motta-junior, 2008).

Between 06:00 and 09:00 hr, sampling was carried out within *cabruca* sites, focusing on forest species that only occasionally fly above the canopy (Thiollay, 1989), but also searching for soaring species that commence flight activity later. An active search was carried out throughout the sampling grid using Yukon Futurus Pro 10 × 50 binoculars and the aforementioned voice recorder to record vocalizations whenever possible. Additionally, we performed playbacks at two points located at the beginning and the end of each sampling grid (Figure 3), separated by a mean linear distance of 665 ± 160 m (which is consistent with previous studies of Carvalho Filho, Zorzin, Canuto, Carvalho, & Carvalho, 2009; Vázquez-Pérez, Enríquez-Rocha, & Rangel-Salazar, 2009).

We performed targeted playbacks to detect the presence of a set of diurnal raptors known to respond to calls (Zorzin, 2011; JABM [pers. obs., November, 2012]) using a modified version of the methods proposed by Granzinolli and Motta-junior (2008). These species included gray-headed kite (*Leptodon cayanensis*), barred forest-falcon (*Micrastur ruficollis*), collared forest-falcon (*Micrastur semitorquatus*), bicolored Hawk (*Accipiter bicolor*), and black hawk-eagle (*Spizaetus tyrannus*). We used recordings from Wiki Aves (http://www.wikiaves.com/), preferentially selecting those from the study region, and avoiding aggressive vocalizations and duets. At each playback point, recordings of all focal species were played in a pre-established order considering both body size and aggressive behavior, since larger-bodied species could repel smaller raptors. Thus, we played the vocalizations of the smallest and least aggressive raptor first. Each vocalization was played continuously for 3 min, holding the speaker at ~2 m above the ground and rotating it 360° at a constant rate, followed by a 3-min on-site wait.

Most raptors start soaring when thermals are well-formed, so the best period to perform point count techniques is between 09:00 and 12:00 hr (Mañosa et al., 2003; Thiollay, 1989). During this period, we recorded all individuals using visual or vocal cues from a fixed point located on hilltops adjacent to the study area (Mañosa et al., 2003). At six of the 16 sites where the relief was very flat, we performed two complementary point counts located at ~100 m from the edge of the *cabruca*, separated by mean distances of 690 ± 170 m. We split our efforts between these two points so that we remained at each point for 1 hr 30 min.

Except for single point counts, we changed the location of the initial sampling point in the second visit to ensure the detection of species with different activity peaks at all points (Jones, 2000). Given that even small raptors occupy home ranges of up to 100 ha (Thiollay, 1989), repeated detections of the same species in the same site were attributed to the same individual, unless more than one individual was observed simultaneously. Based on these records, we estimated the total abundance of aerial predators at each *cabruca* site. Overall sampling effort amounted to 64 playback points (4 per site), 91 hr 11 min of active searches (4 hr 48 min– 6 hr 45 min per site), and 96 hr of point counts (6 hr per site).

2.4 | Habitat structure and quality

Several features of the habitat structure and management of *cabruca* were sampled within seven 200 m^2 plots (Figure 3) at each site in the same period of GHLT surveys to assess 15 variables (Table S4): (a) density of shade trees; (b) canopy height; (c) canopy connectivity; (d) vertical stratification; (e) species richness of shade trees; (f) equitability of shade tree species; (g) Importance Value Index (IVI; Curtis & McIntosh, 1951) of key resource trees; (h) IVI of jackfruit trees; (i) mean diameter at breast height (DBH) of shade trees; (j) abundance of woody lianas; (k) abundance of bromeliads; (l) abundance of banana trees; (m) management intensity; (n) density of cacao trees; (o) percentage of shading. Variables 5–8 were calculated as a single value for the entire study sites, but the others were calculated at the plot scale. In these cases, we summed the values obtained in each plot to create a unique value for each variable per site, which we treated as an abundance index in the statistical analyses. Besides these variables, we also recorded any signs of hunting (e.g., waiting stations, gunshots) and selective logging (stumps) to describe the degree of human disturbance at each site.

