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How many shade trees are enough? Identifying the threshold for golden-headed lion tamarin presence in cocoa agroforests of Southern Bahia, Brazil

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A B S T R A C T

Cocoa agroforestry systems offer potential for sustainable development by supporting biodiversity conservation alongside agricultural production and rural livelihoods. However, the effect of shade-tree management on biodiversity within these systems remains unclear, as research has largely focused on comparisons with other land-use systems. We investigate the effects of shade-tree management on the presence of the golden-headed lion tamarin (*Leontopithecus chrysomelas*), an endangered primate species highly dependent on shaded cocoa agroforests, and terrestrial medium- and large-sized mammals in southern Bahia, Brazil. We conduct playback surveys to determine *L. chrysomelas* presence and use camera traps to record mammal detections across 18 farms with cocoa agroforestry systems, and analyse the relationship between shade-tree management and *L. chrysomelas* occupancy and mammal detection rates using occupancy modelling and generalized linear mixed models. Our findings show that reduced shade cover is associated with lower *L. chrysomelas* occupancy and decreased mammal detections, highlighting the negative effects of intensified shade management on biodiversity. The threshold required for *L. chrysomelas'* persistence is 65% shade cover, corresponding to 100 native shade trees per hectare. This is much higher than the shade levels allowed by the current Bahian shade-tree management decree, which permits thinning to 40 native shade trees per hectare. Our findings suggest that the current shade-tree management policy in Bahia needs to be adjusted to ensure adequate shade cover for biodiversity conservation in cocoa agroforests. These insights are valuable for policymakers developing strategies to mitigate trade-offs between management intensification and biodiversity conservation in cocoa-growing landscapes.

1. Introduction

As global demand for agricultural commodities continues to rise, biodiversity and ecosystem services are rapidly declining due to forest conversion for agriculture and the intensification of agricultural systems (De Beenhouwer et al., 2013; Lenzen et al., 2012; Pendrill et al., 2022). Among these commodities, cocoa (*Theobroma cacao*) has raised significant sustainability concerns due to the environmental and socio-economic impacts associated with its production systems (Boeckx et al., 2020; Kalischek et al., 2023; Renier et al., 2023; Van Broeck and Akaribo, 2024). Cocoa agroforestry systems (CAFS), where cocoa is cultivated under a canopy of native shade trees retained after forest thinning, have been advocated as a sustainable solution for supporting biodiversity conservation alongside cocoa production while providing decent livelihoods for farmers (Blaser et al., 2018; Niether et al., 2020; Steffan et al., 2007). However, farmers in many cacao growing regions throughout the tropics increasingly shift towards unshaded or low-shaded cocoa cultivation, driven by expectations of higher yields and the need to secure short-term income (Steffan et al., 2007; Tscharntke et al., 2011).

While the ecological benefits of agroforestry are well-documented, most studies have primarily focussed on comparing biodiversity outcomes to other land-use systems or farming systems, treating agroforestry as a distinct land-use type (Cassano et al., 2012; De Beenhouwer et al., 2013; Etana et al., 2021; Ferreira et al., 2020; Niether et al., 2020). This approach overlooks the substantial variability within CAFS, which can range from intensively managed agroforestry systems with few shade trees and limited species diversity to highly shaded and diversified systems (Schroth et al., 2015). Although some research has addressed the effects of management intensification within CAFS on biodiversity, studies in South America remain scarce (Aaron et al., 2024; Cabral et al., 2021; Cassano et al., 2014; Ferreira et al., 2025; Waldron et al., 2012),

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despite evidence indicating that biodiversity responses to intensification are highly region-specific and that biodiversity declines are among the highest on this continent (De Beenhouwer et al., 2013).

Brazil is the world's seventh largest cocoa producer and has experienced a 57% increase in domestic cocoa production in the past two decades (FAOSTAT, 2023). The country's major cocoa-producing region, southern Bahia, accounts for 47% of the country's total production (IBGE, 2023) and provides livelihoods for approximately 69,000 households (Chiapetti et al., 2020; Rocha et al., 2024). Traditionally, cocoa cultivation in this region occurs within shaded agroforestry systems locally known as *cabrucas*, which remain widespread and account for 78% of cocoa-producing properties (Chiapetti et al., 2020). *Cabrucas* are structurally complex and highly diversified systems, with an average of 197 shade trees per hectare (ranging from 70 to 480) and approximately 63% native tree species (Schroth et al., 2015). As a result, *cabrucas* provide habitat for native and endangered species of the Atlantic Forest biome (Cassano et al., 2009; Faria et al., 2007; Schroth et al., 2011), one of the world's most threatened biodiversity hotspots (Myers et al., 2000). Despite their ecological significance, *cabrucas* are under increasing pressure from intensification. Southern Bahia's ambition to double its cocoa production to 400,000 tons by 2030 (Ministério da Agricultura e Pecuária, 2024) could have substantial environmental implications for the sustainability of its traditional agroforestry systems. This goal is legally supported by a state decree established in 2014, allowing landowners to reduce the number of shade trees in *cabrucas* to a minimum of 40 native trees per hectare (State Decree No. 15180/2014, Seção IV, Art. 19, Bahia; hereafter referred to as "*shade tree management decree*"), a threshold well below the densities typically observed in traditional *cabrucas* (Schroth et al., 2015). While the intention is to boost production, this ambition aided by the *shade tree management decree* risks simplifying the structural complexity of these traditional agroforests, potentially diminishing their biodiversity conservation value.

Recent studies highlight the role of southern Bahia's CAFS in supporting diverse mammal communities as well as other forest biodiversity, including endemic and threatened species, while also enhancing landscape connectivity in a highly fragmented landscape (Almeida-Rocha et al., 2020; Cabral et al., 2021; Cassano et al., 2014; Ferreira et al., 2020, 2024). The ability of *cabrucas* to sustain mammal populations is strongly influenced by the landscape context, particularly the extent of surrounding forest cover (Ferreira et al., 2020, 2025). Yet, *cabrucas* can support a significant portion of the mammal fauna even in landscapes with reduced forest cover, provided they remains the dominant land-use type in the landscape (Ferreira et al., 2020). While the role of landscape context is well-documented (Faria et al., 2007; Ferreira et al., 2020, 2025; Raboy et al., 2010; Teixeira et al., 2024), the effects of intensified shade-tree management on mammal communities, particularly for species of conservation concern, remain insufficiently understood, as highlighted by previous studies (Almeida-Rocha et al., 2020; Ferreira et al., 2025). Given the trend of intensified shade-tree removal not only in CAFS of southern Bahia but throughout the tropics, understanding how such management practices, alongside resource availability and anthropogenic disturbances, affect mammal communities is crucial for developing effective conservation strategies.

