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Species richness and relative abundance of terrestrial mammals in an area with different managements in Costa Rica

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ABSTRACT

Introduction: While essential, protected areas are sometimes insufficient to conserve wildlife. Terrestrial mammals often move between protected and unprotected sites, and the abundance of one species may influence the occurrence of others.

Objectives: To compare mammal species richness and relative abundance between three nearby sites with different management approaches in a tropical dry forest.

Methods: We placed 18 camera traps in three contiguous sites under different management schemes (a national park – high protection; forest reserve – medium protection; and a non-protected site) in Northwest Costa Rica between December 31, 2021, and March 31, 2022, and compared the richness and relative abundance of terrestrial mammal species occurring in each site.

Results: We recorded 730 independent captures corresponding to 18 species. The highest number of species was recorded in the forest reserve (16 species), but 10 species were found at all three locations. The most abundant species were white-tailed deer, jaguars and tapirs in the National Park, ocelots in the Forest Reserve, and white-faced capuchins, white-nosed coatis, common opossums, raccoons, and coyotes in the non-protected site. Generalist species were more commonly detected in the unprotected site, whereas specialist species were highly reported in the protected sites.

Conclusions: Different management restrictions could affect the presence and relative abundance of terrestrial mammals. However, other factors such as the presence of rivers, trails, and/or roads could also affect movements

and influence distribution. A detailed analysis of the factors driving species abundance in sites with different management could improve species protection throughout their range.

Key words: tropical dry forest; camera trapping; Guanacaste Conservation Area; Santa Rosa National Park; Horizontes Forest Reserve; Playa Cabuyal; protection level.

RESUMEN

Riqueza y abundancia relativa de mamíferos terrestres en un área con diferentes manejos en Costa Rica

Introducción: Las Áreas Protegidas son fundamentales para la conservación de la vida salvaje, pero podrían ser insuficientes. Los mamíferos terrestres suelen moverse entre zonas protegidas y no protegidas, y la abundancia de una especie puede influir en la presencia de otras.
Objetivos: Comparar la riqueza y abundancia relativa de mamíferos terrestres en tres sitios cercanos con diferentes enfoques de manejo en un bosque seco tropical.
Métodos: Colocamos 18 cámaras trampa en tres localizaciones contiguas bajo diferente régimen de manejo (parque nacional – alta protección; reserva forestal – protección media; y una localización sin protección) en el noroeste de Costa Rica entre el 31 de diciembre de 2021 y el 31 de marzo de 2022, y comparamos la riqueza y abundancia relativa de especies de mamíferos terrestres en cada localización.
Resultados: Registramos 730 capturas independientes correspondientes a 18 especies. El mayor número de especies se registró en la reserva forestal (16 especies), pero 10 especies fueron encontradas en las tres localidades. Las especies más abundantes fueron el venado de cola blanca, jaguar y tapir centroamericano en el Parque Nacional, el ocelote en la Reserva Forestal y el mono carablanca, coatí de nariz blanca, zarigüeya común, mapache y coyote en la zona no protegida. Más especies generalistas fueron encontradas en la localización no protegida y más especialistas en las zonas protegidas.
Conclusiones: Diferentes restricciones de manejo pueden afectar la presencia y abundancia de mamíferos terrestres. Sin embargo, otros factores como la presencia de ríos, senderos y/o carreteras también podrían influir en su distribución. Un análisis detallado de los factores que determinan la abundancia en localizaciones de diferente manejo podría mejorar la protección de especies a lo largo de su rango de distribución.

Palabras clave: bosque tropical seco; fototrampeo; Área de Conservación Guanacaste, Parque Nacional Santa Rosa; Estación Experimental Forestal Horizontes; Playa Cabuyal; nivel de protección.

INTRODUCTION

The rates of global biodiversity loss due to anthropogenic activities have been increasing during the last few decades (Johnson et al., 2017). Therefore, as a worldwide strategy to protect wildlife, conservationists set a goal of increasing the world's network of protected areas (PAs) (Naughton-Treves et al., 2005). Creating PAs is one of the most efficient mechanisms to protect wildlife (González-Maya et al., 2015; Pinheiro et al., 2020). With a clearly defined geographical space, these areas might be managed to achieve long-term protection and conservation of species, with associated ecosystem services and cultural values (Kareiva & Marvier, 2015). But unfortunately, due to the extension and the lack of resources, many PAs face uneven protection and external threats that could limit their conservation success (Mora & Sale, 2011). PAs are crucial in providing refuge to terrestrial mammal species from direct persecution and other anthropogenic disturbances (Sáenz-Bolaños et al., 2020). Nevertheless, species may require large areas for foraging or migration, which may exceed the boundaries of what PAs can provide (González-Maya et al., 2015). Thus, the current extent of many PAs is likely insufficient to protect many vertebrate species across their entire range (Wen et al., 2022).

