



An assessment of the terrestrial mammal communities in forests of Central Panama, using camera-trap surveys



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ABSTRACT

The Isthmus of Panama, part of the planet's third largest megadiversity hotspot, and connecting the faunas of North and South America, has lost more than half of its forest due to agriculture and economic development. It is unknown to what degree the remaining forest, which is fragmented and subject to poaching, still supports the wildlife diversity found in intact forests. Here, we use camera-trap surveys to assess whether forests in Central Panama, the narrowest and most disturbed portion of the Isthmus, still have intact communities of medium- and large-bodied terrestrial mammals. During 2005–2014, we collected camera-trap survey data from 15 national parks and forest fragments on both sides of the Panama Canal, and compared these to similar data from two sites in the intact Darién National Park in Eastern Panama, the nearest available reference. We found that most sites in Central Panama – including some of the national parks – had lower mammal species richness and evenness than the reference sites, and less structurally-complex mammal communities. Forests in Central Panama had little or no apex predators and large terrestrial frugivores, with the exception of two sites directly connected to the reference site. Our results indicate that the terrestrial mammal community in forests of Central Panama is currently degraded, even inside national parks. These data provide a baseline for evaluating the success of conservation efforts to prevent the Panamanian Isthmus to become a bottleneck for movement of animals.

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Introduction

The formation of the Isthmus of Panama 3 million years ago facilitated a massive exchange of animal and plant species between North and South America, a biogeographical event known as the Great American Interchange (Marshall et al. 1982). The land bridge contributed to Central America becoming the planet's third largest 'megadiversity hotspot', harbouring 5–12% of the planet's biodiversity on just 0.5% of the land surface (Grandia 2007). Today, however, migration along the Isthmus of Panama may be more difficult for many organisms. The country of Panama has been experiencing

rapid economic development, which has resulted in massive loss and fragmentation of natural habitat (Heckadon Moreno 1993). Panama lost 14.3% of its forest cover between 1990 and 2010, and just 43.7% of this narrow country remains forested (Food and Agriculture Organization of the United Nations 2010). Moreover, economic development, population growth, agricultural expansion, forest conversion and fragmentation, traffic and poaching pose an increasing threat to wildlife (Griffiths & van Schaik 1993; Heckadon Moreno 1993; Wright et al. 2000). Anthropogenic pressure is especially intense in Central Panama, due to the presence and expansion of two major cities – Panama City and Colon – with associated infrastructure including the Panama Canal (Heckadon Moreno 1993).

Economic development in the Canal watershed has led to dramatic changes of its ecosystems (Heckadon Moreno 1993). Large-bodied terrestrial mammals may be declining, as they are

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vulnerable to local extinction in fragmented landscapes because of their relatively large home ranges, small population sizes and persecution by humans (Crooks 2002; Kinnaird et al. 2003; Urquiza-Haas et al. 2011; Moreno et al. in press). However, quantitative studies on the presence and abundance of terrestrial mammals in this region are rare and consider small scales only (Ibáñez et al. 2002; Mendez-Carvajal 2012). This is problematic as data on the status of biodiversity in Central Panama are essential for assessing the effectiveness of conservation programs aimed at restoring the connectivity of forests for facilitating wildlife movement. The Mesoamerican Biological Corridor project (MBC), for example, seeks to establish a biological corridor for wildlife between Southern Mexico and eastern Panama (Grandia 2007).

An important reason why the current status of wildlife in Central Panama remains unclear is that many species of interest are secretive and/or nocturnal and therefore difficult to survey objectively by direct observation or line transects counts (Silveira et al. 2003). Over the past decade, however, camera-based surveys have become a feasible, reliable and non-invasive alternative method for surveying communities of rare and cryptic terrestrial mammals (Tobler et al. 2008; Ahumada et al. 2011; Kays et al. 2011). Camera-trap surveys can yield data on the relative abundance of species, as the number of instances at which animals of a species are photographed is positively correlated with that species' abundance (O'Connell et al. 2011).

In this study, we used camera-trap data to test the hypothesis that terrestrial mammal communities in the forests of Central Panama are degraded, having (1) lower species richness and evenness, and a higher index of defaunation and (2) a poor representation of large-bodied species, compared to "intact" reference communities. Moreover, we hypothesized that (3) degradation of mammal communities in Central Panama is greater for forest fragments than for national parks, and (4) greater towards the West, thus further away from the larger protected forests lying on the

Eastern side of the Canal. We collected data from camera-trapping surveys from 15 forest sites across Central Panama, and two sites in the Darién NP in Eastern Panama, a forest relatively intact that qualifies as reference (Condit et al. 2001; Moreno 2006).

Methods

Study area

Panama lies in the moist tropics with an average annual daytime temperature of 31 °C. The dry season runs from late December to early May, and the annual rainfall amounts 1700–3000 mm on the Pacific and Atlantic coasts but increases with altitude to 6000 mm in the Darién (Ibáñez et al. 2002). Around half of the forest in Central Panama has been cleared (Food and Agriculture Organization of the United Nations 2010). Outside of the national parks, the area is a mosaic of both old-growth and secondary forest patches surrounded by plantations, grasslands and human settlements (Condit et al. 2001). The region is intersected by the Panama Canal, a busy shipping route that may constitute a barrier for many terrestrial species (Moreno et al. in press), and two highways that connect the cities of Colón and Panamá. Two biological corridors that have been proposed as part of the MBC project would run through this area (Fig. 1) (USAID 2009).

