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ORIGINAL ARTICLE

Medium and large-sized mammals in dry forests of the Colombian Caribbean

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Abstract

Mammalian populations are fundamental at functional and ecological levels within ecosystems and are in constant threat of reduction worldwide and in the Neotropic. We evaluated population variables, habitat use, and threats to medium and large mammals (weight > 1kg.) in the terrestrial part of the Tayrona National Natural Park (Santa Marta - Colombia). We carried out indirect annual observations with camera traps between 2012 and 2017, both in rainy and dry seasons. We estimated the richness, relative abundance (RAI), and functional diversity of the mammals present in the area. We recorded 15 species, distributed in seven orders (Carnivora, Rodentia, Pilosa, Cingulata, Lagomorpha, Didelphimorphia, and Cetartiodactyla), 11 families and 13 genera. The species with the highest capture frequency was *Dasyprocta punctata* (142, RAI = 0.85), followed by *Cuniculus paca* (56, RAI = 0.33), *Odocoileus virginianus* (51, RAI = 0.30), and *Cerdocyon thous* (41, RAI = 0.24). We observed a marked use and preference of habitat in the seasonal dry evergreen forest. This finding coincides with the highest value of functional richness (S1 = 293.88) for this ecosystem, probably due to its features, such as green vegetation and abundant water streams. Our results reveal stability of the species richness across the years studied, suggesting good health of the mammal populations in the studied area.

Keywords: Habitat occupation; dry forest; taxonomic diversity; functional diversity; Mammalia

Introduction

Mammals perform multiple ecological roles including -but not limited to- seed dispersal, species control, and plant species recruitment. Despite their importance, mammals currently are after amphibians, sharks, and rays the third group of vertebrates most vulnerable to extinction

(Schipper *et al*., 2008; IUCN, 2019). More than 30 % of mammals are in some degree of threat (Ripple *et al*., 2014) due to habitat fragmentation, degradation, or loss (Murphy & Lugo, 1986; Sala *et al*., 2000; Pennington *et al*., 2009; Pekin & Pijanowski, 2012). These phenomena reduce food availability (Sinclair & Krebs, 2002) and refuge areas (McNab, 1986; Carbone *et al*., 2007). Other stressful factors particularly for medium and large mammals are illegal hunt/trade and coexistence conflicts with other species present in close-by human communities (Conover, 2001; Schipper *et al*., 2008; Macdonald *et al*., 2010). Furthermore, some natural characteristics of mammals, such as reduced population density, slow reproductive cycles (Damuth, 1981), and the need for large areas for permanence and survival (Bodmer *et al*., 1997; Jerozolimski & Peres, 2003) represent important challenges for the conservation, recovery, rehabilitation, and restoration of their threatened populations.

Tropical dry forests constitute one of the vegetation covers occupied by Mammals (Pizano & Garcia, 2014). Tropical dry forests represent 50 % of the forested areas in Central America and 22 % in South America (Murphy & Lugo, 1986) and are one of the most threatened plant formations globally (Janzen, 1988). In Colombia, about 92 % of the original tropical dry forest coverage has been converted (García *et al*., 2014) for agricultural use, urbanization, and mining (Etter *et al*., 2015). Due to its vulnerability, this type of forest has been classified as a critically threatened ecosystem and is listed as a priority for conservation (Miles *et al*., 2006; Sánchez-Azofeifa & Portillo-Quintero, 2011). However, tropical dry forests are underrepresented in the plan of protected areas in Colombia. A decade ago, only 0.5 % of these forest areas were included in the plan (Forero-Medina & Joppa, 2010; Banda *et al*., 2016), and this figure has not increased in the present.

A Colombian dry forest in recovery and in a good state of conservation is the Tayrona National Natural Park (TNNP). This tropical dry forest is large (3 119.5 ha) and exhibits the highest species richness values in Colombia (Barbosa-Rojas *et al*., 2012). This area counts with baseline studies, inventories and species lists, documented by Sánchez *et al*. (2006); UAESPNN and PROCAT (2012), and Jiménez-Alvarado *et al*. (2015). We characterized the diversity of medium and large mammals across several years in the TNNP continental area. We determined the occupation, use, and habitat preference of mammals and calculated an approximation for their functional diversity in typical dry formation coverage, according to Rangel-Ch & Carvajal-Cogollo (2012).

The aspects evaluated in our study incorporate key characteristics that help to understand the relationships between diversity, community structure, and subsequent ecosystem functioning (Tilman *et al*., 1997; Chapin *et al*., 2000; Díaz & Cabido 2001; Naeem & Wright 2003). We hypothesized that (i) large mammals with weights larger than 2.5 k, would have reduced populations, due to the lack of conservation to which they have historically been subjected in the vicinity and within the actual protected area. (ii) Medium-sized mammals would show abundant populations for some species. In terms of functional diversity, we assumed that the ecological roles played by mammals in the protected area are sufficient to maintain a balanced e cosystem. Our results are essential for the management and conservation of mammals in the TNNP continental protected area, and contribute to the definition of strategies for managing its resources.

Materials and methods

Study area

The TNNP has both terrestrial and marine areas; its terrestrial area covers a total of 12 597.52 ha. The Park is located in the northern Caribbean region of Colombia (11 ° 16'20"N, 74 ° 12'56"W - 11 ° 21'33"N; 73 ° 53'11"W) in the foothills of the north-western flank of the Sierra Nevada de Santa Marta, in the department of Magdalena (**Fig. 1**). The TNNP has an elevation gradient between 0 and 1 000 m.a.s.l., mainly covered by seasonal tropical dry forest and evergreen tropical dry forests linked to the marine areas of the park (Espinal & Montenegro, 1963; Carbonó-De la Hoz & García-Q, 2010) (Fig. 1). Among the floral species recorded in the study area there are representatives of the Cactaceae, Leguminosae, Burseraceae, and Capparaceae families. The genus *Capparis* (Capparaceae) is particularly well represented in this area with a large number of eatable species known as caparbushes, which constitute important food sources for the local fauna (Carbonó-De la Hoz & García-Q, 2010).