One of the world's most threatened ecosystems is the tropical dry forest, particularly in Central America, where it has been reduced to less than 20 % of its original extent (Klemens et al., 2011; Siyum, 2020). In the Northwest of Costa Rica, large areas of dry forest were converted to pastures for cattle grazing and

to selective logging of high-value tree species during the early XIX century (Klemens et al., 2011), thereby reducing the extent of dry forest to a few isolated small patches (Janzen, 1986). Considering this, in 1971, the Santa Rosa National Park (SRNP) was created, followed by the Horizontes Forest Reserve (HFR) in 1989. Both sites were designed to protect the largest remnant of tropical dry forest in the Neotropical region (Janzen, 1986; Janzen & Hallwachs, 2020). Outside SRNP and HFR, the remaining patches of dry forest are highly fragmented (Yaney-Keller et al., 2019) and threatened by anthropogenic fires, land conversion for hotel developments, or livestock grazing (Reyes, 2012; Vargas, 2016).

In Costa Rica, the national system of PAs (Sistema Nacional de Áreas de Conservación [SINAC], for its Spanish acronym) has 12 management categories, each with specific restrictions based on conservation goals (Sistema Nacional de Áreas de Conservación [SINAC], 2023). For example, SRNP is protected as a "national park", which allows tourism and low anthropogenic alteration and prohibits extraction (Dudley, 2008). HFR is classified as a "forest reserve", which allows active forest restoration and sustainable timber extraction (Organización de las Naciones Unidas para la Alimentación y la Agricultura [FAO], 2010). It is surrounded by "fincas" (farms for cattle and agriculture) without use restrictions, creating a landscape with differing management regimes (SINAC, 2023). These differences in protection level and adjacent land use suggest that PAs may experience contrasting degrees of anthropogenic pressure, with potential consequences for wildlife communities. For example, Sáenz-Bolaños et al. (2020) found that different levels of protection affected the species richness and relative abundance of mammal species in Costa Rican tropical rainforests. In addition, Naing et al. (2015) reported that within a protected area (PA) in the subtropical rainforests of Myanmar, locations with higher human infrastructure had lower species richness than those that were less impacted by humans. More recent studies further indicate that anthropogenic pressure negatively affects mammal assemblages, reducing species richness and occupancy even within PAs (Gallego-Zamorano et al., 2020; Streicher et al., 2025; Zwicker et al., 2025).

Mammal species play a key role in the ecosystems, and conserving their populations is essential to ensure the long-term functionality of PAs (González-Maya et al., 2015; Dorji et al., 2019). Previous studies suggest that by comparing mammal diversity inside and outside PAs, or among sites with different levels of protection, decision-makers can get baseline information to support conservation efforts (Dorji et al., 2019; Sáenz-Bolaños et al., 2020).

In this study, we used automatic camera traps to compare terrestrial mammal richness and relative abundance among contiguous sites of different conservation management categories: 1) Santa Rosa National Park, 2) Horizontes Forest Reserve, and 3) an adjacent unprotected site: Playa Cabuyal. Previous studies have shown that there is a lower number of mammal species in disturbed areas and a generally higher number of species in PAs, including in regions of Costa Rica (Sáenz-Bolaños et al., 2020; Vargas-Soto et al., 2022; Cambronero et al., 2023; Johnson et al., 2023). Thus, we hypothesized that richness and relative abundance of terrestrial mammals would differ between our study sites. Specifically, we predicted higher richness and relative abundance in sites with greater protection, with progressively lower values in the less protected sites.

MATERIALS AND METHODS

Study area: Our research was conducted in the Guanacaste Conservation Area (GCA), located in Northwestern Costa Rica along the Pacific coast (10°53'01" N & 85°46'30" W). This area encompasses one of the largest remnants of tropical dry forest ecosystems in Central America, and the vegetation community is characterized by a mosaic of evergreen and deciduous forests, mixed with grasslands and secondary growth at different regeneration stages (Janzen & Hallwachs, 2020; Kalacska et al., 2004). The precipitation regime is highly seasonal,

with an annual average rainfall of 1 600 mm, a well-defined dry season from December to April (months ≤ 100 mm of rain), and a rainy season from May to November (Fuller et al., 2020). The mean annual temperature is 25 °C, with maximum temperatures of 31 °C during the rainy season and above 35 °C during the dry season (Jiménez et al., 2016; Fuller et al., 2020). We selected three sites inside the GCA corresponding to three different management categories: 1) the Santa Rosa National Park (hereinafter SRNP, 10°50'35.2" N & 85°42'13.0" W), a site with high protection restrictions since 1971; 2) the Horizontes Forest Reserve (hereinafter HFR, 10°42'56.2" N & 85°34'0.7" W), a site with intermediate protection, and regulated human activities and use since 1989; 3) Playa Cabuyal (hereinafter PC, 10°40'32" N & 85°39'11" W), a site without protection designation, with a relatively high anthropogenic presence on the beach during peak tourist season (December to April) but low during the rest of the year (Fig. 1).

