

Snapshot of the Atlantic Forest canopy: surveying arboreal mammals in a biodiversity hotspot

MARIANE C. KAIZER, THIAGO H.G. ALVIM, CLAUDIO L. NOVAES
ALLAN D. McDEVITT and ROBERT J. YOUNG

Abstract The Atlantic Forest of South America supports a rich terrestrial biodiversity but has been reduced to only a small extent of its original forest cover. It hosts a large number of endemic mammalian species but our knowledge of arboreal mammal ecology and conservation has been limited because of the challenges of observing arboreal species from ground level. Camera trapping has proven to be an effective tool in terrestrial mammal monitoring but the technique has rarely been used for arboreal species. For the first time in the Atlantic Forest, we obtained data on the arboreal mammal community using arboreal camera trapping, focusing on Caparaó National Park, Brazil. We placed 24 infrared camera traps in the forest canopy in seven areas within the Park, operating them continuously during January 2017–June 2019. During this period the camera traps accumulated 4,736 camera-days of footage and generated a total of 2,256 photographs and 30-s videos of vertebrates. The arboreal camera traps were able to detect arboreal mammals of a range of body sizes. The mammal assemblage comprised 15 identifiable species, including the Critically Endangered northern muriqui *Brachyteles hypoxanthus* and buffy-headed marmoset *Callithrix flaviceps* as well as other rare, nocturnal and inconspicuous species. We confirmed for the first time the occurrence of the thin-spined porcupine *Chaetomys subspinosus* in the Park. Species richness varied across survey areas and forest types. Our findings demonstrate the potential of arboreal camera trapping to inform conservation strategies.

Keywords Arboreal mammals, Atlantic Forest, Brazil, camera trapping, canopy research methods, Caparaó National Park, conservation, protected area

Supplementary material for this article is available at doi.org/10.1017/S0030605321001563

MARIANE C. KAIZER (Corresponding author, orcid.org/0000-0001-9105-9478, m.dacruzkaizer@edu.salford.ac.uk) School of Science, Engineering & Environment, Peel Building, University of Salford, Salford, M5 4WT, UK

THIAGO H.G. ALVIM and CLAUDIO L. NOVAES (orcid.org/0000-0002-1692-369X) Rede Eco-Diversa para Conservação da Biodiversidade, Tombos, Brazil

ALLAN D. McDEVITT (orcid.org/0000-0002-2677-7833) and ROBERT J. YOUNG (orcid.org/0000-0002-8407-2348) University of Salford, Salford, UK

Received 10 March 2021. Revision requested 6 April 2021.

Accepted 26 October 2021. First published online 17 October 2022.

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Oryx, 2022, 56(6), 825–836 © The Author(s), 2022. Published by Cambridge University Press on behalf of Fauna & Flora International doi:10.1017/S0030605321001563

<https://doi.org/10.1017/S0030605321001563> Published online by Cambridge University Press

Introduction

Tropical forest canopies host between half and two-thirds of terrestrial biodiversity yet remain poorly explored because of the difficulty of access (Linsenmair et al., 2001; Lowman, 2009; Lowman et al., 2013). Approximately three-quarters of terrestrial forest vertebrates in the tropics, including a diversity of mammals, live strictly or partially in the arboreal realm (Eisenberg & Thorington, 1973; Kays & Allison, 2001). For many years, tropical arboreal mammals were inventoried and observed traditionally, using ground-based methods, which often failed to record cryptic, fast-moving or nocturnal species (Lowman & Moffett, 1993; Kays & Allison, 2001; Whitworth et al., 2016; Bowler et al., 2017; Moore et al., 2020). These methods are also difficult to implement in remote areas and on a large scale. Recent advances in canopy access techniques (Lowman, 2009) and the incorporation of emerging technologies into conservation (Pimm et al., 2015; Marvin et al., 2016) have proven useful for overcoming these difficulties, thereby increasing our knowledge of arboreal mammals (e.g. arboreal camera traps: Gregory et al., 2014; drones: Kays et al., 2019; passive acoustic recording: Duarte et al., 2018; environmental DNA: Sales et al., 2020).

Identifying effective approaches for assessing and monitoring the arboreal mammal community is vital for driving management and conservation. Arboreal mammals comprise a high proportion of rainforest animal biomass and play fundamental functional roles in the maintenance of forest ecosystems (Kays & Allison, 2001), including pollination, top-down regulation of prey, folivory, seed dispersal and maintenance of forest carbon storage (Kays & Allison, 2001; Jorge et al., 2013; Bello et al., 2015; Bufalo et al., 2016; Bogoni et al., 2019). Arboreal mammals are sensitive to habitat disturbance (Whitworth et al., 2019), and so anthropogenic impacts could lead to the decline or loss of such species (Dirzo et al., 2014). This could cause changes in community composition and functional diversity (Jorge et al., 2013; Dirzo et al., 2014; Bovendorp et al., 2019).