TNNP's temperatures range between 22 °C and 27 °C throughout the year and rainfall ranges from 1 200 mm per year in the driest zone (Western sector) to 2 000 mm per year (Eastern sector) (INDERENA, 1978). Topography and maritime effects in the north and the continental effects in the south influence the park's relative humidity (80-95) (IDEAM, 2014). The area has a history of transformations dating back to the mid-20th century, due to different human migrations that generated erosion, felling, and soil compaction because of livestock and agriculture. These processes have created a highly heterogeneous landscape allowing the presence of different mammal species such as two species of large cats, primates, rodents, armadillos and even wild dogs (Jiménez-Alvarado *et al*., 2015).

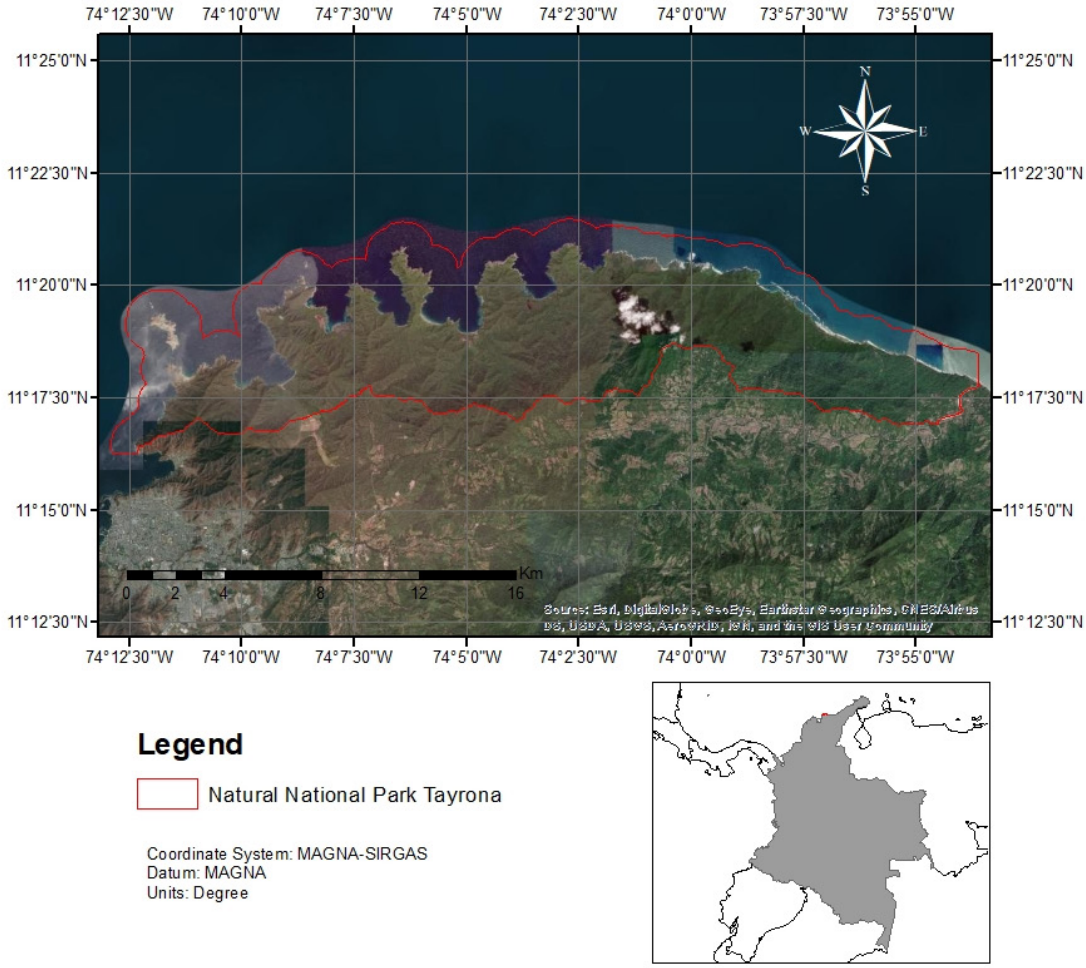

Figure 1. Location of the study area, in the Colombian Caribbean.

We defined six sectors within the protected area, according to their location, orientation, and plant structure (Sánchez *et al*., 2006): Cañaveral (S1) and Pueblito (S2), which correspond to dry evergreen forest ecosystem (DEF); Arrecifes (S3) and Cedro (S4) with seasonal dry forest ecosystem (SDF); finally, Gayraca (S5) and Bahía Concha (S6) with thorny scrub (TS). In each of the types of plant coverage, we identified the habitats of forest clearing (FC), roadside (RS) and semi-open areas (SA).

Camera trapping

Our research covered a multi-year period during the dry and rainy seasons of 2012, 2013, 2014, 2016, and 2017. We used 25 Bushnell camera traps, model No. 119436 and set 12 traps in dry evergreen forest, seven in seasonal dry forest, and six in thorny scrub. The difference in the number of cameras in each ecosystem was due to its percentage of coverage in the protected area, its capacity to house medium-sized mammal species due to the availability of resources (UAESPNN & PROCAT, 2012), and the presence or proximity to anthropogenic activities (e.g. tourism). We divided each type of forest coverage into quadrants (grids) of 1.5 km^2 and randomly chose those grids in which the cameras were located. These grids were separated from each other by at least 1 km to guarantee independence of samples (Srbek-Araujo & Chiarello, 2013).

