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Source: Tropical Conservation Science, 11(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082918809617

Tropical Conservation Science
Volume 11: 1–10

DOI: 10.1177/1940082918809617
journals.sagepub.com/home/trc
SAGE

Status of Large Terrestrial Vertebrates in the Monteverde-Arenal Bioregion, Northwestern Costa Rica

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Abstract

Protected areas have been important in reducing tropical forest biodiversity loss. Costa Rica has been a model country in protecting forests and promoting conservation. However, many Costa Rican protected areas are surrounded by highly modified habitat and may be losing species, either because they are too small to support viable populations or are too isolated to allow for population connectivity. We used camera traps to study terrestrial mammal and terrestrial bird populations in the Monteverde-Arenal Bioregion of northwestern Costa Rica. We sampled core protected areas and nearby unprotected, fragmented habitats. Of 33 species historically found in the region, we detected 25. However, most species were rarely detected, and only five were found more than once per 30 days of camera time. The most commonly detected species represented major feeding groups, including obligate herbivores, omnivores, and obligate carnivores. Most ungulates were rare and may not have viable population sizes. However, a top predator, the puma (*Puma concolor*), was commonly detected. Fragmented areas had lower abundance and fewer species detected; a few species were not detected at all, even though some of them were abundant in the core protected areas. We suggest that conservation efforts are protecting some terrestrial mammals and birds, and there is a functioning food web. However, many species are either rare or extirpated, indicating the Monteverde-Arenal Bioregion is a partially defaunated landscape.

Keywords

arenal, camera study, conservation, Costa Rica, Monteverde, terrestrial birds, terrestrial mammals

Introduction

Tropical forests support high levels of biodiversity but are undergoing rapid deforestation, and it has been estimated that there has been a 62% acceleration in deforestation of humid tropics from 1990 to 2010 (Kim, Sexton, & Townshend, 2015). Because of the interest in conservation of tropical forests, many locations have some level of protection, although effectiveness of conservation efforts varies (Andam, Ferraro, Pfaff, Sanchez-Azofeifa, & Robalino, 2008; Börner et al., 2016; Bruner, Gullison, Rice, & Da Fonseca, 2001; Hayes, 2006). Costa Rica has been particularly effective at conserving its tropical forests (Sánchez-Azofeifa, Daily, Pfaff, & Busch, 2003), with about 26% of land currently under formal protection and national rates of forest cover that have increased considerably in the last 20 years (González-Maya, Víquez-R, Belant, & Ceballos, 2015). Although some large blocks of protected tropical forest probably contain most native fauna historically present, many important protected areas are relatively small and isolated. A large body of

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Received 26 July 2018; Revised 4 October 2018; Accepted 5 October 2018

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research (reviewed in Fahrig, 2013) shows that isolated habitat, even when well protected, tends to lose biodiversity. Fragmentation of tropical forests tends to disproportionately impact large animals and specialized species (Fritz, Bininda-Emonds, & Purvis, 2009; Turner, 1996). Large terrestrial birds (e.g., guans and tinamous), which are an important component of neotropical forests, are sensitive to fragment size, level of isolation, and amount of edge habitat, and they tend to be extirpated from small, isolated patches (Thornton, Branch, & Sunquist, 2012). Declines in large animals due to forest fragmentation have been linked to changes in habitat and increased hunting pressure (Peres, 2001). The greater specialization of tropical forest mammals and their greater intolerance to disturbed areas or willingness to travel across deforested areas (Laurance et al., 2002) may further increase their risk of extinction in fragmented areas (Peres, 2001). A possible solution for this dilemma is the creation of functional biological corridors, a strategy that is currently underway in Costa Rica (Chassot & Monge-Arias, 2012; Fung et al., 2016; Gamboa & Salom, 2015; Viveiros de Castro & Fernandez, 2004).