The Atlantic Forest of South America is one of the hottest global biodiversity hotspots because it harbours one of the greatest diversities of plants and vertebrates, has a high level of endemism and contains many threatened species (Myers et al., 2000; Laurance, 2009). This originally vast biome (1.5 million km²) has been reduced to only c. 12% (c. 163,000 km²) of its original forest cover in Brazil, most of which persists as highly fragmented areas of < 50 ha

(Ribeiro et al., 2009). Over 300 species of mammals occur in the Atlantic Forest, with c. 30% of these being endemic (Paglia et al., 2012; Quintela et al., 2020). Although the mammals of the Atlantic Forest are mostly arboreal (Paglia et al., 2012), the majority of studies that have focused on mammals > 1 kg have been conducted using ground-based methods, such as transect censuses and terrestrial camera traps, along with the use of indirect evidence obtained from vocalizations, tracks, faeces and carcasses (Chiarello, 2000; Srbeek-Araujo & Chiarello, 2005; Oliveira et al., 2013; Geise et al., 2017). Given that loss of mammals has been widely documented throughout the Atlantic Forest biome (Canale et al., 2012; Galetti et al., 2017; Sousa & Srbeek-Araujo, 2017; Bogoni et al., 2018, 2020) and probably will continue to increase because of ongoing anthropogenic activities and climate change, there is a need to gather more reliable data on the distribution and population status of arboreal mammals to inform conservation plans.

Camera traps have proven to be an effective non-invasive method to detect rare and elusive species, even in remote areas and over large spatial and temporal scales (Burton et al., 2015; Wearn & Glover-Kapfer, 2019). Although camera traps have become a ubiquitous method in ecological studies and conservation programmes for terrestrial mammals (Glover-Kapfer et al., 2019), with great potential for global network monitoring (Ahumada et al., 2011; Steenweg et al., 2017), only recently has this method begun to be applied to surveying arboreal mammals in tropical forest canopies (Olson et al., 2012; Gregory et al., 2014; Whitworth et al., 2016; Bowler et al., 2017; Kaizer, 2019; Hongo et al., 2020; Moore et al., 2020). Here we present the first study using arboreal camera trapping to survey arboreal mammals in the Atlantic Forest. Our aims were to (1) assess the efficiency of camera traps for inventorying arboreal mammals in two forest types (semideciduous and ombrophilous forest) and (2) examine variation in the species richness, relative abundance, community composition and functional traits of the arboreal mammal assemblage in Caparaó National Park, Brazil. Although Caparaó National Park is one of the last significant Atlantic Forest remnants in terms of size, in south-east Brazil there is a lack of studies on the vertebrate biodiversity of the Park and its arboreal mammal community is largely undocumented.

Study area

The 31,853 ha Caparaó National Park lies on the border between the states of Minas Gerais and Espírito Santo in south-east Brazil (Fig. 1). The protected area is within the Caparaó massif, part of the northern Mantiqueira mountain range, and stretches for c. 40 km from north to south, with altitudes of 630–2,892 m. (ICMBio, 2015). The vegetation types include Mountainous and High Mountainous Ombrophilous Dense Forest and Mountainous Semideciduous Seasonal Forest below 1,500 m, cloud forest at 1,500–1,900 m and high-altitude

grasslands above 1,900 m (Veloso et al., 1991; ICMBio, 2015). Semideciduous Seasonal Forest occurs predominantly on the western side of the Park and Mountainous Ombrophilous Dense Forest mostly on the eastern side (ICMBio, 2015). The landscape surrounding the Park is dominated by coffee plantations, pastures and isolated, small forest patches. The climate is humid with a temperate summer (Alvares et al., 2013). Mean annual temperature is c. 19 °C at lower altitudes and 9.4 °C at higher altitudes (Alvares et al., 2013). Mean annual rainfall is c. 1,500 mm and the air relative humidity is high (> 70%) during most of the year (ICMBio, 2015). There is a rainy season during October–April and a dry and cool season, with monthly rainfall < 50 mm, during May–September (Alvares et al., 2013; ICMBio, 2015).

Methods

Infrared camera traps (Bushnell Trophy Cam, Bushnell, Overland Park, USA) were deployed in Caparaó National Park during January 2017–June 2019 as part of a larger project monitoring the resident northern muriqui *Brachyteles hypoxanthus* population (Kaizer, 2019). We surveyed 24 sites (each with a single camera trap) in the canopy in seven valleys within the Park (Aleixo, Calçado, Facão de Pedra, Santa Marta, Rio Norte, Rio Preto and Rio Veado). Survey sites covered an altitude range of 1,000–1,768 m, with 10 sites on the western side of the Park (Montane Semideciduous Seasonal Forest) and 14 sites on the eastern side (Montane Ombrophilous Dense Forest). In 2017, we placed eight cameras each in two of these valleys (one in the west and one in the east) along an altitude gradient (Fig. 1; Kaizer, 2019). In 2018 and 2019, we placed eight more camera traps in the other valleys within the Park (Fig. 1). We placed the arboreal camera traps > 250 m apart, strapping them to trees at a mean height of $12.0 \pm \text{SD } 3.1$ m (range: 7.5–17.0 m) from the ground. We chose the arboreal camera-trap locations independently of tree species, based on tree connectivity; i.e. trees connected to at least three other trees where animals could cross the canopy and that were considered to offer safe access for climbers (Gregory et al., 2014; Kaizer, 2019; Whitworth et al., 2019). To prevent bias, we chose trees that were not fruiting or flowering on the day of installation, as food resources could attract certain species more than others and thus affect detection rates. We did not bait the camera traps or orientate them to the east or west (which would avoid direct sunlight and reduce shadows and false positive/negative triggers) and we placed them facing along a horizontal branch of the tree or towards a horizontal or vertical branch of an adjacent tree. The camera traps were active continuously and set to hybrid mode (two photographs and one 30-s video on each trigger event), with 10-s intervals between triggers and low night-time light-emitting diode intensity. We identified animals in the photographs using *Wild.ID*

