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ORIGINAL PAPER

Mammal richness and diversity in a Himalayan hotspot: the role of protected areas in conserving Bhutan's mammals

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Abstract

More than 51% of Bhutan is in a protected area (PA) network and our study demonstrates its effectiveness in conserving large and medium mammal species. We conducted camera trapping in Bhutan's PAs, biological corridors (BCs) and intervening non-protected areas (NPAs) to investigate the richness and diversity of mammals, and assess the network's efficacy in protecting mammals. 1858 camera traps were deployed within 1129 5-km × 5-km grids over 536 days between 2014 and 2015, resulting in 148,598 trap-nights (mean = 80 traps-nights/camera) which yielded nearly 10 million photos (mean = 5368 photos/camera trap). Fifty-six mammal species (65% of Bhutan's 86 medium and large terrestrial mammal species) representing 18 families within seven orders were identified, of which, 18 (32.16%) are listed as threatened by the International Union for Conservation of Nature. There was a significant difference in mammal diversity between PAs, BCs, and NPAs (PERMANOVA test; $p < 0.001$; Pseudo-F = 6.40; unique perms = 9921), with the strongest difference between PAs and NPAs. Additionally, Hill's numbers $q = 0$ (species richness), $q = 1$ (Shannon's entropy index) and $q = 2$ (Simpson's concentration index) revealed a higher mammal diversity in PAs compared to BCs and NPAs. Higher mammal diversity in PAs can be attributed to the added presence of threatened species, including the tiger *Panthera tigris*, red panda *Ailurus fulgens*, Asian elephant *Elephas maximus*, and golden langur *Trachypithecus geei*. However, BCs and NPAs share similar patterns of mammal diversity, and globally threatened species such as the Chinese pangolin *Manis pentadactyla* and Indian pangolin *Manis crassicaudata* were only detected in NPAs. Although Bhutan's PA network is effective in conserving much of the country's mammal diversity, realignment of some protected areas and biological corridors would ensure the long-term protection of several threatened mammal species.

Keywords Mammals · Eastern Himalayas · Protected areas · Camera trapping · Species richness and diversity · Bhutan

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Introduction

To prevent mass species extinction, halt global biodiversity loss, slow earth's rising temperature, and ensure continued provision of essential ecosystem services, scientists advocate the protection of 50% of earth's land and seas through inter-connected protected areas (Dinerstein et al. 2017; Wilson 2016; Wuerthner et al. 2015). However, Büscher et al. (2017) argued that a half-earth protection is impractical and would result in widespread negative consequences for human populations, especially in developing countries. Bhutan, nevertheless, achieved the Half-Earth target by setting aside 51.4% of the country's area in a protected area (PA) and biological corridor (BC) network, including a commitment to protect 17% of global terrestrial land and inland water areas by 2020 through Achi Target 11 (Convention on Biological Diversity 2010). Although Bhutan's PAs are well managed in partnership with local communities, they are experiencing increased pressure from infrastructure development, grazing, resource collection, human-wildlife conflict, and climate change (Dorji et al. 2012; Dorji 2016; Sangay and Vernes 2008; Thinley et al. 2018; Wang and Macdonald 2006). Previous studies on the nation's PA management effectiveness indicated that scientific data on PA functionality and effectiveness is lacking which, in turn, hinders adaptive management to changing land use pressure and climate (Choden 2016; Lham et al. 2018; Tshering 2003).

Mammals are key indicators for measuring anthropogenic impacts on biota (Ceballos and Ehrlich 2002), and important for the maintenance and functionality of ecosystems through seed and fruit dispersal, pollination, nutrient recycling, and plant succession (Davidson et al. 2012; Ripple et al. 2015). Mammals also benefit people through the provision of food, recreation, and income (Naidoo et al. 2016; Velho et al. 2016). Therefore, knowledge on presence and distribution of mammals is crucial for planning and evaluating conservation strategies for a region or country (Tobler et al. 2008). Despite their importance, detailed understanding of mammal diversity, distribution, and abundance are lacking in many regions including the Eastern Himalayas (Dorji et al. 2018).

