ARTICLE

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Mammal diversity among vertical strata and the evaluation of a survey technique in a central Amazonian forest

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Abstract. Mammal groups have a vast variety of habitats, which include aquatic, aerial, arboreal, and terrestrial. For terrestrial habitats, camera traps are used as a common technique to record mammals and other vertebrates and have been recently utilized to observe arboreal animals as well. Here, we compare the difference in mammal diversity between floor and canopy strata and evaluate the use of camera trapping in a lowland forest in central Amazon. We installed nine paired camera traps, one in the canopy stratum and other in the floor stratum, in the Alto Cuieiras Biological Reserve (Brazilian Amazon). With a sampling effort of 720 camera-days, we recorded 30 mammal species: nine in canopy strata, 14 in floor strata, and seven in scansorial strata (sharing both strata). On the forest floor, the species with the greatest abundance was *Myoprocta acouchy;* in the canopy, *Isothrix paguros* had the greatest abundance; and among the scansorial species, *Proechymis* sp. was the most abundant. Our results show the differences in mammal diversity between floor and canopy strata; canopy strata contained more small and frugivorous mammals. Although we obtained a relatively low sampling effort with the camera-trap method compared with other studies utilizing different techniques, our results were especially similar to those of previous studies that worked with canopy and floor strata. Thus, camera trap can be very effective for recording short periods of time, and this method is less physically exhaustive and expensive for researchers to study vertical strata.

Keywords. Mammals assemblage; Lowland forest; Canopy and floor strata; Monitoring.

INTRODUCTION

Mammals are one of the most charismatic groups and have a broad variety of habitats, such as aquatic, aerial, terrestrial and arboreal (Ceballos & Ehrlich, 2002; Wright *et al.,* 2007). Due to the diversity of species, mammals play important roles in ecosystem functioning, and information on their species diversity can elucidate broad ecological processes, such as seed dispersal (de Almeida *et al.,* 2018; Escribano-Avila *et al.,* 2014), seed predation (Mendoza & Dirzo, 2007), the beetle-mammal network (Raine *et al.,* 2018), and population control of other species by carnivores (Ford & Goheen, 2015).

The Brazilian Amazon is home to 409 mammal species with 248 species being exclusive for this biome; these species are mostly arboreal (55.7% excluding aerials) and occupy all the vertical strata (Paglia *et al.,* 2012; Quintela *et al.,* 2020). Regarding vertical strata, 40% to 70% of nonvolant mammalian biomass is represented in the canopy stratum (Eisenberg & Thorington, 1973). Despite the existence of different survey field techniques to monitor mammals in this habitat (*e.g.,* Palmeirim *et al.,* 2019), the canopy stratum is one of the least known environments in the world, termed as the "last biotic frontier" (Bouget *et al.,* 2011; Erwin, 1988; Whitworth *et al.,* 2019a).

Among possible survey techniques, the most commonly used are line transects, live trapping, and camera trapping. The line transect technique (hereafter LnTT) is broadly used to survey mid-size to large-bodied mammals, especially those

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with terrestrial and diurnal behaviors (Munari *et al.,* 2011; Peres & Cunha, 2011; Pontes, 2004). The live-trapping technique (LvTT), which includes Sherman, Tomahawk, and pitfall traps, is especially used for nonvolant small mammals (< 1 kg) (Ardente *et al.,* 2017; Malcolm, 1991), which can be located in the canopy stratum (José *et al.,* 2019). Finally, the camera-trapping technique (CTT) is one of the newest to be implemented to mammal surveys, and its use has drastically increased in recent years (Burton *et al.,* 2015; Wearn & Glover-Kapfer, 2017). This technique can be used to reach a vast variety of difficult habitats, such as canopy habitats, and record elusive and rare species in the wild with more success than the previously described techniques (Bowler *et al.,* 2017; Wearn & Glover-Kapfer, 2017). While cost-benefit studies show that CTT should be, despite the high initial costs (Silveira *et al.,* 2003), the most appropriate technique for mammal surveys in all environmental conditions (Palmeirim *et al.,* 2019). Nevertheless, most surveys utilizing CTT have focused on the floor stratum (Rowcliffe, 2017; Network, 2011; Tobler *et al.,* 2008), and few recent surveys in the eastern Amazon have focused on the canopy stratum (Gregory *et al.,* 2014; Whitworth *et al.,* 2019b). In this study, we compare the differences in mammal diversity between floor and canopy strata and evaluate the use of CTT compared with other techniques between the vertical strata in a lowland central Amazonian forest. We hypothesize that the canopy strata will have a higher abundance of small and frugivorous mammals than those of the floor and CTT will be more efficient than other techniques recording a large number of species in a short period of time.