SRNP is a site in the process of restoration since the 1980s that currently includes the largest remnant of dry forest ecosystem in the country, covering 387 km^2 with a variety of successional stages (Klemens et al., 2011; Janzen & Hallwachs, 2020). The HFR comprises an area of 72.93 km^2, and it is in the early successional stage compared with SRNP, where intensive forest uses are carried out (Rigg, 2013). Playa Cabuyal (PC) includes an important nesting beach for sea turtles (Santidrián et al., 2015), surrounded by a mangrove swamp and fragments of tropical dry forest and cattle farms (Yaney-Keller et al., 2019). Although the mangrove forest is protected under the Law on the Maritime Terrestrial Zone No. 6043 (Sistema Costarricense de Información Jurídica [SCIJ], 1977), PC lacks official protection and has a relatively high influx of tourists during the day.

Data collection: We used 18 camera traps, of which six cameras were deployed in PC, seven in HFR, and five in SRNP, covering a total area of 2.67 km^2, 5.02 km^2, and 4.65 km^2, respectively (Table 1). We georeferenced each camera trap location using a Global Positioning System unit (GPS; model Garmin eTrex

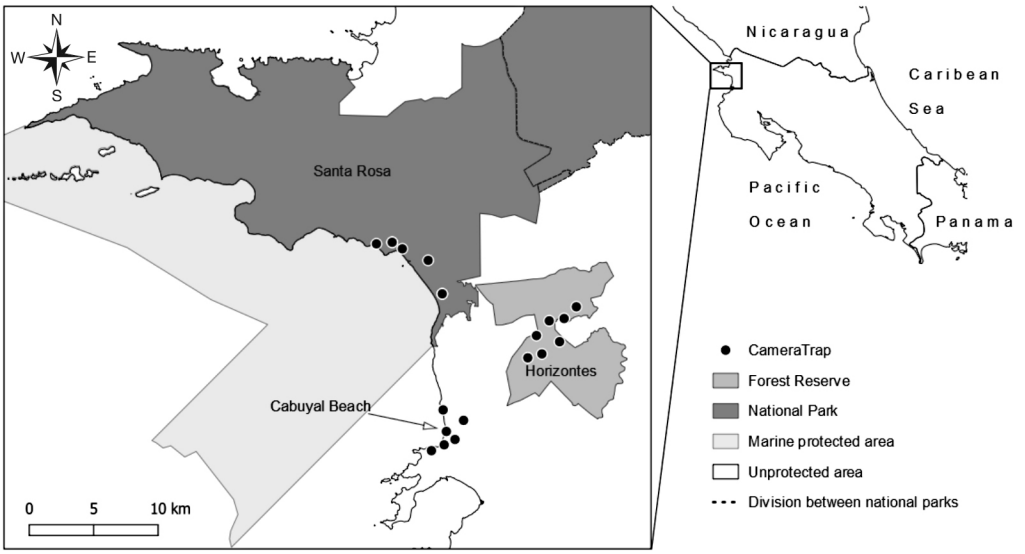

Fig. 1. Study area and location of the camera traps established between December 31, 2021 and March 31, 2022. In dark grey are national parks (Santa Rosa and Guanacaste National Park, the latest not included in this study), in medium grey is the forest reserve (Horizontes Forest Reserve), in light grey is protected marine site and in white is site non-protected, all of them within the Guanacaste Conservation Area. Circles indicate the location of camera traps at Santa Rosa National Park, Horizontes Forest Reserve and Playa Cabuyal.

Table 1
Minimum, maximum, and mean distances (km) between the cameras placed between December 31, 2021 and March 31, 2022 and the total extension (km^2) that comprised the cameras in each locality.

	PC	HFR	SRNP
Min. Dist. (km)	1.83	1.17	1. 87
Max. Dist. (km)	3.43	5.47	6.38
Mean Dist. (km)	1.94	2.08	6.64
Total extension (km^2)	2.67	5.02	4.65

Min. Dist.: Minimum distance, Max. Dist.: Maximum distance, Mean Dist.: Mean distance, PC: Playa Cabuyal, HFR: Horizontes Forest Reserve, SRNP: Santa Rosa National Park.

10, Olathe, Kansas, USA) and placed all the cameras at a minimum distance of 1-2 km apart and 30-40 cm above the ground, following recommendations by Montalvo (2020). We set the cameras to be active for 24 hours per day and to take three photos per shot at 15 s intervals when triggered to avoid recording the same event (Naing et al., 2015). The cameras used a medium-sensitivity passive infrared (PIR) sensor to minimize false activations. Videos were recorded over 15 or 30 s per shot in three of Santa Rosa's cameras. We checked the cameras every 10-20 days. During each visit, we downloaded the information, replaced the memory card, and changed the batteries as necessary. We collected data between December 31, 2021 and March 30, 2022 in PC, January 16, 2022 and March 31, 2022 in HFR, and December 31, 2021 and March 31, 2022 in SRNP.