In each chosen grid we set up camera traps, attaching each camera to a tree approximately 40 cm above the ground. The specific sites where the cameras were installed were on the edge of the road, forest clearings, and close to lotic bodies of water. We made sure that camera sensors were pointed parallel to the ground to maximize the extent of the detection zone (Kelly, 2008; Debata & Swain, 2018). Trap cameras were configured to operate 24 hours a day and programmed to take sequential photographs for 30 seconds, recording the date and time of each record. Trap cameras in each coverage were left to operate for a maximum of 35 days and were verified at fortnightly intervals to download photos and replace their batteries.

Data analysis

We inspected all images taken and identified the animals photographed to species level. For felines, we used identification guides by Payán Garrido & Soto Vargas (2012) and Hunter (2015). The tail of spotted small cats (genus *Leopardus*) was measured superficially on the photographs (estimating tail to body size ratios), we also took into account the direction and features of the spots (Ramírez-Barajas, 2014). For other mammals, we used the guidebooks of Morales Jiménez (2004), Alberico *et al.* (2002), and Tirira (2017). We considered photographs separated by a 24-hour period as independent records. In the event that the photographs contained more than one individual, we considered one of them as an independent record (Hernández-Pérez *et al.*, 2015). Images of animals for which we were unable to accurately determine their species were discarded.

We calculated species diversity by measuring sampling coverage through accumulation curves (rarefaction and extrapolation) and with Hill Numbers. With these, we estimated $q = 0$, measuring the total species richness (true diversity); $q = 1$, that expressed the exponential of the Shannon entropy index; and $q = 2$ that corresponded to the inverse of the Simpson index (Chao *et al.*, 2014). For each analysis, the procedure outlined by Chao & Jost (2012) in the iNEXT program V2.0.12 (Hsieh *et al.*, 2016) was used.

We recorded the number of mammal detections and calculated the relative abundance index (RAI) for each species (Goulart *et al.*, 2009). The RAI was estimated for each species observed during the two seasons of the year (rain and drought) in each ecosystem with the following formula:

$$(1)\ RAI = \frac{A}{N} x 100 \quad (1)$$

Where A is the total number of detections of a species by all cameras, N is the total number of camera trap days in the entire study area, and 100 is the standard correction factor. RAI is interpreted as the average number of photos of each species per 100 days. We used R studio (Allaire, 2012) to graphically show the frequencies of each species for each ecosystem.

In order to assess functional diversity, a matrix with functional traits was constructed taking into account the presence of a species and the role it plays in the ecosystem. The functional traits, considered key determinants of behavior, were weight, trophic guild, dental formula, and tooth function. In addition, we used captured frequencies as a weight factor in the analyses.

We calculated three multidimensional multi-trait indices. (i) Functional richness (FRic), which is the amount of functional space occupied by the species of a community regardless of their abundances (Villéger *et al.*, 2010). A low functional richness indicates that some of the resources for potential use in the community are not in use and could result in a reduction of productivity in that ecosystem (Mason *et al.*, 2005). (ii) The Functional fairness index (FEve) informs on the uniformity in the distribution of the species abundances of a community in a functional space (Villéger *et al.*, 2010). A low index of functional equity indicates that some parts of the space available for a niche are occupied but underutilized, causing a reduction in productivity and increasing the opportunity for possible invaders to establish themselves (Mason *et al.*, 2005). Finally, (iii) the functional divergence index measures the regularity with which species are distributed in functional space based on their characteristics. This index takes values between zero (0), when it is completely lacking in equity, and one (1), when it has complete equity; namely, when the abundances of all species are uniform (Villéger *et al.*, 2010). A high divergence reflects a high degree of niche differentiation between dominant species (predators), which could reduce competition and increase the magnitude of ecosystem processes as a result of more efficient use of resources (Mason *et al.* 2005). These index calculations were made in the fDiversity package in R.

We described use, preference, niche width, and habitat occupation through the index of Colwell & Futuyma (1971) with estimates of Shannon (1948) and the Baltz preference indices (1990), following II- Jacobs (1974). These two indices were calculated with an interval of 95 % (alpha = 0.5 %).

The analyses were carried out in the Havistat V2.02 program (Montenegro *et al*., 2014).

Results

Diversity of medium-sized mammals in the Tayrona Natural National Park.

We obtained 357 independent records from 5 328 photographs with a sampling effort of 3 263 trap cameras / day. The data obtained showed a specifies richness of 15 species distributed in seven orders (Carnivora, Rodentia, Pilosa, Cingulata, Lagomorpha, Didelphimorphia, and Cetartiodactyla), 11 families, and 13 genera (**Fig. 2**).

Of the 15 registered species, eight belonged to the order Carnivora and were distributed in four families. The most representative family within this order was Felidae with five species, followed by Canidae, Procyonidae and Mephitidae with one species each. The second most common order was Rodentia with two families, each with one species. The remaining five orders got one record with one species each (**Table 1**).