One of the most important areas in Costa Rica for both biodiversity and ecotourism is the Monteverde-Arenal Bioregion (MAB). The MAB encompasses several state-owned and privately owned reserves in northwestern Costa Rica, including Arenal Volcano National Park, Santa Elena Cloud Forest Reserve, and Alberto Manuel Brenes Biological Reserve (all state-owned), plus the Children's Eternal Rainforest and Monteverde Cloud Forest Biological Reserve (privately owned). The region is known for its extremely high biodiversity and large number of habitat types, known as Holdridge life zones (Holdridge, 1967). The MAB has a relatively large area of protected forest (48,500 ha); however, it is surrounded by fragmented and heavily deforested areas. The nearest large protected areas are Tenorio Volcano National Park, and various preserves in the Central Volcanic Range, which are 17.5 km and 23.1 km distant, respectively. The MAB likely has enough habitat to support viable populations of some species. Nevertheless, due to the relative isolation of this block of protected forest, movement of animals between MAB and other protected areas can be difficult, reducing gene flow in populations of animals that are unwilling to disperse across human-dominated landscapes. For mammals that have low population densities to begin with and strong negative interactions in human modified lands, such as the jaguar (*Panthera onca*), the MAB area probably cannot maintain viable populations.

Costa Rica has also been a leader in ecotourism development, in part motivated by concerns of deforestation. Tourism is Costa Rica's largest source of foreign exchange (Inman, Mesa, Oleas, & de los Santos, 1998; Institute of Costa Rican Tourism, 2016) and is likely important for improvements in the country's economy and reductions in poverty (Andam, Ferraro, Sims, Healy, & Holland, 2010). However, the question of whether ecotourism effectively protects biodiversity remains debatable. Within the MAB, the Monteverde Cloud Forest Biological Reserve alone attracts over 200,000 tourists per year, and the local economy is heavily dependent on the tourism industry (Institute of Costa Rican Tourism, 2009). Because much of Monteverde's tourism can be considered "ecotourism," the local human population presumably has a strong economic interest in conservation. Many tourists visit the area to see iconic wildlife (e.g., the Resplendent Quetzal, *Pharomachrus mocinno*), experience the famous cloud forests of the area, and view the Arenal Volcano. The MAB has been described as a model for ecotourism that benefits both humans and nature (Aylward, Allen, Echeverría, & Tosi, 1996). Because the local economy depends in part on biodiversity, there is perhaps a greater interest in wildlife conservation (Alexander, 2000; Aronson, Clewell, Blignaut, & Milton, 2006; Walpole & Goodwin, 2001; Wells, 1997). If the average citizen of the region is aware that they benefit economically from wildlife, then they may be more inclined to engage in activities that are nondestructive toward nature. Although large animals are often more popular with tourists (Goodwin & Leader-Williams, 2000; Macdonald et al., 2015), only a few studies have investigated terrestrial mammal and terrestrial bird populations in the MAB and how they are faring in this important ecotourism and conservation region (but see Arévalo, Méndez, Roberts, Alvarado, & Vargas, 2015; Wheelwright, 2000).

This study had two objectives: (a) to determine relative abundance and diversity of terrestrial mammals and terrestrial birds in core protected areas of the MAB, in order to ascertain which species populations have been maintained and which have been extirpated or reduced and (b) to determine abundance and diversity of terrestrial mammals and terrestrial birds in core protected areas versus the surrounding fragmented landscape.

Methods

Study Site

Our study site was located in the MAB, in the Tilarán Mountains of northwestern Costa Rica. Core protected areas were defined as the Children's Eternal Rainforest (CER; property of the Monteverde Conservation League) and the private reserve on the University of Georgia Costa Rica campus (UGA-CR) in San Luis de Monteverde (Figure 1). The CER covers about 22,600 ha, making it the largest protected area in the

