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STUDY OF THE IMPORTANCE OF COPAÍBA (COPAIFERA TRAPEZIFOLIA) FOR A PRIMATE COMMUNITY IN THE BRAZILIAN ATLANTIC FOREST USING ARBOREAL CAMERA TRAPS.

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ABSTRACT

Due to the severe degradation and fragmentation of the Brazilian Atlantic Forest, primates are highly subjected to population declines and species extinctions. *Copaifera trapezifolia* – a large and tall canopy tree species – was studied from December 2024 to June 2025 using arboreal camera traps within the Carlos Botelho State Park to assess its use by a unique primate community. It includes the southern muriqui (*Brachyteles arachnoides*), brown howler monkey (*Alouatta guariba*), black-horned capuchin (*Sapajus cucullatus*) and black lion tamarin (*Leontopithecus chrysopygus*). The Carlos Botelho State Park is considered as a crucial climate refuge for primates, providing optimal climatic conditions for their conservation and survival. Primates spent 147 nights in the copaíbas during the seven-month data collection, with multiples climatic factors, such as temperature, wind and precipitation, impacting their stay in the trees at night. Diurnal and nocturnal activity were studied, illustrating high activity of all primate species around their average sleeping and waking up times, as well as a significant activity at night when primates are expected to be sleeping. Moreover, temporal and spatial overlaps were calculated, indicating significant overlaps between primate species for the use of *C. trapezifolia*, and confirming the high probabilities of interspecific interactions and competition within these trees. Behavioural data permitted a more precise analysis of the activity in the trees, revealing varying uses of these trees by the primate community. These temporal, behavioural and spatial analyses provided a better understanding of this unique primate community, offering valuable insights for the ecology of primate and conservation efforts.

KEYWORDS: Arboreal camera traps, Atlantic Forest, Brazil, *Copaifera trapezifolia*, Primate community, Sleeping site, Southern muriqui

1. INTRODUCTION

Considered as one of the most diverse and threatened biodiversity hotspots in the world, the Brazilian Atlantic Forest is currently suffering from a high biodiversity crisis (Myers et al., 2000; Joly et al., 2014). The main drivers of this ongoing crisis are natural resource exploitation, infrastructure expansion, selective logging, and global climate (Carlucci et al., 2021; Cunha et al., 2021; Pinto et al., 2023). Brazil's Atlantic Forest originally covered around 150 million hectares, but only 11.7% of this area remains today (Bergamin et al., 2017). As a result, the conservation of large forest fragments within this forest ecosystem is necessary to ensure a suitable habitat for species sensitive to habitat loss, such as primates and large mammals (Casano et al., 2012).

Primates constitute a high biomass of tropical forests and play major ecological roles by serving as effective indicators of environmental changes (Lee et al., 1988; Zanette et al., 2020). Brazil hosts the greatest diversity of primate species with a total of 102 species, of which 39% are considered as threatened (Estrada et al., 2018; Pinto et al., 2023). Of these species, 26 are inventoried in the Atlantic Forest of South America, with 19 considered as endemic (Culot et al., 2019). However, predictive models reveal that Atlantic Forest primates are expected to lose significant climatic suitable range by 2050, leading to potential population declines and range shifts (Pinto et al., 2023).

The Carlos Botelho State Park (CBSP) – part of the largest continuous remnant of Atlantic Forests situated in southern Brazil and considered as a key climate refuge for primates – hosts a high diversity and abundance of species, including a unique primate community containing four species: *Brachyteles arachnoides*, *Alouatta guariba*, *Sapajus cucullatus*, and *Leontopithecus chrysopygus* (Ribeiro et al., 2009; Viveiros de Castro et al., 2021). The CBSP is the only known location where these four species coexist, identifying it as an important site for conservation programs. Moreover, these primates play a significant role in seed dispersal thanks to their frugivorous-folivorous diet, with more than 70% of the seeds they ingest being dispersed (Bufalo et al., 2016; Vasquez et al., 2025). Extinctions of primate populations would significantly impact the seed rain, leading to the extinction of plant species and alter forest ecosystems (Fuzessy et al., 2018; Gardner et al., 2019).

The discovery of black lion tamarins (*Leontopithecus chrysopygus)* in the CBSP in 2013 may have provided evidence of range shifts affecting Atlantic Forest primate populations due to climate change (Meyer et al., 2014; Garbino et al., 2016). High densities of primate species within forest fragments enhance their coexistence and competition, requiring a deep understanding of these species and their niche partitioning (Sobral et al., 2023). Niche partitioning, which assesses the differences of spatial and temporal resource use between species, reveals how primates coexist within the same area (Chesson, 2000). Sleeping sites constitute another crucial resource of the ecological niche of primates. Their optimal selection helps to avoid competition and predation while ensuring a safe environment for the night (Cheyne et al., 2012). In contrast, niche overlap can also occur between sympatric primate species due to similar dietary resources and temporal activity, leading to potential competition in the canopy (Iwanaga et Ferrari, 2001; Campera et al., 2019).

Nowadays, multiple monitoring methods are available to survey wildlife in forest ecosystems (Bowler et al., 2017). The use of camera traps (CT), which became more popular with the improvement of camera technology and the reduction in equipment prices (Tobler et al., 2008; Fonteyn et al., 2021), constitutes a non-invasive and cost/effective monitoring method (Gregory et al., 2014). Compared to other inventory methods, CT minimize the influence of human on data collection by reducing the disturbance on wildlife and observer bias (Ahumada et al., 2013). Valuable information about wildlife communities can be collected using this technique, such as species diversity, abundance, habitat use, activity patterns and niche partitioning (Ahumada et al., 2011; O'Brien, 2011; O'Connell et al., 2011). One of the main advantages offered by this method is the uninterrupted monitoring (Tan et al., 2013).