We surveyed 15 forest sites east and west of the Panama Canal, including large protected areas (national parks, nature reserves and a Nature Monument, henceforth referred to as "national parks") as well as forest fragments within the agricultural matrix that were scattered in between the protected sites (Fig. 1, Table 1). As reference sites for comparison, we used Cana and Pirre in the Darién NP, one of the largest protected areas in Mesoamerica, located on the far eastern side of Panama along the Colombian border, <300 km from Central Panama. The park, listed as a Biosphere Reserve, contains the most diverse and species-rich terrestrial ecosystems of

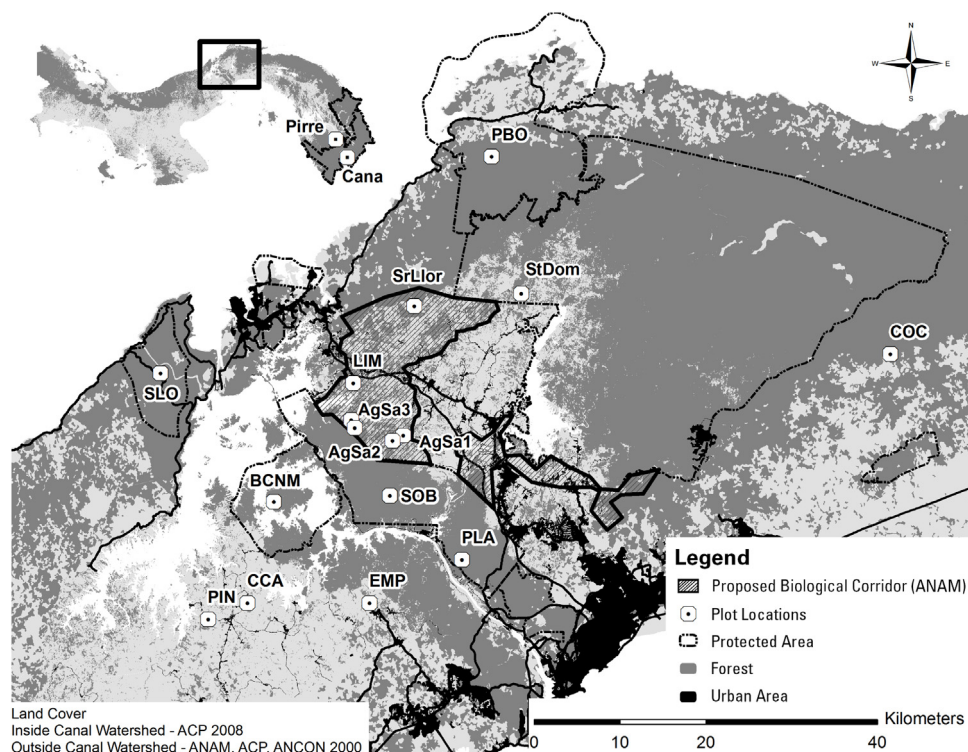


Fig. 1. Location of the 17 sites where camera trapping surveys were conducted. See Table 1 for site codes.

Table 1
Characteristics of the 15 study sites in Central Panama and the 2 reference sites in Darién, with specifications of camera trapping surveys conducted in these sites.

Code	Name	Status	Size (km ²)	Sampling				
				Period	Area covered (km ²)	No. stations	Interspacing (km)	Total effort (days)
<i>Reference sites</i>								
CAN	Cana	NP	5970	2005/06	110	44	1–3.2	2049
PIR	Pirre	NP	5970	2014	73	44	0.8–1.5	3372
<i>Sites east of the Panama Canal</i>								
COC	Cocobolo	PA	4	2013	1	16	0.33	603
PBO	Portobelo	NP	349	2013/14	1	29	0.33	766
StDom	Sant Domingo	PL	0.8	2012/13	0.8	31	0.03	695
SrLlor	Sierra Llorona	PL	2.1	2012/14	1	29	0.33	673
LIM	Limon	PL	0.02	2012/13	0.02	30	0.03	739
AgSa1	Agua Salud 1	PL	0.3	2012/14	0.3	30	0.03	798
AgSa2	Agua Salud 2	PL	0.2	2012/14	0.2	24	0.03	595
AgSa3	Agua Salud 3	PL	0.3	2012	0.3	16	0.03	575
SOB	Soberania	NP	225	2011/12/13	120	87	1.4	2864
PLA	Plantation Road	NP	225	2013/14	1	29	0.33	723
<i>Sites west of the Panama Canal</i>								
EMP	Nuevo Emperador	PL	0.4	2013/14	0.4	29	0.1	583
BCNM	Barro Colorado	NM	54	2011/12/13	54	87	1.4	2937
SanLo	San Lorenzo	NP	97	2012	25	24	0.3–0.5	624
CCA	Cerro Cama	PL	0.1	2013/14	0.1	30	0.03	610
PIN	Piña	PL	0.02	2013/14	0.02	26	0.03	529

NP = National park; PL = Forest fragment in a private land; NM = Nature Monument; PA = Private protected area. Area covered is the size of the camera trap survey. Interspacing is the distance in km between the cameras. Total effort is the total number of camera days.

Central America and is relatively intact (Condit et al. 2001; Moreno 2006).

Camera trap surveys

Camera-trapping surveys were conducted as part of different projects with different objectives and thus different designs and protocols. All surveys used unbaited camera traps deployed during the dry season and accounted for > 500 trapping nights (Table 1) to have a sufficient sampling effort; it usually takes around 400 trap nights to record most of the common species in tropical forests (Tobler et al. 2008). The surveys in Darién were designed to estimate jaguar density, while the other surveys were designed to randomly capture any terrestrial mammal species. The 15 sites in Central Panama were surveyed with camera traps (Reconyx PC 900 Hyperfire–Reconyx, Inc, WI, USA) placed at 16–30 computer-generated points in grids. The surveys in the Barro Colorado Nature Monument (BCNM) and Soberania NP followed the protocol of the Tropical Ecology Assessment and Monitoring Network (TEAM Network 2011; Jansen et al., 2014). The Darien sites were surveyed with 45 stations of cameras (Cuddeback Capture–Cuddeback, WI, USA) set up in pairs along trails and ridges. Cameras in large areas were placed in a subset of the area, while cameras in small fragments were set up in a way that the entire site was sampled (Table 1).