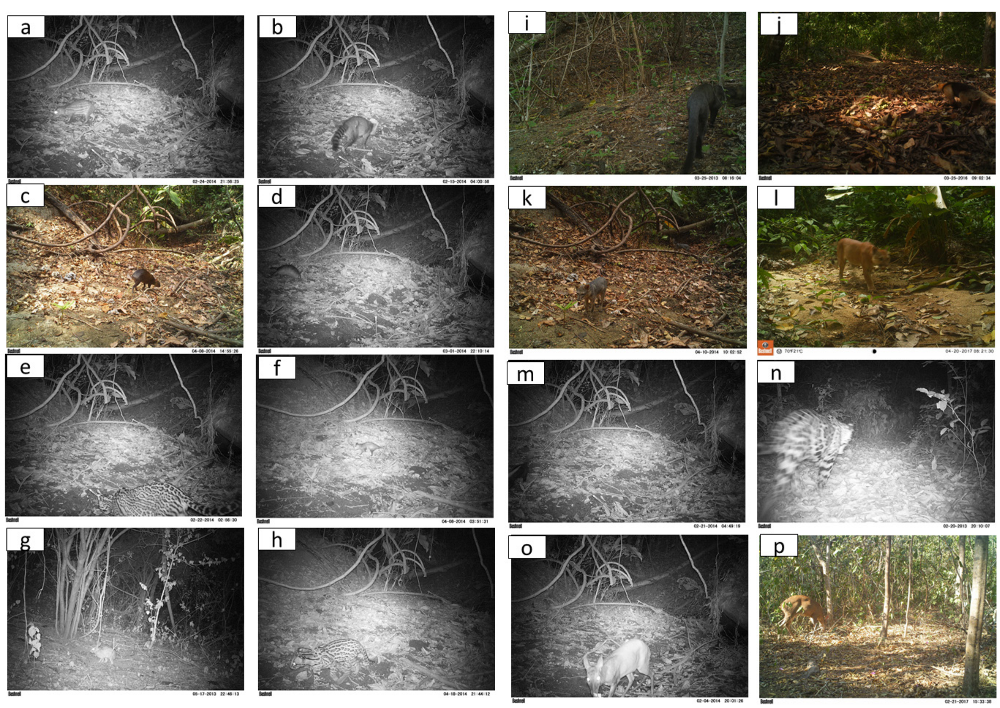

Figure 2. Photographic record of mammals found in dry vegetation cover of the Tayrona National Natural Park. (**A**) *Cuniculus paca*, (**B**) *Procyon cancrivorus*, (**C**) *Dasyprocta punctata*, (**D**) *Dasypus novemcinctus*, (**E**) *Leopardus pardalis*, (**F**) *Didelphis marsupialis*, (**G**) *Sylvilagus cf. floridanus*, (**H**) *Leopardus wiedii*, (**I**) *Herpailurus yagouaroundi*, (**J**) *Tamandua mexicana*, (**K**) *Cerdocyon thous*, (**L**) *Puma concolor*, (**M**) *Conepatus semistriatus*, (**N**) *Panthera onca*, (**O**) *Odocoileus virginianus* (black and white photo), (**P**) *Odocoileus virginianus*.

Table 1. Richness, composition, and frequency of observations of medium and large mammals per site in Tayrona National Natural Park, Colombia.

Order	Family	Species	S1	S2	S3	S4	S5	S6
Carnivora	Felidae	*Leopardus pardalis*	1	1	4	0	0	2
		Leopardus wiedii	1	1	2	0	0	0
		Herpailurus yagouaroundi	0	0	1	0	0	1
		Puma concolor	1	1	0	0	0	0
		Panthera onca	2	1	0	0	0	0
	Canidae	*Cerdocyon thous*	11	14	11	0	0	5
	Procyonidae	*Procyon cancrivorus*	2	10	3	0	0	0
	Mephitidae	*Conepatus semistriatus*	0	0	2	0	0	0
Rodentia	Cuniculidae	*Cuniculus paca*	12	11	33	0	0	0
	Dasyproctidae	*Dasyprocta punctata*	36	16	81	7	0	2
Pilosa	Myrmecophagidae	*Tamandua mexicana*	2	0	0	0	1	0
Cingulata	Dasypodidae	*Dasypus novemcinctus*	0	1	6	0	0	0
Lagomorpha	Leporidae	*Sylvilagus floridanus*	0	0	0	0	0	3
Didelphimorphia	Didelphidae	*Didelphis marsupialis*	6	0	10	2	0	0
Cetartiodactyla	Cervidae	*Odocoileus virginianus*	13	1	6	1	4	26

The accumulation curves (rarefaction-extrapolation) indicated that the scope of the sampling covered a considerable proportion of the medium-sized mammals present at the different sites (e.g. 90 % at S4, 98 % at S5, and above 75 % for the remaining sites) (**Fig. 3B**). The estimated richness in relation to the values of the sampling scope (base value of 80 %) revealed differences among sites. In sites S1 and S2 (dry evergreen forest) and S3 (seasonal dry forest), around five species were present; whereas in sites S4 (seasonal dry forest) and S6 (thorny scrub) around three species were present. In S5 approximately two species were recorded (Fig. 3C).

Structure of the assemblage of medium-sized mammals

The highest capture frequency occurred in the seasonal dry forest with 169 individuals (S3 = 159 and S4 = 10), followed by the dry evergreen forest, with 144 individuals (S1 = 87 and S2 = 57) and the thorny scrub with 44