However, assessing multiple primate species simultaneously tends to be challenging and requires the use of an effective canopy-adapted monitoring technique, commonly referred as arboreal camera trapping (Séguigne et al., 2022). Studies of arboreal species using direct observations often result in incomplete data, especially at night, due to the dense canopy of most tropical trees (Kays et Allisson, 2001). Arboreal CT facilitate this monitoring with both diurnal and nocturnal activities being continuously recorded (Munari, 2013). While the use of CT to monitor arboreal species increases with time, half of the current arboreal studies set traps at a height below 10 meters, resulting in an incomplete vertical coverage of the canopy (Haysom et al., 2021; Nazareth et al., 2024). Although this technique remains recent and unexplored, with only a few studies existing, it demonstrates its high potential for arboreal studies, especially primates (Olson et al., 2012; Bowler et al., 2017).

This study assesses the high potential and the effectiveness of arboreal camera-trapping for monitoring medium- and large-bodied primates in a canopy-dominant tree species (*Copaifera trapezifolia*) within the Brazilian Atlantic Forest, known to be used as a sleeping site. Compared to the other primate species, *Leontopithecus chrysopygus* mostly occupy low canopy levels, up to 10 meters, which explains its absence in copaíba trees (Passos and Alho, 2001).
This study aimed to 1) Assess and compare the nocturnal use of *Copaifera trapezifolia* for each primate species using temporal data, 2) Compare the diurnal and nocturnal activity between each species of primate within *Copaifera trapezifolia* using temporal and behavioural data, and 3)

Assess whether temporal and/or spatial overlap occurs among the primate species in their use of *Copaifera trapezifolia* and how they affect the coexistence and niche partitioning in the studied trees.

2. METHODS

2.1. Study area

This study was conducted in the northern part of the Carlos Botelho State Park (CBSP), located in the south of São Paulo State, in Brazil (24° 7' 53" S, 47° 56' 57" O). This protected area was created in 1982 and covers 37,644 ha of Atlantic Forest, considered as one of the most threatened biomes in the world (São Paulo, 2008; Metzger, 2009). Following the Köppen climate classification, the climate is classified as a humid subtropical climate (Cfa), characterized by evenly distributed precipitations throughout the year and a hot summer (Kottek et al., 2006). The mean annual temperature reaches 20.5°C (Agritempo, n.d.), with annual precipitation averaging 1626mm in 2024 (Carlos Botelho State Park, 2025). The altitude of the CBSP ranges from 500 to 1000m above sea level (Talebi et Soares, 2005), which is explained by the formation of valleys and mountains marked by steep slopes (Lima and Gandolfi, 2009; Talebi and Lee, 2010). While pasture and agriculture represent about 73% of land covers in the state of São Paulo (Shimabukuro et al., 2023), the main land covers surrounding the CBSP are Atlantic Rainforest remnants, eucalyptus plantations, grape vineyards, as well as other crops and pasture (Monero et al., 2024).

2.2. Studied primate species

Table 1 : Description of each species included in the sympatric primate community studied within the study area.

	Brachyteles arachnoides	***Alouatta guariba***	***Sapajus cucullatus***
Vernacular name	Southern muriqui	Brown howler monkey	Black-horned capuchin
Native range	Brazil's Atlantic Forest[a]	Brazil & Argentina[c]	Eastern Brazil & northeastern Argentina[f]
IUCN status	CR[a]	VU[c]	NT[g]
Alimentation	Frugivores (pristine forests) Folivores (fragmented forests)[b]	Folivores-frugivores[d]	Frugivores-insectivores[g]
Average weight	Male: 9.6 kg Female: 8.4 kg [b]	Male: 6.7 kg Female: 4.4 kg[e]	2.4 kg[h]

[a]Talebi et al., 2019 ; [b]Talebi et al., 2005 ; [c]Jerusalinsky et al., 2016 ; [d]Milton, 1986 ; [e]Smith and Jungers, 1997 ; [f]Szynwelski et al., 2024 ; [g]Di Bidetti et al., 2020 ; [h]Chagas et al., 2018

2.3. Studied tree species

Copaifera trapezifolia is a tree species endemic to the Brazilian Atlantic Forest, belonging to the Fabaceae family. The *Copaifera* genus includes 70 species that can be found in South America, Africa, and Asia, with 16 species being endemic to Brazil (Carneiro et al., 2024). Nowadays, *C. trapezifolia* is commonly referred to as copaíba, a name originally given by indigenous peoples to the tree's exudate (da Trindade et al., 2018). Considered as high and large trees with a slow growth, copaíbas can reach a height of 40 meters and a diameter of 4 meters (Martins-da-Silva et al., 2008). Small and apetalous flowers grouped into axillary panicles are found on this tree species, along with fruits characterized by an ovoid seed surrounded with a voluminous and colourful aril (Veiga Junior and Pinto, 2002). Although *C. trapezifolia* is commonly exploited for wood and oleoresins (Martins-da-Silva et al., 2008; Carneiro et al., 2024), this tree also provides important resources to primates, including fruits and optimal sleeping sites. The studied *C. trapezifolia* had an average circumference of 210.5 ± 39.6 cm and a mean height of 25.8 ± 3.1 m.

A tree inventory was conducted in the study area to evaluate the presence of *Copaifera trapezifolia* (Appendix S1). Out of the 1784 trees, only 6 *C. trapezifolia* were inventoried, corresponding to 6 trees/ha. Despite their medium circumference at breast height (55.68 ± 38.18 cm), these trees have an average height (16.5 ± 5.92 m) considerably higher than the average height of all inventoried trees (9.84 m). Copaíbas stand out for their remarkable height, enhancing their use potential by the primate community.

2.4. Arboreal camera trapping

To assess the use and importance of *C. trapezifolia* for the primate community, 20 arboreal CT were installed in the canopy of 10 selected copaíbas within the study area from December 2024 to June 2025, covering 212 days of recording (Figure 1). Each tree was selected for its significant role as a sleeping site for the primate community, based on 6 months of simultaneous field observations of the four species collected by researchers in the park. Due to the large dimensions of the canopy, 2 CT were installed per tree, both facing different zones to monitor specific locations such as natural bridges between trees and sleeping locations.