Photos from BCNM and Soberania NP were processed in DeskTEAM (Fegraus et al. 2011), photos from Darién NP and San Lorenzo NP were annotated in Excel 2007 (Microsoft Corporation, Redmond WA, USA), and photos from the other sites in Central Panama were processed in the ForestGEO camera-trapping database (as in Kays et al. 2011; <http://www.forestgeo.si.edu>). Photos were manually grouped into sequences that represented the same visit of an animal or group of animals (notably coatis *Nasua narica* and pecarries species *Tayassu pecari* and *Pecari tajacu*) in a 2 h-interval, which triggered the same camera one or multiple times depending on movement speed and residence time. This filter assured that visit events were independent despite the fact that some species, especially the Central American agouti *Dasyprocta punctata*, can spend a longer time in the area around the camera. Animal identifications were based on Reid (2009). We excluded strictly arboreal mammal species (primates and Rothschild's porcupine

Coendou rothschildi), species that are mostly aquatic or riverine (capybara *Hydrochoerus isthmus* and Neotropical river otter *Lontra longicaudis*), small species that are not systematically detected by the camera traps (mouse species and *Marmosa robinsoni*) and all bird species. We calculated the detection rates for species, a measure of relative abundance, as the number of visits photographed per 100 trap days. We assumed that for most species, the number of visits that the cameras recorded is proportional to the local density of the species, i.e. cameras will record a species more often where it is more abundant (O'Connell et al. 2011).

Data analysis

To account for differences in sampling effort when estimating species richness for each site, we generated sample-based rarefaction curves in EstimateS v.9.0 (Colwell 2013). Curves were fitted to deployments – i.e. a run of a camera trap at a single point within a site – and then rescaled to the number of animal detections in that deployment as given by the variable “individuals” in the output of Estimate S. We used the Jackknife 1 estimator of species richness because it performs better with camera trapping data than do the Chao indices (Tobler et al. 2008), and gave the closest estimation to the total number of 30 species known for Darién (Reid 2009). Pielou's evenness index, a measure of diversity related to the relative abundance of species in a community, was calculated using standard methods (Shannon & Weaver 1963). The index of defaunation (D) is a quantitative/weighted measure of dissimilarity between a focal assemblage of a given location and a reference assemblage that represents an unperturbed state (Giacomini & Galetti 2013). We calculated D of each community in Central Panama with respect to two reference communities, i.e. Cana and Pirre, following the index proposed by Giacomini and Galetti (2013): $(r, f) = \frac{\sum_{k=1}^S w_k(N_{k,r} - N_{k,f})}{\sum_{k=1}^S w_k(N_{k,r} + N_{k,f})}$ with r the reference community i.e. Pirre or Cana, f the focal community, i.e. the sites in Central Panama, S the total number of species, k the particular species, N the occurrence (presence/absence) of species k in the reference and the focal community, W_k the importance of a species k assigned by the body size (kg) raised to the power of 0.75 (Table 2).

Table 2

Terrestrial mammal species recorded by camera traps across 17 forest sites in Panama, their diet, body size, size, and the number of sites where they were recorded.

	Species	Common name	Diet	Body size (kg)	Size class	No. sites recorded	
						Darién	Central Panama
DIDELPHIMORPHIA							
Didelphidae	<i>Metachirus nudicaudatus</i>	Brown four-eyed opossum	IO	0.4	S	1 (of 2)	8 (of 15)
	<i>Philander opossum</i>	Gray four-eyed opossum	IO	0.7	S	0	8
	<i>Didelphis marsupialis</i>	Common opossum	FO	1.4	S	2	15
CINGULATA							
Dasypodidae	<i>Cabassous centralis</i>	Northern naked-tailed armadillo	MY	3.3	M	0	9
	<i>Dasyplus novemcinctus</i>	Nine-banded armadillo	IO	4.7	M	2	15
PILOSA							
Myrmecophagidae	<i>Tamandua mexicana</i>	Northern tamandua	MY	5.5	M	1	12
	<i>Myrmecophaga tridactyla</i>	Giant Anteater	MY	36	L	1	0
RODENTIA							
Cuniculidae	<i>Cuniculus paca</i>	Lowland paca	FG	8.3	L	2	14
Dasyproctidae	<i>Dasyprocta punctata</i>	Central American agouti	FG	3.1	M	2	15
Echimyidae	<i>Hoplomys gymnurus</i>	Armored rat	FO	0.4	S	1	12
	<i>Proechimys semispinosus</i>	Tome's spiny rat	FG	0.4	S	2	11
Sciuridae	<i>Sciurus granatensis</i>	Red-tailed squirrel	FG	0.3	S	2	14
LAGOMORPHA							
Leporidae	<i>Sylvilagus brasiliensis</i>	Forest rabbit	HZ	1	S	2	6
CARNIVORA							
Canidae	<i>Cerdocyon thous</i>	Crab-eating fox	CA	5.9	M	2	1
	<i>Canis latrans</i>	Coyote	CA	12.8	L	0	2
Felidae	<i>Leopardus tigrinus</i>	Oncilla	CA	2.2	M	1	0
	<i>Leopardus wiedii</i>	Margay	CA	3.6	M	2	5
	<i>Puma yagouaroundi</i>	Jaguarundi	CA	6.5	L	1	10
	<i>Leopardus pardalis</i>	Ocelot	CA	11.1	L	2	13
	<i>Puma concolor</i>	Puma	CA	46.8	L	2	2
	<i>Panthera onca</i>	Jaguar	CA	76.6	L	2	1
Mustelidae	<i>Galictis vittata</i>	Greater grison	CA	3.2	M	1	3
	<i>Eira barbara</i>	Tayra	FO	4.3	M	2	13
Procyonidae	<i>Nasua narica</i>	White-nosed coati	FO	4.3	M	1	14
	<i>Procyon cancrivorus</i>	Crab-eating racoon	FO	5.7	M	1	10
	<i>Procyon lotor</i>	Northern racoon	FO	5.5	M	0	1
PERISSODACTYLA							
Tapiridae	<i>Tapirus bairdii</i>	Baird's tapir	FH	260	L	2	1
ARTIODACTYLA							
Cervidae	<i>Mazama temama</i>	Red brocket deer	FH	22.8	L	2	7
	<i>Odocoileus virginianus</i>	White-tailed deer	HB	41.2	L	0	6
Tayassuidae	<i>Pecari tajacu</i>	Collared peccary	FO	19.8	L	2	10
	<i>Tayassu pecari</i>	White-lipped peccary	FH	33.8	L	2	1

Diet class was taken from [Robinson and Redford \(1986\)](#): CA: carnivore, FH: frugivore-herbivore, FG: frugivore-granivore, FO: frugivore-omnivore, HB: herbivore-browser, HZ: herbivore-grazer, IO: insectivore-herbivore, MY: myrmecophage. Body size was taken from [Smith et al. \(2003\)](#), and size class follow the classification of [Peres \(2000\)](#): S: small, M: medium, L: large.