In this paper, we summarize the results of a nation-wide camera trapping survey between 2014 and 2015, and compare the richness and diversity of mammals in Bhutan's protected areas, biological corridors, and intervening non-protected areas. We further ascertain the adequateness of Bhutan's protected area and corridor network in conserving large and medium sized mammals.

Study area and methods

Altitude in Bhutan ranges from 150 to 7570 m above sea level (m asl) and there are three distinct eco-floristic zones: Alpine (> 4000 m asl), Temperate (2000–4000 m asl) and Subtropical (150–2000 m asl) (Ministry of Agriculture and Forests 2014). This study was conducted across Bhutan's ten PAs, nine BCs that link PAs, and the intervening landscape comprising 14 Territorial Divisions ('non-protected areas' hereafter called 'NPAs'). Our study area covered 33,909 km^2 (88.30% of the country's area) from 150 m asl to approximately 4500 m asl, and was divided into 5 × 5 km survey grids. It was segregated into two blocks (southern and northern; Fig. 1) which were sampled in two consecutive phases because of human resource constraints, camera trap availability, weather conditions, and funding availability. In each grid, we set up a camera station consisting of a pair of

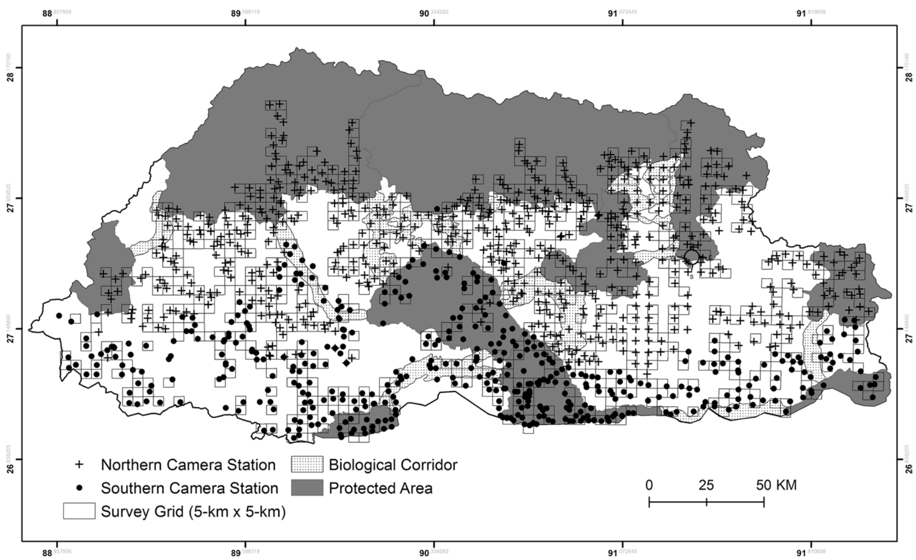


Fig. 1 Distribution of camera traps within 5-km × 5-km survey grids (square boxes) in this camera trap study of mammals in Bhutan from 2014 to 2015. Black circles indicate a camera station in the southern block and crosses indicate a camera station in the northern block

opposing un-baited cameras set 10–30 m apart at a height of 30–60 cm from the ground, and maintained a minimum distance of 2 km between any two camera stations for independence. We chose the 30–60 cm height range to document large and medium size mammals such as tigers and their prey, resulting in limitations to capturing small and aboreal mammals. Cameras were deployed along trails in areas with pronounced animal signs (tracks, scrapes, etc.) (Aung et al. 2017; Meyer et al. 2015; Moo et al. 2018; Tobler et al. 2008).