Species identification and sampling effort: We used CPW Photo Warehouse (https://cpw.state.co.us) to archive, identify, summarize, and analyse photo data (Newkirk, 2016). Species identification was conducted following Reid and Gómez-Zamora (2022). We considered that photos were independent captures when: 1) photos were separated by more than 60 min, 2) in consecutive photos of the same species, we could identify animals at an individual level, and 3) photos of individuals of the same species were separated by photos of another species (Montalvo, 2020; O'Brien et al., 2003). To estimate sampling effort, we counted the number of nights each camera was active, adjusting those periods when cameras were inactive or malfunctioned. If the camera was not pointing in the correct direction or height, the photos were excluded, and the corresponding nights were subtracted from the sampling effort. We plotted accumulation curves with a logistic adjustment to compare species richness (number of species within a defined region) at the three sample sites, counting the number of camera trap nights required to reach the expected number of species in each site, following Naing et al. (2015) and Sáenz-Bolaños et al. (2020). We assessed inventory completeness using incidence-based nonparametric richness estimators with camera nights as the sampling unit (presence/absence per species per operational camera-night) following Rovero et al. (2016). Expected richness was estimated using Chao2, and completeness was calculated as the ratio between observed and expected richness. Inventory completeness ranges from 0 to 1, with values closer to 1 indicating a more complete species inventory.

We calculated the relative abundance index (RAI, number of independent captures / 100 trap nights) (Montalvo et al., 2023; Rovero & Marshall, 2009) of each species for each camera and averaged the RAI for each species for all cameras at each location. Statistical analyses and comparisons were made considering the mean RAI. For species with more than 10 detections in total, we performed a Chi-square test to compare RAI between the three locations (Naing et al., 2015; Sáenz-Bolaños et al., 2020), using the R "stats" package (R Core Team, 2017).

To quantify the differences between mammal communities under the three management categories, we used two dissimilarity indices: (1) the Chao estimator of shared species, which estimates the number of shared species between each site (Chen et al., 1995), and (2) the Chao-Jaccard (C-J) similarity estimator, which is a measure of beta-diversity and ranges from 0 (completely distinct communities) to

1 (identical communities; Chao et al., 2000). Both metrics correct for under-sampling bias by estimating the number of 'unseen' shared species between sites (Chao et al., 2005). To visualize the difference in mammal assemblages between sites, we performed a non-metric multidimensional scaling (NMDS) ordination with two axes, using the C-J similarity estimator and metaMDS function of the vegan package version 2.6.10 (Oksanen et al., 2014). Statistical differences in species composition between the three sites were tested using permutational multivariate analysis of variance (PERMANOVA), with the adonis function from the vegan package (Oksanen et al., 2014). Finally, we used the envfit function from the vegan package and applied 999 permutations to the species detections and ordination axis scores to identify the key species that contributed most to variation in assemblage structure among camera trap locations (Oksanen et al., 2014).

RESULTS

We recorded a total of 17 470 photos with an effort of 842 camera trap nights. Additionally, we obtained 2 290 photos of terrestrial mammals of which, 558 photos were obtained at PC over 286 nights, 771 photos at HFR over 330 nights, and 961 photos at SRNP over 226 nights.

We recorded 728 independent captures and identified 18 species of terrestrial mammals between all sites. We detected 14 species of mammals in PC from 11 families and six orders, 16 species in HFR from 12 families and seven orders, and 13 species in SRNP from nine families and six orders (SMT 1).

The number of shared species was similar between all sites (Table 2). Among them, ten species were present in PC, HFR, and SRNP: Central American agoutis (*Dasyprocta punctata*), white-nosed coatis (*Nasua narica*) (Fig. 2A), raccoons (*Procyon lotor*), white-faced monkeys (*Cebus imitator*), ocelots (*Leopardus pardalis*), pumas (*Puma concolor*) (Fig. 2B), Baird's tapirs (*Tapirus bairdii*) (Fig. 2C), tayras (*Eira barbara*), white-tailed deers (*Odocoileus virginianus*), and common opossums (*Didelphis marsupialis*). The C-J similarity index indicates that HFR and SRNP had the highest similarity in species composition (0.93 C-J similarity

Fig. 2. Photo captures. **A.** A white-nosed coati (*Nasua narica*) in PC. **B.** A puma (*Puma concolor*) in HFR. **C.** A Baird's tapir (*Tapirus bairdii*) in PC. **D.** A jaguar (*Panthera onca*) in HFR (d).

Table 2
Number of shared taxa and Chao-Jaccard similarity index between three areas with different management categories.

Study sites	PC	HFR	SRNP
PC		10 (14.9)	13 (17.8)
HFR	0.74		11 (12.7)
SRNP	0.88	0.93	

Playa Cabuyal (PC), Horizontes Forest Reserve (HFR), and Santa Rosa National Park (SRNP). Upper diagonal: observed number of shared taxa (Chao-estimated number of shared taxa in parentheses). Lower diagonal: Chao–Jaccard similarity index (0–1; higher values indicate greater community similarity). Gray diagonal cells indicate within-site comparisons.

index). PC and SRNP also had a relatively high similarity (0.74 C-J similarity index, Table 2), although it was lower than that of HFR and SRNP. Three species were only found in PC and HFR: coyotes (*Canis latrans*), collared peccaries (*Dicotyles tajacu*), and grey foxes (*Urocyon cinereoargenteus*); and two species in HFR and SRNP: striped hog-nosed skunks (*Conepatus semistriatus*) and jaguars (*Panthera onca*) (Fig. 2D). Also, three species were unique to each site: spotted skunk (*Spilogale angustifrons*) in PC, tamandua (*Tamandua mexicana*) in HFR, and jaguarundi (*Herpailurus yagouaroundi*) at SRNP. These differences in species composition were further confirmed by permutation tests (PERMANOVA: $F = 2.45$, $p < 0.001$). Additionally, NMDS ordination revealed high correlations between several species and specific sites. For example, coyotes ($R^2 = 0.60$, $p < 0.01$) and raccoons ($R^2 = 0.32$, $p < 0.05$) were associated with PC, while ocelots ($R^2 = 0.37$, $p < 0.05$), striped hog-nosed skunks ($R^2 = 0.39$, $p < 0.05$), and Central American agoutis ($R^2 = 0.30$, $p < 0.05$) were associated with HFR (Fig. 3).