Body size is a proxy for vulnerability to extinction and conservation concern ([Giacomini & Galetti 2013](#)). An index close to the upper limit 1 indicates a higher defaunation where most species are absent in a focal community while an index close to 0 occurs when the two communities are similar and when little defaunation has occurred.

We used the 95% confidence intervals of each curve to test for differences in species richness between sites ([Gotelli & Colwell 2001](#); [Colwell et al. 2004](#)). Residuals of species evenness were normally distributed (Shapiro–Wilk $df = 15$, $p = 0.622$) so we used one-sample t -tests in SPSS 19 ([SPSS Inc. 2011](#)) to determine whether evenness was lower in Central Panama than at the two reference sites in Darién. Residuals of the defaunation indices were normally distributed when either Cana or Pirre were used as a reference site (Shapiro Wilk, $df = 15$, $p_{\text{cana}} = 0.495$, $p_{\text{pirre}} = 0.507$) and Levene's tests confirmed homogeneity of variances ($F_{\text{pirre}} = 0.065$, $p = 0.937$, $F_{\text{cana}} = 0.070$, $p = 0.933$). We therefore conducted a one-way ANOVA and a Tukey–Kramer post-hoc test in SPSS to test whether the index of defaunation was different at a significant level of 0.05 between national parks and fragments east and west of the Panama Canal. The capture rate of each species, centered by species, was compared between sites with a Principal Component Analysis (PCA) on the species \times sites matrix using the software CANOCO 5 ([Braak & Smilauer, 2002](#)) with square-root transformed detection rates.

Results

A total of 31 terrestrial mammal species from 15 families were recorded, of which only three were captured in all 17 sites: agouti, nine-banded armadillo and common opossum ([Table 2](#)). Species richness was highest in one reference site, Pirre ($\hat{S} = 27$), followed by two national parks in the Canal area, BCNM and Soberania ($\hat{S} = 23$ and $\hat{S} = 22$, respectively; [Fig. 2A](#); [Table 3](#)). Richness was lowest in Cerro Cama (CCA: $\hat{S} = 14$), a small fragment on the western side of the Panama Canal, and in one site of Agua Salud (AgSa3: $\hat{S} = 15$; [Fig. 2B](#); [Table 3](#)). Overall, small forest fragments tended to have fewer species for a given number of individuals photographed than did protected sites ([Fig. 2](#)). Species richness was significantly higher at the reference site Pirre than all the other sites, as shown by non-overlapping confidence intervals of the species accumulation curves ([Table 3](#)), while richness was significantly lower for the fragments StDom and CCA than for Soberania and BCNM but not the other sites. The rest of the sites did not differ significantly from each other in terms of species richness.

Species evenness tended to be higher in the reference site Cana and at Cocobolo, and lowest in San Lorenzo and Barro Colorado ([Table 3](#)), mainly due to relatively high detection rates of agouti at the latter sites ([Table 3](#)). Compared to sites in central Panama, evenness was higher in Cana but lower in Pirre (One-sample t -test, $df = 14$, $t_{\text{cana}} = 4.465$, $p_{\text{cana}} = 0.001$ and $t_{\text{pirre}} = 2.144$, $p_{\text{pirre}} = 0.05$).

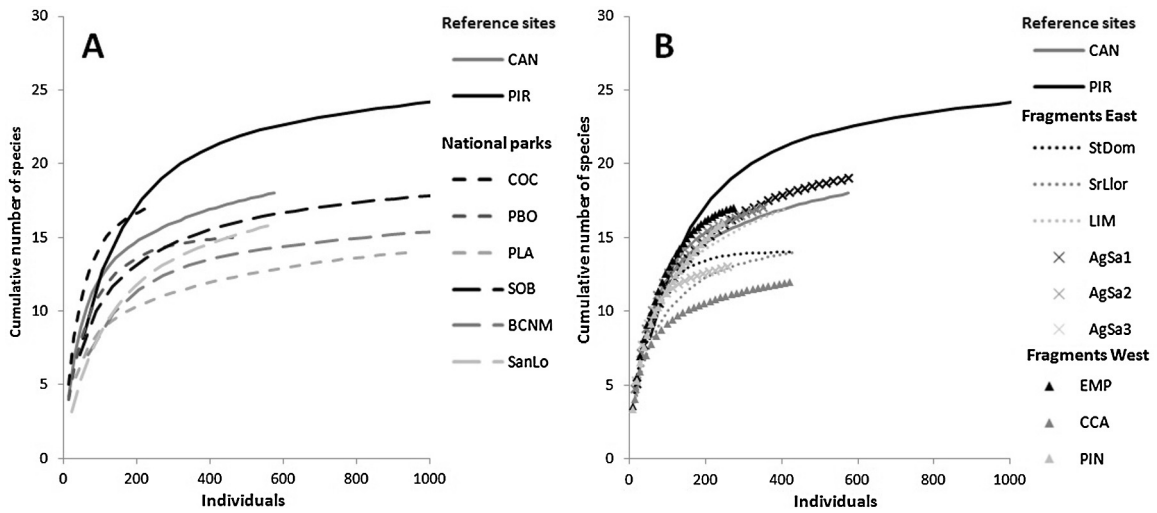


Fig. 2. Sample-based rarefaction curves, based on camera-trapping data of 15 sites in Central Panama (National parks—(A) and forest fragments—(B)) and two reference sites in Darién. See Table 1 for site codes.

Table 3
Observed and estimated species richness with 95% confidence intervals, evenness and index of defaunation based on two different reference sites of the terrestrial mammal communities recorded in camera trapping surveys in 2 sites of Darién and 15 sites of Central Panama, ranked east to west. Sites with different letters present significantly different species richness, while letters shared in common between the sites indicate no significant difference in species richness.