Installed at an average height of 24.2 ± 3.7 m, CT were attached to large branches using buckle straps to withstand weather conditions. The sun exposure, wind and vegetation disturbance were considered while setting up the traps to prevent unusable data. CT were active 24 hours a day and recorded a 30-second footage after each trigger, with a 10-second delay between consecutive events. The camera lens sensitivity was set to low or medium, based on each canopy configuration, to ensure the recording of all individual's presence in the camera range, while reducing the number of false-triggered videos. A 256 Go memory card was used in each camera trap, as well as 6 non-rechargeable *Energizer* lithium batteries. Each month, memory cards were swapped out from the CT to retrieve the data, while the batteries were checked and changed if needed. A pilot study was conducted between October and December 2024 to adjust camera trap orientations towards the most frequently used canopy locations, and to reduce the significant number of false triggers in problematic trees.

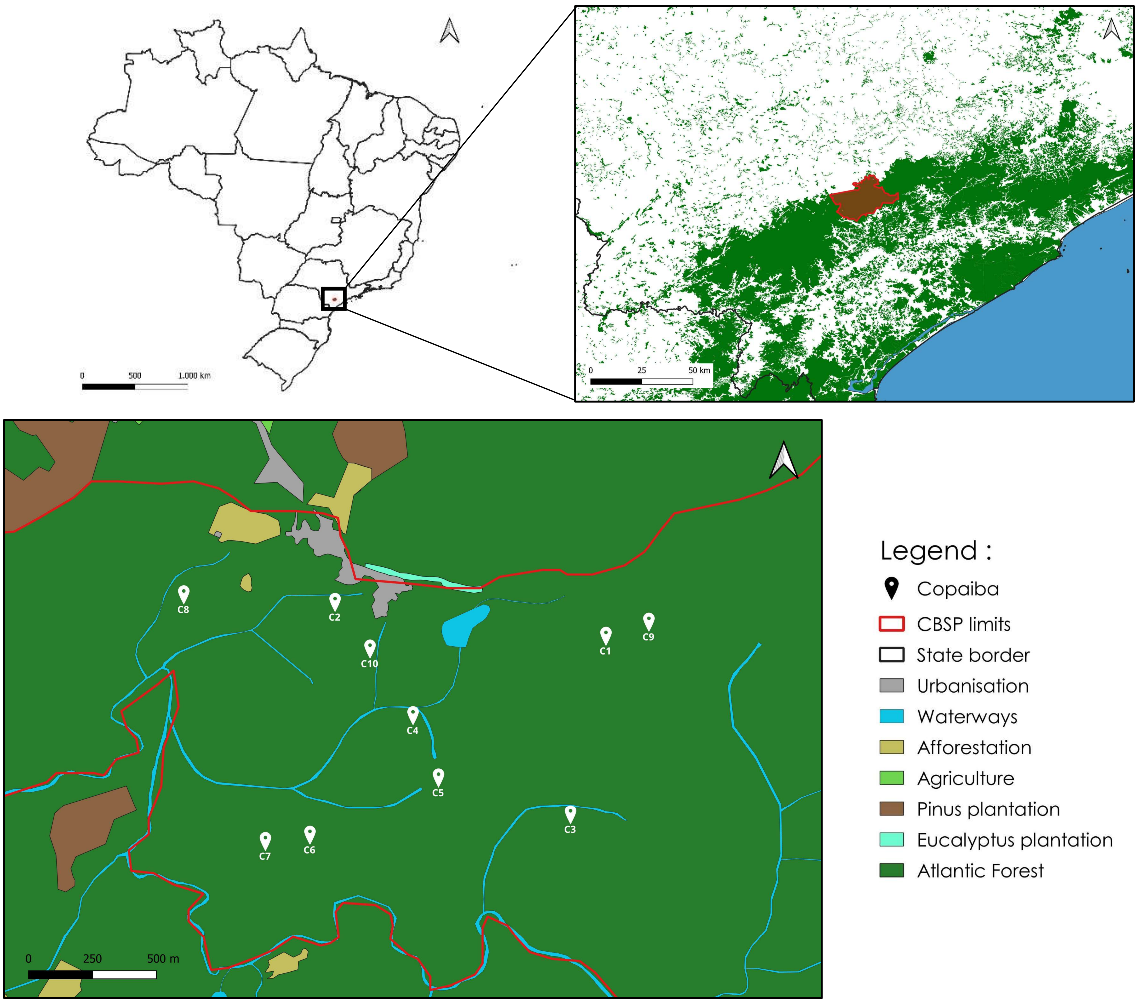

Figure 1 : Location of the study area situated in the northern part of the Carlos Botelho State Park in Brazil. The land cover is illustrated to highlight the dominance of Atlantic Forest remnants in the region

2.5. Data analysis

Each 30-second video was processed using *Timelapse* software (Greenberg et al., 2019). Multiple parameters were recorded to extract as much information as possible per video, including the date and time, species, number of individuals, main behaviour, and sometimes an additional behaviour (Table S1 & Table S2). The behavioural analysis was made using a variant of instantaneous scan sampling, describing the main behaviour as the behaviour predominating among all individuals in each footage, to focus on group activity rather than individual behaviours (Altmann, 1974). The collected information was ultimately compiled into a CSV file for statistical analyses in *R studio*.

2.5.1. Temporal analysis

The first analysis conducted on the dataset was the estimation of the number of nights spent in the studied trees for each primate species. To determine whether primates spent the night in a tree, species-specific sleeping hours were defined based on their habitual sleeping schedules observed during daily follows conducted by researchers, together with sunset and sunrise hours. A primate species was considered to have spent the night in a copaíba if either (1) a detection occurred within the shortest nighttime window of this species, OR (2) a detection occurred between the latest arrival time and the earliest departure time of this species. This method accounted for nights during which primates occupied the trees during nighttime without being detected.

To assess the temporal use of *Copaifera trapezifolia* for each species, observations were compiled into occurrences based on the tree identification and primate species. Each occurrence indicates the presence of a specific species in a given tree within a 15-minute time bin. Multiple observations within the same time bin were grouped as a single occurrence. Occurrences during estimated nights were also generated to account for the time when primates were in the tree but not observed due to inactivity. These occurrences were calculated based on the average sleeping times, estimated individually for each day. This data gathering prevented the overestimation of primate presence resulting from the dual camera trap setup installed in each tree.