Whenever possible, shade trees were identified in situ to the level of species, with the help of an experienced local field parabotanist. Whenever necessary, voucher specimens were collected for further identification at the herbarium in the Department of Botany, State University of Santa Cruz. For the IVI of key resource trees, we first calculated the arithmetic sum of relative density, dominance, and frequency of all shade tree species recorded at each site, according to Curtis and McIntosh (1951). Then, based on checklists of tree species used by GHLTs for food and shelter (Cardoso, 2008; Catenacci, De Vleeschouwer, & Nogueira-Filho, 2009; Catenacci, Pessoa, Nogueira-Filho, & De Vleeschouwer, 2016; Oliveira et al., 2010, 2011), we identified the key tree species recorded in our study sites (Table S5). Finally, we summed the IVI values of these key tree species per site. We also used the jackfruit trees IVI separately for the analysis due to its particular importance in the diet of GHLTs at *cabruca* sites (Oliveira et al., 2010). Further details on this index and all other habitat variables are presented in the Supplementary Material (Table S4).

2.5 | Landscape context

Based on Landsat 8 images from 2016 (30 m resolution) provided by Google Earth (Google, 2016) and using the *raster* package (Hijmans et al., 2016) in R 3.3.1 (R Core Team, 2019), we measured the minimum linear distance between each playback point to the nearest household and fragment edge. We calculated the percentage of vegetation cover in the surroundings of each *cabruca* site by defining a 1-km radius buffer from the survey area' boundaries (Figure 3) and extracting all visually identified clear-cut areas from this region using the Quantum GIS 2.18.2 (http://www.qgis.org/). The spectral difficulty of accurately distinguishing *cabrucas* from forests using satellite images did not pose a problem for our analysis because we were primarily interested in quantifying the total amount of available habitat for GHLTs, and *cabruca* is habitat for this species (Oliveira et al., 2011).

2.6 | Occupancy modeling

Occupancy estimate (Ψ) represents the proportion of an area that is occupied by a given species (Mackenzie et al., 2002). Using Mark 8.x software (White & Burnham, 1999), we fitted *single-season* occupancy models—which assume that the population is closed to changes in occupancy inside each sampling unit during the survey season—to estimate GHLTs occupancy in *cabrucas*, and modeled the detection probability (p) as imperfect, considering that GHLTs may be present in an area but may not always be detected.

A GHLT detection history (1 = detected; 0 = undetected) was created for each playback point per site based on the three independent visits, so playback events served as independent sampling units for the analysis. In doing so, the assumption of population closure may not have been achieved, since GHLTs can move over 200 m (the distance between neighboring playback points), thus exiting or entering sampling units many times during the season. As proposed by Mackenzie et al. (2006), we dealt with this problem by interpreting the occupancy estimate as to the proportion of the area "used" by the species, rather than the true occupancy, and detectability as the probability of detecting the species when it is present in the area *and* using the sampling unit during the survey, assuming that GHLT movements through their home range are random (see similar interpretations in Kalan et al., 2015; Keane, Hobinjatovo, Razafimanahaka, Jenkins, & Jones, 2012).

Before analyses, we assessed the pairwise correlations between all variables collected in the field and extracted from satellite images through a Spearman correlation test, using the *Stats* package in R (R Core Team, 2019). For each pair, we excluded one highly correlated variable ($r \geq .6$), always keeping the variables that enabled us to test all hypotheses. In this way, we removed shade tree species richness, bromeliads, canopy height, and connectivity from the analyses. We then examined levels of multicollinearity among all remaining variables through the Variance Inflation Factor (VIF) using the *CAR* package in R (R Core Team, 2019), and excluded variables with

VIF > 4: percentage of shading, IVI of key resource trees, density of shade trees and vertical stratification. This resulted in 12 remaining covariates to model —(a) equitability of shade tree species, (b) IVI of jackfruit trees, (c) DBH of shade trees, (d) abundance of woody lianas, (e) abundance of banana trees, (f) management intensity, (g) density of cacao trees, (h) abundance of nonaerial predators, (i) abundance of aerial predators, (j) distance to households, (k) distance to the nearest fragment edge, and (l) vegetation cover—and four covariates to model p—(a) density of cacao trees, (b) playback time, (c) mean temperature, and (d) mean air humidity during the visit.