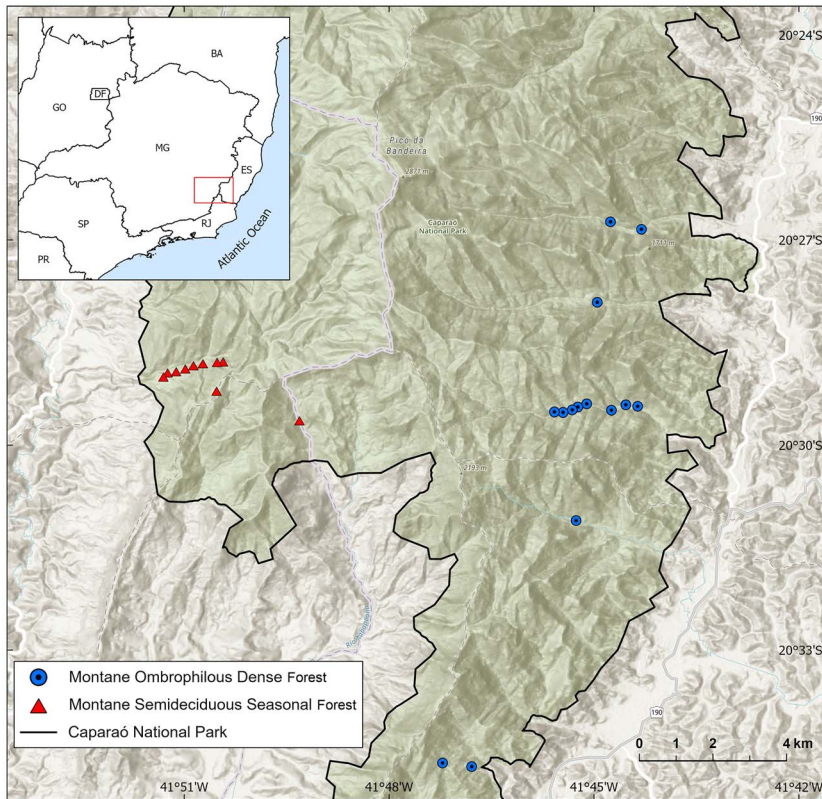


FIG. 1 Locations where arboreal camera-trap surveys were conducted in ombrophilous and semideciduous forests in Caparaó National Park, south-eastern Brazil.

0.9.3.1 (TEAM Network, 2015). As we set the camera traps to hybrid mode we defined a detection event as a set of two photographs and one 30-s video. To ensure independence between events, we used a minimum interval of 1 h between species-specific detection events (Oliveira-Santos et al., 2008; Debrulle et al., 2020).

We defined detection rates for arboreal mammals as the ratio of independent detection events to the number of camera-trap days; the latter is the number of 24-h periods from camera-trap placement until its battery ran out or we retrieved the camera, multiplied by 100 (Rovero & Marshall, 2009). We used the mean camera-trap detection rate as an index of the relative abundances of arboreal mammal species (Rovero & Marshall, 2009; Pal et al., 2020).

We conducted all analyses in R 3.6.3 (R Core Team, 2020). To assess arboreal camera-trapping efficiency we estimated rarefied species richness per camera, accounting for differences in the number of camera-trap days, and used a first-order jackknife estimator available in the *vegan* package of R (Oksanen et al., 2019). We performed a Wilcoxon rank-sum test to examine whether species richness and camera-trap detection rate (i.e. relative abundance) differed between semideciduous and ombrophilous forests. We used the Jaccard index, calculated by dividing the total number of species trophic guilds shared in both semideciduous and ombrophilous forests by the total number of trophic guilds occurring in either forest, to examine the similarities in species trophic guilds between the two forest types.

We categorized all mammal species into trophic guilds (Table 1), which are not mutually exclusive (folivore, frugivore, granivore, gumivore, insectivore, myrmecophage, omnivore, carnivore), and according to their foraging habits (arboreal, scansorial, terrestrial). The morpho-ecological traits of the mammal species are based on Paglia et al. (2012) and Wilman et al. (2014), and taxonomy follows Abreu et al. (2021).