Multiple environmental variables were tested using a binomial generalized linear model (GLM) to study their potential effects on the nocturnal presence of primates in the trees. The binomial data classified each day as the presence (=1) or absence (=0) of primates during the night, according to the estimated nights determined previously. The tested variables included minimum temperature, maximum temperature, average wind speed, maximum wind speed, total daily precipitation, and moon phase. The GLM was applied only to days with at least one operational camera per tree. The correlation between all covariates was calculated to avoid any potential multicollinearity issues. For each species of primate, the final regression model was chosen based on the Akaike information criterion (AIC), with $\Delta AIC > 2$, indicating a greater accuracy compared to other models (Buscemi et Plaia, 2020).

Ultimately, the number of daily occurrences were used to calculate, for each species, the monthly occurrence proportions, ranging between 0 and 1. This enabled the evaluation of the temporal overlap between species pairs within each tree using the Schoener index (Klein et Bay, 1994; de M. Santos et al., 2013), which indicates the proportion of similarity in temporal patterns (Appendix S3). The overall temporal overlap for each pair of species was obtained by averaging the Schoener index values of all trees. Finally, a Wilcoxon signed rank test was conducted to define whether temporal overlaps between species pairs were significantly different (Rosner et al., 2006).

2.5.2. Behavioural analysis

The behavioural activity was examined to better understand the use of *C. trapezifolia* by primates. Visits, defined as a series of detections separated by less than 15 minutes from one another, were used instead of occurrences to consider all behaviour records rather than just one behaviour per occurrence. Estimated nights were not included to focus exclusively on observed data. Visit duration was determined by the time between the first and last detection, with an additional 30 seconds to account for the last detection. Each visit was analysed with its corresponding behaviours to calculate their time proportion. Following this, the duration of each behaviour was summed to summarize the behavioural activity in all trees.

Furthermore, interspecific interactions observed in some of the monitored trees were also considered in this study, to illustrate and explain the competition occurring within *C. trapezifolia*.

2.5.3. Spatial analysis

Kernel Density Estimates (KDE) were built using the KernedUD function of the *adehabitatHR* package to explain the spatial use of the 10 copaíbas by primates (Denoël et Ficetola, 2015; Panda et al., 2023). To achieve this, all occurrences – including the ones within nights – were gathered in a unique dataset, with the geographic coordinates of each copaíba in which they occurred. Three isopleths – 95%, 75%, and 50% – were calculated to illustrate the spatial use intensity for each month. The Sørensen–Dice index, ranging from 0 to 1, was adapted to calculate the monthly spatial overlap similarity between each pair of species (Li et al., 2020), illustrating the proportion of core area (50% isopleth) shared by both species (Appendix S4). Similarly to the temporal overlap analysis, the Wilcoxon signed rank test was conducted to provide information on the intensity of the spatial overlap between each pair of species. However, this overlap doesn't assess the similarity of the *C. trapezifolia* used, meaning that two pair of species may have comparable intensities of overlap while using different trees.

3. RESULTS

Out of 29,000 videos gathered during the data collection, 4,440 videos contained an animal detection, indicating that almost 85 percent of the collected videos were false triggers. Among the detection-positive videos, 4,390 were primate detections and 50 featured other animal species, comprising 10 mammal species and at least 9 identified bird species (Table S3).

3.1. Temporal analysis

Over the seven-months data collection period, 146 nights recorded the presence of primate species in the studied *C. trapezifolia*. Muriquis were observed on 90 nights across 9 of the 10 monitored trees, whereas brown howler monkeys and capuchins were recorded on 32 and 24 nights in 9 and 5 of the 10 selected copaíbas, respectively (Table S4). On average, the trees were used during 14,6 ± 16,3 nights, with the number of nights per tree ranging from 1 to 46. Among the estimated nights, some were recorded on the same day but in different trees, involving either two different species, distinct groups of the same species, or both. In total, 29 days recorded the simultaneous nocturnal use of two or three trees as sleeping sites by the primate community.

Two graphics were generated using the density of occurrences to illustrate and compare the activity of each species of primate during daytime and nighttime based exclusively on observed data (Figure 2). Occurrence densities were used instead of occurrence counts to provide a better representation of the activity, given the uneven number of occurrences between species. During daytime, capuchins' activity remained significantly low compared to morning and evening peaks. The use by southern muriquis remained relatively stable throughout the day, with two activity peaks observed prior to their average wake-up time and near their sleeping time. These peaks are less significant than those observed for capuchins, implying that southern muriquis do not use *C. trapezifolia* only as a sleeping site, but also for additional purposes during daytime. Brown howler monkeys opted for a contrasting activity during daytime, with three activity peaks found in the morning and a decreasing activity during the afternoon.

During the early hours of the night, capuchins contained a high density of occurrences due to its late average sleeping time, while howler monkeys' activity declined due to its early sleeping time. Capuchins did not show any significant activity for the rest of the night, confirming the hypothesis that this species uses *C. trapezifolia* mostly as a sleeping site. Similar to its daytime activity, Muriquis' nocturnal activity remained relatively stable and diverse. In comparison, howler monkeys' activity remained low at the beginning of the night and slightly increased during the second half of the night.

276 ***Figure 2 :*** Density plots illustrating the activity of each primate species in Copaifera trapezifolia: (A)
277 Daytime activity from 05:00 to 19:00, based on the longest day, with the average sleep schedule of each
278 species indicated with vertical lines. (B) Nighttime activity from 19:00 to 05:00, based on the shortest
279 night.

The correlation test made on the environmental variables reported that none of the variables were correlated, as all correlation coefficients are below 0.7 (Table S5). The model tested for muriqui determined that this species preferred to sleep in the copaíbas on warmer and windier days, respectively with $p < 0.001$ and $p < 0.01$ (Table S6). The brown howler monkey model results showed that this species was more likely to spend the night in copaíbas on warmer days ($p < 0.1$), low windy days ($p < 0.01$) and when precipitation were abundant ($p < 0.1$) (Table S7). Finally, the capuchin model indicated that this species only tended to use *C. trapezifolia* during warmer nights, similarly as the two other primate species (Table S8).