Since we were primarily interested in determining the most important covariates that influenced Ψ and p, we built a model set based on all possible additive covariate combinations (Doherty, White, & Burnham, 2012), which resulted in 2,517 competing models. We then calculated the cumulative AIC_c weight (w_+) for each covariate to interpret their relative importance on the estimates (Burnham & Anderson, 2002). The final estimates of Ψ and p were model-averaged considering the weighted mean among all competing models (Burnham & Anderson, 2002). We assessed the fit of the most general model (i.e. the model with the greatest number of parameters) by estimating the overdispersion parameter *c-hat* through 10,000 bootstrap samples (Mackenzie & Bailey, 2004) in the PRESENCE 11.7 software (http://www.mbr-pwrc.usgs.gov/software/presence.shtml).

3 | RESULTS

3.1 | GHLT and predator surveys

We obtained 31 GHLT responses at 29 playback points within eight sites (50%). At two additional sites, we did not obtain playback responses, but we occasionally detected GHLTs while walking between playback points. The playbacks also elicited responses from diurnal raptors, including some potential predators such as the Southern Caracara (*Caracara plancus*), the Crane Hawk (*Geranospiza caerulescens*), the Mantled Hawk (*Pseudastur polionotus*), the Roadside Hawk (*Rupornis magnirostris*), and the Black Hawk-eagle.

A total of 10 native mammal species plus domestic dogs, domesticated livestock, and humans were recorded at *cabruca* sites using camera traps. Such records included three potential predators assigned to low to moderate GHLT predation probabilities (Table 1): domestic dogs (PPI = 11), recorded in 15 *cabruca* sites (94%); coatis (PPI = 9), recorded in three *cabruca* sites (19%); and tayras (*Eira barbara*; PPI = 11), recorded in two *cabruca* sites (13%). Except for domestic dogs, all potential predators were recorded within low activity *cabruca* plots near regenerating forest patches. Capuchin monkeys (PPI = 11) were occasionally recorded at one site while moving between playback points (Table 1).

We recorded at least 18 species of diurnal raptors, including 15 potential predators with varying GHLT predation probabilities (Table 2). The most common of these were assigned to medium to high potential to prey on GHLTs (Table 2): the Southern caracara (PPI = 19), recorded in 15 *cabruca* sites (94%); and the Roadside Hawk (PPI = 25) and the Zone-tailed Hawk (*Buteo albonotatus*; PPI = 19), both of which recorded in at least 11 *cabruca* sites (70%).

3.2 | Habitat structure and quality, and landscape context

Cabruca sites have a mean density of 623 ± 182 cacao trees/ha and 182 ± 60 shade trees/ha, with a mean shade tree diameter of 37.2 ± 30.7 cm, median canopy height of 15.6 ± 2.6 m, and mean shade cover of 73% ± 10% (Table S6). A total of 79 shade tree species were identified (15 ± 5 species/site), 46 of which are used by GHLTs for food and/or shelter (Table S5).

The IVI of those key resource tree species, and particularly of jackfruit trees, ranged between 15–78% and 0–19%, respectively (Table S6). Direct or indirect signs of hunting (traps, hunters, and/or shotgun blows) and logging (chainsaw noise and stumps) were recorded at 10 and 9 of the 16 sites, respectively (Table S6). Vegetation cover in the surroundings ranged from 73% to 96% between *cabruca* sites (Table S6).

3.3 | GHLT occupancy

Our goodness-of-fit test revealed no evidence of overdispersion $\chi^2 = 15.17$; P = 0.29; *c-hat* = 1.09). The most parsimonious model explaining GHLT occupancy had a low AIC_c weight (w_+ = 0.15), suggesting a high degree of uncertainty as to which is the best model (Table 3), which was not surprising considering the large number of competing models. The estimated p at each playback point per visit was 0.08 (95% CI: 0.03; 0.17), being positively affected by the density of cacao trees (w_+ = 0.81; Table 4; Figure 4). The estimated Ψ was 0.47 (95% CI: 0.06; 0.93), being most influenced negatively by the IVI of jackfruit trees (w_+ = 0.87) and positively by the DBH of shade trees (w_+ = 0.85; Table 4; Figure 5).

4 | DISCUSSION

We investigated the determinants of GHLT occupancy within *cabrucas* of southern Bahia, Brazil, focusing on the specific influence of vegetation structure, habitat quality, agroforestry management intensity, landscape context, and predation pressure. The two features that most affected GHLT occupancy—the preponderance of jackfruit trees and the diameter of shade trees—are related to the availability of key resources (food and shelter) and both may be directly affected by the intensification of management practices.