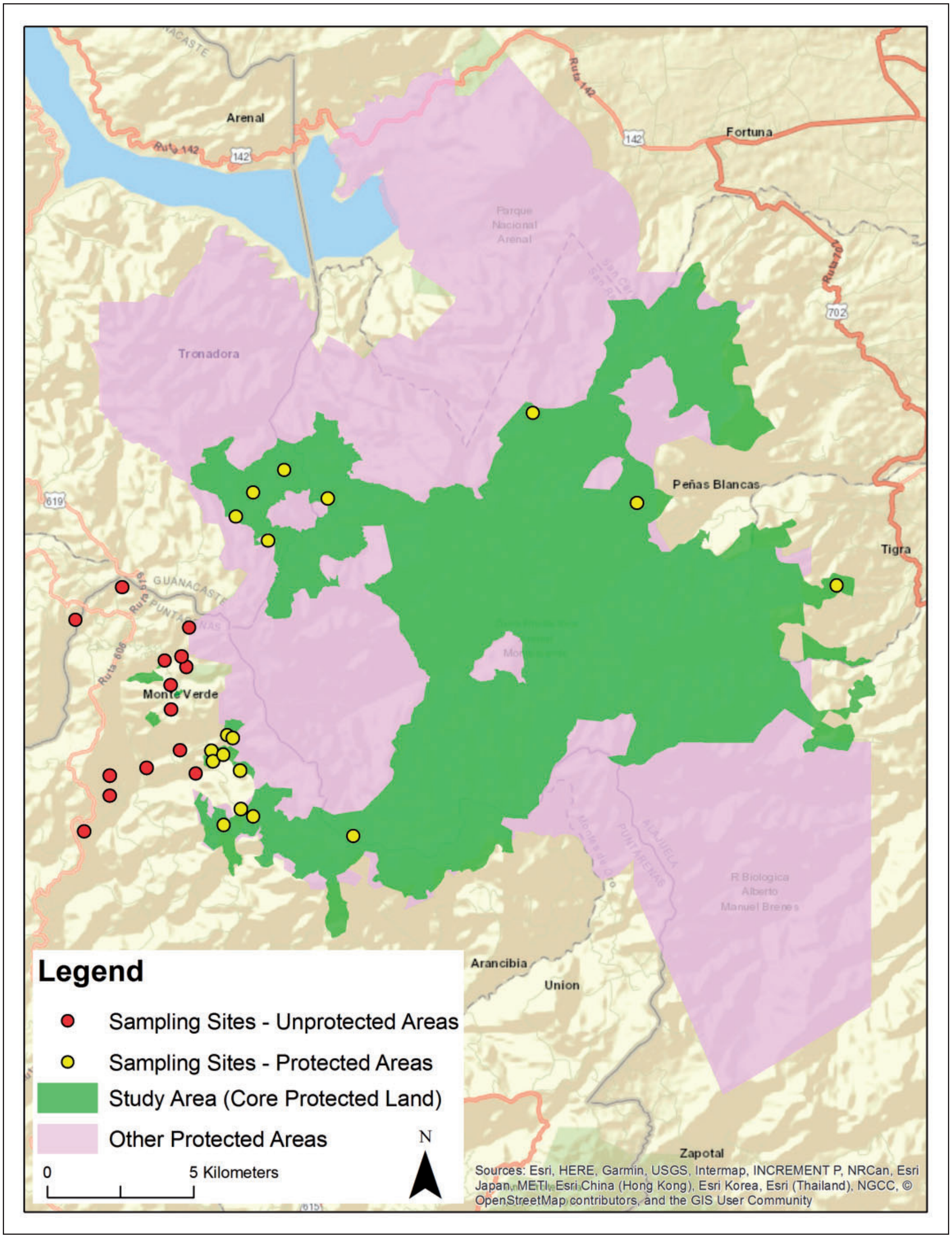

Figure 1. Map of sampling sites within the Monteverde-Arenal Bioregion.

region as well as Costa Rica's largest private reserve. The UGA-CR property comprises 62 ha and borders the CER. Together, the sites are more than 95% forested (primary and secondary) and directly adjacent to other protected areas, including Arenal Volcano National Park, Monteverde Cloud Forest Biological Reserve, Santa Elena Cloud Forest Reserve, Alberto Manuel Brenes Biological Reserve, and several smaller preserves, which together total about 48,000 ha of contiguous, protected tropical forest. The areas sampled (CER and UGA-CR) cover a great range of elevation (400–1,800 m) and cover both the Pacific and Caribbean slopes of Costa Rica.

Core Protected Area Census. We established a total of 20 camera sites in the two core protected areas (18 in CER and two in UGA-CR) during a 16-month period from June 2016 through September 2017 (Figure 1). Each camera was fixed to a tree trunk at 0.5 m above the ground. As we only had cameras placed at ground level, we did not detect primarily arboreal species (e.g., primates) and may have had reduced detection frequency of those animals whose behavior include both terrestrial and arboreal activity (Whitworth, Braunholtz, Huarcaya, MacLeod, & Beirne, 2016). All cameras were placed on or near hiking or access trails, which have been shown to have increased animal use (Beaudrot et al., 2016). Many parts of the CER have inaccessible terrain, so we were unable to place camera locations in many interior portions of the preserves. This limited our camera coverage of the CER so that large portions were not surveyed. Cameras were active 24 h a day. Data from cameras were periodically downloaded and stored in a central database. Each camera site was sampled for at least 30 days. In total, we sampled 49,776 camera hours in core areas.