The golden-headed lion tamarin (*Leontopithecus chrysomelas*), an endangered primate endemic to the Atlantic Forest, is an emblematic species of the *cabrucas* of southern Bahia and particularly relies on these shaded agroforestry systems for its persistence in the fragmented landscape (Oliveira et al., 2010, 2011). *Cabrucas* provide essential trophic and structural resources for *L. chrysomelas*, with shade trees in particular offering key food sources (such as fruits, flowers, nectar, gums), and providing sleeping sites, primarily tree holes (Oliveira et al., 2010). In *cabrucas*, *L. chrysomelas* also depend on bromeliads, which are concentrated on shade trees and serve as foraging sites for animal prey (Rylands, 1989; Oliveira et al., 2011), and exotic jackfruit trees (*Artocarpus heterophylus*) when other key resources are scarce (Oliveira et al., 2011). Among native shade tree species, those belonging to the Sapotaceae and Myrtaceae families are especially important, being the most frequently used for both feeding and sleeping (Oliveira et al., 2010). Although cabrucas contain fewer individual trees used by *L. chrysomelas* compared to forests, the frequency of use per tree is higher in cabrucas (Oliveira et al., 2010), suggesting that individual trees play an important role in supporting the species' resource use (Oliveira et al., 2011). Moreover, large-diameter shade trees have been found to be associated with a higher probability of the species' occurrence, likely due to their suitability as sleeping sites (Almeida-Rocha et al., 2020). Additionally, shade trees enhance canopy connectivity, offering travel routes that facilitate movement across the fragmented landscape (Cassano et al., 2014). Over the last 30 years, *L. chrysomelas*' geographic range has contracted by 42% and its population size has declined by 60% due to extensive deforestation (Teixeira et al., 2024), with approximately 60% of the species' remaining habitat is comprised of CAFS (Zeigler et al., 2010). Despite *L. chrysomelas*' reliance on shade trees in *cabrucas*, the effects of shade-tree management on its occurrence remain unstudied, leaving it unclear whether the current *shade tree management decree*'s threshold is adequate to sustain their populations.

This study addresses these research gaps by evaluating how shade-tree management intensification influences our focal species, the golden-headed lion tamarin, and the terrestrial medium- and large mammal community within cocoa agroforestry systems in Southern Bahia, Brazil. Specifically, it examines whether the current state-mandated intensification threshold of 40 native shade trees per hectare is sufficient to sustain *L. chrysomelas* and whether shade tree management recommendations for this species may also provide co-benefits for the terrestrial medium- and large mammal community in *cabrucas*. To this end, data on shade tree management intensity (i.e., shade tree density and cover), vegetation structural complexity (e.g., height of shade trees and canopy connectivity), and the availability of key trophic resources for *L. chrysomelas* (e.g., presence of bromeliads and key tree species) were collected across 18 cabrucas in southern Bahia, Brazil. Using playback surveys and camera traps, *L. chrysomelas'* presence and terrestrial medium- and large-sized mammal detections were assessed, respectively. We expect that intensified shade-tree management, characterized by reduced tree density, will be associated with lower levels of shade cover, and predict that both *L. chrysomelas* occupancy and mammal detections will decrease under such management in CAFS.

This research on the effects of shade-tree management intensification on biodiversity has the potential to inform evidence-based policy adjustments to the *shade tree management decree*, guiding the establishment of shade-tree density thresholds that better support biodiversity conservation in cocoa agroforestry systems. In particular, it aims to enhance understanding of the tipping point at which shade tree management intensification negatively affects species of conservation concern, such as *L. chrysomelas*. Our insights help to promote sustainable agroforestry practices in the southern Bahia's cocoa landscape, as well as for other cocoa-producing landscapes facing similar intensification pressures.

2. Data and methods

2.1. Research area

We conducted our research in the south-eastern cocoa region of Bahia, in north-eastern Brazil (Fig. 1A). The region is characterized by a mean annual temperature and rainfall of 24 °C and 2500 mm, respectively, with no distinct seasonality (Mori et al., 1983). A total of 18 *cabrucas* were surveyed, all located across six major cocoa-producing municipalities (Fig. 1B), which constitute the eastern part of the golden-headed lion tamarin's distribution range (Teixeira et al., 2024). According to the most recent and comprehensive assessment of *L. chrysomelas* distribution (Teixeira et al., 2024), the eastern region is characterized by a higher species occurrence and harbours its most viable populations (Zeigler et al., 2010). This area consists of a relatively continuous complex of coastal evergreen tropical rainforest, along with

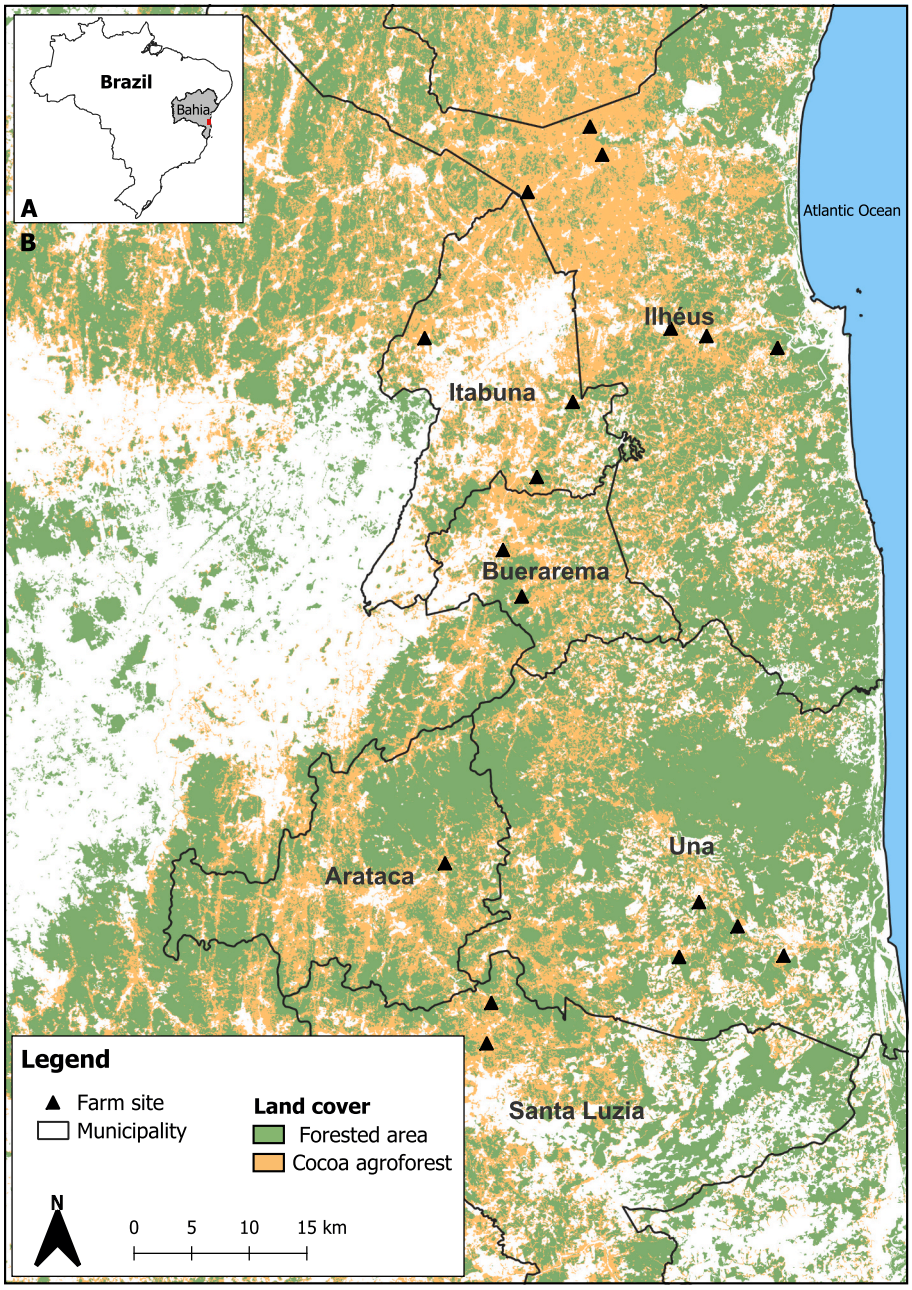

Fig. 1. (A) Location of the state Bahia (grey) and the research area (red) in Brazil. (B) Distribution of the 18 farm sites across six municipalities in southern Bahia. Land cover data obtained from MapBiomas Cacau (MapBiomas Cacau, accessed on 1 October 2024, via: https://brasil.mapbiomas.org/en/mapbiomas-cacau/). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

an increasingly fragmented landscape of *cabrucas*, pasture, other agricultural crops, and urban areas (Zeigler et al., 2010). In contrast, the western part of the species' range has undergone extensive anthropogenic modification through agriculture and livestock (Zeigler et al., 2010), resulting in lower *L. chrysomelas* occurrence (Teixeira et al., 2024) and near total absence of cocoa plantations and is therefore out of scope for our research area.