We found a negative relationship between the IVI of jackfruit trees and GHLT occupancy. At first, this may seem counterintuitive since jackfruits represent one of the most important food resources for GHLTs within *cabrucas* (Oliveira et al., 2010). However, as the IVI index was derived from key resource trees, high values of jackfruit

TABLE 1 Camera trapping records (number of individuals/groups) of mammalian species at 16 *cabruca* sites, and species classification according to their capacity to prey on GHLTs (y = yes, n =no) based on their Potential Predation Index (PPI)

Species	Predator	PPI	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Eira barbara	y	11					1		1									
Canis familiaris	y	11	4	3	2	1	8	3	3	1	5	2		4	1	2	3	2
Sapajus xanthosternos[a]	y	11											1					
Nasua nasua[a]	y	9								1			1		1			
Cerdocyon thous	n	6	2	1–2	1	1			6		3							1
Procyon cancrivorous	n	3				1	1		1									
Cuniculus paca	n	0	1						1		1							
Dasypus novencinctus	n	0	1					1										
Didelphis aurita	n	0	1		1													
Mazama sp.	n	0	1	2		1					1			2				1
Pecari tajacu	n	0												1				
Livestock	n	0		2							2			2			3–5	
Unidentified species	–	–										1					1	
Lost records[b]	–	–	3	1	1							1	4				1	
Predator species richness			1	1	1	1	2	1	2	2	1	1	2	1	2	1	1	1
Predator abundance			4	3	2	1	9	3	4	2	5	2	2	4	2	2	3	2

Note: Details of PPI calculation can be found in Table S1.

[a]The abundance of *S. xanthosternos* and *N. nasua* are shown as the number of groups recorded per area.

[b]Images were damaged due to the accumulation of moisture, preventing the identification of the recorded species.

trees IVI imply a prevalence of this species over other key food species—such as *Myrtaceae* trees, which are largely used as food resources by GHLTs in *cabrucas* (Oliveira et al., 2010)—resulting in lower availability of complementary resources. This suggests that, when sites become highly dominated by jackfruit trees, they may fail to provide enough complementary resources to satisfy the metabolic and nutritional requirements of GHLTs. This situation may occur whenever farmers favor cacao shading by fast-growing tree species with dense crowns — as is the case of jackfruit trees and *Erythrina* spp.—rather than maintaining a diversified native tree composition in which old-growth species are more common (Rolim & Chiarello, 2004).

We found that *cabrucas* retaining wide-diameter shade trees were more likely to contain GHLTs, which is probably related to the availability of suitable sleeping sites (Hankerson, Franklin, & Dietz, 2007). In addition to boosting GHLT occupancy, retaining larger trees also contributes to climate change mitigation, since trees larger than 35 cm in diameter account for a disproportionate fraction of the carbon storage within *cabruca* systems (Schroth et al., 2015). The tree diameter profile of *cabrucas* will vary depending on which species are used to shade the cacao understory and on the frequency with which the understory is weeded (Sambuichi & Haridasan, 2007), which can therefore largely determine the extent to which *cabrucas* are wildlife-friendly. Since natural regeneration of most shade trees is suppressed through weeding (Rolim & Chiarello, 2004), *cabrucas* are composed of an unstable land-sharing system in which the long-term persistence of GHLTs, as well as many other vertebrate species, depends heavily on replanting key resource species. A possible way to improve the conservation value of *cabrucas* under production intensification is to prioritize the retention/replanting of larger diameter tree species that have already been identified as important for the regional fauna (Oliveira et al., 2010), ensuring a diversified and balanced tree species composition.