Differences in the number of recorded species were illustrated by the species accumulation

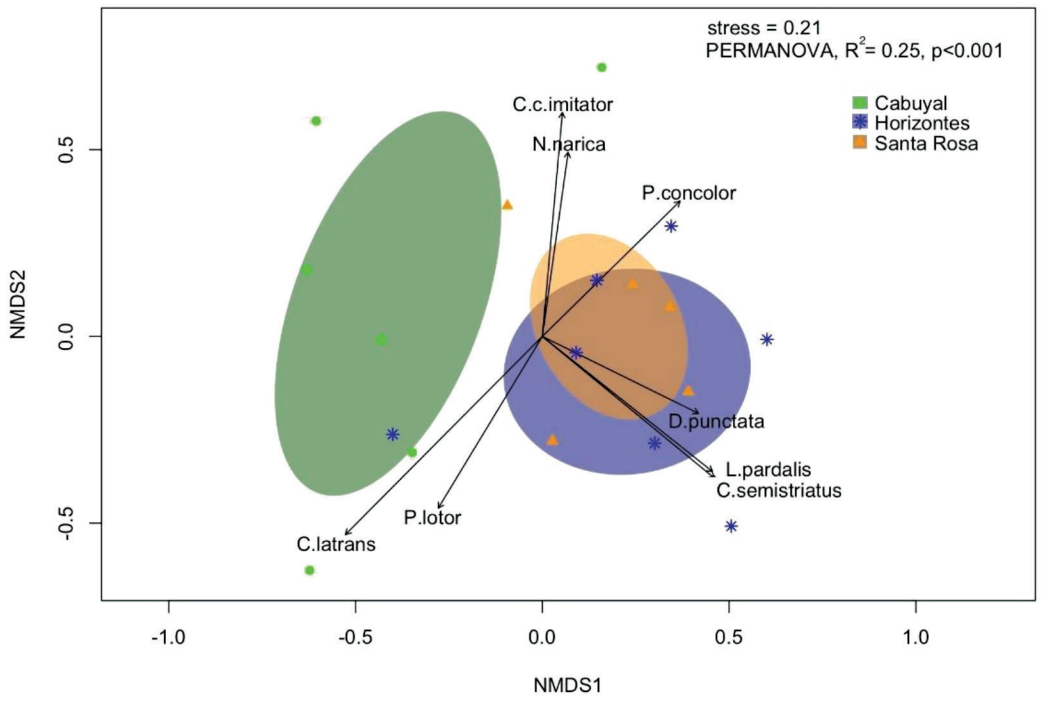

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of the terrestrial mammal species composition detected by camera traps in Playa Cabuyal, Horizontes Forest Reserve, and Santa Rosa National Park. The NMDS plot area is derived from relative abundance data for each species at each site. The species represented in the graph contributed the most to the difference in species composition between the sites.

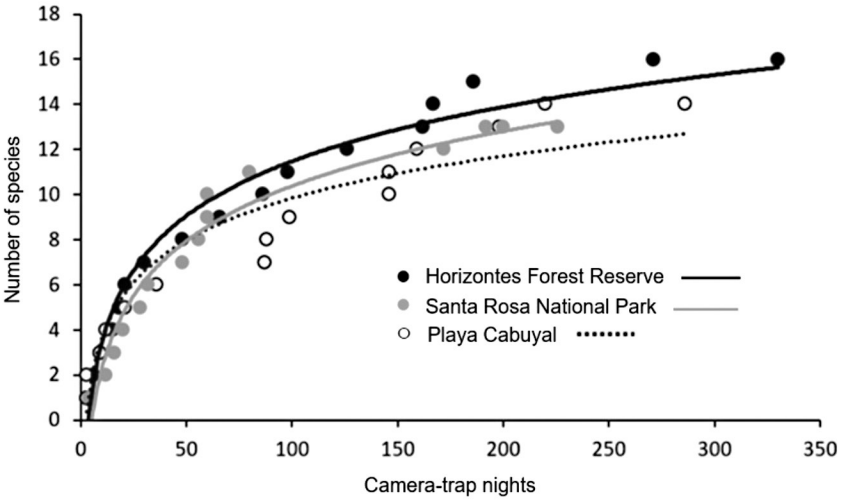

Fig. 4. Species accumulation curves. Trend lines for the total cumulative number of species based on the number of camera trap nights (effort) in Horizontes Forest Reserve (HFR: black line and dots), Santa Rosa National Park (SRNP: grey line and dots), and Playa Cabuyal site (PC: dashed line and white dots) between December 2021 – March 2022 sampling period.