2.2. Sampling

Between June and September 2022, we systematically selected 18 traditional CAFS (i.e. *cabrucas*) along a gradient of shade-tree density, ensuring the inclusion of sites ranging from intensively managed to highly shaded agroforestry systems (60 to 310 shade trees ha^{-1}, with a diameter at breast height (DBH) >10 cm). This approach ensured that the study design effectively met its objective of quantifying changes in biodiversity along a shade-tree management gradient. Sampling sites were at least 2.5 km apart. Environmental data collection was conducted from January to October 2023. All sampling was performed by the first author with the help of an experienced field assistant.

2.3. Golden-headed lion tamarin survey

Playback surveys were conducted to detect the presence of *L. chrysomelas* in each CAFS. This sampling method, which involves broadcasting the long call vocalization of *L. chrysomelas* along a point-transect to elicit intraspecific responses and stimulate countercalls (Kierulff and Rylands, 2003), is particularly effective for detecting territorial primates that rely on long-distance vocalizations to signal the presence of other individuals or groups in their territory, such as *L.*

chrysomelas. Its effectiveness has been demonstrated in several field studies targeting *L. chrysomelas* (Almeida-Rocha et al., 2020; Pinto and Rylands, 1997; Raboy et al., 2010; Teixeira et al., 2024) as well as other primate species (Gestich et al., 2017; Hilário et al., 2022).

To ensure standardized sampling, a 200 × 200 m grid was overlaid on satellite imagery of the CAFS using QGIS *3.22.5* (QGIS Development Team, 2024). Playback points were established at each grid intersection, with points spaced 200 m apart, as recommended by previous studies to prevent overlap within the species' auditory range (~100 m) and to reduce the likelihood of detecting the same group more than once on the same day (Kierulff and Rylands, 2003). The number of playback points surveyed per farm ranged from 3 to 10, proportional to farm size, following the sampling design of Almeida-Rocha et al. (2020). Up to 10 points were surveyed during a single morning (06:00–11:00 h), the maximum achievable during the peak activity period *of L. chrysomelas* in agroforests (Almeida-Rocha et al., 2020). Surveyed areas included a 100 m buffer from the agroforest edge. In the field, the location of each playback point was pinpointed using a handheld GPS (Model Garmin GPSMAP 66S).

At each playback point, one recorded long-call from an adult male and female was broadcast in each cardinal direction using a JBL Charge 5 speaker (frequency response: 60 Hz–20 kHz), followed by a 4-min waiting period for responses from *L. chrysomelas*. This procedure was repeated three times at each point before moving to the next point along the transect. The total time spent at each playback point was 15 min. When *L. chrysomelas* groups were detected, either through vocal responses or direct observation, their geographic location was recorded, the time of detection, and, when possible, the number of individuals and their group composition (adults, juveniles, and infants) to ensure that the same group was not counted more than once on the same survey day.

The number of visits (three) to CAFS was determined a priori based on the detection history of *L. chrysomelas* from previous studies using the same sampling method (Almeida-Rocha et al., 2020; Teixeira et al., 2024). To prevent habituation, playback surveys were conducted over three non-consecutive days, with at least one week between visits to the same CAFS. When *L. chrysomelas* was not detected after the third visit, the species was considered absent in the CAFS. A thermo-hygrometer was used to record mean air temperature and humidity during each visit to model the influence of survey-specific covariates on species detectability. Playback surveys were avoided during rainy or windy weather conditions.

2.4. Terrestrial medium- and large-sized mammal survey

Camera traps were used to assess the presence of the terrestrial medium- and large-sized mammals (defined as those larger than >500 g) in the CAFS. This widely recognized, non-invasive method is effective for surveying mammal communities and simultaneously recording multiple species with minimal disturbance (Bruce et al., 2018; Etana et al., 2021; Lhoest et al., 2020; Wearn and Glover-Kapfer, 2017). Camera traps (Browning Spec Ops Elite HP5) were placed on each grid intersection point 400 m apart, based on similar studies on terrestrial large mammals in agroforestry systems (Almeida-Rocha et al., 2020; Espartosa et al., 2011; Etana et al., 2021, 2024). The number of camera traps per farm ranged from 1 to 5, proportional to farm size, following the sampling design of Almeida-Rocha et al. (2020). At each predefined point, one camera was attached at a random location to a tree trunk, 20-50 cm above ground level. No bait was used to prevent differences in detection probability among mammal species. Cameras were operational for 24 h a day and set to take a minimum of 5 consecutive rapid-fire pictures per trigger, with 1 s delay between consecutive triggers. They were checked every 8–20 days to replace SD cards and maintain camera functionality. Cameras remained in the field for a one-month period, depending on uncontrollable conditions, including malfunctions. When possible, malfunctioning cameras were replaced and kept operating longer to compensate for any losses in sampling effort. Independent detection events were defined as consecutive pictures of the same species taken >60 min apart (Bruce et al., 2018; Tobler et al., 2008) across all cameras within the same farm to reduce the likelihood of counting the same individual multiple times at different camera traps within the same farm. The sampling effort for each camera trap was quantified in camera trap days, defined as the total number of days the camera was operational. To account for differences in sampling effort, mammal detection rate for each camera was then standardized as the number of independent detections per 100 effective camera trap days.

2.5. Vegetation survey

Vegetation surveys were conducted in each CAFS to assess a set of local vegetation variables related to and influenced by shade tree management practices. Plots of 500m^2 (20mx25m) were established at each CAFS at 400 m intervals, following the sampling design of Almeida-Rocha et al. (2020). In each plot, cocoa trees were counted as well as native and non-native shade trees with a diameter at breast height (DBH) of ≥10.0 cm) to determine shade tree density within each plot. The percentage of shade cover within each plot was estimated using a hand-held concave spherical densiometer (Forestry Suppliers, Inc., Jackson, MS, USA). Shade measurements were taken along the centre-line of the plot, at every 10 m along the 20 m axis. Shade-tree density and shade cover are indicators of shade tree management intensification within agroforestry systems (Blaser et al., 2018), i.e. lower tree density or shade cover reflect higher levels of shade-tree management intensification in the CAFS. The DBH of shade trees and their height were recorded using a hypsometer (Forestry Pro, Nikon Co., Ltd., Tokyo, Japan). Shade trees were identified in situ at the lowest possible taxonomic level by experienced local field assistants. Shade tree species used by *L. chrysomelas* for food and sleeping sites were identified based on previous studies (Catenacci et al., 2009, 2016; Oliveira et al., 2010, 2011; Raboy and Dietz, 2004; Couto and Oliveira, 2019; Table S2, Appendix A). Jackfruit trees were also included as a separate variable due to their particular importance in the diet of *L. chrysomelas* in CAFS (Oliveira et al., 2011). Other main habitat requirements for *L. chrysomelas* were identified: i) presence of bromeliads on shade trees; ii) canopy connectivity, defined by the number of crown connections with adjacent shade trees and iii) number of banana trees.