Fragment-Core Study. From May to August 2017, we established 32 camera trap locations in both core protected areas ($N = 18$) and unprotected forest fragments ($N = 14$) that ranged between 0.1 and 3.8 km from the boundary of the core protected areas (Figure 1). All of these unprotected areas were partially deforested and inhabited by people, mostly as small farms. All cameras were placed in forested fragments. Sampling methods were the same as described earlier. Each site was sampled for a minimum of 26 days. In total, we sampled 23,040 camera hours in the fragment-core study.

Data Management

All photographs were downloaded to a central database. Whenever possible, animals were identified to species. If the photograph was not clear enough to achieve species identification, then that datum point was removed. The one exception was the oncilla (*Leopardus tigrina*) and margay (*Leopardus wiedii*), which are not easily distinguishable in photographs, but are together distinguishable from all other felids. These two species, which are both known to inhabit the region (Wainwright, 2007; James Wolfe, personal communication), were counted as one group. To reduce the probability of multiple counting of the same individuals, we utilized a 1-h time delay from detection before we counted another individual of that species.

Based on historical ranges of terrestrial mammals and birds, we developed a list of species that we would expect to find in our study area (Stiles & Skutch, 1989; Wainwright, 2007). We narrowed this list to include only species >0.5 kg in size, as animals smaller than that are unlikely to consistently trigger the wildlife camera sensors. Each "expected species" was assigned a trophic position of obligate herbivore, obligate carnivore, or omnivore based on feeding behavior. We also analyzed Aves (birds) and ungulates as distinct taxonomic groups (see Appendix).

To indicate if our cameras had detected all species present at a site, we plotted the cumulative mammal species detection over time, assuming that a curve showing a close approach to the inverse function asymptote would indicate that cameras had been in the field long enough to capture all or most species present. We analyzed these data by curvilinear regression using the inverse curve estimation ($Y = b0 + b1/t$) model fit (SPSS®). We then calculated the detection frequency of each species at each camera site, standardized as number of detections per 30 days of camera time.

To compare detection frequency between core protected areas and unprotected, fragmented sites, we used a Mann–Whitney U test on the median values for the different taxonomic and trophic groups described earlier. To compare presence or absence of different groups between the core protected areas and the unprotected fragmented sites, we performed a χ^2 analysis of independence. As the statistical tests require samples to be independent, we performed a spatial autocorrelation analysis (Moran's I) using the spatial analysis tool in Arc GIS® to determine if the detection frequency was significantly clustered or uniform in its dispersion pattern.

Results

Of the 33 species of terrestrial mammals and birds historically found in the study area, we detected 25 (76%, Appendix, Figure 2). There was neither a taxonomic nor a trophic pattern among those detected; every order and trophic level had most species present. Of the mammals not detected, two species, the neotropical river otter (*Lutra longicaudis*) and water opossum (*Chironectes minimus*), were unlikely to be detected with our methods, because these species prefer aquatic habitats. One species, the giant anteater (*Myrmecophaga tridactyla*), has likely been extirpated entirely from Costa Rica (Wainwright, 2007). The white-tailed deer (*Odocoileus virginianus*), although common in other parts of Costa Rica, may not have historically ranged into our study area (Janzen, 1983). The remaining undetected species which included the grison (*Galictis vittata*), northern