MATERIAL AND METHODS

Study Site

Our study area was in the Cuieiras Biological Reserve located approximately 60 km northwest of Manaus (02°37′ to 02°38′S, 60°09′ to 60°11′W) (Fig. 1). It has an area of approximately 38,000 ha and is delimited by the BR-174 highway and the Cuieiras River basin (Higuchi, 1981).

The area contains lowland forest habitats with a relatively open understory and dense uniform canopy, with a height range of 30-39 m and the emergent layer reaching up to 55 m in height. The soils in these habitats are nutrient-poor sandy and clayey oxisols. The topography is undulating with an average elevation varying between 40 and 160 m above sea level (m.a.s.l.) (Prance *et al.,* 1990). These variations have a great influence on the forest structure; the forests have visibly different vegetation formations associated with hilltops and slopes of varying inclination. In addition, flooded bottomland swamps may occasionally occur in areas where plateaus are dissected by streams (Oliveira *et al.,* 2008). The av-

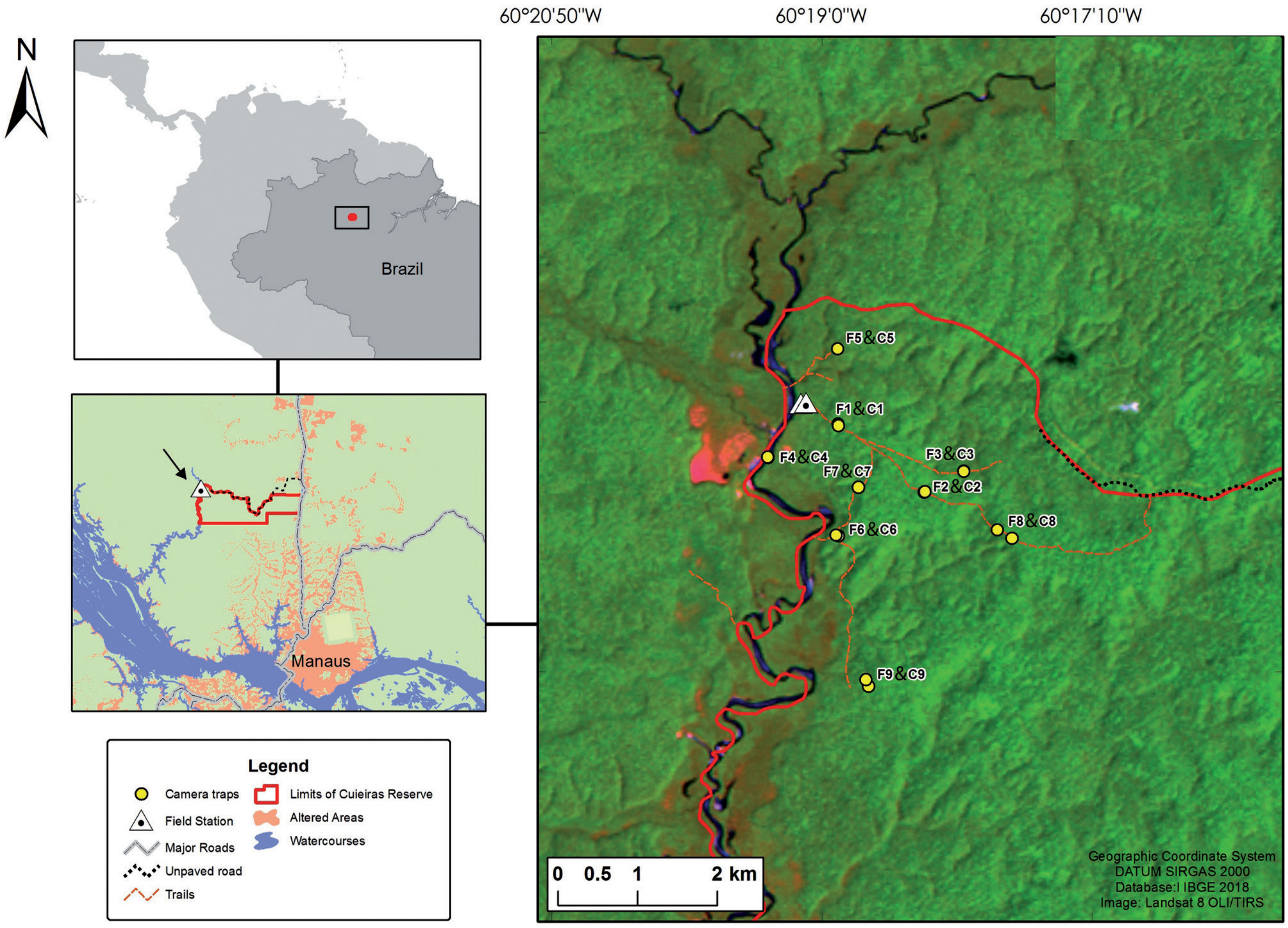

Figure 1. Locations of the nine paired camera traps located in the Cuieiras Biological Reserve, Brazil. F represents the floor stratum and C represents the canopy stratum.

erage temperature is 26°C, and the seasons are well defined; most rain fall occurs from December to May (211-300 mm monthly average), and a marked dry season occurs from June to November (42-162 mm monthly average) (Ribeiro & Adis, 1984).

Data collection and analysis

We carried out a 40-day camera trap survey from March to April 2018 during the peak of the rainy season. The camera traps were paired; one camera trap focused on the floor stratum and another was placed in the canopy stratum with a total of 22 points (eleven in each stratum) (Fig. 1). The distance among them was between 0.6 and 2 km, covering 600 ha. We used Reconyx UltraFire XR6 (Holmen, WI, USA) passive infrared cameras, which were sealed with silicon for protection from the rain. The cameras recorded continuously 24 hours a day. All cameras were unbaited and programed to record three pictures followed by one video of 15 seconds without