Landscape characteristics were accounted for by including data on elevation, surrounding forest cover, and the distance to the closest urban area and road accessible for car transportation, extracted in QGIS software. For elevation, the Digital Elevation Model (USGS, 2015) were used. The percentage of surrounding forest cover within a 2 km radius buffer from the CAFS centroid was used, based on previous studies in the region that identified this threshold as the most relevant for landscape analysis of medium- and large-sized mammals (Faria et al., 2023; Ferreira et al., 2020). Forest cover data were obtained from MapBiomas Cacau and urban area data from the broader MapBiomas Project (MapBiomas, accessed on 1 October 2024, via: https://brasil.mapbiomas.org/en/mapbiomas-cacau/)—both part of a collaborative initiative involving interdisciplinary teams from universities, NGOs, and technology companies. The underlying classification methodology has been validated in peer-reviewed literature (Souza et al., 2020). While a known challenge in MapBiomas Cacau is distinguishing degraded forests or agroforestry systems from native forests, this is unlikely to significantly affect the reliability of our analysis, as these habitat types are used by *L. chrysomelas*. Farmers were interviewed about their pesticide use (R$ ha^{-1}) within their CAFS in 2023 as part of a socioeconomic survey conducted in 2024.

2.6. Data analyses

Vegetation variables were first calculated at plot-level and median values were subsequently computed for each variable to obtain farm-level estimates for each CAFS. Shade tree diversity was quantified

using Hill-Simpson's diversity index, which was selected above Hill-Shannon's due to its robustness to sample size (Roswell et al., 2021). The contribution of key trees species to the shade tree community composition on CAFS was weighted using the Importance Value Index according to (Curtis and McIntosh, 1951). IVI integrates relative values of frequency, density, and dominance (through basal area). Tree species with the highest IVI are considered more dominant (Tesfay et al., 2022). IVI of key tree species for *L. chrysomelas* and IVI of jackfruit were calculated as a single value for each CAFS.

Variables were selected a priori to reflect key ecological processes and different aspects of shade management intensification relevant to our main hypothesis, with demonstrated or hypothesized importance for either *L. chrysomelas* or terrestrial medium- and large-sized mammals, based on previous studies (Almeida-Rocha et al., 2020; Cassano et al., 2014; Etana et al., 2021, 2024; Ferreira et al., 2025; Teixeira et al., 2024). Multicollinearity among predictor variables was assessed using Spearman correlations ($|r| < 0.6$; Fig. S1; Appendix A) and Variance Inflation Factors (VIF < 4.0) using the *car* package (Etana et al., 2024; Zuur et al., 2010). For each pair of highly correlated variables ($r \geq 0.6$), we excluded one, prioritizing the retention of variables that enabled us to test our main hypotheses. As a result, we removed banana density, IVI of key tree species for *L. chrysomelas*, native shade tree density, and canopy height. We excluded the following variables due to high multicollinearity as indicated by Variance Inflation Factors (VIF > 4): non-native shade tree density, shade tree species richness, DBH of shade trees and elevation. Additionally, distance to roads and cocoa density were excluded due to high multicollinearity (VIF > 4), to prioritize the retention of canopy connectivity for *L. chrysomelas*.

Due to differences in survey method and resulting data structure, we applied complementary analytical approaches. The focal species of this study, *L. chrysomelas*, was surveyed using playback surveys, generating detection–non-detection data suitable for single-season occupancy modelling that accounts for imperfect detection (Mackenzie et al., 2002). In contrast, data on terrestrial medium- and large-sized mammals were obtained from unbaited camera traps deployed continuously for a one-month period in each farm. Given the limited sampling duration, we calculated detection rates standardized by camera trap effort and modelled these using a Generalized Linear Mixed Model (GLMM). All statistical analyses were done in R version 4.3.1 (R Core Team, 2024).

2.6.1. Occupancy modelling

Single-season occupancy modelling (Mackenzie et al., 2002) was used to investigate the influence of shade tree management on *L. chrysomelas* occupancy (ψ) in *cabrucas*, while accounting for imperfect detection (p). A detection history matrix was constructed for each playback point (sampling unit i), with species detections (1) and non-detections (0) across three survey occasions (sampling occasion j). Detection probability (p) was modelled as a function of survey-specific covariates (i.e. temperature, humidity, time of visit) along with sampling effort and neighbouring forest cover. Occupancy (ψ) was modelled using variables related to CAFS management and vegetation characteristics (i.e. shade-tree density and diversity, shade cover, basal area and pesticide use), key habitat variables for *L. chrysomelas* (i.e. canopy connectivity, vertical stratification, IVI of jackfruit trees and the presence of bromeliads) as well as landscape characteristics (i.e. distance to urban area). To account for the nested sampling design and spatial non-independence between playback points (i.e. the sampling unit) within the same farm, a random effect of farm was included in the occupancy model (Kellner et al., 2023). As *L. chrysomelas* can move between playback points and across farm boundaries, potentially exiting or entering sampling units during the survey period, the assumption of population closure was not met. Consequently, as proposed by Mackenzie et al. (2006), occupancy should be interpreted as the proportion of the area being used by the species, rather than true occupancy.

Model building followed a stepwise approach. First, a null model with constant detection and occupancy probabilities was constructed. Detection probability was then modelled, with the best-supported detection model subsequently used to model occupancy (Table S3, Appendix A). Considering that survey effort may influence the detectability of primates, we included sampling effort as a covariate to model detection probability. Since the model including the sampling effort covariate had less support than the null model and showed no significant effect, this covariate was not retained in the subsequent occupancy model (Table S3), following the approach of (Greco et al., 2023; Sushma et al., 2022). To reduce the risk of overfitting and ensure robust parameter estimation, we limited candidate models to a maximum of two covariates. Models were fitted using the function 'occu' from *Unmarked* package. Model ranking and selection were based on the smallest Akaike information criterion corrected for small samples (AICc). AICc allows identifying the model that explains the most variation with the fewest variables: the model with the lowest AICc best explains the data (Burnham and Anderson, 2002). *L. chrysomelas* occupancy was predicted using the best-supported model, and covariate effects were extracted. The fit of the global model (i.e. including all covariates) was assessed by estimating the overdispersion parameter (*c-hat*) through 1000 bootstrap simulations, using the *AICcmodavg* package.

2.6.2. Generalized linear mixed model

The influence of shade tree management on medium- and large-sized mammal detections was analysed using a GLMM with a Negative Binomial distribution to account for the count-based structure of the data and overdispersion. The total number of independent mammal detections was used as response variable. Similar for occupancy modelling, a random effect of farm was included in the model to account for the nested sampling design and spatial non-independence between camera trap points (i.e. the sampling unit) within the same farm. We also accounted for differences in camera trap sampling effort by including a log-offset for camera trap effort (i.e., number of camera trap days) in the model. Explanatory variables included CAFS management and vegetation characteristics (i.e. shade tree cover, shade tree density and diversity, basal area, pesticide use, cocoa density and IVI of jackfruit trees) as well as landscape characteristics (neighbouring forest cover, distance to road and urban areas) relevant for terrestrial medium- and large-sized mammals. Candidate models were generated using the *MuMIn* package and the most parsimonious model was selected based on the smallest ΔAICc value. Mammal detections were predicted using the best-supported model and covariate effects were extracted.