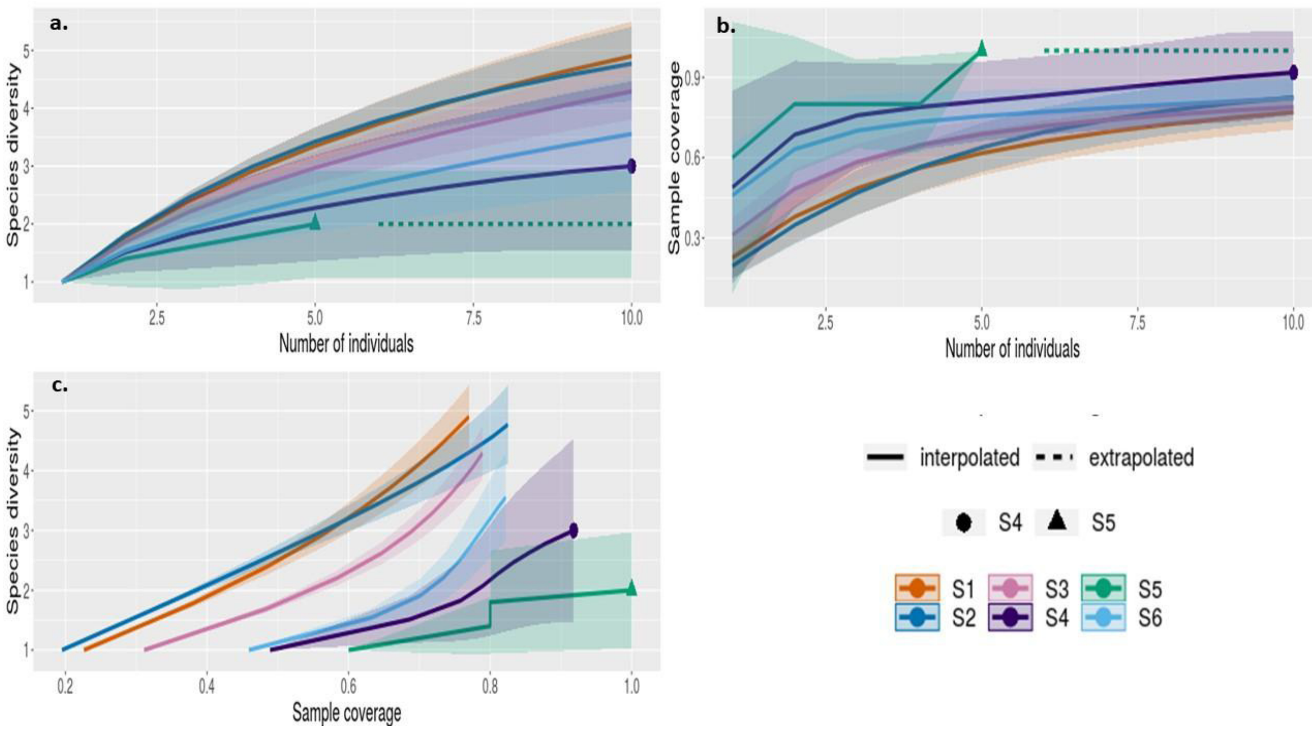

Figure 3. (A) Rarefaction based on sample size (solid line) and extrapolation (dashed line), was up to double the size of the smallest sample of mammal richness. The dots indicate the reference samples. (B) Sampling scope as a function of double the reference size, for rarefaction (solid line) and extrapolated (dotted line) samples. (C) Rarefaction (solid line) and extrapolation (dashed)

individuals (S5 = 5 and S6 = 39; **Fig. 4**). The species with the highest frequency of capture was *Dasyprocta punctata* (142) followed by *Cuniculus paca* (56), *Odocoileus virginianus* (51), and *Cerdocyon thous* (41). There were species with medium capture frequencies such as *Procyon cancrivorus* (18) and *Didelphis marsupialis* (15), and the species with the lowest capture frequency per site were cats such as *Leopardus pardalis* (8), *Leopardus wiedii* (4), *H. yaguoarondi* (2), *Puma concolor* (2), and *Panthera onca* (3). Other least frequent species from other families included: *Tamandua mexicana* (3), *Dasypus novemcinctus* (7), *Conepatus semistriatus* (2), and *Sylvilagus* cf. *floridianus* (3).

Regarding RAI, the species *Dasyprocta punctata* scored highest (RAI = 0.85) and the minimum for *Herpailurus yaguaroundi*, *Puma concolor* (RAI = 0.012) and *C. semistriatus* (RAI = 0.012). In general, the RAI values for the feline species were low, *L. pardalis* (RAI = 0.05), *L. wiedii* (RAI = 0.024) and *Panthera onca* (RAI = 0.018). For species with omnivorous and herbivorous feeding habits, the RAI