Site	Species richness				Sig. difference	Shannon Evenness	Index of defaunation	
	Observed	Jack 1	Lower CI	Upper CI			Cana	Pirre
CAN	18	20.92	15.26	20.74	ab	0.78	–	–
PIR	26	26.98	25.21	26.79	c	0.63	–	–
COC	17	18.88	15.48	18.52	ab	0.83	0.35	0.42
PBO	15	15.97	10.13	19.87	ab	0.71	0.39	0.43
StDom	14	14.00	14.00	14.00	a	0.77	0.66	0.70
SrLlor	14	15.93	9.02	18.98	ab	0.64	0.50	0.56
LIM	17	20.87	13.52	20.48	ab	0.64	0.59	0.65
AgSa1	19	21.9	16.26	21.74	ab	0.72	0.40	0.47
AgSa2	17	19.88	11.76	22.24	ab	0.70	0.54	0.60
AgSa3	13	14.88	11.17	14.83	ab	0.75	0.51	0.57
SOB	20	21.98	18.1	21.9	b	0.66	0.37	0.44
PLA	14	15.93	9.02	18.98	ab	0.67	0.44	0.50
EMP	17	19.12	12.29	21.58	ab	0.70	0.46	0.53
BCNM	20	22.97	17.23	22.77	b	0.54	0.11	0.19
SanLo	16	19.83	11.54	20.46	ab	0.48	0.37	0.44
CCA	12	13.93	6.94	17.06	a	0.74	0.69	0.73
PIN	16	21.77	10.32	21.68	ab	0.63	0.57	0.63

Bold sites are protected. CI = 95% confidence interval.

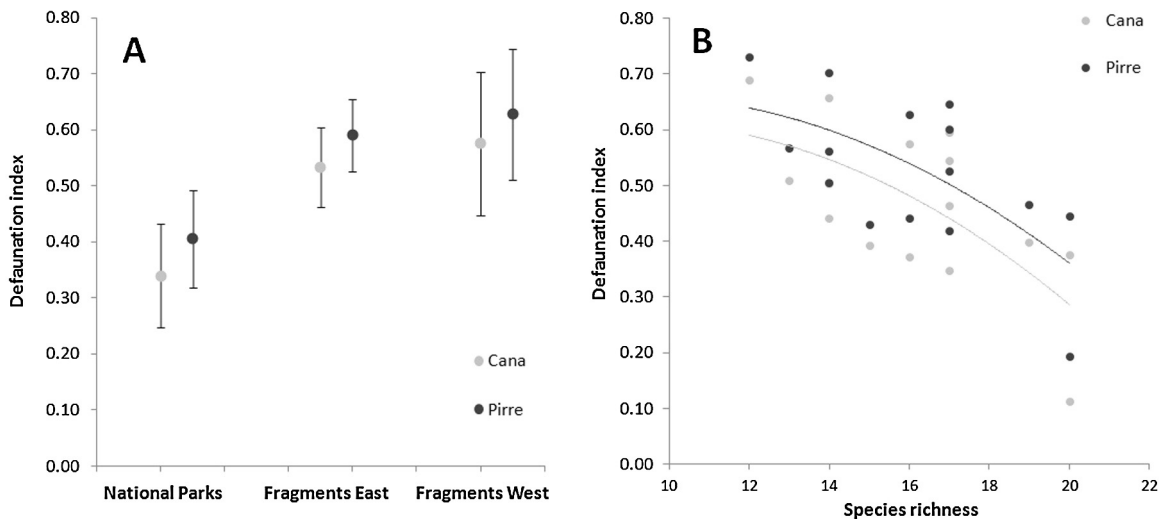


Fig. 3. Mean defaunation index (D) with error bars based on body size in mammal communities of Central Panama with respect to reference communities in Pirre and Cana in Darién (A) and as a function of species richness (B).

The indices of defaunation were different between the national parks and the fragments east and west when either Pirre or Cana were used as reference sites (ANOVA, $df=2$, $F_{\text{Cana}}=7.221$, $p_{\text{Cana}}=0.009$ and $F_{\text{Pirre}}=8.101$, $p_{\text{Pirre}}=0.006$) (Table 3). Specifically, there was no difference between the fragments east and west of the Panama Canal but the defaunation in the national parks of Central Panama was lower than in the forests fragments (Fig. 3A). The index of defaunation varied substantially at the same richness but tended to decrease with species richness ($R^2_{\text{Cana}}=0.45$ and $R^2_{\text{Pirre}}=0.43$) (Fig. 3B).

Community composition varied widely among sites (Fig. 4). The first two axes of the ordination diagram explained 56.0% of the total variation in the community composition of terrestrial mammals among sites. The first axis (36.7% of the total variation) explained the variation in species community structure among the protected sites in Panama, and was strongly related to the relative abundance of game species (i.e. lowland paca, collared peccary, white-tailed deer and red brocket deer) and species that are persecuted because of the damage they induce to crops (i.e. coati). Their abundance increased along the first axis and was highest in the larger protected sites of Central Panama (i.e. Soberania, San Lorenzo and especially Barro Colorado and Plantation road) and where large predators and frugivores were not detected. The second axis (17.3% of the total variation) explained the differences between the small sites in Central Panama and the larger, more remote sites in Portobelo and Darién, and was related to the abundance of two groups of species. The first group included tapir, white-lipped peccary, giant anteater, jaguar and puma, which are large indicator species that require large tracts of contiguous forest, and that are locally in danger of extinction. While relatively abundant in Darién, these species were not detected in Central Panama except at the two most remote sites, where they were rare. The second group consisted of small- to medium-sized species that are habitat generalists and are not actively targeted by hunters (e.g., rats, opossums and armadillos). These species were relatively abundant in the smaller, unprotected forest fragments.

Discussion

This study used camera-trapping surveys to assess the composition of terrestrial mammal communities in the forests of Central Panama, the narrowest and most disturbed part of the Isthmus of Panama, and a key area for conservation in the region. We found that most sites in Central Panama had lower species richness and a relatively poor representation of large-bodied species compared to the relatively undisturbed reference sites. These findings indicate that the terrestrial mammal community in forests of Central Panama is currently degraded, even inside national parks.