3. Results

3.1. Management and vegetation characteristics of cocoa agroforestry systems

Shade tree density and shade levels demonstrated considerable variation across the 18 CAFS, ranging from 60 to 310 (±59.42) shade trees ha^{-1} and 46.18% to 88.33% (±11.06) shade cover, respectively (Table S1, Appendix A). Spearman correlation test on plot-level measurements indicated a significant positive correlation between shade tree density and shade cover ($\rho = 0.34$, $p < 0.05$; Fig. S2) and a significant negative correlation between shade tree density and DBH ($\rho = -0.45$, $p < 0.001$). A total of 64 shade tree species from 30 families were recorded, of which 39 were identified as key tree species for *L. chrysomelas* (Table S2, Appendix A). The IVI of those key resource tree species, and particularly of jackfruit trees, ranged between 39.07 and 269.62% and 0–80.53%, respectively (Table S1, Appendix A). Cocoa tree density ranged between 465 and 990 trees ha^{-1} (±156.94).

3.2. Golden-headed lion tamarin occupancy

A total of 21 detections of *L. chrysomelas* were recorded across 17 playback points in 11 CAFS. The maximum number of groups detected on a single farm during the same sampling occasion was two. We

recorded solitary individuals and groups with up to 10 individuals. Additionally, groups of *Callithrix kuhlii* were regularly observed, often forming mixed-species groups with *L. chrysomelas*. The playbacks also elicited responses from Black-headed titi *(Callicebus melanochir*).

The estimated detection probability (p) was 0.20 (95% CI: 0.08; 0.42). Based on the lowest AICc value and highest Akaike weights, the model including the percentage of forest cover around CAFS improved detection probability of *L. chrysomelas* in CAFS (Table S3, Appendix A). The estimated occupancy probability (Ψ) was 0.29 (95% CI: 0.12; 0.55). The best supported occupancy model (ΔAICc = 0.00; Table S3) showed that the probability of occupancy of *L. chrysomelas* increased significantly with higher shade cover percentage ($\beta = 0.15 \pm 0.24$; $p < 0.01$; Table 1; Fig. 2), with *L. chrysomelas* remaining absent below 65% shade cover and occupancy reaching its maximum at approximately 75%. This indicates that the threshold required for *L. chrysomelas'* persistence is 65% shade cover, corresponding to approximately 100 native shade trees per hectare in our sampled CAFS (Fig. S2). The best supported occupancy model also indicated a significant positive effect of importance value index (IVI) of jackfruit, indicating an increase in *L. chrysomelas* occupancy with higher dominance of jackfruit trees ($\beta = 0.15 \pm 0.24$; $p < 0.01$; Table 1). However, the species' occupancy probability was already high (~0.95) in cocoa agroforestry systems where jackfruit was either absent or not the dominant shade tree species (Fig. S3). The goodness-of-fit test of the global model indicated no evidence of overdispersion ($\chi^2 = 4.83$; $P = 0.26$; *c-hat* = 0.95).

3.3. Terrestrial medium- and large-sized mammal detections

Throughout the study period, a total sampling effort of 1811 operational camera-trap days was achieved across 18 CAFS, with a mean of 37.72 ± 5.06 days per camera trap. A total of 14 medium-and large-sized terrestrial mammals were recorded, belonging to six orders and 13 families (Table 2). Three arboreal mammal species (*L. chrysomelas*, *Callithrix kuhlii* and *Coendou insidious*) were recorded that were not the target of this camera trap survey. Beside for *L. chrysomelas*, which is classified as 'Endangered' on the IUCN Red List, *C. kuhlii* is also classified as 'Vulnerable' and considered a species of conservation concern. The most frequently detected medium-and large-sized terrestrial mammal species were crab-eating fox (*Cerdocyon thous*) and nine-banded armadillo (*Dasypus novemcinctus*). The Amazonian brocket (*Passalites nemorivagus*) was identified in three distinct CAFS. This species, previously thought to be restricted to the Amazon region, was also recently documented in Una Biological Reserve (Oliveira et al., 2020) in southern Bahia.

Based on the best-supported model (ΔAICc = 0.00; Table S4, Appendix A), mammal detections significantly increased with increasing shade cover ($\beta = 0.32 \pm 0.10$; $p < 0.01$; Table 3; Fig. 3). However, a decrease in total basal area of shade trees was significantly associated with decreasing mammal detections ($\beta = -0.44 \pm 0.12$; $p < 0.001$; Table 3). The fit of the best-supported model was assessed by checking for overdispersion (Fig. S4), with a Pearson overdispersion value of 1.12, indicating no overdispersion (Zuur et al., 2009). Additionally, Nagelkerke's R-squared value of 0.34 indicated a moderate model fit (Nagelkerke, 1991). Among models with ΔAICc <2, additional models incorporating distance to road, shade tree diversity, and pesticide use were evaluated. However, these variables were not statistically significant ($p > 0.1$), suggesting the inclusion of these variables did not contribute to the model fit.

The best-supported model for total mammal detections was subsequently applied to both mammal species sensitive and insensitive to forest conversion into cocoa agroforests, as classified by Ferreira et al. (2025). The results suggest that for insensitive species, mammal detections significantly decreased with increasing basal area of shade trees ($\beta = -0.55 \pm 0.16$; $p < 0.001$; Table S5). In contrast, for sensitive species, mammal detections significantly increased with increasing shade cover ($\beta = 0.37 \pm 0.15$; $p < 0.05$; Table S5), while mammal detections decreased with increasing basal area ($\beta = -0.40 \pm 0.13$; $p < 0.01$; Table S5).

Table 1
Covariates used to model occupancy (ψ) and detection (p) probability, along with parameter estimates from the best-supported model (ΔAIC = 0.00), for *L. chrysomelas* in 18 cocoa agroforestry systems in southern Bahia, Brazil.

Covariates	Estimate	SE	Z	*P*-value
ψ(Intercept)	4.97	0.48	10.39	<0.001
ψ(Shade cover)	7.52	0.01	1338.03	< 0.01
ψ(IVI Jackfruit)	2.04	0.38	5.39	< 0.01
p(Intercept)	−2.48	0.23	−10.72	<0.001
p(Forest cover)	0.15	0.24	0.61	0.54

4. Discussion

4.1. Linking shade tree density to shade cover and the shade tree management decree

The significant positive correlation between shade tree density and shade cover suggests that reductions in shade tree density influence shade cover levels, underscoring the important role of shade tree density in shaping the canopy structure in CAFS. While shade cover can be provided by either many small trees or fewer large trees (Blaser et al., 2018), our results indicate a significant negative correlation between shade tree density and DBH of shade trees, suggesting that higher shade cover in CAFS is associated with a higher density of smaller trees. While shade cover can be provided by either a high density of small shade trees or a lower density of large, mature shade trees (Blaser et al., 2018), our results indicate a significant negative correlation between shade tree density and DBH, suggesting that higher shade cover in CAFS is associated with a higher density of smaller trees. The correlation between shade tree density and shade cover also allows us to convert the threshold set by the *shade tree management decree*, specified as shade tree density, into shade cover. Under the decree, famers are allowed to thin their CAFS to 40 native shade trees per hectare, which is equivalent to <35% shade cover based on plot-level measurements. This threshold is much lower than the shade tree density and shade cover observed in our sampled CAFS, which raises concerns about the structural simplification that could result from the *shade tree management decree*.