We studied the temporal overlap by representing, for each tree, the density of occurrences over time (Figure 3). This figure highlights considerable variations of temporal activity and temporal overlap across studied trees and primate species. In addition, the Schoener index gave contrasting values after averaging the index values from the 10 selected trees. *B. arachnoides – A. guariba* (*BA – AG*) obtained an index value of 0.512 ± 0.166, followed by 0.442 ± 0.160 for *B. arachnoides – S. cucullatus* (*BA – SC*), and 0.402 ± 0.203 for *A. guariba – S. cucullatus* (*AG – SC*). The standard deviations associated with each index value range from 0.160 to 0.203 suggested higher temporal overlaps in some trees. The Wilcoxon signed rank test related to the temporal overlap indicates that none of these overlaps between species pairs are significantly different as $p_{BA\text{-}AG\ \&\ AG\text{–}SC} = 0.4961$, $p_{BA\text{-}AG\ \&\ BA\text{–}SC} = 0.3594$ and $p_{AG\text{-}SC\ \&\ BA\text{–}SC} = 0.1289$.

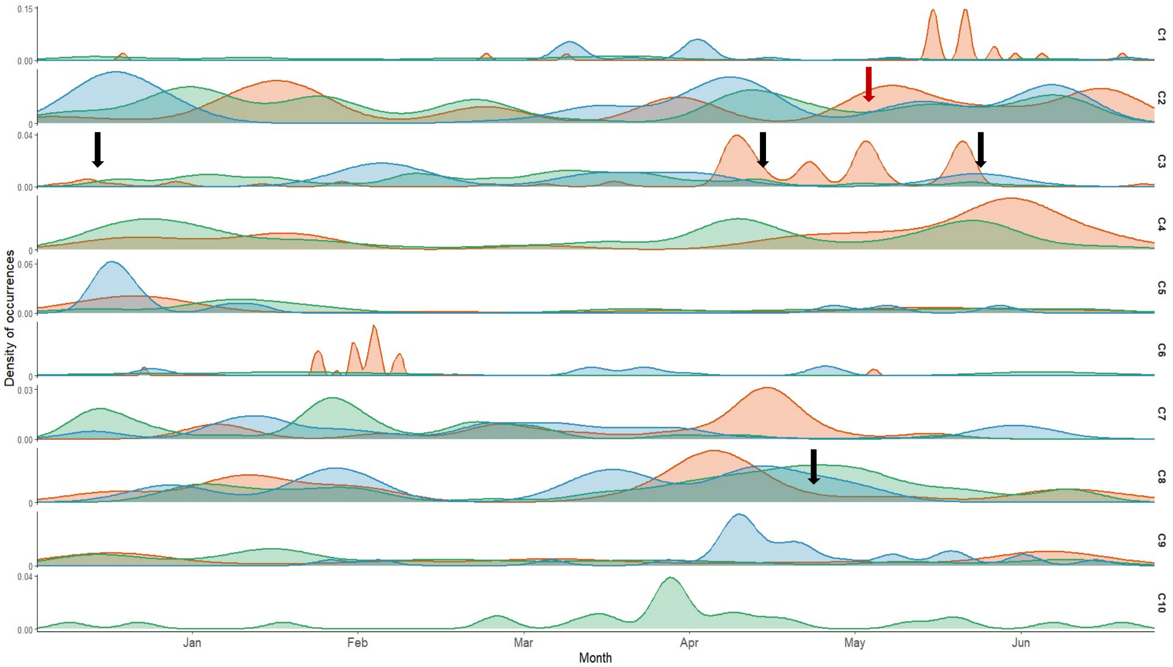

Figure 3 : Illustration of the primate species' activity and the temporal overlap throughout the months for each monitored Copaifera trapezifolia. Interspecific interactions observed during the data collection between southern muriquis and brown howler monkeys are indicated with black arrows, while the one between brown howler monkeys and black-horned capuchins is indicated in red.

3.2. Behavioural analysis

The behavioural activity was assessed using bar chart graphs illustrating the time percentage of each behaviour for each primate species during daytime and nighttime (Figure 4). Both graphs revealed similarities, as the dominant behaviours of each species – resting, traveling and moving – remains similar between both time periods. This figure also shows a high proportion of time spent in behaviours other than resting during the night, highlighting an intense nocturnal activity, also varying between species.

The daytime graph shows that *A. guariba* spent over 60% of the time resting, with traveling and moving observed for 23% and 8%, respectively. Muriquis use *C. trapezifolia* similarly to brown howler monkeys but in different proportions, with over 50% of the time spent traveling and about

30% resting. *S. cucullatus* shows a more evenly distributed time for its most frequent behaviours – 40% traveling, 25% resting, 18% moving and 15% feeding – indicating the importance of copaíbas also as a feeding site for this species.

Although *B. arachnoides* traveling behaviour declines during nighttime likely due to an increased resting, other behaviours such as moving, playing and inactive were still recorded, indicating a consistent diverse activity at night. The activity of *A. guariba* during the night aligned to daytime activity, with only a slight decline in time proportion for feeding, inactive and playing, indicating that this species is the least active during the night. The nighttime activity of *S. cucullatus* remains high, with moving and traveling becoming the most frequent observed behaviours, followed by resting and playing.