Results

Across the 24 arboreal camera-trap sites our survey effort totalled 4,736 camera-trap days, of which 2,151 and 2,585 camera-trap days were in semideciduous and ombrophilous forest, respectively. The camera traps were active for a mean of $57.0 \pm \text{SD } 43.6$ days (range 1–285 days), dependent in part on whether cameras malfunctioned or batteries failed. There was a total of 27,310 trigger events, of which 2,256 were of mammals, birds or lizards (8.3%).

We obtained 2,200 events of arboreal mammals, of which 1,396 were independent events. From these we identified 1,216 records (87.2% of the total number of mammal events), with 15 mammals identified to species, two to genus and one to family (Table 1). Unidentifiable events ($n = 178$) were small mammals, including opossums and rodents. The identified mammals represent 12 families and eight orders (Table 1). Rodentia was the richest order (five species),

TABLE 1 List of mammals recorded by arboreal camera trapping in Caparaó National Park, Brazil, with their IUCN Red List status (IUCN, 2022), number of independent events, detection rates (independent photographs/trap days \times 100) in two forest types, altitude range (Fig. 3) and camera height. Information of mammals' morpho-ecological traits from Paglia et al. (2012) and Wilman et al. (2014).

Order/family/species	Weight (g)	Habit ¹	Trophic guild ²	Red List status ³	No. of events	Detection rate (independent photographs/trap days \times 100)			Altitude range (m)	Camera height (m)
						Semideciduous	Ombrophilous	Overall		
Carnivora										
Felidae										
Margay <i>Leopardus wiedii</i>	3,000–9,000	Sc	Ca	NT	2	0.00	0.19	0.08	1,367	7.6
Mustelidae										
Tayra <i>Eira barbara</i>	4,000–10,000	Te	Fr/On	LC	27	0.00	2.51	1.14	1,367	7.6
Procyonidae										
South American coati <i>Nasua nasua</i>	5,100	Te	Fr/On	LC	6	0.00	0.56	0.25	1,304–1,367	7.6–9.0
Kinkajou <i>Potos flavus</i>	2,600	Ar	Fr/On	LC	13	0.00	1.21	0.55	1,099–1,238	9.0–15.9
Chiroptera										
Phyllostomidae										
Unidentifiable bat species					1	0.00	0.09	0.04	1,426	8.5
Didelphimorphia										
Didelphidae										
Bare-tailed woolly opossum	140–390	Ar	Fr/On	LC	66	2.71	2.88	2.79	1,099–1,511	7.6–15.9
<i>Caluromys philander</i>										
Southeastern four-eyed opossum	220–680	Sc	In/On	LC	1	0.00	0.09	0.04	1,367	7.6
<i>Philander quica</i>										
Brazilian gracile opossum	12–52	Ar	In/On	LC	29	2.24	0.00	1.22	1,316–1,528	10.9–16.0
<i>Gracilinanus microtarsus</i>										
Tate's woolly mouse opossum	120–175	Sc	In/On	LC	1	0.00	0.19	0.08	1,303	9.0
<i>Marmosa (micoureus) paraguayana</i>										
Pilosa										
Myrmecophagidae										
Southern tamandua <i>Tamandua tetradactyla</i>	5,200	Sc	Myr	LC	1	0.00	0.09	0.04	1,367	7.6
Primates										
Atelidae										
Northern muriqui <i>Brachyteles hypoxanthus</i>	13,000	Ar	Fr/Fo	CR	283	14.62	8.74	11.95	1,238–1,768	7.5–17.0
Callitrichidae										
Buffy-headed marmoset <i>Callithrix flaviceps</i>	400	Ar	Fr/In/Gu	CR	128	6.77	3.72	5.38	1,367–1,528	7.5–16.0
Cebidae										
Black-horned tufted capuchin <i>Sapajus nigritus</i>	3,000–4,000	Ar	Fr/On	NT	148	4.41	8.14	6.10	1,099–1,768	7.5–15.9

TABLE 1 (Cont.)

Order/family/species	Weight (g)	Habit ¹	Trophic guild ²	Red List status ³	No. of events	Detection rate (independent photographs/trap days × 100)			Altitude range (m)	Camera height (m)
						Semideciduous	Ombrophilous	Overall		
Rodentia										
Cricetidae										
Climbing mouse <i>Rhipidomys</i> sp.	40–87	Ar	Fr/Se		23	0.00	2.14	0.97	1,367–1,426	7.6–8.5
Echimyidae										
Atlantic tree-rat <i>Phyllomys</i> sp.	170–320	Ar	Fo		193	2.86	14.50	8.15	1,304–1,768	8.5–10.0
Erethizontidae										
Thin-spined rat <i>Chaetomys subspinosus</i>	1,300	Ar	Fr/Fo	VU	8	0.00	0.73	0.34	1,099–1,364	10.0–15.9
Spiny tree porcupine <i>Coendou spinosus</i>	1,200–1,300	Ar	Fr/Fo	LC	196	2.79	5.76	4.14	1,099–1,511	7.5–15.9
Porcupine <i>Coendou</i> sp.					98	0.31	0.00	0.17	1,316	10.9
Sciuridae										
Southeastern squirrel <i>Guerlinguetus brasiliensis ingrami</i>	125–216	Sc	Fr/Gr	LC	186	0.00	17.29	7.85	1,304–1,442	15.9
Unidentifiable spp. (rats & opossums)					178				1,190–1,707	7.5–10.2
<i>Total</i>					1,396				1,099–1,768	7.5–17

¹Ar, arboreal; Sc, scansorial; Te, terrestrial.²Ca, carnivore; Fo, folivore; Fr, frugivore; Gr, granivore; Gu, gumivore; In, insectivore; Myr, myrmecophage; On, omnivore.³LC, Least Concern; NT, Near Threatened; VU, Vulnerable; CR, Critically Endangered.

followed by Carnivora and Didelphidae (four each), Primates (three), and Pilosa and Chiroptera (one each).