Our hypothesis that terrestrial mammal communities in the forests of Central Panama are degraded was supported by the survey data. First, as predicted, communities in Central Panama had lower species richness compared to the reference communities in Darién, and were less structurally-complex revealing the rarity of top predators and large frugivores in most Central Panamanian sites. Large frugivores (i.e. tapirs) were only detected on Barro Colorado Island (BCI), which is intensively patrolled by game wardens, whereas other indicator species were only detected in the more remote, protected sites that lie adjacent to the large tracts of forests that run continuously along the Atlantic coast towards Darién. The patterns observed agree with tropical studies where species richness decreased in forest fragments (Turner 1996), smaller sites in the Brazilian Atlantic Forest (Chiarello 1999) and in sites surrounded with higher disturbance (Ahumada et al. 2011). Evenness was higher in Cana but lower in Pirre, in contrast to Ahumada et al. (2011) who did not find differences in evenness between sites with

different sizes and disturbance degree. The index of evenness is related to the abundance of species in a community, and a low index of evenness thus indicates the dominance of one or several species. The abundance of the agouti was much higher than the other species in most sites with the exception of Cana, which could explain the low evenness values.

Second, we hypothesized that degradation of mammal communities would be greater for forest fragments than for national parks, and greater towards the West, further away from the larger protected forests blocks lying on the Eastern side of the Canal. These predictions were partially supported by the data. Most national parks had relatively high species richness and our results show a high heterogeneity in structure among wildlife communities throughout Central Panama. However, there was no difference between the fragments east and west of the Panama Canal; they were equally degraded. In general, small forest fragments were characterized by small- to medium sized mammals with smaller home ranges and that can therefore persist in these smaller disturbed habitats, just as Chiarello (1999) found in the Atlantic Forest in Brazil. In contrast, larger common species, i.e. the deer and collared peccary, were more frequently detected in sites east of the Canal that were relatively large and protected, or forest fragments adjacent to these protected areas. This was further corroborated by the index of defaunation which was higher in the fragments indicating that communities of Central Panama tended to become impoverished by losing larger species similarly to what Giacomini and Galetti (2013) had already showed. Small fragments usually cannot sustain large vertebrates (Peres 2001) and bias of mammal communities towards smaller species is a well-known effect of fragmentation (Chiarello 1999; Kinnaird et al. 2003). Habitat loss and fragmentation also promote hunting by increasing forest accessibility to poachers who prefer to harvest medium- to large sized herbivores and granivores (Peres 2001; Wright et al. 2000). Although illegal, hunting pressure is high throughout Central Panama (Wright et al. 2000; RM & NM pers. obs.) including protected areas that are easily accessible (RM & NM pers. obs.).

Hunting coupled with fragmentation may explain the absence or rarity of large vulnerable species such as tapir, white-lipped peccary, giant-anteater, jaguar and puma in Central Panama. Outside of BCI, tapirs are extremely rare in Central Panama and have not been reported for decades (Meyer et al. 2013). White-lipped peccaries require large areas of several thousand hectares to maintain breeding populations and are highly sensitive to hunting (Reyna-Hurtado et al. 2009), especially in Panama where they are the favored game species and have gone locally extinct in many areas (Moreno & Meyer 2014). The elusive giant-anteater has never been reported in sites adjacent to the Canal, but was sighted in 2012 in Boquerón close to our sites in Santo Domingo (R. Morales pers. com.). Jaguars and pumas do still occur in Central Panama, though at a very low density as they have never been photographed in the protected sites adjacent to the Canal (i.e. Soberania, San Lorenzo, Barro Colorado), except for one individual that spent 6 months in BCI in 2009 (Willis 2009). However, sightings and tracks are sporadically reported by researchers and game wardens working in Barro Colorado and in Soberania, and by local people in the matrix of Central Panama (Moreno et al. in press). These individuals might be migrating through the landscape rather than being residents in the area, because they have very large home ranges and are heavily persecuted by people (Moreno et al. in press).

Our camera traps recorded two species that are relatively newcomers to Central Panama. The coyote, known from North America, was recorded in Piña, close to the Panama Canal. This species has already been reported more south at the border with the Darién Province (Mendéz-Carvajal and Moreno 2014). The crab-eating fox, native to South America, was recorded next to a cleared area near an indigenous community in Darién, and along the Panama Canal

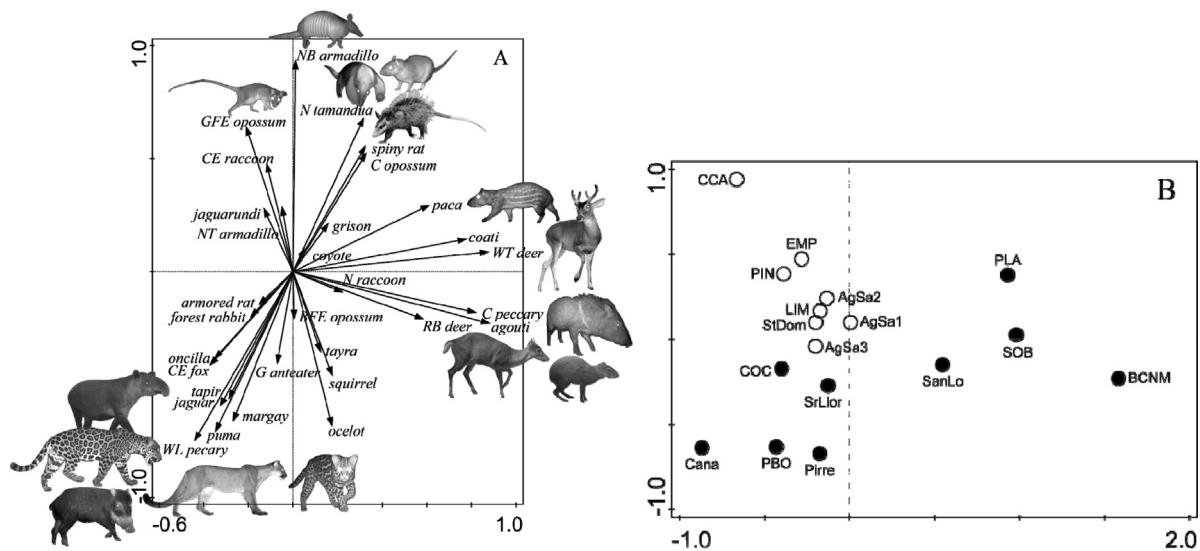


Fig. 4. Results of a Principal Component Analysis of terrestrial mammal communities, based on capture rates by camera traps, at 15 forest sites in Central Panama and two 2 reference sites in Darién, for species (A) and sites (B). Arrows in (A) indicate the direction of maximum change in relative abundance across the ordination plot, where arrow length is proportional to the change. Black circles in (B) represent sites that are protected, and open circles represent forest fragments. See Table 1 for site codes. The distances between sites indicate their similarity in terms of species composition and abundance.

in Limon. The two species are habitat generalists and are thus well adapted to survive in fragmented landscapes that may in fact have facilitated their range expansion (Faria-Corrêa et al. 2009; Mendéz-Carvajal and Moreno 2014).