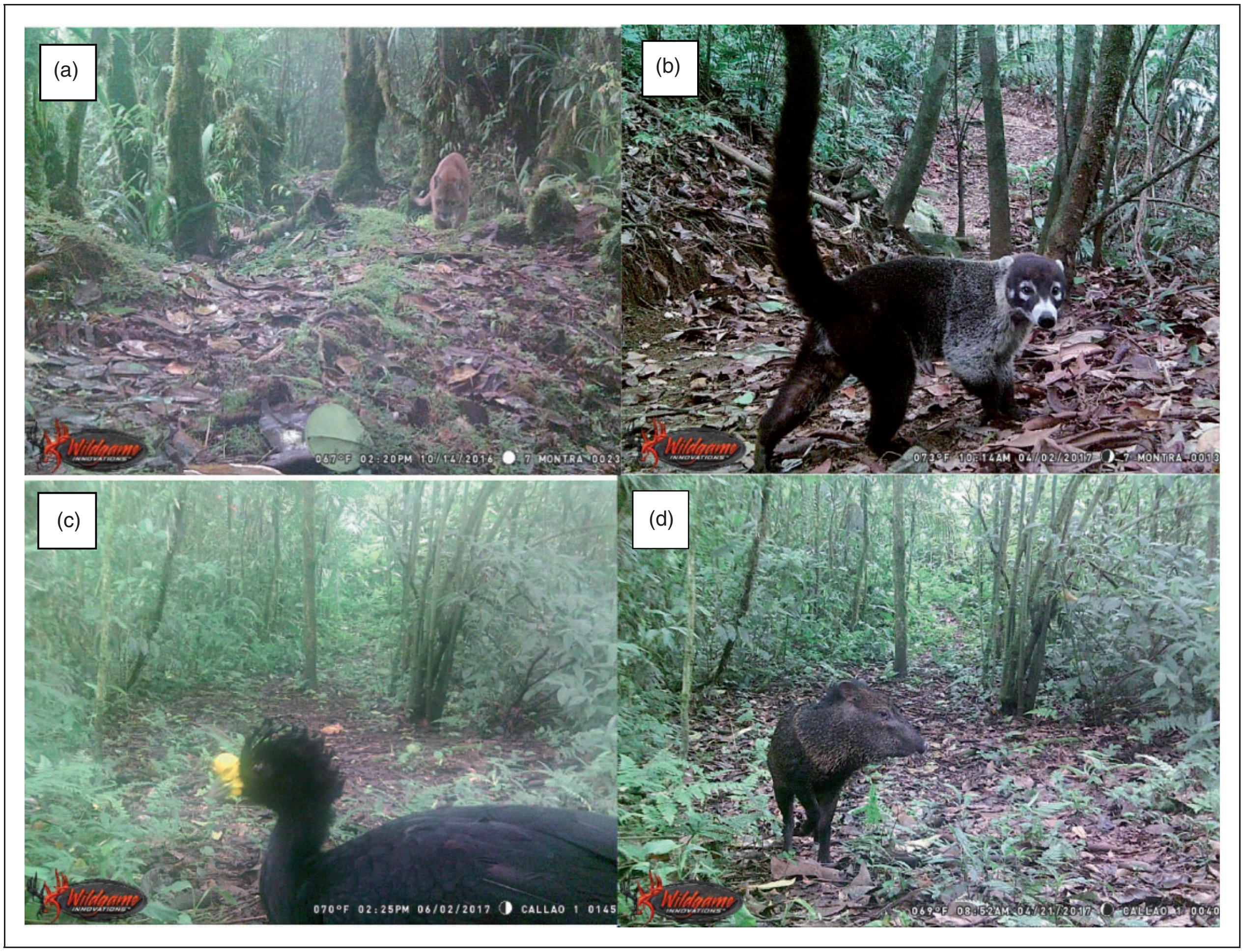

Figure 2. Representative photographs taken by wildlife cameras showing (a) puma (*Puma concolor*), (b) white-nosed coati (*Nasua narica*), (c) great curassow (*Crax rubra*), and (d) collared peccary (*Tayassu tajacu*).

naked-tailed armadillo (*Cabassous centralis*), northern raccoon (*Procyon lotor*), and white-lipped peccary (*Tayassu pecari*), appear to be extremely rare or extirpated from the region. It should be noted that a confiscated group of white-tailed deer were reported to have been released in the area by Sistema Nacional de Áreas de Conservación around the year 2000 and have been seen by local people in recent times, indicating a small population may persist (G. Alvarado, personal communication).

By the fifth month of the core area study, we had detected 80% of the total species we would eventually capture with our cameras (Figure 3). Between the 6th and 12th month, we detected the remaining five, presumably rare, species. No new species were found during the remaining 4 months of the study. The cumulative detection curve was a close fit to an inverse curve model (curvilinear regression, $p < .001$, $R^2 = .83$).