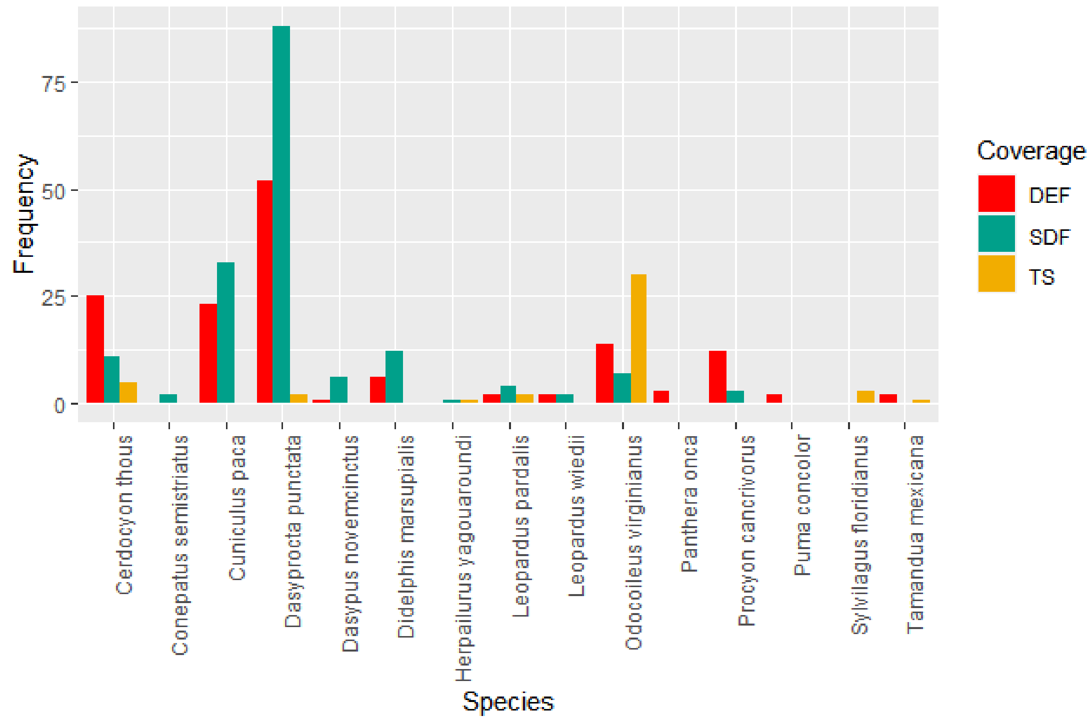

Figure 4. Frequency of capture of mammal species in each coverage. DEF: Dry evergreen forest; SDF: Seasonal Dry Forest; TS: Thorny Scrub.

values varied. *Cerdocyon thous* (RAI = 0.24), *Cuniculus paca* (RAI = 0.33) and *Odocoileus virginianus* (RAI = 0.30) presented low values. *Sylvilagus* cf. *floridianus* and *T. mexicana* (RAI = 0.017), *D. novemcinctus* (RAI = 0.04) and *D. marsupialis* (RAI = 0.11) presented RAI values that corresponded to the individual capture frequencies in the study area.

Occupation, use, and habitat preference

We observed a marked preference of the mammals for the seasonal dry forest coverage. Likewise, we noticed a marked evasion for the cover of thorny scrub (TS). In terms of habitat preference, the habitat that presented the least evasion was the forest clearing habitat (FC) and the greatest evasion occurred in the semi-open area (SA) habitat. Most felines showed a strong preference for the dry forest (SDF) ecosystem (**Table 2**).

The species with the largest niche width was *Leopardus pardalis* (0.91), followed by *Dasyprocta punctata* (0.9), *Odocoileus virginianus* (0.87), *Conepatus semistriatus* (0.86), and *Puma concolor* (0.83). The remainder of the individuals had a niche width that was intermediate, and the smallest niche widths were those of *Tamandua mexicana* (0.56) and *Panthera onca* (0.5).

Table 2. Habitat preference scores of medium-sized mammals observed in this study. Dry Evergreen Forest (DEF), Thorny Scrub (TS), Seasonal Dry Forest (SDF), Forest Clearing (FC), Roadside (RS), Semi-open Area (SA).

Species	DEF	TS	SDF	SA	FC	RS
Leopardus pardalis	-0.6	0	0	0	0	0.3
Leopardus wiedii	-0.1	-1	-0.1	-1	-1	0.4
Herpailurus yaguoarondi	0	0.6	0	-1	-1	-1
Puma concolor	0.9	-1	-0.8	-1	-0.4	-0.5
Panthera on	0.8	-1	-1	-1	0.1	-0.1
Cerdocyon thous	-0.9	-0.4	-0.1	-0.4	-0.6	0.3
Procyon cancrivorus	0.8	-1	-0.9	-0.7	-0.7	-0.2
Conepatus semistriatus	1	-1	-1	-1	-1	-1
Cuniculus paca	-0.8	-1	-0.6	-0.2	0.3	0.7
Dasyprocta punctata	-0.8	-0.7	0	0.1	0.4	0.1
Tamandua mexicana	-1	0.5	-0.1	0.8	0.5	-1
Dasypus novemcinctus	0.9	-1	-1	-1	-1	-1
Sylvilagus floridanus	0.8	0.1	-0.3	-1	-1	-0.4
Didelphis marsupialis	-1	-1	-1	-1	0.7	-1
Odocoileus virginianus	-1	0.5	0.3	0	-0.3	0.3
Rank: -1 to 1						
If -1< Index Value < -0.5 Strong Evasion						
If -0.49 Index Value < -0.26 Moderate Evasion						
If 0.25 < Index Value < 0.25 Indifference						
If 0.26 < Index Value < 0.49 Neutral Selection						
If 0.50 < Index Value < 1 Strong Selection						

Approach to the functional diversity of mammals in the Tayrona Park

Dry evergreen forest exhibited the greatest functional richness, followed by dry forest and thorny scrub. This same pattern was observed for the FEve index. The multi-trait functional divergence (FDiv) index was largest in thorny scrub, followed by the dry evergreen forest and finally by the dry forest. Each one of the sites followed the same pattern shown for the ecosystems. At the site level, these followed the same pattern shown for the coverage to which they belonged (**Table 3**).

Table 3. Functional diversity for the studied vegetation coverages and sampled sites. Functional wealth (FRic), Functional equity (FEve), and Multi-trait functional divergence (FDiv).