Two key assumptions are underlying our analysis. The first is that all mammals found in our Darién surveys have originally occurred in Central Panama before any defaunation took place in historic years. Indeed, all species photographed in Darién, except for oncilla and giant anteater, were also photographed in our sites in Central Panama, although none of the surveys recorded all species in a single site. Moreover, these species are also present in Donoso, a primary forest near central Panama at the opposite side (Moreno unpub. data), and old studies report the presence of most species in Central Panama (Goldman 1920). The second assumption was that the surveys in the respective forests sites described the composition of the mammal communities in a sufficiently comparable manner, despite the fact that designs differed between surveys. We believe that the difference of camera traps settings (on/off-trail) between Darién and Central Panama – which may cause differences in detection of large felids that preferentially use trails (Harmsen et al. 2009) – was not a problem in our study, as on-trail camera-trapping surveys undertaken in Soberania and BCNM – not included in this study – confirm the rarity of large cats in Central Panama (Moreno and Willis, unpub. data). Also, the reference communities were logically positioned in the ordination results rather than being outliers. Variation in camera spacing should have had little impact on the results (Tobler et al. 2008) because in most sites the species accumulation curves reached an asymptote. Nevertheless, in the future, further standardizing the study design may help reducing variation in detection rates across surveys (cf. Sollmann et al., 2013).

Our study provides a baseline for the monitoring of mammal communities in Central Panama forests over time. Evaluating the mammal community on a regular basis with the surrounding development activities will help to evaluate the effectiveness of measures, if they are taken, to increase protection and restore connectivity to prevent the Panamanian Isthmus becoming a bottleneck for the movement of animals. Our study does not allow to identify the mechanisms underlying the degradation of mammal communities that we observed, but it is probable that

hunting, forest degradation, physical barriers and isolation, or a combination of these are involved. Actions that could possibly lead to recovery would then include: (1) Enhance connectivity between parks and fragments, for example by implementing biological corridors and creating wildlife overpasses over the road network along the Canal to facilitate mammal movements and gene flow between forests now separated (Olsson et al. 2008); (2) Enhanced forest protection coupled with better education of local people to reduce poaching (Moreno et al. in press); (3) Reduce forest conversion and degradation, for example by implementing a program of payments for ecosystem services (Rodríguez 2014).