The probable reason why we failed to detect significant effects of presumably important habitat features, such as shade tree density and canopy connectivity, is that our study sites did not span critical thresholds for such features. This is not a failure of our study design but the reality of traditional *cabrucas*. We can reasonably expect these features to become more important if legally sanctioned management intensification is implemented. If intensification is unavoidable, we strongly recommend the monitoring of *cabruca* plots both before and after intensification, so that we can understand how intensification will impact GHLT populations (and other species from the regional fauna) and design mitigation strategies accordingly. Similarly, we failed to detect a significant influence of the amount of vegetation cover within surrounding *cabruca* landscapes probably because the range of values estimated for our study sites was high. Our approach considered *cabrucas* in estimates of vegetation cover because this agroecosystem is a key habitat for GHLTs (Oliveira et al., 2011), so these high values reflect the regional context at the

TABLE 2 Records of diurnal raptor species (number of individuals), species classification as potential predators (y = yes; n =no) of golden-headed lion tamarins (*Leontopithecus chrysomelas*) based on their Potential Predation Index (PPI), and estimates of species richness and abundance of diurnal raptors at 16 *cabruca* sites

			Study sites															
Species	**Predator**	**PPI**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Spizaetus tyrannus	y	34	1		1		1	2				2			1	1	1	
Accipiter bicolor	y	25		1[a]	1[a]			1[a]										1[a]
Rupornis magnirostris	y	25	1		2	1		1	2	1	1[a]			1	2	2	2	1
Spizaetus melanoleucus	y	25			1	1[a]	1				2							
Leptodon cayanensis	y	23	1	1	1	1[a]		1		1[a]		1		2			1[a]	
Geranospiza caerulescens	y	23	1[a]		1		1	1				1						1
Micrastur semitorquatus	y	20		2	1[a]			1										
Buteogallus urubitinga	y	20		2	1								1[a]			1		
Buteo albonotatus	y	19	2	3	1	1	1	1[a]	1	2	1	2	1[a]	1[a]	1[a]		1	2
Caracara plancus	y	19	2	4	1	2	1	1		2	1	1	1	2	1	2	2	1
Buteo brachyurus	y	18	1[a]		1													
Buteo nitidus	y	18	1[a]	1[a]	1		2											
Pseudastur polionotus	y	18		1		2	2	1	1		1		1		1	2		2
Milvago chimachima	y	18	1	1		2	1			1				2	1	1	1	
Buteogallus meridionalis	y	13											1[a]				1	
Herpetotheres cachinnans	n	9	1	1	1	1	1	1		2		1		1	2	1	2	1
Falco femoralis	n	8			1[a]		1[a]											
Sarcoramphus papa	n	7					1									1		
Chondrohierax uncinatus	n	5			1							1						
Harpagus diodon	n	5					1[a]	1[a]										
Falco rufigularis	n	3			1[a]		1[a]											
Rostrhamus sociabilis	n	3											1[a]					
Unidentified individuals			3	0	2	3	1	2	2	1	2	2	1	1	0	3	2	1
Predator species richness			7–10	8	10–15	5–10	8–9	7–9	3–5	5–6	4–7	5–7	2–6	4–6	5–6	6–9	6–9	5–7
Predator abundance[b]			9–13	15	11–15	8–13	10–11	8–12	4–6	6–8	5–8	7–9	2–6	7–9	6–7	9–12	8–11	7–9

Note: Details of PPI calculation can be found in Table S2.
[a]Uncertainty in species identification. These uncertainties were considered in the estimates of species richness and abundance.
[b]For the occupancy modeling, we used the minimum expected abundance in the site.

time of this study. We, therefore, highlight that our results apply to landscapes containing high amounts of habitat availability for GHLTs. However, landscape-scale habitat amount would likely become more important for GHLTs should this study be repeated in highly deforested landscapes.

Contrary to our expectations, predators apparently do not play a decisive role in GHLT occupancy of *cabrucas* currently. The few records we obtained of wild nonaerial predators were restricted to low activity *cabruca* plots near forest patches, suggesting that these species may be transient in *cabrucas*. An alternative explanation for this low detectability may be the elevated hunting pressure throughout this region (Cassano, Barlow, & Pardini, 2012). For instance, we found unambiguous hunting signs at 62% of our study sites. Although our data did not confirm a previously suggested negative relationship between domestic dogs and GHLT occupancy (Cassano et al., 2014), it does not mean that dogs did not exert any influence on this. Dogs can affect other carnivores and prey species indirectly by inducing changes in the use of space, foraging behavior, and activity pattern (e.g. time allocated to play or vigilance), as well as by spreading diseases, increasing stress level and thus affecting species fitness (Sheriff, Krebs, & Boonstra, 2009; Vanak & Gompper, 2009). All of these indirect impacts may lead to future changes in vertebrate occupancy patterns (Silva-Rodríguez & Sieving, 2012; Vanak & Gompper, 2010). Santos et al. (2018) assessed direct