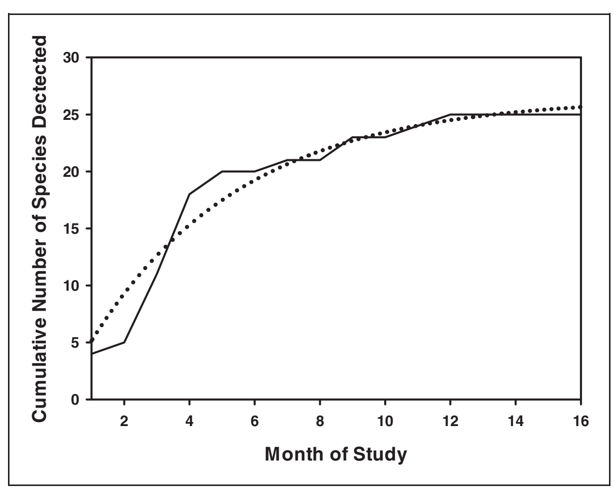

Figure 3. Cumulative number of species detected over time during the course of the study. Solid line = number of species detected in field, dotted line = inverse curve model.

Of the 25 species detected, only 5 were photographed more than once per 30 days of camera time (Figure 4). In other words, the vast majority of species were rarely detected. It is worth noting that the five most common species represented a variety of trophic positions (obligate herbivores, obligate carnivores, and omnivores), including one top predator, the puma (*Puma concolor*).

Mammal and bird communities differed between core protected areas and unprotected forest fragments. The median number of obligate carnivores and ungulates was significantly greater in the core areas (Mann–Whitney *U* test, Table 1). When analyzed for presence or absence as each site, total number of animals detected, obligate carnivores, and ungulates were more likely to be detected in core areas (χ^2, Table 1). Interestingly, collared peccaries (*Tayassu tajacu*), while the second most frequently detected species in core protected areas, were never detected in fragmented landscapes. It is noteworthy that although the median detection frequency for birds was zero for both types of habitat, they were never detected in fragmented forest. By contrast, in core protected areas, they were usually not detected (i.e., most camera sites were zero), but in a few sites, they were fairly abundant.

The spatial autocorrelation analysis indicated that two groups, ungulates and birds were significantly clustered (i.e., positive spatial autocorrelation, Table 1). The dispersion pattern of other groups was not significantly different from random. Therefore, the statistically significantly differences for ungulates should be interpreted with caution.

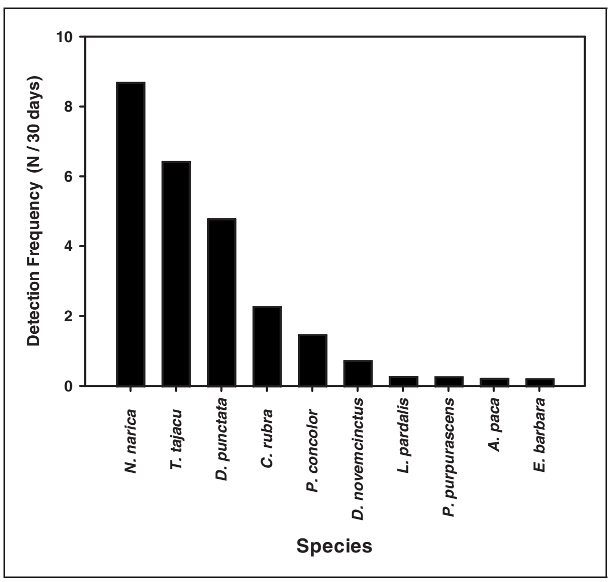

Figure 4. Detection frequency (number of detections per 30 days of camera time) in the core protected areas (Study 1) for those species with a minimum frequency of 0.20.

Discussion

Most species we expected to be present based on historical records were detected during the study; only eight species were classified as absent from the study area. This area appears to have a functional food web that contains animals in abundance representing all trophic levels, including a top predator, the puma. However, we view this food web as simplified, because some animals, especially large herbivores (e.g., tapir, white-tailed deer) and the largest carnivore, the jaguar, were rarely detected or not detected at all. The rarity or absence of these species can be attributed to the protected area being too small to support low-density populations, lack of dispersal corridors to other protected areas, and ongoing human impacts (Crooks, 2002; Laurance et al., 2011; Valiente-Banuet et al., 2015). By contrast, larger and better connected protected areas of similar habitat in Costa Rica do appear to have a nearly complete mammal and bird fauna present (Beaudrot et al., 2016; Rojas, 2006). Although we do not have data on changes in population sizes of mammals in our study area, the higher abundance and fewer missing species

Table 1. Comparison of Median Detection Frequency (per 30 Days of Camera Time) and Presence/Absence Between Core, Protected Camera Sites and Adjacent, Fragmented, Private Land.