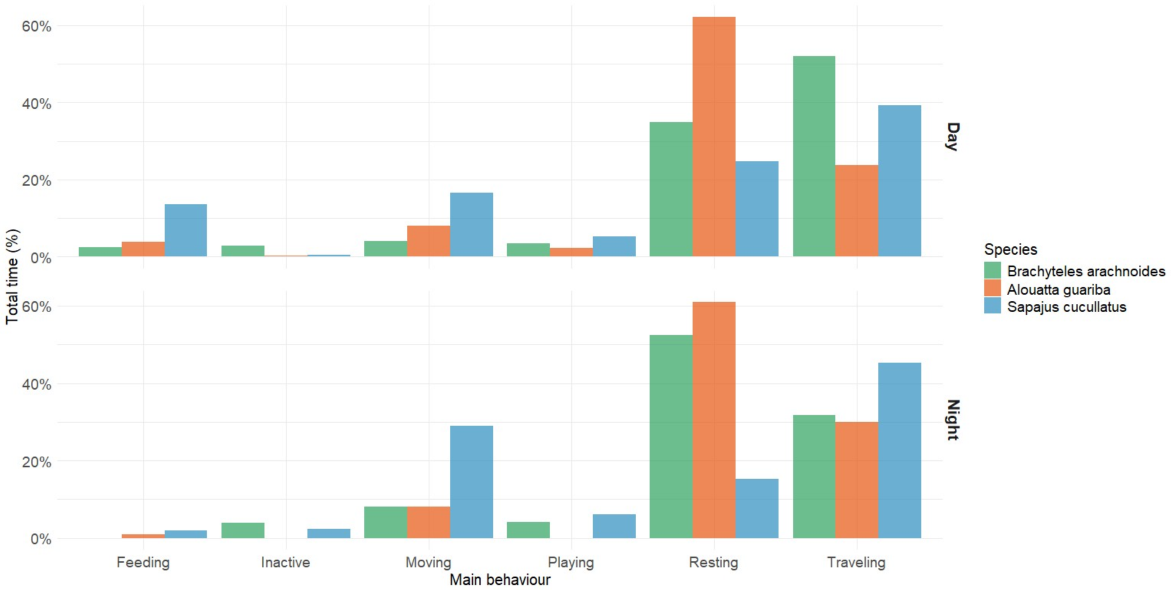

Figure 4 : Bar charts showing the percentage of time spent on each main behaviour by species during daytime and nighttime in Copaifera trapezifolia.

Moreover, five interspecific encounters were observed inside the studied copaíbas through camera traps. Four interactions involved *B. arachnoides* and *A. guariba* individuals, during which southern muriquis were observed having aggressive behaviours and were chasing brown howler monkeys out of the tree. The fifth interaction was a passive encounter between *A. guariba* and *S. cucullatus* individuals.

3.3. Spatial analysis

KDE (50, 75, and 95%) were calculated for each primate species based on their monthly occurrence in the copaíbas (Figure 5).

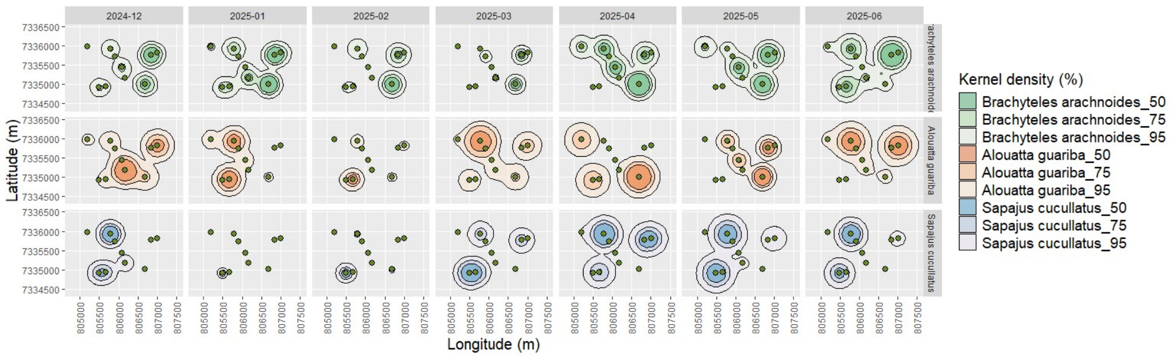

Figure 5 : Heatmaps illustrating the 50%, 75%, and 95% kernel density isopleths of spatial use calculated for each primate species and each month. Each row of heat maps corresponds to a primate species, and each column corresponds to the months during which data were collected. The core area (50% isopleth) is shown in darker colours while the 95% isopleth appears in lighter colours. Monitored Copaifera trapezifolia were illustrated as green circular points.

The values of the Sørensen-Dice index (mean ± SD) reveal variations of spatial overlap between species. BA – SC obtained an index value of 0.067 ± 0.116, 0.299 ± 0.334 for BA – AG, and 0.116 ± 0.209 for AG – SC. Finally, the Wilcoxon signed rank test results related to the spatial overlap showed that the spatial overlap values between species combinations are not significantly different, with $p_{BA\text{-}AG\ \&\ AG\text{–}SC} = 0.4017$, $p_{BA\text{-}AG\ \&\ BA\text{–}SC} = 0.1003$ and $p_{AG\text{-}SC\ \&\ BA\text{–}SC} = 0.4185$. Although these spatial overlaps are not significantly different, we still observe a higher overlap between AG – BA than BA – SC. This can be observed with Figure 5, where the core areas used between AG – BA looks more similar than those between BA – SC or AG – SC.

4. DISCUSSION

Results obtained in this study confirm the strong potential of arboreal camera trap monitoring to assess the presence, activity and competition of primates in the canopy, which have been already reported in previous studies using distinct monitoring methods (Olson et al., 2012; Tan et al., 2013; Whitworth et al., 2016; Nazareth et al., 2024). Although primate communities are intensely studied to assess their spatial segregation among species based on habitat use (Mitani et al., 1991; Bermejo, 1999; Marshall et al., 2014), arboreal CT method remains underutilized despite its potential illustrated in this study. This study is the first to evaluate the significance of *C. trapezifolia*, which contributes to a better understanding of the ecology of this unique primate community. Despite being cost/effective, arboreal CT surveys also require consideration of additional costs for climbing equipment, extra time to setup and inspect CT, and inherent limitations (Haysom et al., 2021). One of the main limitations is the high number of false triggers caused by vegetation, wind and sunlight, which can drain CT batteries and fills memory cards in a short period of time (Gregory et al., 2014; Moore et al., 2021). Nevertheless, minimising false triggers during the pilot study allowed the complete assessment of *C. trapezifolia* use by the primate community.