intervals between them; we consider this series as one record. For the floor stratum, we installed cameras 20-30 cm above the floor, in areas with signs of mammal presence (*e.g.,* footprints, tracks, feces, and other signs). In these floor areas, we cleared 5 × 5 m area in front of each camera of foliage and herbs to prevent falsely triggering cameras and to ensure clear recording and easy identification of observed animals. For the canopy stratum, we installed cameras at a height of 15-20 m in trees with potential animal footbridges. The points were not necessarily in the same trees where forest floor recordings took place. Four cameras were excluded from the analysis due to malfunctions (two in the canopy stratum and two in the floor stratum).

We processed the camera trap records using the freely available software Timelapse2 (Greenberg & Godin, 2015). The records were considered independent if taken at least 30 min apart; when the same species were recorded the same day on the same camera, we used these records as a proxy for abundance (Rovero & Zimmermann, 2016).

To compare the rate at which new species accumulated in each stratum, we generated sample-based rarefaction/extrapolation curves for species richness and compared them using 95% confidence intervals drawn from 1,000 randomizations. These rates were also estimated using the first-order jackknife estimator. We considered the richness between strata distinct when the confidence intervals did not overlap curves (Magurran, 2004). We also assessed whether the sampling effort was sufficient enough to record mammal species using these curves. Richness analyses were carried using the iNEXT package (Hsieh *et al.,* 2013). To test the similarity between assemblages, we reduced the matrix dimensionality of midsize to large-bodied mammal species recorded on the floor and canopy strata using a non-metric multidimensional scaling (NMDS) based on the Bray-Curtis similarity index using the "vegan" package (Oksanen *et al.,* 2019). We standardized the camera trap station weights by divid-

Table 1. Sampling effort compared with other techniques in different vertical strata in the Amazon.