Of the mammal species recorded, two are categorized as Critically Endangered, one as Vulnerable and two as Near Threatened on the IUCN Red List (IUCN, 2020; Table 1). Seven species, including three primates (*B. hypoxanthus*, *Callithrix flaviceps* and *Sapajus nigritus*), one porcupine (*Chaetomys subspinosus*), one squirrel (*Guerlinguetus*

brasiliensis ingrami), one tree-rat (*Phyllomys* sp.) and one opossum (*Gracilinanus microtarsus*) are endemic to the Atlantic Forest. The detection of the thin-spined porcupine *C. subspinosus* is the first confirmed occurrence of the species in the Park and in western Espírito Santo state (Giné & Faria, 2018). The arboreal camera traps detected mammals spanning a wide range of body sizes (Plate 1, Table 1), with nine > 1 kg (Table 1). The largest-bodied species



PLATE 1 Some of the arboreal mammal species photographed by camera traps in the canopy of the Atlantic Forest of Caparaó National Park, Brazil (Fig. 1): (a) northern muriqui *Brachyteles hypoxanthus*, (b) buffy-headed marmoset *Callithrix flaviceps*, (c) black-horned capuchin *Sapajus nigritus*, (d) tayra *Eira barbara*, (e) South American coati *Nasua nasua*, (f) kinkajou *Potos flavus*, (g) southern tamandua *Tamandua tetradactyla*, (h) thin-spined rat *Chaetomys subspinosus*, (i) spiny tree porcupine *Coendou spinosus*, (j) rusty-sided Atlantic tree-rat *Phyllomys* sp., (k) bare-tailed woolly opossum *Caluromys philander*, and (l) Brazilian gracile opossum *Gracilinanus microtarsus*.

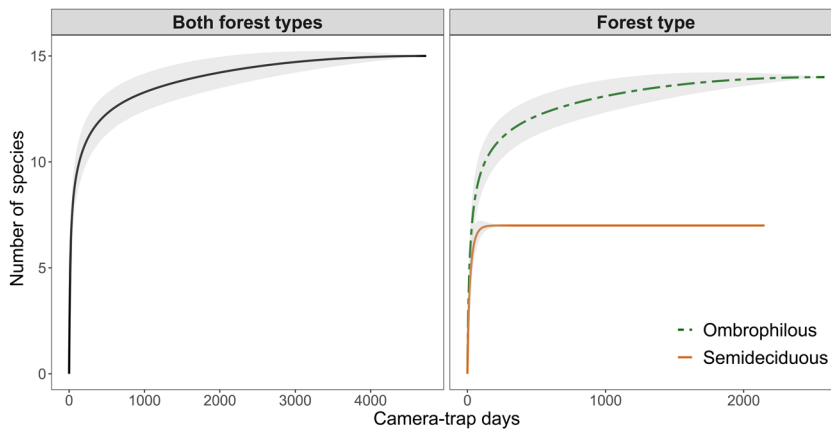


FIG. 2 Species accumulation curves in Caparaó National Park, Brazil, with 95% CIs, for all mammal species detected, and for mammal species detected only in ombrophilous and semideciduous forests, by arboreal camera traps.

detected was a primate, the northern muriqui *B. hypoxanthus*, and the smallest-bodied mammals were *G. microtarsus*, *Rhipidomys* sp., *Marmosa (micoureus) paraguayana*, *G. b. ingrami*, *Caluromys philander*, *Phyllomys* sp., *Philander quica* and *C. flaviceps* (Paglia et al., 2012; Faria et al., 2019). The majority of the mammal species are arboreal but five are scansorial (*G. b. ingrami*, *M. m. paraguayana*, *P. quica*, *Tamandua tetradactyla* and *Leopardus wiedii*) and two are terrestrial (*Eira barbara* and *Nasua nasua*).