curve (Fig. 4). The curves indicated that HFR had the highest species richness (n = 16, R^2 = 0.97), followed by SRNP (n = 13, R^2 = 0.95), and PC (n = 14, R^2 = 0.91) (Fig. 4). None of the curves reached an asymptote. Nevertheless, inventory completeness was high for HFR (0.89) and SRNP (0.85), suggesting that sampling captured most of the species present at these sites. In addition, Chao2 estimated 18.0 and 15.2 species respectively, suggesting that only 2-3 species may have been undetected. In contrast, PC exhibited a lower completeness (0.52), with Chao2 estimating 25.2 species, compared with 14 observed, implying that ~ 12 species may have been undetected.

The most abundant species across the sample sites were white-tailed deer and common opossums. We found statistically significant differences in relative abundances among locations for eight species: white-nosed coatis, white-faced monkeys, common opossums, raccoons, and coyotes were significantly more abundant in PC, whereas white-tailed deer, jaguars, and tapirs were more abundant in SRNP, and ocelots in HFR (p-value < 0.05 all cases) (Table 3, SMF 1).

Though we did not find statistically significant differences considering all the analysed species, we recorded a higher number of captures of Central American agoutis in HFR (RAI = 7.54) than in SRNP (RAI = 5.70) and PC (RAI = 0.61). Pumas detection was higher in SRNP (RAI = 3.44), followed by HFR (RAI = 2.68) and PC (RAI = 0.43). We detected more striped hog-nosed skunks in HFR (RAI = 4.75), followed by SRNP (RAI = 2.16), with no records of presence in PC (Table 3). The observed differences in species RAI between sites are further supported by the results of the NMDS ordination (Fig. 3).

Six of the species we detected were listed as endangered (ocelot, puma, tapir, jaguar, jaguarundi, and spotted skunk), and one additional species (peccary) was locally threatened according to the official list of endangered species in Costa Rica (SCIJ, 2017). Tapirs and jaguars were also listed as endangered and near threatened, respectively, under the IUCN Red List of Threatened Species (IUCN, 2024).

DISCUSSION

We hypothesized that terrestrial mammal richness and relative abundance would differ among the studied sites, predicting higher

Table 3
Relative abundance indices (RAI) for each sampled site and the Chi-square test results.

Scientific name	Common name	Conservation status		RAI			X^2	p-value
		CR	IUCN	PC n = 286	HFR n = 330	SRNP n = 226		
Didelphis marsupialis	Common opossum	NC	LC	24.30*	1.36	7.42	25.63	2.70E-06
Cebus imitator	White-faced monkey	NC	VU	15.09*	1.94	0.36	22.09	1.26E-05
Nasua narica	White-nosed coati	NC	LC	7.93*	1.13	1.44	8.42	0.01
Canis latrans	Coyote	NC	LC	6.63*	3.90	0	6.33	0.04
Procyon lotor	Northern raccoon	NC	LC	5.13*	0.21	0.72	7.25	0.03
Leopardus pardalis	Ocelot	EN	LC	0.28	9.94*	1.74	13.60	0.001
Odocoileus virginianus	White-tailed deer	NC	LC	0.61	12.59	100.99*	157.93	2.2E-16
Panthera onca	Jaguar	EN	NT	0	2.99	12.81*	17.06	0
Tapirus bairdii	Baird's tapir	EN	EN	0.28	2.93	7.86*	0.018	0.02
Dasyprocta punctata	Central American agouti	NC	LC	0.61	7.54	5.70	5.58	0.06
Puma concolor	Puma	EN	LC	0.43	2.68	3.44	2.24	0.33
Conepatus semistriatus	Striped hog-nosed skunk	NC	LC	0	4.75	2.16	4.91	0.09
Dicotyle tajacu	Collared peccary	T	LC	0.38	2.47	0	3.72	0.16
Eira barbara	Tayra	NC	LC	0.19	0.84	1.01	-	-
Herpailurus yagourandi	Jaguarundi	EN	LC	0	0	0.36	-	-
Urocyon cinereoargenteus	Grey fox	NC	LC	0.61	4.23	0	-	-
Tamandua mexicana	Northern tamandua	NC	LC	0	0.31	0	-	-
Spilogale angustifrons	Spotted skunk	EN	LC	0.28	0	0	-	-

PC: Playa Cabuyal, HFR: Horizontes Forest Reserve, SRNP: Santa Rosa National Park. Statistically significant differences between the three locations are highlighted with an asterisk (*). The n value was the number of camera trap nights. The conservation status of each species followed the official list of species in danger of extinction and with reduced and threatened populations of Costa Rica (referenced as CR in the table; abbr.: EN – Endangered, T – Threatened, and NC – Not catalogued; SCIJ, 2017) and The IUCN Red List of Threatened Species (referenced as IUCN in the table; abbr.: EN – Endangered, VU – Vulnerable, NT – Near threatened, and LC – Least concerned; International Union for Conservation of Nature [IUCN], 2024).

values in areas under stricter protection. Our results partially supported this prediction. Although mammal composition was similar between sites, we found differences in species richness and relative abundance. Contrary to our prediction, the highest species richness was recorded in the forest reserve, followed by the national park and the unprotected site. However, several species showed higher relative abundance in the national park compared to the other sites. Species typically associated with disturbed habitats were more frequent in the unprotected area.