TABLE 3 Results for the 10 top-ranked models of occupancy (Ψ) and detection (*p*) probabilities of the golden-headed lion tamarin (*Leontopithecus chrysomelas*) in 16 *cabrucas* of southern Bahia, Brazil

Model	AICc	Δ AICc	AICcW	Dev
{Ψ(MAN + JAC + DBH) *p*(CAC)}	195.35	0.00	0.15	182.94
{Ψ(EQUI + JAC + DBH) *p*(CAC)}	196.01	0.66	0.10	183.60
{Ψ(VEG + JAC + DBH) *p*(CAC)}	196.18	0.83	0.10	183.77
{Ψ(CAC + JAC + DBH) *p*(CAC)}	196.49	1.14	0.08	184.08
{Ψ(LIA + JAC + DBH) *p*(CAC)}	196.75	1.40	0.07	184.34
{Ψ(BAN + JAC + DBH) *p*(CAC)}	197.36	2.02	0.05	184.95
{Ψ(JAC + DBH) *p*(CAC + HUM)}	197.77	2.43	0.04	185.36
{Ψ(JAC + DBH) *p*(CAC)}	198.44	3.10	0.03	188.15
{Ψ(EQUI + JAC + DBH) *p*(HUM)}	199.45	4.11	0.02	187.04
{Ψ(EQUI + CAC + DBH) *p*(CAC)}	199.87	4.53	0.02	187.47

Note: The table shows the values of the Akaike information criterion corrected for small samples (AIC_c), the difference between the AIC_c value of each model and the top-ranked model (ΔAIC_c), the Akaike weight (AIC_cW), and the model adjustment (i.e., the deviance, Dev). All models included the intercepts of Ψ and *p*.
Abbreviations: BAN, abundance of banana trees; CAC, density of cacao trees; DBH, diameter of shade trees at breast height; EQUI, equitability of shade tree species; HUM, air humidity during the visit; JAC, jackfruit tree Importance Value Index (IVI); LIA, abundance of woody lianas; MAN, management intensity; VEG, percentage of vegetation cover in the surroundings.

(chasing and predation) and indirect (urine and fecal deposition) interactions between domestic dogs and wildlife in *cabrucas*. Although only one direct interaction with GHLTs (chasing) was observed by the authors, dogs are very active within *cabrucas* and there is still no information on how GHLTs can be indirectly affected by such activity, calling for future studies on this topic.

The high incidence of potential aerial predators, that is diurnal raptors, at *cabruca* sites may be related to increased foraging efficiency, since prey can be more exposed in structurally simplified habitats such as *cabrucas* (Alves, 1990; Piana, 2015). The higher rate of encounters between GHLTs and raptors in *cabrucas* compared to forests (Oliveira & Dietz, 2011) suggests such increased efficiency. Although we did not detect a direct effect of raptors on GHLT occupancy, it is important to consider that the predator-prey relationship could be quite different in highly intensified *cabrucas*. If *cabrucas* become even more simplified, that is with a lower density of shade trees and canopy connectivity, GHLTs will become more exposed to predators due to even more reduced canopy connectivity, lower midstory foliage density, and reduced availability of natural shelters. Besides, a decline in food resources could lead to longer travel distances to key food trees thereby exposing GHLTs to greater predation risk (Garber & Bicca-Marques, 2002). Accordingly, monitoring efforts of GHLT groups are required in highly intensified *cabrucas* to investigate these possible outcomes.

TABLE 4 Cumulative AIC_c weight for covariates used to model occupancy (Ψ) and detection (*p*) probabilities of the golden-headed lion tamarin (*Leontopithecus chrysomelas*) at 16 *cabruca* sites of southern Bahia, Brazil