4.2. Golden-headed lion tamarin response to shade-tree management and vegetation variables

Shade cover was the most important determinant of *L. chrysomelas* occupancy in CAFS. *Cabrucas* with higher shade cover were significantly more likely to contain *L. chrysomelas*, with *L. chrysomelas* remaining absent below 65% shade cover and occupancy reaching its maximum at approximately 75%. This suggests that a minimum threshold of 65% shade cover is required for the species' persistence in agroforestry systems, corresponding to an estimated 100 native shade trees per hectare in our sampled CAFS. This is much higher than the 35% of shade cover as promoted by the *shade tree management decree*. While the decree aims to enhance cocoa production, its low shade-tree threshold raises concerns that intensifying shade-tree management may render agroforestry systems unsuitable for *L. chrysomelas* conservation, as highlighted by previous research of Almeida-Rocha et al. (2020).

Although Almeida-Rocha et al. (2020) emphasized the importance of large-diameter shade trees—likely due to their role in providing preferred sleeping sites—our findings indicate that shade cover is a more important predictor of *L. chrysomelas* occupancy in cabrucas than DBH or basal area of shade trees. *L. chrysomelas* may be more likely to rely on cabrucas primarily for foraging and as movement corridors between isolated forest patches, where increased shade cover offers greater ecological benefits. In particular, increased shade cover likely mitigates

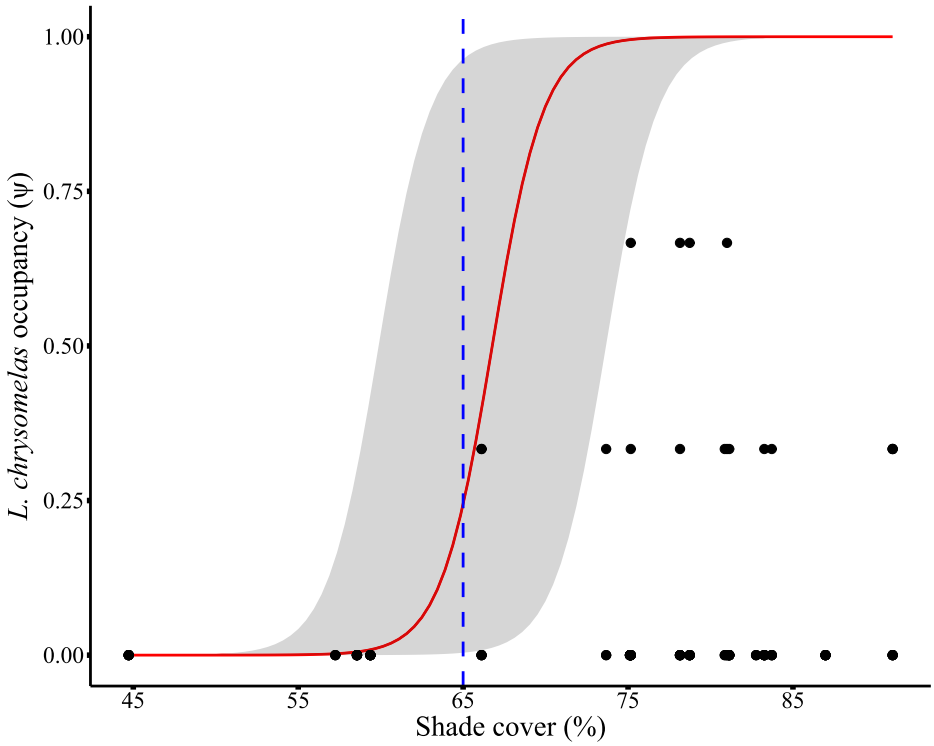

Fig. 2. Predicted occupancy (Ψ) of *L. chrysomelas* within cocoa agroforestry systems as a function of shade cover (%). The prediction was based on the model from Table 1. The red line and the colour-coded area represent the estimates and the 95 % confidence intervals, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

predation risk, which is especially important in cabrucas, where *L. chrysomelas* is more exposed to predation due to reduced canopy connectivity and increased use of upper canopy strata compared to relatively undisturbed forests (Oliveira and Dietz, 2011). Although *L. chrysomelas* typically prefer lower canopy levels in forests, they tend to use the higher canopy strata more frequently in cabrucas (De Almeida Rocha et al., 2015), further increasing their vulnerability in less shaded cabrucas, which may be directly affected by intensified shade-tree management practices.

In contrast, a study in the coffee agroforestry landscape of Ethiopia—the only one to our knowledge comparing primate occurrences across agroforestry systems of varying management intensities—found no significant differences in primate detections between intensively managed and traditional coffee systems with low levels of management intensity (Etana et al., 2021). However, 99% of detections involved olive baboons (*Papio anubis*), a primarily terrestrial and generalist species (Etana et al., 2024). This difference may suggest that terrestrial generalist primates may be more resilient to intensifying shade-tree management compared to primarily arboreal species like *L. chrysomelas*. Arboreal primates, which are highly dependent on canopy connectivity and habitat complexity for movement and foraging, may therefore benefit more from structurally complex, shaded agroforestry systems (Cassano et al., 2014; Estrada et al., 2012). While responses to shade-tree management likely vary among primate taxa, promoting shade tree management practices that maintain higher shade-tree cover may be especially important for conserving canopy-dependent species like *L. chrysomelas* within agroforestry landscapes.

Furthermore, we found a significant positive association between the IVI of jackfruit trees and *L. chrysomelas* occupancy, suggesting that cabrucas with a higher prevalence of jackfruit trees were more likely to contain *L. chrysomelas*. However, this contrasts with the findings of Almeida-Rocha et al. (2020), who reported a negative relationship between jackfruit dominance and *L. chrysomelas* occupancy in cabrucas. This discrepancy may reflect differences in both local CAFS characteristics and broader landscape context. In our study, jackfruit trees were more dominant (higher IVI values), yet *L. chrysomelas* showed a high probability of occupancy even in cabrucas where jackfruit was absent or not the dominant shade tree species. This suggests that while the presence of jackfruit trees enhances occupancy of *L. chrysomelas*, it likely serves as a supplementary food source rather than a limiting factor for species' occupancy. This aligns with previous research highlighting the importance of jackfruit as a food resource for *L. chrysomelas* (Oliveira et al., 2010, 2011), particularly during seasons of native fruit scarcity (Costa et al., 2022). Additionally, Almeida-Rocha et al. (2020) included sites outside the core distribution range of *L. chrysomelas* (Teixeira et al., 2024), where anthropogenic disturbances are more pronounced, forest fragments are more isolated by pasture, and *L. chrysomelas* populations are more vulnerable to local extinction (Raboy et al., 2010; Teixeira et al., 2024; Zeigler et al., 2010). In such degraded landscapes, local habitat features—such as jackfruit dominance—may play a more unfavourable role in determining *L. chrysomelas* occupancy, particularly in areas with reduced native food resources.