Site	FRic	FEve	FDiv
S1	293.87	0.46	0.58
S2	77.67	0.29	0.56
S3	101.33	0.25	0.56
S4	109.49	0.03	0.65
S5	64.07		0.65
S6	20	0.63	0.9

Discussion

Species diversity

During our multi-year observation study, we registered 15 of the 21 medium and large mammal species (exlcuding primates) for which records exits in the TNNP (Jiménez-Alvarado *et al*., 2015). However, due to the shape of the sampling coverage curves (Fig. 3), we infer that the species composition agrees with the complete inventory for the study area. The absence of species in our records, such as *Eira barbara*, *Galictis vittata*, *Mazama sanctaemartae*, *Pecari tajacu*, *Myrmecophaga tridactyla*, and *Cabassous centralis*, can, arguably, be explained by behavioral and physical factors, plant cover, camera placement, weather (O'Connell *et al*., 2010), and other characteristics associated with the specific type of life history of each species. For instance, the absence of mustelids, *Eira barbara* and *Galictis vittata* can be attributed to their tendency to be arboreal or their marked competition with other carnivorous mammals (Presley, 2000), the former alone can explain why these animals were not photographed. A similar explanation can be provided for the absence of the armadillo, *Cabassous centralis*. Having semi-fossorial habits, this armadillo is difficult to detect in the different vegetation covers sampled. Other species have a history of conflict with humans or other animals, which reduces their population sizes (UAESPNN & PROCAT, 2012). This may be the cause of their few or no detections in our study.

The highest species richness values were found, in decreasing order, in seasonal dry forest, dry evergreen forest, and thorny scrub. Dry evergreen forests, with year-around water availability, can support a greater richness of medium and large mammals (Mooney *et al*., 1995; Miles *et al*., 2006). A particular case is shown by carnivore richness, represented by large predators (e.g. *Puma concolor*), for which the availability of prey is high (e.g. the Central American Agouti, *Dasyprocta punctata*), allowing the establishment of these populations in this type of vegetation. The seasonal dry forest also has high mammalian species richness, but strong seasonality acts as a stressor. When conditions change throughout several months in one year (Mooney *et al*., 1995), resources decrease, and water becomes a limiting factor for mammal populations. We gather that the vegetation covers sampled are in contact with each other and local movements occur between them. This guarantees a greater number of species and individual occupation of the dry forest with water availability, because of the annual stability of this vegetation type.

The pattern of the relative abundances shows the typical characteristics of an assemblage of large and medium-sized mammals (Debata & Swain, 2018). The largest relative abundances are triggered by species with a high tolerance to different environments and of their fluctuations. Dry plant formations of the Caribbean region and even some disturbed environments constitute two examples of this type of environments. The Central American Agouti, *Dasyprocta punctata*, exhibited the highest relative abundance values (RAI = 0.85). Similarly, the species *Cuniculus paca* and *Cerdodyon thous* had medium abundances (∼ 50 individuals) which were superior to those of other species (e.g. *Silvilagus floridanus*., *L. pardalis, L. wiedii*); some of these species have high tolerances to a wide range of environments and this allows them to exploit different resources and survive (Ceballos & Oliva, 2005).

The white-tailed deer, *Odocoileus virginianus* was the only species of Cervidae found in the entire terrestrial extent of the park, although Jiménez-Alvarado *et al*. (2015) recorded *Mazama sanctaemartae* in the park. *Odocoileus virginianus* had a low relative abundance, despite being considered a species with high adaptability that can cover large areas in a short time (Galindo-Leal & Weber, 1998; Gallina *et al*., 2008; Villarreal, 2008). The least abundant species correspond mostly to carnivores that require a more extensive area to survive (Rabinowitz & Nottingham, 1986; Macdonald & Loveridge, 2010), so they may not be abundant in the area at the time of sampling; and; furthermore, they adjust their distributions according to the supply of prey (Lindsted *et al*., 1986; Crawshaw & Quigley, 1991; Grigione *et al*., 2002; Dillon & Kelly 2008).

Occupation, use and habitat preference

The preference registered for the dry evergreen forest is a consequence of the advantages, in terms of roles, that this type of ecosystem entails, such as water supply (essential in the driest times of the year), nutrient retention (Jacobs *et al*., 2007), biological corridors (Beier & Noss, 1998), besides other types of resources. Furthermore, the dry evergreen forest had marked importance in terms of preference by mammals, because it constitutes a refuge and food source for carnivores (Perault & Lomolino, 2000; Hilty *et al*., 2006; Pereboom *et al*., 2008). The dry evergreen forest has the densest forest cover, and it is widely distributed in the protected area (UAESPNN & PROCAT, 2012). The evasion of thorny scrubs was observed in the majority of species; this ecosystem creates behavioral changes in the fauna available in the disturbed sites. In this way, in the thorny scrubs there are changes at a higher trophic level in terms of populations and communities. These changes modify the species distribution and behavior due to disturbances (Sutherland & Crockford, 1993; Beale & Monaghan, 2004).

The differences observed in the composition of mammals among different biotic covers are due to the proximity to the Colombian Caribbean coastline and the modification of their territories and plant cover over the years (Etter, 2015). Therefore, we highlight the importance and the need for protection of patches with heterogeneous plant cover for the maintenance and conservation of wild species. The loss of a species or population can lead to irreversible effects on the functionality of the ecosystem and the services it provides (Ceballos & Ehrlich, 2002). In the case of the tropical dry forest (a critically threatened ecosystem; Janzen, 1988), it is important to know the ecological values that each species contributes.

Ecological role and functional diversity

The functional diversity of some sites in the present study was high. This result shows that a portion of the functional space in each sampled vegetation cover is occupied by the species of each functional group. This result is important if we take into account that the functionality and health status of a given ecosystem can be measured by the distribution of the functional traits possessed by the species (Mason *et al*., 2005), for example, the biomass and dental formula of first-order predators such as the big cats. On the other hand, the high values of functional fairness show a homogeneous distribution of the abundances of species with functional traits that play an important ecological role for the functioning of the ecosystem, for example, the biomass contribution of *Dasyprocta punctata* and the joint abundances of the species in trophic guilds (Villéger *et al*., 2010).