Covariate	Cumulative AIC_c weight	β parameters		
		Estimate	LL	UL
Detection (*p*)				
Density of cacao trees	0.81	5.64	2.10	9.18
Mean air humidity	0.20	0.07	−0.04	0.18
Playback time	0.03	0.00	0.00	0.01
Mean temperature	0.03	0.01	−0.06	0.07
Occupancy (Ψ)				
Jackfruits IVI	0.87	−0.54	−1.05	−0.03
DBH of shade trees	0.85	0.04	0.00	0.08
Abundance of lianas	0.23	1.90	−0.73	4.54
Equitability of shade tree species	0.22	14.95	−6.14	36.05
Management intensity	0.18	−1.45	−3.05	0.15
Density of cacao trees	0.15	−11.97	−30.30	6.37
Vegetation cover in the landscape	0.13	0.17	−0.09	0.43
Abundance of banana trees	0.07	0.17	−0.25	0.59
Distance to fragment edge	0.05	0.00	0.00	0.01
Abundance of diurnal raptors	0.04	−0.26	−0.96	0.44
Distance to households	0.03	0.00	−0.01	0.01
Abundance of non-aerial predators	0.03	−0.12	−1.03	0.79

Note: The covariate effects (β parameters) were derived from the most parsimonious model including each covariate. LL and UL represent the lower and upper limits of the confidence interval (95%), respectively.

5 | CONSERVATION IMPLICATIONS

Considering the landscape composition within the current geographic range of GHLTs, one can easily conclude that a GHLT conservation plan that fails to explicitly consider *cabrucas* is likely doomed to failure. Unfortunately, the role of *cabrucas* in assisting GHLT conservation can be threatened by imminent prospects of widespread management intensification, as attempts to increase cacao yields typically involve thinning of shade canopy trees, which is likely to affect the main predictors of GHLT occupancy in this habitat. However, some studies have shown that it is possible to combine high crop yields with high biodiversity levels in cacao agroforests (Clough et al., 2011). In southern Bahian *cabrucas*, shade cacao crop yields can increase two-fold compared to the regional average productivity by simply adjusting appropriate levels of mineral fertilizers

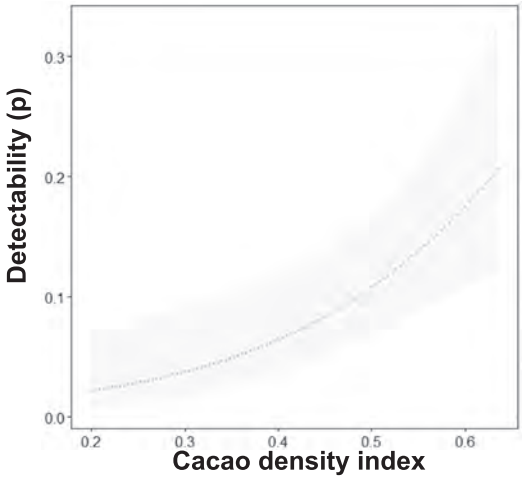

FIGURE 4 Probability of detecting golden-headed lion tamarins (*Leontopithecus chrysomelas*) at each playback point within *cabrucas* (p) as a function of the density of cacao trees (represented as the sum of density values per plot for each *cabruca* site). The dotted line and the color-coded area represent the estimates and the 95% confidence intervals, respectively

and restricting overall canopy shading to 55%, without necessarily reducing shade tree density (Schroth et al., 2014).

Under current policies in which *cabruca* management intensification is incentivized, it has been proposed that exotic shade species, such as jackfruits, should be preferentially removed instead of native species, as exotic species are expected to have a lower ecological value for the native fauna (Schroth et al., 2014). Considering previous findings (Oliveira et al., 2011) and our results here, both complete removal and complete dominance of jackfruits would detrimentally impact GHLTs. As such, although we agree native species should be favored, we recommend that removal of exotic species should be done with caution since exotic fruits have become staple resources for GHLTs and other frugivores in human modified-habitats (Canale et al., 2016; Oliveira et al., 2011). Currently, there is no official mechanism to regulate the thinning rate of exotic species from *cabrucas*, which is necessary as the removal of jackfruit trees can substantially reduce habitat carrying capacity for the attendant fauna (Gosper & Vivian-Smith, 2009). The impact of removing exotic species from intensified *cabrucas*, that is those containing a low-density of shade trees, can be even higher than in traditional *cabrucas* such as those in this study.