4.3. Mammal responses to shade-tree management and vegetation variables

Our findings confirm that *cabrucas* harbour diverse assemblages of medium and large terrestrial mammals, reinforcing their conservation value within human-modified landscapes. This aligns with previous studies from the region (Cassano et al., 2012, 2014; Ferreira et al., 2020, 2025), which demonstrate the role of *cabrucas* in supporting mammal populations, even in landscapes dominated by shaded cocoa cultivation and reduced forest cover (Ferreira et al., 2020). However, our results provide a more nuanced perspective, identifying that shade cover is as a key driver of terrestrial mammal detections within *cabrucas*, particularly for species sensitive to forest conversion. Specifically, total mammal detections, as well as detections for sensitive mammal species, declined significantly in *cabrucas* with reduced shade cover. This finding

Table 2
Medium- and large-sized mammals recorded during the camera trap survey at 18 cocoa agroforestry systems in southern Bahia, Brazil. Number of records (i.e. independent detections events per 100 trap days) is given for each species across all sites. Species are classified as either sensitive (X) or insensitive (–) to forest conversion into CAFS based on classification of Ferreira et al. (2025).

Taxon	Common name	Sensitive	IUCN status	N° records
Artiodactyla				
CERVIDAE		X		79
Mazama rufa (Illiger, 1815)	Red brocket deer		LC	
Passalites nemorivagus (Cuvier, 1817)	Amazonian brown brocket		LC	
TAYASSUIDAE				
Pecari tajacu (Linnaeus, 1758)	Collared peccary	X	LC	57
Carnivora				
CANIDAE				
Cerdocyon thous (Linnaeus, 1766)	Crab-eating fox	–	LC	286
MUSTELIDAE				
Eira barbara (Linnaeus, 1758)	Tayra	X	LC	48
Nasua nasua (Linnaeus, 1766)	South American coati	X	LC	14
FELIDAE				
Leopardus wiedii (Schinz, 1821)	Southern margay	–	NT	30
PROCYONIDAE				
Procyon cancrivorus (*G. Cuvier*, 1798)	Crab-eating raccoon	–	LC	67
Cingulata				
CHLAMYPHORIDAE				
Euphractus sexcinctus (Linnaeus, 1758)	Six-banded armadillo		LC	5
DASYPODIDAE				
Dasypus novemcinctus (Linnaeus, 1758)	Nine-banded armadillo	–	LC	102
Didelphimorphia				
DIDELPHIDAE				
Didelphis aurita (Wied-Neuwied, 1826)	Black-eared opossum	X	LC	37
Pilosa				
MYRMECOPHAGIDAE				
Tamandua tetradactyla (Linnaeus, 1758)	Southern tamandua	X	LC	33
Primates				
CALLITRICHIDAE				
Callithrix kuhlii (Coimbra-Filho, 1985)	Wied's marmoset		VU	4
Leontopithecus chrysomelas (Kuhl, 1820)	Golden-headed lion tamarin		EN	1
Rodentia				
CUNICULIDAE				
Cuniculus paca (Linnaeus, 1766)	Spotted paca	–	LC	74
DASYPROCTIDAE				
Dasyprocta leporina (Linnaeus, 1758)	Red-rumped agouti	X	LC	14
ERETHIZONTIDAE				
Coendou insidiosus (Lichtenstein, 1818)	Bahia porcupine		LC	2

International Union for Conservation of Nature (IUCN) status: critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC).

underscores the dual importance of preserving *cabrucas* as a land-use system and implementing effective shade-tree management practices that maintain adequate shade cover. Such practices not only benefit species of conservation concern, such as the *L. chrysomelas*, but also the terrestrial mammal community.

These findings align with those of Ferreira et al. (2025), who reported that higher shade-tree density positively influenced mammal assemblage structure, benefiting both species that are insensitive and

Table 3
Estimates of parameters predicting total mammal detections as a function of shade cover (%) and total basal area of shade trees (m^2 ha^{-1}) analysed using a Generalized Linear Mixed Model (GLMM; family = Negative Binomial).

Response variable	Covariates	Estimate	SE	Z	P-value
Total mammal detections	Intercept	−0.89	0.10	−8.64	< 0.001
	Shade cover	0.33	0.10	3.11	< 0.01
	Total basal area	−0.43	0.12	−3.59	< 0.001

sensitive to forest conversion into CAFS. Moreover, Ferreira et al. (2020) observed that intensified cocoa agroforests - where cocoa is cultivated predominantly under exotic tree species - contained less diversified mammal assemblages than *cabrucas* with a predominance of native trees and forests, even in highly forested landscapes. This further emphasizes the necessity of maintaining a diversified, dense native shade-tree canopy in agroforestry systems to support mammal populations and enhance community composition.

Similar trends have been observed in coffee agroforestry systems across the tropics. A meta-analysis by Manson et al. (2024) found that mammal presence is significantly higher in agroforestry systems with higher shade cover (Manson et al., 2024). For instance, Etana et al. (2021) found that traditional coffee agroforestry systems in Ethiopia supported higher overall species richness, diversity, and detection of mammals compared to intensively managed coffee plantations, where intensive tree thinning and undergrowth removal likely reduced the potential natural plant regeneration (Hundera et al., 2013), ultimately diminishing mammal diversity.

In addition to shade cover, the total basal area of shade trees was also a significant driver of medium and large terrestrial mammal abundances. However, unlike shade cover, mammal detections were negatively associated with total basal area of shade trees. Shade-tree cover in agroforests can be provided through either a high density of small shade trees or a low density of large, mature shade trees (Blaser et al., 2018). Our findings suggest that mammals were more frequently detected in agroforestry systems with high shade-tree cover provided by greater density of smaller shade trees, likely reflecting agroforests in early stages of forest regeneration (DeWalt et al., 2003) and less intensively managed systems. The tree diameter profile of *cabrucas* varies depending on the shade species used and the intensity of management practices, such as tree thinning and understory weeding (Sambuichi and Haridasan, 2007). In intensively managed systems, these practices limit natural regeneration of most shade-tree species (Hundera et al., 2013), likely reducing habitat complexity and resource availability for mammals, especially in agroforests with fewer shade trees.

Together, these findings highlight the importance of preserving traditional agroforestry systems that maintain adequate shade cover, supported by a sufficient density of native shade trees. However, since shade cover in agroforests is also determined the DBH of shade trees, a potential trade-off may exist that could influence habitat use across taxa. For instance, *L. chrysomelas* may benefit from higher shade cover provided by larger, mature trees, which offer preferred sleeping sites, whereas terrestrial mammals may favour agroforests with higher shade cover provided by a higher density of smaller shade trees. Ultimately, limiting the intensification of shade management is key to preserving the biodiversity conservation value of cocoa agroforests.