The number of species predicted by the jackknife 1 estimator was $17 \pm \text{SD } 1.4$ (Fig. 2), suggesting that c. 88% of species present can be captured within the first 1,000 camera-trap days (41.7 days for each of our 24 cameras), which is the minimum effort needed to detect the arboreal mammal assemblage in tropical rainforest (Bowler et al., 2017). The cumulative curves for species richness increased substantially during the first 500 camera-trap days in both forest types (Fig. 2) but took longer to stabilize for the ombrophilous forest, which indicates that it could require greater effort to detect rare and cryptic species there. Although arboreal camera traps documented greater species richness and relative abundance for the mammal community in Ombrophilous Dense Forest (Supplementary Figs 1 & 2), there were no significant differences between forest types (richness: $W = 90$, $P = 0.245$; abundance: $W = 72$, $P = 0.931$). The estimated detection rates for mammals were highly variable, from 0.04 for *M. m. paraguayana*, *Philander quica*, *T. tetradactyla* and Phyllostomidae bats to 12.00 for *B. hypoxanthus* (Table 1). The estimates for mammals in semideciduous forest ranged from 2.2 for *G. microtarsus* to 14.6 for *B. hypoxanthus*, whereas in ombrophilous forest the detection rates ranged from 0.1 for *M. m. paraguayana*, *P. quica*, *T. tetradactyla* and Phyllostomidae bats to 17.3 for *G. b. ingrami*. *Brachyteles hypoxanthus* and the black-horned capuchin *S. nigritus* were detected widely (20 and 17 canopy sampling locations, respectively) and across an altitude gradient (Fig. 3). However, *M. m. paraguayana*, *P. quica*, *T. tetradactyla* and Phyllostomidae bats were detected only once and

L. wiedii was detected only twice during the survey period. The kinkajou *P. flavus* and *C. spinosus* were detected at two and three sampling locations, respectively, close to streams in the ombrophilous forest type at altitudes up to 1,364 m (Fig. 3).

The Jaccard index revealed a dissimilarity of 0.375 in trophic guilds between the forest types. Ten species were recorded exclusively in the Montane Ombrophilous Dense Forest and only one species was recorded exclusively in the semideciduous forest (Fig. 3, Table 1). The species richness of frugivores–omnivores and frugivores–folivores was high in both forest types. However, two trophic guilds were missing in the semideciduous forest: carnivores and myrmecophages. The mean relative abundance was greatest for folivore (8.1, $n = 1$), frugivore–granivore (7.9, $n = 1$), frugivore–folivore ($5.5 \pm \text{SD } 5.9$, $n = 3$) and frugivore–insectivore–granivore (5.4, $n = 1$) species. The frugivore–insectivore–gumivore (6.8, $n = 1$), frugivore–folivore ($5.9 \pm \text{SD } 7.7$, $n = 3$) and folivore (2.9, $n = 1$) species had the greatest mean relative abundances in the semideciduous forest, whereas frugivore–granivore (17.3, $n = 1$), folivore (14.5, $n = 1$) and frugivore–folivore ($5.1 \pm \text{SD } 4.0$, $n = 3$) species had the greatest mean relative abundances in the ombrophilous forest.

Discussion

We examined the species richness, community composition and functional traits of arboreal mammals in the Atlantic Forest canopy. As far as we are aware, this is the first study using arboreal camera trapping to assess mammal assemblages in the canopy of this biodiversity hotspot (except for low-height camera-trap studies; Kierulff et al., 2004; Oliveira-Santos et al., 2008). Our results demonstrate the efficiency of this method for detecting arboreal mammals of various body sizes and for detecting rare and highly cryptic species such as the buffy-headed marmoset, tree-rats and the thin-spined porcupine. Furthermore, we compiled evidence that this protected area has high species richness and a functional community of arboreal mammals,