Reference	Site[a]	Nonvolant mammal group	Number of species by stratum[b]		Sampling effort by stratum[c]					
					Forest floor			Canopy		
			Forest floor	Canopy	LnTT	LvTT	CTT	LnTT	LvTT	CTT
Peres (1997)	Jurua river, western Amazon	Primates	—	19	—	—	—	1564	—	—
Michalski & Peres (2007)[d]	Alta Floresta, southern Amazon	Midsize to large	9	30	1824	—	3086	—	—	—
Tobler *et al.* (2008)[e]	Los Amigos, southwestern Amazon	Midsize to large terrestrial	35	3	—	—	3780	—	—	—
Munari *et al.* (2011)[f]	Uacari Sustainable Development Reserve, western Amazon	Midsize to large terrestrial	20	—	343	—	932	—	—	—
Gregory *et al.* (2014)[g]	Pagoreni, lower Urubamba river, southwestern Amazon	Small to large	18	6	—	—	1950	—	—	3608
Abrahams *et al.* (2017)	Médio Juruá and Uatumã regions, central-western Amazon	Small to large	23	6	—	—	11490[h]	—	—	—
Ardente *et al.* (2017)[i]	Carajás National Forest, southeastern Amazon	Small	19	13	—	28080	—	—	34560	—
Blake *et al.* (2017)	Tiputini Biodiversity Station, northwestern Amazon	Small to large	24	7	—	—	5540	—	—	—
Bowler *et al.* (2017)	Maijuna-Kichwa Regional Conservation Area, nortestern Amazon	Midsize to large arboreal	4	16	—	—	—	2014	—	3147
Mendes-Oliveira *et al.* (2017)	Agropalma private landholding, eastern Amazon	Small to large	28	9	627	—	6720	—	—	—
Palmeirim *et al.* (2019)	Archipelagic landscape of the Balbina Hydroelectric Reservoir, central Amazon	Small	12	13	—	19584[j]	6600	—	—	—
Whitworth *et al.* (2019b)[k]	The Manu Biosphere Reserve, southwestern Amazon	Midsize to large	27	21	—	—	11253	—	—	20364
Present study	Alto Cuieiras Biological Reserve, central Amazon	Small to large	22	14	—	—	360	—	—	360

[a] In Amazon biome only.
[b] According locomotor classification from Paglia *et al.* (2012). Scansorial is counted for floor and canopy stratum.
[c] Sampling effort: as census effort (km for LnTT, trap-days for LvTT, and camera-days for CTT).
[d] In this study, line transect census and armadillo surveys were utilized. For practicality, we consider both techniques as line transects only.
[e] Excluding arboreal, aquatic, and small mammals.
[f] Including species of uncertain identification.
[g] Authors recorded 16 species in the floor stratum and four in the canopy stratum. To calculate the floor stratum sampling effort, we multiplied the points where the camera traps were installed (13) by the survey days in that stratum (150).
[h] Calculation of the camera trap station (383) multiplied by the survey days (30). Authors used interviews to complement their records also.
[i] In this study, pitfall trapping and live trapping were utilized. For practicality, we consider both techniques as live trapping only. Authors placed live traps in three strata: ground, understory, and canopy. For practicality, we calculated the sampling effort for understory and canopy as canopy stratum only. Authors used baited traps.
[j] In this study, pitfall trapping and live trapping were utilized. For practicality, we consider both techniques as live trapping only. In the case of live trapping, authors used baited traps.
[k] Authors recorded 26 species in the forest stratum and 24 in the canopy stratum; two of these species were escansorial.

Table 2. Checklist of mammals recorded in vertical strata from Cueiras Biological Reserve.