The values of wealth and equity, the distribution of functional traits, and the abundance that they possess —in addition to the trophic guilds of the mammals found— cover a large part of the food types of the trophic chain (carnivores, omnivores, and herbivores). Altogether, these reveal a good state of health for the ecosystem, mainly for the forest cover including both the dry evergreen forest and the seasonal dry forest. Other species (e.g. *Cerdocyon thous, Tamandua mexicana*, and *Odocoileus virginianus*) are essential for the proper functioning of the ecosystem, and they may have no replacement in the trophic chain and in the functions they perform in the study area (seed dispersal, species control).

Implications for conservation in protected areas

The reduced population abundances in a multitemporal time scale for some species may be due to several factors, one of such being incomplete compliance to regulations within the TNNP. Therefore, pressures continue decreasing the population density of the species. Lately the TNNP has had high tourist growth and, thus, interventions and contamination are increasing within the area. Implications of low abundance for some species in the area can trigger problems at the ecological level, influencing food chains and the ecological roles that the species fulfill in relation to the protected area and the BST. An optimal area for the conservation of species is vital in order to maintain the ecosystem services that they provide. Our study constitutes an essential source of data about the distribution and roles of mammals in the TNNP to inform management and monitoring plans that are currently being developed in this protected area.

Conclusions

This study found that the mammal populations in the studies protected area are still under threat even if environmental laws are in force. In the case of the dry forest at TNNP, some mammal populations are worrisome because of their low abundance in the five-year period of this investigation. Also, in the dry forest, water streams play an important role for the mammal population: in the dry season, these streams sustain the necessary plant coverage for mammals to survive in marked dry seasons. Conservation plans are needed due to the importance of this type of ecosystem at local, regional, and national levels.

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Conflict of interest

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest (such as honoraria, educational grants, participation in speaker's membership, employment, consultancies, stock ownership, or other equity interest, and expert testimony or patent arrangements) in the subject matter or materials discussed in this manuscript.

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Mamíferos medianos y grandes en bosques secos del Caribe colombiano

Resumen: Las poblaciones de mamíferos son fundamentales a nivel funcional y ecológico en los ecosistemas y están en constante amenaza de reducción alrededor del mundo y en el Neotrópico. En este estudio se evaluaron las variables poblacionales, el uso del hábitat y las amenazas a mamíferos medianos y grandes (peso > 1 kg.) en la parte terrestre del Parque Nacional Natural Tayrona (Santa Marta, Colombia). Se llevaron a cabo observaciones indirectas anuales con cámaras trampa entre 2012 y 2017, tanto en estaciones lluviosas como secas. Se estimaron la riqueza, abundancia relativa (RAI) y diversidad funcional de los mamíferos presentes en el área. Se registraron 15 especies, distribuidas en 7 órdenes (Carnivora, Rodentia, Pilosa, Cingulata, Lagomorpha, Didelphimorphia, Cetartiodactyla), 11 familias y 13 géneros. Las especies con más a frecuencia de captura fueron *Dasyprocta punctata* (142, RAI = 0.85), seguida de *Cuniculus paca* (56, RAI = 0.33), *Odocoileus virginianus* (51, RAI = 0.30) y *Cerdocyon thous* (41, RAI = 0.24). Se observó un uso marcado y preferencia de hábitat en el bosque seco siempre verde estacional. Este hallazgo coincide con el valor más alto de riqueza funcional (S1 = 293.88) para este ecosistema, probablemente debido a sus características, como vegetación verde y abundantes corrientes de agua. Estos resultados revelan estabilidad de la riqueza de especies a lo largo de los años de estudio y sugieren buena salud de las poblaciones de mamíferos en el área estudiada.

Palabras clave: ocupación del hábitat; bosque seco; diversidad taxonómica; diversidad funcional; Mammalia.

Mamíferos de médio e grande porte em florestas secas do Caribe colombiano

Resumo: As populações de mamíferos são fundamentais a nível funcional e ecológico nos ecossistemas e estão em constante ameaça de redução ao redor do mundo e na zona Neotropical. Neste estudo foram avaliadas as variáveis populacionais, o uso do habitat e as ameaças a mamíferos de médio e grande porte (peso > 1kg) na parte terrestre do Parque Nacional Natural Tayrona (Santa Marta, Colômbia). Realizaram-se observações indiretas anuais com armadilhas fotográficas entre 2012 e 2017, tanto em estações chuvosas como secas. Estimaram-se a riqueza, abundância relativa (RAI) e diversidade funcional dos mamíferos presentes na área. Registraram-se 15 espécies, distribuídas em 7 ordens (Carnívoca, Rodentia, Pilosa, Cingulata, Lagomorpha, Didelphimorphia e Cetartiodactyla), 11 famílias e 13 géneros. As espécies com mais frequência de captura foram *Dasyprocta punctata* (142, RAI = 0,85), seguida de *Cuniculus paca* (56, RAI = 0,33), *Odocoileus virginianus* (51, RAI 0,30) e *Cerdocyon thous* (41, RAI = 0,24). Observou-se um uso marcado e preferência de hábitat em floresta perene seca sazonal. Estes resultados coincidem com o valor mais alto de riqueza funcional (S1 = 293,88) para esse ecossistema, provavelmente devido a suas características, como vegetação verde e abundantes correntes de água. Estes resultados revelam estabilidade na riqueza de espécies ao longo dos anos de estudo e sugerem boa saúde das populações de mamíferos na área estudada.

Palavras-chave: ocupação do habitat; floresta seca; diversidade taxonômica; diversidade funcional; Mammalia.

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