Finally, managing cacao farm landholdings to facilitate coexistence with GHLTs and other native wildlife is not just good conservation practice, it can also accrue additional economic benefits. GHLTs play a critical role as natural seed dispersers, yet they do not raid cacao fruits nor damage cacao trees, thereby contributing to the regeneration and maintenance of traditional *cabrucas* (Catenacci et al., 2009). Also, the GHLT is a flagship species in the Atlantic Forest of southern Bahia, which can attract tourists to those *cabrucas* where they still occur. Although this tourism potential remains largely unexplored in this region, some producers are already using the public image of GHLTs in their commercial logos or exploring them as a focal species for ecotourism ventures. Primate watching can be both a profitable economic activity and a successful conservation strategy whenever benign tourism practices are adopted (Macfie & Williamson, 2010; Russon & Wallis, 2014). For example, the Lion

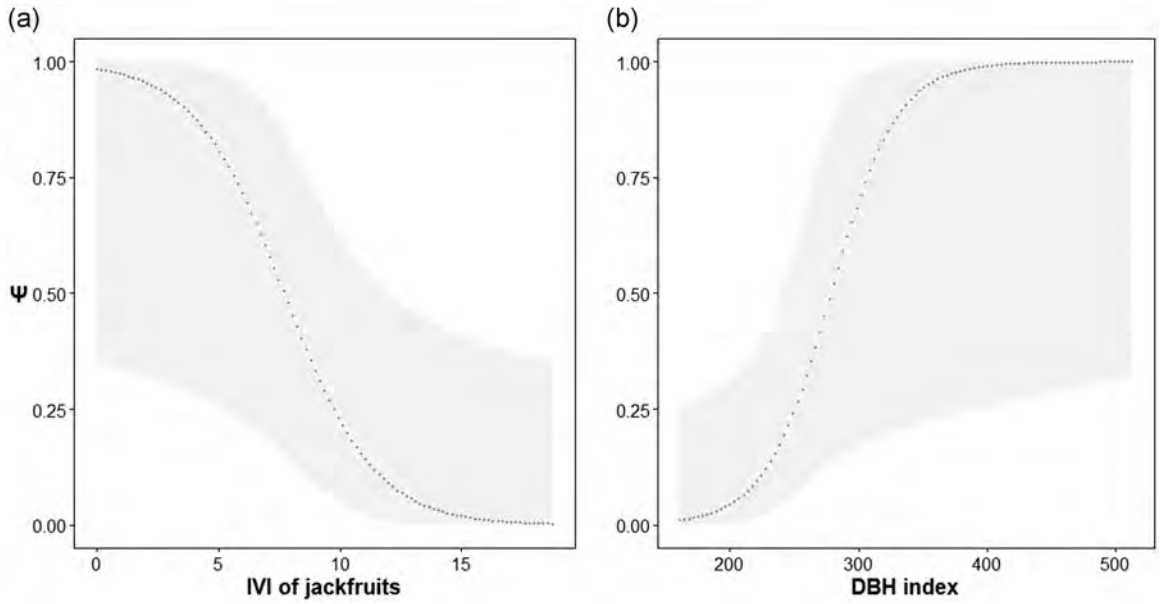

FIGURE 5 Occupancy of golden-headed lion tamarins (*Leontopithecus chrysomelas*) within *cabrucas* (Ψ) as a function of (a) jackfruit trees (*Artocarpus heterophylus*) Importance Value Index (IVI), and (b) the diameter at breast height (DBH) index (calculated as the sum of median DBH values for shade trees recorded per plot at each *cabruca* site). The dotted line and the color-coded area represent the estimates and the 95% confidence intervals, respectively

Tamarin Association (http://www.micoleao.org.br/) has achieved very positive results from sustainable tourism activities focused on the endangered golden lion tamarin (*Leontopithecus rosalia*) showing that this activity has potential in other parts of Brazil. Promoting sustainable ecotourism as an alternative source of local income, combined with biodiversity conservation, has already been proposed by the state management decree. Explicitly linking regional economic development with biodiversity conservation, while maintaining the status of traditional *cabrucas* is, therefore, a wise strategy that can likely perpetuate these wildlife-friendly systems.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supporting Information Material of this article.

ORCID

Juliana M. de Almeida-Rocha http://orcid.org/0000-0002-2968-5504
Carlos A. Peres https://orcid.org/0000-0002-1588-8765
Julio A. B. Monsalvo https://orcid.org/0000-0001-9692-2533
Leonardo de C. Oliveira https://orcid.org/0000-0002-1774-0713

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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