Class/Order/Scientific name*	Common name	Records by strata		Locomotor[a]**	Diet[b]**	IUCN	Mean body mass (kg)**	Calculated biomass (Kg)[c]
		Forest floor	Canopy					
MAMMALIA								
Perissodactyla								
Tapirus terrestris (Linnaeus, 1758)	South American Tapir	6	—	Te	Hb/Fr	VU	260	1560
Artiodactyla								
Mazama americana (Erxleben, 1777)	Red Brocket	1	—	Te	Fr/Hb	LC	36	36
Mazama nemorivaga (F. Cuvier, 1817)	Brown Brocket Deer	7	—	Te	Fr/Hb	LC	20	140
Pecari tajacu (Linnaeus, 1758)	Collared Peccary	9	—	Te	Fr/Hb	LC	26	234
Pilosa								
Tamandua tetradactyla (Linnaeus, 1758)	Southern Tamandua	1	1	Sc	Myr	LC	5,2	10,4
Cingulata								
Dasypus spp. (Linnaeus, 1758)	Seven or nine banded Armadillo	11	—	Te	In/On	LC	6,55	72,05
Primates								
Sapajus apella (Linnaeus, 1758)	Brown Tufted Capuchin	—	8	Ar	Fr/On	LC	3,05	24,4
Saguinus midas (Linnaeus, 1758)	Golden-handed Tamarin	—	4	Ar	Fr/In	LC	0,505	2,02
Rodentia								
Cuniculus paca (Linnaeus, 1766)	Spotted Paca	15	—	Te	Fr/Hb	LC	9,3	139,5
Dasyprocta leporina (Linnaeus, 1758)	Red-rumped Agouti	132	—	Te	Fr/Gr	LC	5,75	759
Myoprocta acouchy (Erxleben, 1777)	Red Acouchi	171	—	Te	Fr/Gr	LC	1,2	205,2
Coendou melanurus (Wagner, 1842)	Black-tailed Hairy Dwarf Porcupine	—	10	Ar	Fr/Fo	LC	1,95	19,5
Isothrix pagurus (Wagner, 1845)	Plain brush-tailed Rat	—	26	Ar	Fr/Fo	LC	0,4	10,4
Makalata didelphoides (Desmarest, 1817)	Red-nosed Armored Tree-rat	1	3	Ar	Fo	LC	0,32	1,28
Proechymis spp. Allen, 1899	Spiny-rat	26	2	Te	Fr/Gr	LC	0,36	10,08
Guerlinguetus aestuans (Linnaeus, 1766)	Guianan Squirrel	4	1	Sc	Fr/On	LC	0,19	0,95
Oecomys spp. Thomas, 1906	Arboreal Rice Rat	1	5	Ar	Fr/Se	LC	0,04	1,44
Didelphimorphia								
Didelphis marsupialis (Linnaeus, 1758)	Common Opossum	12	6	Sc	Fr/On	LC	1,35	24,3
Philander opossum (Linnaeus, 1758)	Gray Four-Eyed Opossum	9	—	Sc	In/On	LC	0,49	4,41
Metachirus spp.	Brown Four-eyed Opossum	17	—	Te	In/On	LC	0,39	6,63
Caluromys philander (Linnaeus, 1758)	Bare-tailed Woolly Opossum	—	13	Ar	Fr/On	LC	0,265	3,445
Glironia venusta (Thomas, 1912)	Bushy-tailed opossum	—	4	Ar	In/On	LC	0,15	0,6
Marmosa murina (Linnaeus, 1758)	Linnaeus's Mouse Opossum	—	3	Sc	In/On	LC	0,05	0,15
Marmosa (Micoureus) demerarae (Thomas, 1905)	Woolly Mouse Opossum	—	9	Ar	In/On	LC	0,12	1,08
Carnivora								
Nasua nasua (Linnaeus, 1766)	South American Coati	1	—	Te	Fr/On	LC	5,1	5,1
Potos flavus (Schreber, 1774)	Kinkajou	—	1	Sc	Fr/On	LC	2,6	2,6
Eira barbara (Linnaeus, 1758)	Tayra	1	1	Sc	Fr/On	LC	7,05	14,1
Puma concolor (Linnaeus, 1771)	Cougar	1	—	Te	Ca	LC	46	46
Leopardus pardalis (Linnaeus, 1758)	Ocelot	5	—	Te	Ca	LC	9,55	47,75
Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803)	Jaguarundi	2	—	Te	Ca	LC	4,55	9,1