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References

- Ahumada, J. A., Silva, C. E. F., Gajapersad, K., Hallam, C., Hurtado, J., Martin, E., et al. (2011). Community structure and diversity of tropical forest mammals: Data from a global camera trap network. *Philosophical Transactions of the Royal Society B*, 366, 2703–2711.
- Braak, C. J. F., & Smilauer, P. (2002). *CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5)*.
- Chiarello, A. G. (1999). Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biological Conservation*, 89, 71–82.
- Colwell, R. K., Mao, C. X., & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85, 2717–2727.
- Colwell, R. K. (2013). *EstimateS: Statistical estimation of species richness and shared species from samples*. Version 9. User's Guide and application published at: (<http://purl.oclc.org/estimates>).
- Condit, R., Robinson, W. D., Ibáñez, R., Aguilar, S., Sanjur, A., Martínez, R., et al. (2001). The status of the Panama Canal watershed and its biodiversity at the beginning of the 21st century. *BioSciences*, 51, 389–398.
- Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, 16, 488–502.
- Faria-Corrêa, M., Balbuena, R. A., Vieira, E. M., & de Freitas, T. R. O. (2009). Activity, habitat use, density, and reproductive biology of the crab-eating fox (*Cerdocyon thous*) and comparison with the pampas fox (*Lycalopex gymnocercus*) in a restinga area in the southern Brazilian Atlantic Forest. *Mammalian Biology*, 74, 220–229.
- Fegraus, E. H., Lin, K., Ahumada, J. A., Baru, C., Chandra, S., & Youn, C. (2011). Data acquisition and management software for camera trap data: A case study from the TEAM Network. *Ecological Informatics*, 6, 345–353.
- Food and Agriculture Organization of the United Nations. (2010). *Global forest resources assessment*. ISBN 978-92-5-106654-6.
- Giacomini, H. C., & Galetti, M. (2013). An index for defaunation. *Biological Conservation*, 163, 33–41.
- Goldman, E. W. (1920). Mammals of Panama (with thirty-nine plates). In *Smithsonian miscellaneous collections* 69. City of Washington, USA: Smithsonian Institution.
- Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecological Letters*, 4, 379–391.
- Grandia, L. (2007). Between Bolivar and bureaucracy: the Mesoamerican Biological Corridor. *Conservation and Society*, 5, 478–503.
- Griffiths, M., & van Schaik, C. P. (1993). The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Conservation Biology*, 7, 623–626.
- Harmsen, B. J., Foster, R. J., Silver, S., Ostro, L., & Doncaster, C. P. (2009). Differential use of trails by forest mammals and the implications for Camera-Trap Studies: A case study from Belize. *Biotropica*, 42, 126–133.
- Heckadon Moreno, S. (1993). Impact of development on the Panama Canal environment. *Journal of Interamerican Studies and World Affairs*, 35, 129–149.
- Ibáñez, R., Condit, R., Angehr, G., Aguilar, S., Garcia, T., Martínez, R., et al. (2002). An ecosystem report on the Panama Canal: Monitoring the status of the forest communities and the watershed. *Environmental Monitoring and Assessment*, 80, 65–95.
- Jansen, P. A., Ahumada, J., Fegraus, E., & O'Brien, T. (2014). TEAM: a standardised camera-trap survey to monitor terrestrial vertebrate communities in tropical forests. In P. D. Meek, A. G. Ballard, P. B. Banks, A. W. Claridge, P. J. S. Fleming, J. G. Sanderson, & D. E. Swann (Eds.), *Camera Trapping: Wildlife Research and Management* (pp. 263–270). Melbourne, Australia: CSIRO Publishing.
- Kays, R., Tilak, S., Kranstauber, B., Jansen, P. A., Carbone, C., Rowcliffe, M., et al. (2011). Camera Traps as Sensor Networks for Monitoring Animal Communities. *International Journal of Research and Reviews in Wireless Sensor Networks*, 1, 19–29.
- Kinnaird, M. F., Sanderson, E. W., O'Brien, T. G., Wibisono, H. T., & Woolmer, G. (2003). Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology*, 17, 245–257.
- Marshall, L. G., Webb, S. D., Sepkoski, J. J., & Raup, D. M. (1982). Mammalian evolution and the Great American Interchange. *Science*, 215, 1351–1357.
- Mendez-Carvajal, P. (2012). Estudio de diversidad de mamíferos en cuatro habitats asociados a una plantación de Teca (*Tectona grandis*) dentro de la cuenca del Canal de Panamá. Las Pavas, Chorrera, Panamá. *Tecnociencia*, 14, 55–83.
- Méndez-Carvajal, P., & Moreno, R. (2014). Mammalia, Carnivora, Canidae, *Canis latrans* (Say, 1823): Actual distribution in Panama. *Check List*, 10, 376–379.
- Meyer, N., Moreno, R., & Jansen, P. (2013). Distribution and conservation status of the Baird's tapir in Panama. *Tapir Conservation*, 30, 10–13.
- Moreno, R. (2006). *Parámetros poblacionales y aspectos ecológicos de los felinos y sus presas en Cana*. Parque Nacional Darien, Panamá: National University of Costa Rica (MSc Thesis).
- Moreno, R., & Meyer, N. (2014). Distribution and conservation status of the white-lipped peccary (*Tayassu pecari*) in Panama. *Suiform Soundings*, 13, 32–37.
- Moreno, R., Bustamante, A., Méndez-Carvajal, P., and Moreno, J. (n.d.). *Jaguars (Panthera onca)* en Panamá: Estado actual y conservación. In: R. A. Medellín, J. A. de la Torre, C. Chávez, H. Zarza, and G. Ceballos, editors. *El jaguar en el Siglo XXI: La perspectiva Continental*. Fondo de Cultura Económica, Universidad Nacional Autónoma de México, Ciudad de México.
- O'Connell, A. F., Nichols, J. D., & Karanth, K. U. (2011). *Camera traps in animal ecology: Methods and analyses* (1st ed.). Springer.
- Olsson, M. P. O., Widén, P., & Larkin, J. L. (2008). Effectiveness of a highway overpass to promote landscape connectivity and ovement of moose and roe deer in Sweden. *Landscape and Urban Planning*, 85, 133–139.
- Peres, C. A. (2001). Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology*, 15, 1490–1505.
- Peres, C. A. (2000). Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology*, 14, 240–353.
- Reid, F. A. (2009). *A field guide to the mammals of Central America and Southeast Mexico*. Oxford University Press: USA.
- Reyna-Hurtado, R., Rojas-Flores, E., & Tanner, G. W. (2009). Home range and habitat preferences of white-lipped peccaries (*Tayassu pecari*) in Calakmul, Campeche, Mexico. *Journal of Mammalogy*, 90, 1199–1209.
- Robinson, J. G., & Redford, K. H. (1986). Body size, diet, and population density of Neotropical forest mammals. *The American Naturalist*, 128, 665–680.
- Rodríguez, C. M. (2014). *Carbono, agua y jaguares nueva propuesta de pagos por servicios ambientales en Costa Rica*. Panthera: Conservación de Felinos en América.
- Shannon, C. E., & Weaver, W. (1963). *The mathematical theory of communication*. University of Illinois Press: USA.
- Silveira, L., Jacomo, A. T. A., & Diniz-Filho, J. A. F. (2003). Camera trap, line transect census and track surveys: A comparative evaluation. *Biological Conservation*, 114, 351–355.
- Smith, F. A., Lyons, S. K., Ernest, S. K. M., Jones, K. E., Kaufman, D. M., Dayan, T., et al. (2003). Body mass of late quaternary mammals. *Ecology*, 84, 3403.
- Sollmann, R., Mohamed, A., Samejima, H., & Wilting, A. (2013). Risky business or simple solution—Relative abundance indices from camera-trapping. *Biological Conservation*, 159, 405–412.
- SPSS Inc. (2011). *IBM SPSS for Windows, version 19.0*. Chicago, IL: SPSS Inc (Released).
- TEAM Network. (2011). *Terrestrial vertebrate protocol implementation manual, v. 3.1. Tropical ecology, assessment and monitoring network, center for applied biodiversity science*. Arlington, VA: Conservation International.
- Tobler, M., Carrillo-Percastegui, S., Leite Pitman, R., Mares, R., & Powell, G. (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, 11, 169–178.
- Turner, I. M. (1996). Species loss in fragments of tropical rain forest: A review of the evidence. *Journal of Applied Ecology*, 33, 200–209.
- Urquiza-Haas, T., Peres, C. A., & Dolman, P. M. (2011). Large vertebrate responses to forest cover and hunting pressure in communal landholdings and protected areas of the Yucatan Peninsula, Mexico. *Animal Conservation*, 14, 271–282.
- USAID. (2009). *Marco conceptual y planes de acción de los corredores biológicos del Filo de Santa Rita y Campo Chagres para la conectividad de los Parques Nacionales Soberanía y Chagres*. Proyecto Conservación de la Biodiversidad en la Cuenca del Canal. Panamá: USAID (Unpublished report).
- Willis, J. (2009). Jaguars at the crossroads of the continents. *Jaguar News*, 28, 3.
- Wright, S. J., Zeballos, H., Domínguez, I., Gallardo, M. M., Moreno, M. C., & Ibáñez, R. (2000). Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology*, 14, 227–239.