Temporal analysis provided insights into the nocturnal use of each primate species. Although the distribution of the estimated nights is uneven across the monitored trees, it highlights the high interspecific use of *C. trapezifolia* as a sleeping site. Overall, 8 out of the 10 studied trees were used at night by at least two species of the primate community. Southern muriquis used *C. trapezifolia* for 36% of the nights, highlighting the crucial role of this tree species for this large-bodied primate, known for changing their sleeping sites frequently (Bueno et al., 2013). In certain copaíbas, a high number of *B. arachnoides* nights is associated with a low number of *S. cucullatus* nights, suggesting that black-horned capuchins avoid trees with a high nocturnal presence of southern muriquis for their sleeping site. However, capuchins prefer sleeping in large trees with a wide canopy (Di Bitetti et al., 2000), which aligns with their high number of nights spent in copaíbas (Table F1). In contrast, brown howler monkeys do not appear to be affected by the intense use of copaíbas at night by other primate species. Primates were also observed using multiple *C. trapezifolia* during similar nights. In total, 29 nights involved the simultaneous use of two or three trees, confirming once more the importance of this tree species as a key resource during for primates during nighttime.

Daily activity patterns can also be efficiently studied using arboreal CT. These patterns show variations between each primate species for both diurnal and nocturnal activity (Figure 2). All species reveal high activity around sleeping hours, which confirms the main use of copaíbas as sleeping sites for the primate community. The morning peaks activity for brown howler monkeys may be explained by the frequent moving in the morning to sunbathe, as observed in *Alouatta caraya*, a species of the same genus (Brividoro et al., 2023). The low activity of capuchins during the day confirms their predominant use of the tree at night, compared to muriquis using them continuously during day and night.

Some climatic conditions offer a significant impact on the nocturnal presence of primates in *C. trapezifolia*. All species showed a preference for warmer conditions in the canopy, while other climatic factors impacted specific species. Muriquis also favoured windier days, whereas brown howler monkeys favoured less windy but rainy days. *A. caraya*, is known to prefer open-canopy trees during rainy and warm conditions (Brividoro et al., 2023), which may explain *A.*

guariba's preference to use the tree under similar nocturnal conditions. Although not all trees were visited by every primate species, temporal overlap was observed in most of them (Figure 3), as confirmed by the Schoener index values. Temporal overlaps obtained higher values in certain trees, increasing their probability of interspecific interactions despite niche partitioning within the primate community. Moreover, as none of the temporal overlap values are considered as significantly different, this indicates that all species from the primate community share similar temporal overlap intensity within all monitored trees. However, similar intensity between species does not imply identical activity patterns, which may differ between species to allow their coexistence.

The behavioural analysis provided further information about the use of *C. trapezifolia* by each species of primates (Figure 4). The high percentage of resting behaviour for brown howler monkeys during daytime confirmed their overall low activity (Rímoli et al., 2012). Their high proportion of traveling may also reflect their increased ranging behaviour caused by potential interspecific interactions observed in the study area (Sobral et al., 2023). Muriquis' behaviour proportions differ from Talebi and Soares (2005), who reported higher percentages of resting and feeding, and a lower percentage of traveling. This suggests that, compared to other tree species, copaíbas are primarily used as sleeping sites and natural bridges rather than as feeding sites by this primate species.

While primate species are seen to be using *Copaifera trapezifolia* at different hours of the day and in multiple ways, the spatial use also showed differences between each species across the months (Figure 5). The most significant difference is likely to appear between BA – SC, with the use of mostly distinct trees across the time, especially during nighttime, confirmed with a low Sørensen-Dice index value. The highest spatial overlap can be found between BA – AG, which may explain the high number of interspecific interactions that appeared in copaíbas during the seven-month data collection. The moderate overlap similarity between AG – SC suggests a lower competition in *C. trapezifolia* for these species compared to muriquis and brown howler monkeys. However, these spatial overlaps can reach up higher values during specific months due to the high standard deviation for each pair of species, increasing the probability of interspecific interactions happening between species of the primate community.

As a matter of fact, *Copaifera trapezifolia*'s function as a crucial resource for this sympatric primate community can no longer be questioned. Although *C. trapezifolia* is primarily used as sleeping sites by primates, high and diverse activity was observed, revealing additional functions of this tree, such as serving as a natural bridge between trees, a place to rest during the day, and a feeding resource. The preference for this tree species by primates can also be illustrated by their intense use but low presence in the study area, with an average of 6 individuals found per hectare. Dimension differences between the monitored and the inventoried *C. trapezifolia* also showed how rare large circumference and well-developed canopy copaíbas are in this Atlantic Forest fragment. Moreover, temporal and spatial patterns revealed noteworthy overlaps between species, especially between southern muriquis and brown howler monkeys, supporting the existence of competition in *C. trapezifolia* canopy based on interspecific interactions captured by the CT. The niche partitioning demonstrated in this study shows how can a sympatric primate community relies on a key tree species, and how temporal, behavioural, and spatial differentiation between species within this tree allows their coexistence, despite notable spatial and temporal overlaps.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are not yet online, due to the heavy weight of photographic and film data, but will be openly available in a public repository at the earliest possible time.

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SUPPORTING INFORMATION

Appendix S1 – Forest characterization

The forest vegetation was characterized using the cluster sampling technique – a cost-effective technique commonly used in extensive forest surveys (Scott, 1998). Twenty cluster locations were selected using systematic sampling to ensure the precision of the estimates (Magnussen et al., 2020). Each cluster included five subsampling units (10 × 10 m) arranged in a cross shape: one plot at the designated cluster location, and one plot located 50 m away in each cardinal direction (Figure A1). Within each plot, trees with a circumference at breast height (CBH) ≥ 15 cm were identified and measured. Multiple parameters were referred for each tree such as the CBH, height, species, canopy cover, canopy diameter and connectivity with the closest trees. The canopy cover and the connectivity were assessed on a scale from 1 to 4, with 1 indicating low cover and connectivity, and 4 indicating high levels for both. In total, 100 botanical plots (equivalent to 1 ha) were inventoried across the study area averaging 400 ha. This corresponds to a sampling rate of 0.25%.