* From Quintela *et al* (2020).
** From Paglia *et al.* (2012).
[a] Ar: Arboreal; Sc: Scansorial; Te: Terrestrial.
[b] Hb: Herbivore grazer; Fr: Frugivore; Myr: Myrmecophage; In: Insectivore; On: Omnivore; Gr: Granivore; Fo: Folivore; Se: Seed predator; Ca: Carnivore.
[c] Assuming every record as an individual, we multiplied records by the strata and mean body mass (kg).

ing the number of records of each species by the total number of records of the camera trap station (decostand function, MARGIN = 1). Subsequently, we compared the assemblages of both strata using a multi-response permutation procedure (mrpp function, "vegan" package) based on the Bray-Curtis index with 9,999 permutations (Oksanen *et al.,* 2019). We used the multiple-response permutation procedure (MRPP) test statistic with an R value to determine the degree of similarity between treatments (i.e., strata) (Legendre & Legendre, 1998). All analyses were performed using the R language and environment for statistical computing (R Core Team, 2018).

RESULTS AND DISCUSSION

We obtained a sampling effort of 720 camera-days (360 for each stratum; Table 1). Through this, we obtained 433 independent records for the floor stratum and 97 for the canopy stratum. These records included 30 mammal species representing eight orders: Perissodactyla, Artiodactyla, Pilosa, Cingulata, Primates, Rodentia (with the highest record, 397), Didelphimorphia, and Carnivora (Table 2). As shown in Table 2, we recorded nine nonvolant mammals' species exclusive to the canopy stratum, 14 exclusive to the floor stratum, and seven scansorial

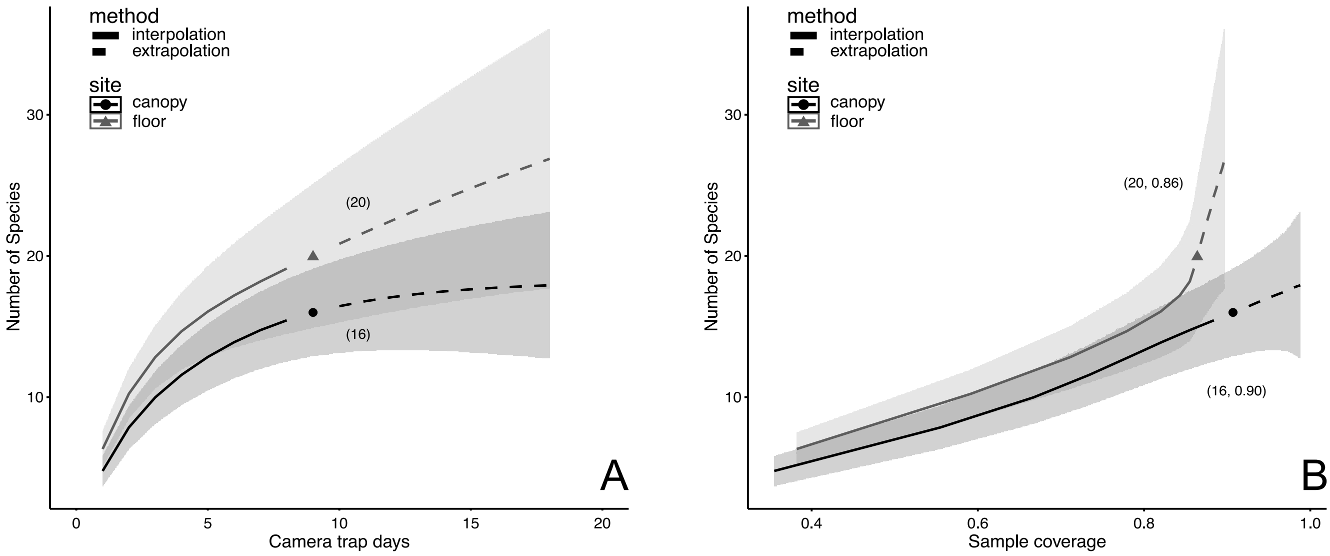

Figure 2. Species accumulation curve for (A) sampling effort (camera trap days) and (B) completeness of vertical strata.