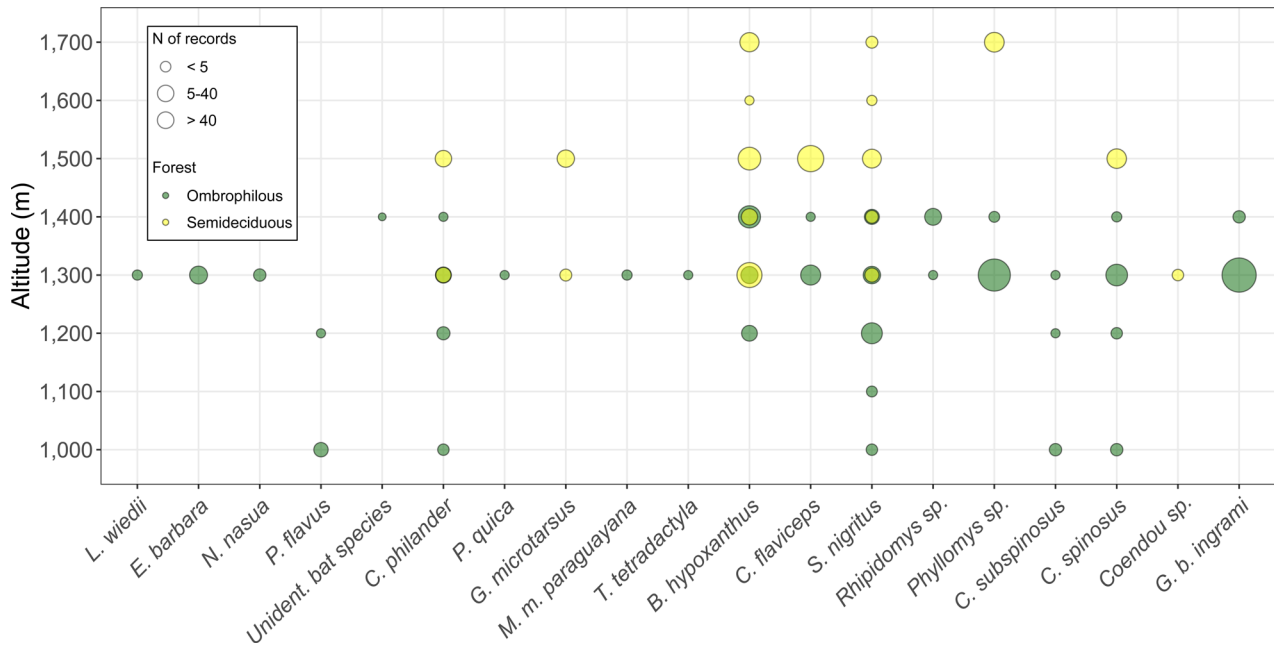


FIG. 3 Bubble graph representing presence–absence and categorical values of the number of independent records in each forest type (semideciduous forest and ombrophilous forest) for each mammal species identified, across an altitudinal gradient in Caparaó National Park, Atlantic Forest, south-eastern Brazil, using arboreal camera traps (Table 1).

including the largest arboreal seed disperser (*B. hypoxanthus*). The results do not indicate any differences in species richness and relative abundance between the semideciduous and the ombrophilous forest types. However, the species richness of the arboreal mammal assemblage in both forest types and our entire study site could be underestimated by arboreal camera traps alone because of the ecology of some species. For example, some terrestrial or scansorial species such as *E. barbara*, *N. nasua*, *T. tetradactyla* and *L. wiedii* also occur in semideciduous forests (Graciano et al., 2021; M.C. Kaizer, pers. obs., 2017) but we only detected them in the ombrophilous forest in our study.

The number of arboreal mammals documented in this study is comparable to the species richness reported in various arboreal camera-trapping studies in other tropical rainforest sites. Previous studies in the Amazon Forest of Peru found the species richness of arboreal mammals as detected by arboreal camera traps to be 18–24 species (18 species: Whitworth et al., 2016; Bowler et al., 2017; 20 species: Gregory et al., 2014; 24 species: Whitworth et al., 2019). In the West African rainforest, arboreal camera traps recorded 19 arboreal mammal taxa in Boumba-Bek and Nki National Parks, Cameroon (Hongo et al., 2020) and 15 arboreal taxa in Nyungwe National Park, Rwanda (Moore et al., 2020). At least six species of primates are known to occur in the rainforest of Caparaó National Park (Culot et al., 2019), of which we detected three. The absence or non-detection of the other three species (*Callicebus nigrifrons*, *Callicebus personatus* and *Alouatta guariba*) could be related to a recent yellow fever outbreak, which caused the deaths of > 5,000 non-

human primates in the Atlantic Forest (Bicca-Marques et al., 2017). The last sightings of *A. guariba* and *C. nigrifrons* in our study area were reported by M.C. Kaizer (pers. obs.) in December 2016 and March 2017, respectively, coinciding with the most severe period of the yellow fever outbreak in south-eastern Brazil (Faria et al., 2018). Our results suggest that further research is necessary to evaluate the current population status of these primate species in the Park and so determine the impact of this yellow fever outbreak.

Defaunation and the collapse of the functional diversity of the mammal community have been reported throughout the Atlantic Forest biome (Jorge et al., 2013; Galetti et al., 2015, 2017; Bogoni et al., 2018, 2020), even in large protected areas (Canale et al., 2012). Historical habitat loss and fragmentation of the Atlantic Forest and historical and recurrent hunting pressures are the major drivers of mammal defaunation and changes in community composition (Jorge et al., 2013; Bogoni et al., 2018). Based on studies conducted during 1983–2015, a mean species richness of 14.7 was reported for mammal assemblages in Atlantic Forest fragments for species > 1 kg (Bogoni et al., 2017). We detected nine species > 1 kg, the majority of which are frugivore–omnivores and frugivore–folivores, which are important for seed dispersal and nutrient cycling in tropical forests. For example, the northern muriqui is important in the dispersal and recruitment of large-seeded plant species, which has consequences for key ecosystem services such as carbon stock (Bufalo et al., 2016). Frugivore–folivore species richness correlates positively with dung beetle species richness across the Atlantic

Forest, which are important in nutrient cycling, soil quality and detritivore food webs (Nichols et al., 2008; Bogoni et al., 2019). Regarding the smaller body-sized species (< 1 kg), our study reveals the occurrence of key species such as large rodents and marsupials of the genera *Phyllomys* and *Caluromys*, which are usually the first groups to disappear from disturbed habitats (Chiarello, 1999).