Group	Core median	Fragmented median	Mann–Whitney *U* significance probability	χ^2 significance probability	SA MI	SA significance probability
All species	8.47	2.60	.17	.003*	−0.06	.25
Obligate carnivores	1.03	0.00	.005*	.005*	−0.05	.60
Obligate herbivores	2.27	0.00	.42	.15	−0.07	.20
Omnivores	1.55	0.43	.24	.14	−0.05	.45
Ungulates	0.90	0.00	.03*	.002*	0.11	<.001*
Aves	0.00	0.00	.61	.49	0.04	.004*

Note. SA = spatial analysis, MI = Moran I.
$^*p < .05$.

in these nearby regions indicates that the MAB has undergone considerable population loss or extirpation of some species.

The species that were frequently detected tended to be smaller in size and habitat generalists. The most abundant mammal was the coati (*Nasua narica*), an omnivore with high reproductive output that prefers secondary growth and can thrive around humans (Cunha, 2010; Hidinger, 1996). It is also possible that a reduction in predator numbers has allowed the coati population to grow (Hidinger, 1996). Even the puma, a top predator detected at relatively high frequency, is known to be a habitat generalist and tolerant of human presence (Sunquist & Sunquist, 2002). That tolerance is shown in that some puma detections were within 100 m of human residences in unprotected, fragmented sites.

The core-fragment comparison indicated that there are general reductions in detection frequency of study species in human-dominated habitats. However, it is noteworthy that most species were detected in both core and fragmented areas, indicating that the food web is relatively similar between the two habitat types. Notable exceptions were the complete absence of collared peccaries and all species of terrestrial birds in the fragmented areas. We suspect that this pattern is due to local hunting pressure, as both of these groups are highly valued for food (Hidinger, 1996) and illegal hunting continues in the region (Monteverde Conservation League, 2017); however, habitat alteration should not be discounted as a possible cause.

The area we sampled protects a wealth of terrestrial mammal and bird biodiversity, but some groups have still suffered population reduction or total extirpation from the region. Currently, the MAB is an island of protected forest surrounded by a sea of fragmentation, and although the area includes some of the most popular ecotourism destinations in the world, it appears to be a partially defaunated landscape. Connecting the MAB to other nearby protected areas, such as the Guanacaste Conservation Area and Central Volcanic Mountain Range, could create enough contiguous habitat to support viable populations of sensitive species and would potentially enhance terrestrial mammal and bird biodiversity (Pardini, de Souza, Braga-Neto, & Metzger, 2005). Increasing species biodiversity may even enhance the ecotourism value of this area, as ecotourists often choose areas with high biodiversity (Dharmaratne, Sang, & Walling, 2000; Lindsey, Alexander, Mills, Romañach, & Woodroffe, 2007) and charismatic megafauna (Goodwin & Leader-Williams, 2000; Macdonald et al., 2015), regardless of the likelihood of observing the species in question. For instance, tourists often list the leopard (*Panthera pardus*) as a motive for visiting African parks, even though the probability of actually seeing a leopard is low (Maciejewski & Kerley, 2014). If conservation efforts in and around the MAB resulted in the increased presence of species that are currently rare or even absent, this would also likely boost the area's ecotourism potential and subsequent economic value.

The MAB is one of the most prominent biodiversity hot spots in Central America, known for its high levels of endemism and many regionally rare species (Lawton, Lawton, Lawton, & Daniels, 2016). As such, considerable conservation resources and ecological research have been dedicated to the region (Nadkarni & Wheelwright, 2000). However, the MAB remains an island of habitat too small to maintain the historic biodiversity of the landscape, resulting in a simplified food web with modified trophic interactions. The reduction or absence of certain species can have profound negative effects on ecosystem function (i.e., keystone species, Mills, Soulé, & Doak, 1993). We recommend that future conservation efforts focus on ways to reestablish or increase populations of historically present species that are currently missing or rare in the region, in order to improve the complexity of the food web and the long-term survival of as many species as possible. An additional benefit of this process would be the enhanced ecotourism and educational value of this heavily visited area.