Our results indicate that the composition of mammal communities exhibits little variation across the studied sites, as evidenced by a C-J similarity index greater than 0.70 in all cases. This high similarity is likely driven by the fact that all sites are located within the same tropical dry forest matrix (Montalvo et al., 2019; Yaney-Keller et al., 2022). In contrast, species richness varied across sites, with both PAs having higher richness than the unprotected site, with the highest richness in HFR, followed by SRNP. However, inventory completeness was low in PC, indicating that the observed richness estimates for this site should be interpreted with caution. The reduced detectability of some species in disturbed, human-transited areas and the presence of transient species at PC may have contributed to an underestimation of richness. Consistent with this interpretation,

Yaney-Keller et al. (2022) reported seven mammal species at PC that were not detected in the present study (e.g., jaguarundi, Virginia opossum, jaguar, Eastern cottontail, variegated squirrel, Northern tamandua), suggesting that additional sampling effort would be required to detect rare or transient species. Similarly coyotes and collared peccaries were not detected in SRNP despite the high inventory completeness, even though both species are known to be present (Montalvo et al., 2015).

Despite higher richness in protected areas, greater richness is not necessarily aligned with stricter protection. Although stricter protection often enhances habitat preservation, sites with lower levels of protection can sometimes host more species due to their diverse management practices and land-use mosaics (Naughton-Treves et al., 2005; Geldmann et al., 2013). Accordingly, mixed-use landscapes, such as HFR, may substantially contribute to conservation by providing complementary habitats that support both generalist and specialist species.

We found differences in the occurrence and relative abundance of some species among the study sites, suggesting that differing levels of protection may shape mammal presence and abundance across the landscape (Jordan et al., 2016; Pérez-Solano et al., 2018; Vargas-Soto et al., 2022). However, it is important to note that although differences were found between sites with varying management, our results do not indicate causality. A more detailed analysis of the different factors that could drive wildlife distributions would help to better pinpoint drivers of abundance. For instance, rivers, streams, trails, or roads can facilitate or impede animal distributions across the landscape (Cusack et al., 2015; Hill et al., 2021), thereby conditioning their presence or absence at each site.

Regardless of causality, differences were detected between sites based on management type. For instance, some large herbivores and carnivores, such as white-tailed deer, tapirs, and jaguars, were more abundant in the National Park. On the other hand, generalist species such as common opossums, raccoons, coyotes, white-nosed coatis, and white-faced monkeys were observed regularly in PC. Sáenz-Bolaños et al. (2020) found a higher abundance of large herbivores and large carnivores in Barbilla National Park compared to other PAs with a lower level of protection (Indigenous territory and forest reserve) in the Northern Talamanca Mountains of Costa Rica. Our study indicated similar results in the PAs, where there was likely less anthropic pressure and high food availability, possibly providing resources to specialist species. On the contrary, generalist species and mesopredators such as white-nosed coatis, raccoons, and common opossums, which can tolerate or thrive in proximity to human settlements and anthropogenic activities, showed higher occurrences outside PAs (i.e., PC), where human impacts are expected to be higher.

Our results showed the same patterns found by Montalvo (2012), who reported low records of coyote, grey fox, collared peccary, and spotted skunks with camera traps in the core of SRNP. On the contrary, Yaney-Keller et al. (2022), also with camera traps, found abundant records of grey foxes, collared peccaries, and spotted skunks at PC. Coyotes are a native species in Costa Rica and have been spotted at the three study sites at different times. It has been suggested that coyote populations are expanding in Central America (Hody & Kays, 2018), which may influence their distribution across the region. However, this seems insufficient to explain the variation in local detection rates.

Disturbed and urbanized sites can increase the number of individuals of generalist species (Prange & Gehrt, 2004; Prange et al., 2004). Our results support that generalist species and mesopredators occur mostly in the most perturbed site among the studied sites. This occurrence, known as mesopredator release, happens when the absence of top predators leads to an increase in generalist species due to reduced predation pressure (Crooks & Soulé, 1999; Prugh et al., 2009). Human-derived food sources may also enhance the success of mesopredators and generalist species (Oro et al., 2013). Among the sample sites, PC was the one with the highest level of anthropogenic activity, as

there is a high transit of tourists that frequently visit the beach during the daytime, especially on weekends. As a result, garbage accumulates during tourist peak season (from November to April), providing food sources to generalist species, such as coyotes and raccoons. On the other hand, predation of sea turtle eggs by raccoons has become a major problem at Las Baulas National Park (Cordero-Umaña et al., 2026), and predation by coyotes has also been confirmed at Cabuyal (unpublished data). These species can rapidly increase their abundance and suppress smaller competitor populations, such as striped hog-nosed skunks or grey foxes (Jachowski et al., 2020). Such dynamics illustrate the critical role that top predators play in maintaining ecological balance and highlight how anthropogenic activities can favor generalist species over specialized ones (Ritchie & Johnson, 2009).