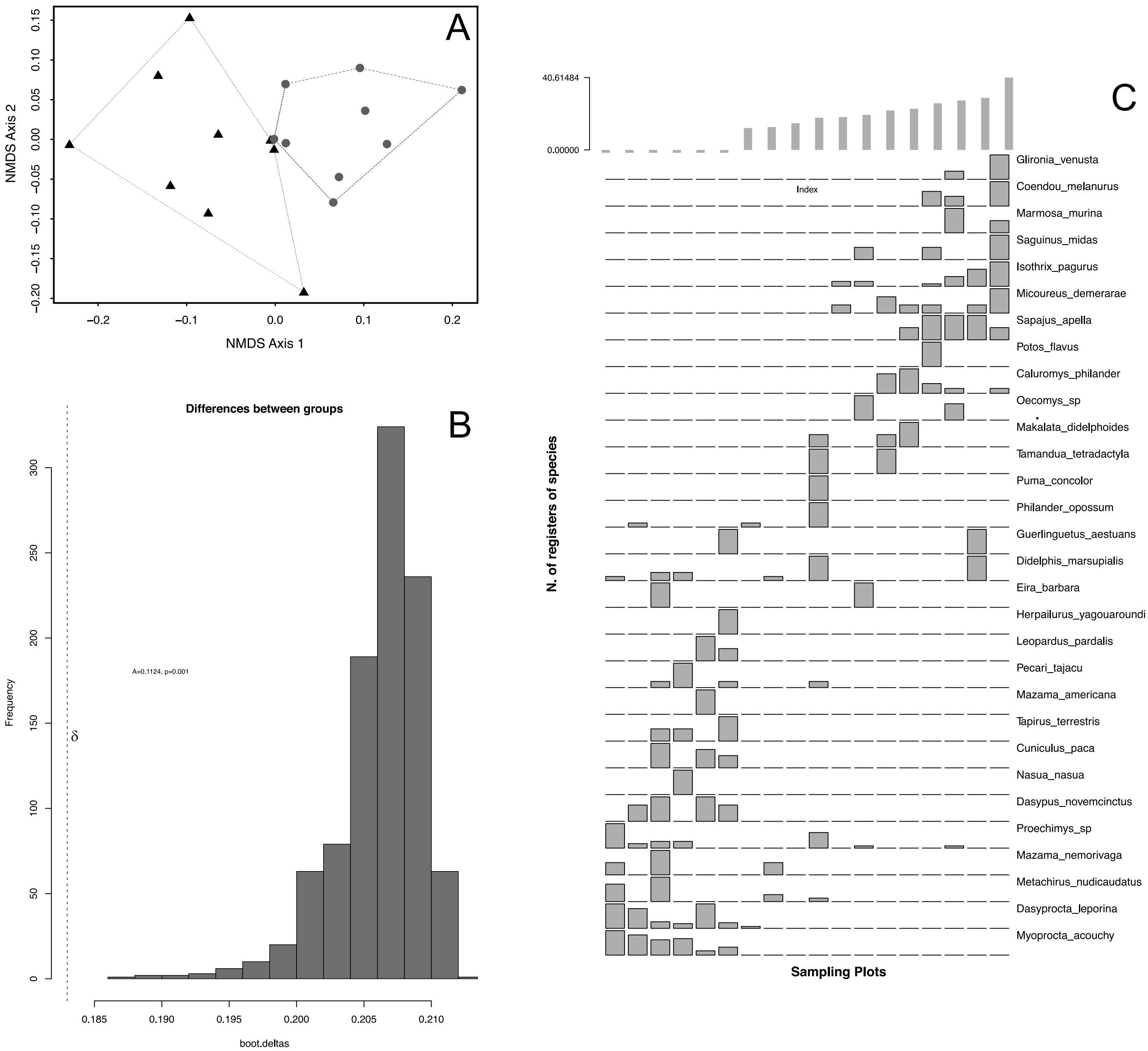

Figure 3. Midsized to large mammal assemblages in vertical strata. (A) Similarity in mammal species composition (black triangles represent the floor assemblage and gray circles represent the canopy assemblage). (B) Differences between groups according to MRPP analyses. (C) Distribution of mammals across sample sites.