4.4. Study limitations and further research

While our study provides valuable insights into the role of shade-tree management in *cabrucas*, some considerations should be noted. Although our sample size is smaller than some studies (Cassano et al., 2014; Ferreira et al., 2025), it is comparable to others assessing biodiversity responses to management intensity in CAFS (Almeida-Rocha et al., 2020; Blaser et al., 2018; Cabral et al., 2021; Steffan et al., 2007),

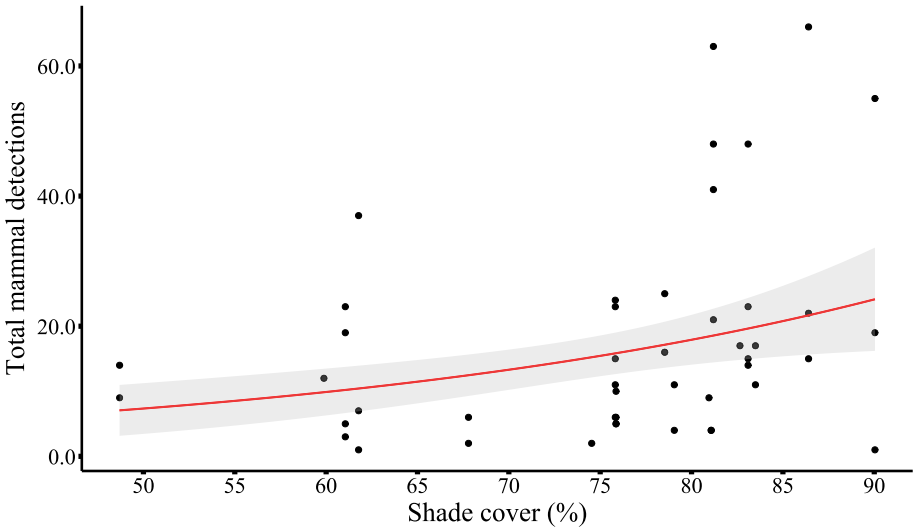

Fig. 3. Predicted total mammal detections as a function of shade cover (%) in 18 cocoa agroforestry systems in southern Bahia, Brazil. The prediction was based on the model from Table 3. The red line and the colour-coded area represent the estimates and the 95% confidence intervals, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and was sufficiently large to detect significant differences in biodiversity across the shade-tree management gradient. Our focus on traditional CAFS, which cannot legally be thinned below a minimum of 40 native shade trees per hectare, limited the inclusion of more intensively managed CAFS. A broader shade tree management gradient, especially at the lowest end, would further strengthen our understanding of biodiversity responses to varying shade tree management intensities.

The occupancy survey for *L. chrysomelas* was conducted during a single season, limiting our ability to account for potential seasonal variation in detection and habitat use. Moreover, as occupancy does not capture population dynamics, our study does not provide insights into abundance, survival, or reproductive success. Future studies should therefore aim to include multi-season population monitoring and demographic assessments to inform long-term conservation strategies for this endangered primate species.

Given that study focused on detecting the presence of *L. chrysomelas* and determining shade tree management thresholds, a species-specific survey approach (i.e., playback surveys) and statistical analysis (i.e., occupancy modelling) were required, which constrained the camera trap deployment period for terrestrial mammals. While our findings provide valuable insights into mammal responses to shade-tree management, future research should extend camera-trap deployment periods, incorporates arboreal camera traps to adopt a community-level approach to assess mammal species richness, diversity, composition, and functional guild responses. Such efforts would contribute to refining shade tree management recommendations to benefit the broader mammal community.

Finally, while our study highlights the ecological benefits of maintaining a dense native shade-tree canopy, integrating the environmental benefits and ecosystem services associated with shade-tree density alongside socio-economic dimensions would provide a more comprehensive perspective on the overall sustainability of CAFS.

4.5. Management implications for conservation and conclusions

Our study highlights the importance of adequate shade-tree management practices in cocoa agroforestry systems for supporting biodiversity conservation, particularly for the golden-headed lion tamarin. We demonstrate that the current intensification threshold of 40 native shade trees per hectare — equivalent to <35% shade cover — set by the Bahian *shade tree management decree*, is insufficient for supporting *L. chrysomelas* conservation in *cabrucas*. Instead, we identify that a minimum threshold of 100 native shade trees per hectare, corresponding to 65% shade cover, is required for *L. chrysomelas* persistence, which would also directly benefit the terrestrial large mammal community. While the decree aims to increase cocoa production, this relatively low threshold raises significant concerns that intensive shade-tree management may render agroforestry systems unsuitable for the conservation of this endangered primate species, highlighting a potential trade-off between agricultural intensification and biodiversity conservation within agroforestry landscapes.

Studies focusing on biodiversity–productivity trade-offs suggest that a win–win scenario can be achieved with 30% to 50% shade-tree cover in cocoa agroforestry systems (Blaser et al., 2018; Clough et al., 2011; Steffan et al., 2007). However, our findings indicate that a minimum of 65% shade cover—equivalent to at least 100 native shade trees per hectare—is necessary to meet the ecological requirements of *L. chrysomelas*. This threshold raises concerns about potential trade-offs for cocoa farmers, as several studies report declining cocoa yields when shade cover exceeds 50–60% (Bisseleua et al., 2009; Blaser et al., 2018; Clough et al., 2011; Wade et al., 2010). Nevertheless, some studies suggest that higher shade levels may support biodiversity without necessarily compromising yields. For example, Waldron et al. (2012) identified 100 shade trees per hectare as a threshold for maintaining farm biodiversity, while also increasing cocoa yields by up to 50% in Ecuadorian cocoa agroforestry systems. Similarly, Ferreira et al. (2023) recommend a 65% shade cover threshold to support bat diversity in African cocoa agroforests, which aligns with our findings for *L. chrysomelas*, although the study did not assess the impact of this threshold on cocoa yield. These findings underscore the importance of region-specific shade-tree management strategies that consider both the ecological requirements of local fauna (De Beenhouwer et al., 2013) and the agronomic contexts of different cocoa-growing regions.

Increased shade-tree cover has been shown to benefit a variety of taxonomic groups, including birds (Bennett et al., 2022; Blaser et al., 2018; Jarrett et al., 2021), bats (Ferreira et al., 2023), and invertebrates (Bisseleua et al., 2009, 2013; Steffan et al., 2007) in both cocoa and coffee agroforestry systems. However, it is also essential to recognize the limitations of agroforests in conserving forest-specialist and threatened species. Numerous studies consistently show that these species are often more abundant and diverse in native forest fragments, particularly those under protection (Bennett et al., 2022; Ferreira et al., 2020; Rodrigues et al., 2018). While agroforestry systems provide valuable habitat for a variety of species, they cannot fully replace the ecological functions and

habitat quality of native forests. This highlights the need for integrated conservation strategies that promote sustainable shade-tree management practices in agroforests with the protection of native forests in human-dominated landscapes, while also accounting for the livelihoods of smallholder farmers and the necessity of crop production.

In this context, further research is needed to explore the interactions between shade-tree density, cocoa yields, and biodiversity conservation. While shade trees offer numerous ecological benefits, including carbon sequestration, soil fertility, and buffering climatic extremes (Blaser et al., 2018; Niether et al., 2020; Tscharntke et al., 2011), competition for land, resources and light can reduce cocoa yields (Abdulai et al., 2018; Blaser et al., 2018). Future studies should assess the environmental and economic trade-offs and synergies under different shade tree management practices. Such research is critical for developing agroforestry systems that simultaneously support biodiversity conservation and the livelihoods of smallholder farmers. Ultimately, the future of cocoa agroforestry systems lies in finding a balance between agricultural productivity and biodiversity conservation, which will guide policy decisions aimed at optimizing both environmental and economic outcomes.

CRediT authorship contribution statement

Steffi Dekegel: Writing – original draft, Funding acquisition, Formal analysis, Conceptualization. **Goedele Van den Broeck:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Leonardo Oliveira:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Kristel De Vleeschouwer:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Ethical statement

The research used non-invasive field techniques, including unbaited, remotely set motion activated camera traps, and hence did not involve direct contact with the animals. 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: 6.729.579 /CAAE: 73531423.3.0000.5526). 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, according to the norms established by Resolution n° 196 of the National Health Council of 10/101996.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT-4 developed by OpenAI in order to improve readability and check grammar of some sentences in this manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111325.

Data availability

Data will be made available on request.

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