Our results reinforce the important role played by protected areas for mammal conservation (Littlewood et al., 2020). It is estimated that < 3% of Atlantic Forest remnants are suitable for the thin-spined porcupine (Bonvicino et al., 2018a). The occurrence of this species in Caparaó National Park is therefore important to the long-term persistence of this species. The first documentation of the tree-rat also demonstrates the potential of the Park to host rare species. Although we were not able to identify this record to species, the rare *Phyllomys lundi* has been reported in a private reserve c. 20 km from our study sites (Faria et al., 2016). This threatened species has been reported previously in only three locations in the Atlantic Forest biome (Faria et al., 2016; Bonvicino, 2018b). Caparaó National Park is also one of the four priority areas for the conservation of the Critically Endangered northern muriqui (Melo et al., 2018). This population is important because it inhabits the greatest altitudinal range of the species (up to 2,000 m; Strier et al., 2017). By using arboreal camera trapping we were able to document this species across an altitudinal gradient, including at high elevations and on slopes, where accessibility for ground-based surveys is limited. Furthermore, the northern muriqui was only recently discovered to occur on the west side of the Park (Kaizer et al., 2016) and its occurrence in ombrophilous forest was reported previously in only a few locations (Mendes et al., 2005). Our findings provide new records for the occurrence of this species at two sites within the Park (Rio Preto and Rio Norte valleys). This demonstrates the importance of this protected area for safeguarding this distinct threatened species (Isaac et al., 2007). However, the high detection rate of the northern muriqui in our study site could have been biased by the large home range of the species (Dias & Strier, 2003; Lima et al., 2019) as it was detected along an array of arboreal camera traps in the same valley and/or in several independent events at distinct locations.

Although c. 12% of the records of mammals in this study were small mammals that could not be identified, including bats, rodents and opossums, our findings demonstrate the ability of arboreal camera traps to detect smaller-bodied species. The record of *Phyllomys* sp. is an example of the potential of arboreal camera traps to detect elusive and arboreal species that are often difficult to record using small mammal traps (Faria et al., 2016; Bonvicino et al., 2018b). However, as most of these records were nocturnal, thus hampering the recognition of some species, the use of camera traps with white flash

functionality could increase the potential effectiveness of this method (Bowler et al., 2017) despite white flashes potentially altering species behaviour or movements (Wearn & Glover-Kapfer, 2017). The configuration of the camera traps to hybrid mode (i.e. to record a short video after taking a still photograph) also increases the likelihood of being able to identify species, and documents fast-moving species such as squirrels and marmosets (including the number of individuals and with potential for collecting data on species behaviour; Caravaggi et al., 2020). Cutting vegetation surrounding the arboreal camera trap station, avoiding facing the camera into direct sunlight and positioning the camera on a horizontal branch could also help increase the likelihood of distinguishing species and reduce the number of false triggers, which is one of the constraints of camera-trapping studies (Gregory et al., 2014; Wearn & Glover-Kapfer, 2017; Kaizer, 2019).

To date, most of the studies reporting the arboreal mammal assemblage in remnants of the Atlantic Forest have been ground-based. Our findings demonstrate the potential of arboreal camera trapping to record rare, nocturnal and cryptic species that are difficult to detect with ground-based methods (Olson et al., 2012; Whitworth et al., 2016; Bowler et al., 2017; Moore et al., 2020). Considering the habits of some scansorial and terrestrial species, we suggest that arboreal camera traps should be paired with terrestrial cameras to reduce the likelihood of failing to detect these species. This would provide a better snapshot of the entire mammal assemblage. In addition, our results illustrate the role played by Caparaó National Park as a stronghold for the conservation of rare and threatened mammalian species endemic to a biodiversity hotspot. We encourage future studies over larger spatial and temporal scales, with the aim of exploring trends in the species composition and functional diversity of the entire mammalian community using emerging biomonitoring technologies (e.g. environmental DNA; Sales et al., 2020). This would provide a more complete understanding of how mammal functional diversity and ecosystem functioning are maintained, and inform evidence-based conservation strategies for this protected area.

Acknowledgements We thank two anonymous reviewers for their critiques; the Brazilian Ministry of Environment/SISBIO for authorizing the research in the Caparaó National Park; the Park managers for logistical support; Francisco H. Gabriel, Leandro Moreira, Rodrigo Silva and Viviane Sodr  for fieldwork assistance; Aryanne Clyvia and Daniel da Silva Ferraz for logistical support; Guilherme Garbino, Michel Faria and Rayque Lanes for the identification of small mammals; Rodolfo Sarcinelli for design of the study area map; the Brazilian Ministry of Education/CAPES (BEX 1 298/2015-01) for the award of a PhD studentship to MCK; Idea Wild and Conquista Montanhismo for equipment grants and the Conservation Leadership Programme (No. 12455) and Mohammed bin Zayed Conservation Fund (No. 162512917) for support to the Capara  Muriqui Project, of which this work is a part; the Conservation Leadership Programme for supporting

MCK to attend a Writing for Conservation Workshop; and the National Geographic Society for supporting MCK as an Early Career National Geographic Explorer.

Author contributions Study design, fieldwork: MCK, CLN, THGA; camera-trap data processing: CLN, MCK; data analysis, writing: MCK, ADM, RJY.

Conflicts of interest None.

Ethical standards This research was approved by the Caparaó National Park (ICMbio/SISBIO No. 49062) and the University of Salford (STR1718-14), and otherwise abided by the *Oryx* guidelines on ethical standards.

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