species (or shared both strata). Of all species recorded in the canopy strata (including scansorial, i.e. 16 species), 62.5% (10 species) were small-bodied mammals.Among small to large species observed in this stratum, 68.75% (11 species) are considered frugivorous according to the classification by Paglia *et al.* (2012). Among records (a proxy for abundance for CTT), with a total of 77 records for all frugivorous species in canopy strata, it was recorded 66.23% (51 records) of small-bodied mammals. For the canopy stratum, the Plain brush-tailed rat *Isothrix pagurus* (Wagner, 1845) was the most abundant species; for the forest floor stratum, the acouchi *Myoprocta acouchy* (Erxleben, 1777) was the most abundant species; and among the scansorial species, *Proechymis* sp. was the most abundant (Table 2).

The species accumulation curves for small to large terrestrial mammal species show more species detected per unit effort on the floor strata (20 ± 3.5 SE) compared with the canopy strata (16 ± 2.6 SE) (Fig. 2a). However, the estimated sampling completeness was lower than 86% for the floor assemblage (Fig. 2b). This finding was reinforced by the accumulation curves that do not show a complete stabilization trend. This outcome indicates that the sampling effort, although good, was not enough to represent all species of mammal fauna in the study site. Therefore, an increase in the sampling effort is expected to reveal some species that were not recorded (Fig. 2).

Species composition by sampling points was hardly grouped between the floor and canopy strata, as shown by the NMDS. The first two axes captured 82% of the variance in the data (Fig. 3a), which can be better represented by MRPP analyses (A = 0.112; p < 0.001) (Fig. 3b), showing species that are exclusive to every stratum with exception of a few species (Fig. 3c).

Although we obtained a relatively low sampling effort with CTT compared with other studies utilizing different techniques (Table 1), we recorded a similar number of mammal species with the other techniques. Our results were especially similar to those of previous studies that worked with canopy and floor strata (Ardente *et al.,* 2017; Gregory *et al.,* 2014; Whitworth *et al.,* 2019b). This finding may indicate a minimum CTT sampling effort for mammal groups in both strata. Furthermore, we believe that to have a larger number of species, it may be necessary to use the other techniques together to complement and increase the records of species that are not easily seen in a short time. Interviews (Michalski & Peres, 2007; Abrahams *et al.,* 2017) and signs (Norris, 2014; Fragoso *et al.,* 2016) are some methods that can complement the previously mentioned methods to help record the presence of species in a short period of time. Some proof of this finding is the difference between the percentages of accumulated biomass (Table 2) for the strata found in our study: 3,200 kg (98.7%) for the floor stratum and 42 kg (1.7%) for the canopy stratum. These results differed from the reports of Eisenberg & Thorington (1973) who found that more than 50% of mammal biomass was composed of sloths and howler monkeys – species found in the canopy stratum – which were precisely the species that we could not record in our study.

CONCLUSION

Monitoring mammal diversity can be expensive, and collecting adequate data is often difficult.

We concluded that the floor forest is more diverse (21 species recorded) and was composed of a broad size of animals (small to large) and more trophic guilds variety than the canopy. However, in the canopy, we mostly observed small, frugivorous mammals that can be great contributors for primary seed dispersal.

CTT can be very effective for recording short periods of time, and this method is less physically exhaustive for researchers to study vertical strata.

If we want to record the total diversity of species in the area, including less abundant and rare species, then we will need a greater sampling effort in combination with other survey techniques.

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AUTHORS' CONTRIBUTIONS

All authors conceived of the presented idea and theory of the manuscript. A.R.A.S. developed the written and led the team. A.L.S.G., K.O., T.Y., and W.R.S. did the fieldwork data collection. A.L.S.G. performed the computations, analyses, and created the map. All authors verified the analytical methods. All authors discussed the results and contributed to the final manuscript. All authors reviewed and approved the final version of the paper.

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