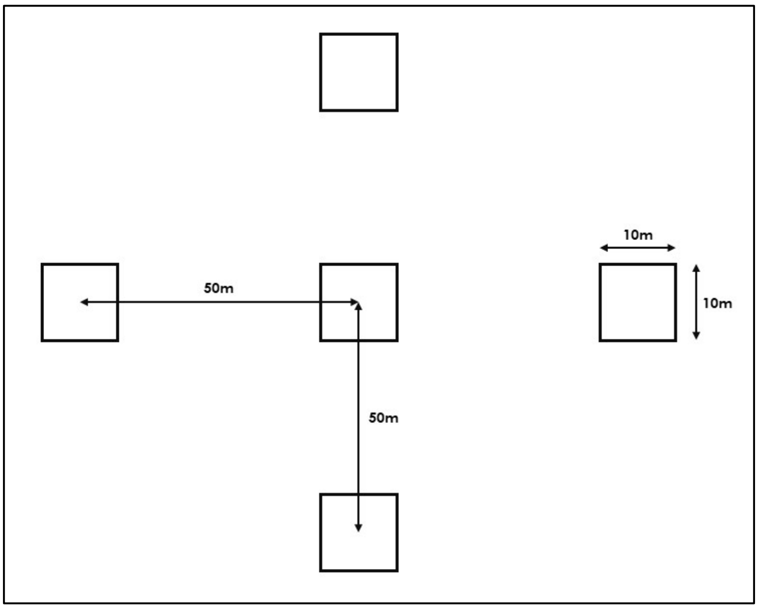

Figure S1 : Illustration of cluster sampling at one of the 20 selected locations using systematic sampling. Each cluster contains five botanical plots of 10 x 10m each.

Appendix S2

Table S1 *:* Ethogram of the main behaviours observed in the primate community.

Main behaviour	Description
Feeding	Searching, collecting or consuming food
Inactive	Immobile in a standing position or scanning the surroundings
Playing	Social interactions including climbing on others, biting or chasing
Moving	Movement within the camera's field of view while staying in the tree
Resting	Sitting or sleeping
Traveling	Moving out of the *Copaifera trapezifolia* or beyond the camera's field of view

Table S2 : List of the additional behaviours observed in the primate community

Behaviour	Description
(Self-)grooming	Cleaning fur by removing parasites or residues
Hugging	Embracing two or more individuals closely together
Copulation	Mating behaviour involving two individuals
Carrying juvenile	Transporting an infant/juvenile on the back/front
Vocalization	Emitting sounds or calls

Appendix S3 – Schoener index formula to calculate the temporal overlap.

$D = 1 - \frac{1}{2} \sum | pi - qi |$ where,

p_i = proportion of occurrences for species 1

q_i = proportion of occurrences for species 2

Appendix S4 – Sørensen-Dice index formula to determine the spatial overlap similarity.

$SD = \frac{2 |X \cap Y|}{|X| + |Y|}$ where,

X = area used by species 1

Y = area used by species 2

Appendix S5

Table S3 *:* List of the inventoried species and their number of observations.

Scientific name	Common name	Number of observations
Brachyteles arachnoides	Southern Muriqui	2858
Alouatta guariba	Brown Howler Monkey	730
Sapajus cucullatus	Black-horned Capuchin	602
Caluromys sp.	Woolly Opossum	23
Nasua nasua	South American Coati	19
Coendou spinosus	Brazilian Porcupine	13
Eira barbara	Tayra	5
Pipile jacutinga	Black-fronted Piping-guan	5
Penelope obscura	Dusky-legged Guan	4
Didelphis aurita	Brazilian Common Opossum	4
Dendrocolaptinae sp.	Woodcreeper	4
/	Rodents	3
Ramphastos dicolorus	Red-breasted Toucan	3
Celeus flavescens	Blond-crested Woodpecker	2
Tamandua tetradactyla	Southern Tamandua	2
Turdus flavipes	Yellow-legged Thrush	1
Pyroderus scutatus	Red-ruffed Fruitcrow	1
Trogon surrucura	Southern Surucua Trogon	1
Spizaetus tyrannus	Black Hawk-eagle	1

Pyrrhura frontalis	Maroon-bellied Parakeet	1

Appendix S6

Table S4 *:* Number of estimated nights spent by each primate species in the 10 studied *Copaifera trapezifolia*.

Species	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	TOTAL
Brachyteles arachnoides	35	6	38	3	2	2	2	0	1	1	90
Alouatta guariba	2	4	8	1	1	5	1	1	1	0	24
Sapajus cucullatus	2	11	0	0	0	4	14	0	1	0	32

Appendix S7

Table S5 *:* Correlation test results between the environmental variables included in the global binomial GLM.

	Max T°	Min T°	Av. wind speed	High. wind speed	Precipitation	Moon phase
Max T°	1	0.66	-0.15	0.13	-0.18	0.01
Min T°		1	0.18	0.21	0.11	0.06
Av. wind speed			1	0.52	-0.0001	0.04
High. wind speed				1	0.09	0.04
Precipitation					1	-0.06
Moon phase						1

Appendix S8

Table S6 : Best binomial linear model testing the effect of minimal temperature, average wind speed and moon phase on the nocturnal presence of Brachyteles arachnoides in the Copaifera trapezifolia.

Covariate	Estimate	SE	z-value	p-value
Maximum temperature	0.2081	0.0494	4.216	$2.49e^{-05}$ ***
Average wind speed	0.6200	0.2010	3.084	0.00204 **
Precipitation	0.03283	0.01705	1.925	0.05425

Table S7 : Best binomial linear model testing the effect of highest wind speed and precipitation on the nocturnal presence of *Alouatta guariba* in *Copaifera trapezifolia*.

Covariate	Estimate	SE	z-value	p-value
Maximum temperature	0.3446	3.4574	1.180	0.03987 *
Highest wind speed	-1.6194	0.5624	-2.879	0.00398 **
Precipitation	1.2445	0.5531	2.250	0.02445 *

Table S8 : Best binomial linear model testing the effect of highest wind speed and precipitation on the nocturnal presence of *Sapajus cucullatus* in the *Copaifera trapezifolia*.

Covariate	Estimate	SE	z-value	p-value
Minimum temperature	0.4022	0.1312	3.065	0.00217 **
Precipitation	0.2590	0.2163	1.197	0.23118