Implications for Conservation

Our study indicates that the MAB is not currently effective at conserving the full community of terrestrial mammals and birds historically found at the site. This result is in spite of the strong conservation practices and characteristics of the region, including well-funded private conservation groups, a strong ecotourism industry, a vigorous ecological research history, and community buy-in to conservation. It has been argued that the MAB is a conservation success story, because of these very characteristics (Aylward et al., 1996; Weinberg, Bellows, & Ekster, 2002). Although these characteristics are valuable and perhaps necessary for any successful conservation plan, the results of our study show that they will not be enough to overcome the ecological limitations of the conservation area, notably its small size and low level of connectivity to other natural areas. We recommend that future conservation planning for this region incorporate land-use and protection strategies that will encourage the increase in animal populations currently rare or absent from the protected areas. In particular, we suggest that fully protected biological corridors to other protected areas will likely be necessary to reestablish viable populations of many larger terrestrial animals.

Appendix. Medium and Large (≥0.5 kg) Terrestrial Mammals and Birds Historically Found in the Study Region and Detected in This Study.

Order	Common Name	Scientific Name	Detected (+, −)	Trophic Position
Mammals				
Didelphimorphia	Common opossum	*Didelphis marsupialis*	+	O
	Common gray four-eyed opossum	*Philander opossum*	+	O
	Water opossum[a]	*Chironectes minimus*	−	OC
Pilosa	Northern tamandua	*Tamandua mexicana*	+	OC
	Giant anteater[b]	*Myrmecophaga tridactyla*	−	OC
Cingulata	Northern naked-tailed armadillo	*Cabassous centralis*	−	O
	Nine-banded armadillo	*Dasypus novemcinctus*	+	O
Rodentia	Central American agouti	*Dasyprocta punctata*	+	OH
	Paca	*Agouti paca*	+	OH
Carnivora	Gray fox	*Urocyon cinereoargenteus*	+	O
	Coyote	*Canis latrans*	+	O
	Northern raccoon	*Procyon lotor*	−	O
	White-nosed coati	*Nasua narica*	+	O
	Grison	*Galictis vittata*	−	OC
	Tayra	*Eira barbara*	+	O
	Striped hog-nosed skunk	*Conepatus semistriatus*	+	O
	Neotropical river otter[a]	*Lutra longicaudis*	−	OC
	Oncilla[c]	*Leopardus tigrina*	+	OC
	Margay[c]	*Leopardus wiedii*	+	OC
	Ocelot	*Leopardus pardalis*	+	OC
	Jaguarundi	*Herpailurus yagouaroundi*	+	OC
	Puma	*Puma concolor*	+	OC
	Jaguar	*Panthera onca*	+	OC
Perissodactyla	Baird's tapir	*Tapirus bairdii*	+	OH
Artiodactyla	Collared peccary	*Tayassu tajacu*	+	OH
	White-lipped peccary	*Tayassu pecari*	−	OH
	Red brocket deer	*Mazama americana*	+	OH
	White-tailed deer[d]	*Odocoileus virginianus*	−	OH
Birds				
Galliformes	Great Curassow	*Crax rubra*	+	O
	Black Guan	*Chamaepetes unicolor*	+	O
	Crested Guan	*Penelope purpurascens*	+	O
Tinamiformes	Great Tinamou	*Tinamus major*	+	O
	Highland Tinamou	*Nothocercus bonapartei*	+	O

Note. O = omnivore; OC = obligate carnivore; OH = obligate herbivore.
[a]Unlikely to be detected due to specialized habitat preference (i.e., semi-aquatic).
[b]Extirpated from Costa Rica.
[c]Oncilla and margay are difficult to distinguish with wildlife camera photographs, but both have been confirmed by other researchers (Jim Wolfe, personal communication).
[d]Study site is on the edge of Costa Rica range and may be naturally absent from region.

Acknowledgments

The authors thank the field staff of the Monteverde Conservation League, who helped greatly with logistics. Three anonymous reviewers made valuable contributions that greatly improved the manuscript.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This study was funded by the Hendrix College Odyssey program.

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