Keystone species with specific ecological requirements, such as large carnivores (e.g., jaguars and pumas) and herbivores (e.g., tapirs and white-tailed deer), were more abundant inside PAs. These species require extensive areas of well-conserved forests that provide shelter from human disturbance (Laidlaw, 2000; Stoner & Timm, 2004). In addition, large species and top predators naturally occur in low population densities and have low reproductive rates, which makes them more vulnerable to habitat degradation and anthropogenic pressures. This makes them at the same time good indicators of the quality of the environment and its change over time (bioindicators; Díaz-Pulido et al., 2015). Therefore, the higher abundance of specialist species, top predators, and large herbivores we found in the PAs could indicate a recovery of the forests and the wild populations that inhabit there compared to the unprotected site (i.e., PC).

The presence of prey influences the presence of predators (Karanth et al., 2004; Montalvo et al., 2015), and in our study, the high abundance of white-tailed deer and the seasonal large availability of sea turtles in SRNP could also explain the high abundance of jaguars (Montalvo, 2012). Jaguars are regular predators of sea turtles in SRNP (Alfaro et al., 2016), particularly at Nancite (Fonseca et al., 2020), where synchronized arribadas of hundreds of turtles occur, providing high-energy and readily accessible prey (Carrillo et al., 2009; Fonseca et al., 2009; Montalvo et al., 2020). This could also explain the high abundance of jaguars in SRNP compared to HFR and PC. In fact, the number of jaguars has increased in recent years, but not the percentage of sea turtles predated (Fonseca et al., 2020). In addition, no jaguars were detected in PC during the study, despite being Cabuyal a sea turtle nesting beach, possibly due to the relatively high level of tourist inflow. In PC, forest patches are structurally disconnected from HFR and SRNP and are dominated by anthropogenic activities (farmlands). Although we did not find jaguars in PC, they have been observed before (Yaney-Keller et al., 2022). One jaguar recorded in HFR in this study was previously spotted in PC in 2020 (Fonseca, pers. Communication). Likewise, a jaguar previously seen in PC was originally identified at SRNP (Yaney-Keller et al., 2022). This may indicate that at least some jaguars naturally move between the three sites, even if their abundance is far greater in the site with the highest level of protection and greatest forest cover and sea turtle abundance.

Interspecific competition and seasonality can also define the composition of mammal communities in the tropical dry forest. Therefore, the harsh conditions that are typical during the dry seasons can limit food availability (Stoner & Timm, 2011). For instance, jaguars are known to directly compete with pumas (Montalvo, 2012; Montalvo et al., 2015; Montalvo et al., 2023), while ocelots can also be outcompeted and displaced by larger carnivore species (Montalvo, 2012; Oliveira et al., 2010). Hence, Montalvo (2012) suggested that the high abundance of jaguars in SRNP pushes pumas to consume smaller prey species, which would normally be species that ocelots prey upon, having a cascade effect on the ecosystem. Our results also support Oliveira et al. (2010) conclusions about interspecific competition since we found a low abundance of ocelots

in SRNP, in contrast with HFR, where ocelot populations were possibly high due to the lower frequency of jaguars and pumas.

Tapirs generally require large areas of well-preserved forest (Chassot et al., 2009; Stoner & Timm, 2011). Thus, a higher abundance obtained in the SRNP compared to other sample sites was expected. Tapirs are listed as endangered in Costa Rica (SCIJ, 2017) and at a global level (IUCN, 2024) and are considered keystone species for the tropical dry forest, due to their important role in seed dispersal and vegetation regeneration (Chassot et al., 2009; O'Farrill et al., 2013). We detected tapirs in all three sites during this study, being the first scientific record of this species in PC. Tapirs are highly dependent on waterholes during the dry season, and their observations are not common outside waterhole sites (Montalvo et al., 2019). The observation of tapirs in PC may, therefore, indicate that non-protected sites could work as transit or occasional use sites for large herbivore species, as suggested by the detection of a white-tailed deer in this study and previous records in 2017 (Yaney-Keller et al, 2022). This indicates that PAs' adjacent sites could be important to the preservation of this threatened species.

Finally, endangered or threatened species were encountered more frequently at SRNP than at HFR or PC. Though differences in relative abundance between sites were not statistically significant for some of the evaluated species, a larger sampling effort would be necessary to obtain more independent captures of rare species. SRNP might act as a source for populating other sites. Previous records indicate that some endangered species (e.g., jaguarundi and jaguars) also utilize PC (Yaney-Keller et al., 2022), though their use is infrequent and was not detected during this study.

In conclusion, our findings suggest that different management strategies could affect the presence and relative abundance of terrestrial mammals at the Guanacaste Conservation Area, likely reflecting a positive impact of PAs on the conservation of the tropical dry forest. The records of top predators, large herbivores, and endangered species at PC suggest that attention should also be paid to unprotected sites in relation to protected ones. A greater effort is needed to conduct more thorough analyses on the different factors that drive wildlife distributions in the Guanacaste Conservation Area and on how management categories could specifically condition their abundance.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

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