We compiled data over 536 days between January 2014 and June 2015, from 1129 camera stations comprising 1858 cameras (excluding malfunctioned cameras, stolen cameras, and cameras destroyed by elephants, rain, and windstorm). Image files were re-labeled according to their time and date using the Program 'Renamer' (http://www.snapfiles.com); sorted manually into species folders; and processed using 'Camerasweet' software (Sanderson and Harris 2014). Sampling effort at a station was calculated as the number of days a camera trap was operational at the location i.e. duration between installation of the last camera and retrieval of the first camera in each location. We assumed images of an individual species taken at least 30 min apart at a camera station to be independent events, and photographic rates or Relative Abundance Index (RAI) were obtained by dividing total events by the number of trap nights and multiplied by 100 (Rovero and Marshall 2009; Tobler et al. 2008). Species identification and conservation status were based on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2018). We broadly characterized the community structure of mammals based on body mass (Smith et al. 2003) as follows: up to 1 kg = small sized mammal; 1–10 kg = medium sized mammal; and > 10 kg = large sized mammal. We further categorized mammals into general trophic categories i.e. carnivore, herbivore, insectivore and omnivore based on dietary literature (Lambert 2014; Nowak and Walker 1999; Wilson et al. 2017). There were only three records of two species of insectivores (Chinese Pangolin *Manis pentadactyla* and Indian pangolin *Manis crassicaudata*) in the NPAs. As such, we excluded them from any analysis.

We assessed the completeness of our sampling by computing the sample size and coverage-based accumulation curves among three treatments (PA, BC & NPA; hereafter called sites) based on the C.hat estimator with 95% confidence intervals as proposed by Chao and Jost (2012). This yields the expected number of species in a community by normalizing bias due to sample size (Chao and Jost 2012; Rovero et al. 2017). We compared species richness and diversity of mammals between the three sites using integrated sample size and coverage-based rarefaction and extrapolation methods, for both abundance and incidence matrices at the 95% confidence interval (Chao et al. 2014; Chao and Jost 2012; Colwell et al. 2012). This allowed a fair comparison of species richness and diversity across sites despite differences in sampling effort (Chao et al. 2014; Hsieh et al. 2016). All the analyses were performed using the R package iNEXT (Hsieh et al. 2016). We also performed a one-factor design, SS Type III (partial) Permutational Multivariate Analysis of Variance (PERMANOVA) test with 9999 permutations, to compare significant differences between site-associated mammal communities using Primer 6 (Primer-E 2008).

Results

Trapping effort, species composition, and species detection rate

From 536 days of camera trapping, 9,975,258 photographs were obtained over 148,598 trap-nights (mean = 80 trap-nights/camera). Pooled data from multiple cameras in a grid returned a total sampling effort of 59,551 trap-nights in 751 survey grids (PA = 248; BC = 116; NPA = 387), from which, 51,017 independent photographs were obtained (20,496 in PAs; 8098 in BCs; 22,423 in NPAs). This comprised 19,448 trap-nights in PAs, 9787 trap-nights in BCs, and 30,316 trap-nights in NPAs (Table 1).

Fifty-six terrestrial mammal species representing 18 families within seven orders were recorded, of which, 18 (32.1%) are listed as threatened by the IUCN. Threatened species included one Critically Endangered (CR) mammal (1.8%; Chinese Pangolin), eight Endangered (EN) mammal species (14.3%; including tiger *Panthera tigris*, red panda *Ailurus fulgens*, golden langur *Trachypithecus geei* and Asian elephant *Elephas maximus*), and nine Vulnerable (VU) mammal species (16.1%; including clouded leopard *Neofelis nebulosi*, Takin *Budorcas taxicolor*, and Binturong *Arctictis binturong*) (Table 2). The remaining 38 mammal species comprised eight Near Threatened (NT) species (14.3%) and 30 species (53.6%) of Least Concern (LC) (Table 2). Carnivores were the most diverse group,

Table 1 Summary of camera trapping data of mammals in protected areas (PA), biological corridors (BC), and non-protected areas (NPA) of Bhutan between 2014 and 2015

Sites	Camera station	Total trap-night	Mean trap-night per camera station	Total event	Mean event
PA	248	19,448	78.4 ± 3.45	20,496	79.4 ± 2.41
BC	116	9787	84.4 ± 4.18	8098	66.4 ± 2.44
NPA	387	30,316	78.1 ± 2.29	22,423	55.5 ± 2.54
Total	751	59,551	80.0 ± 1.77	51,017	67.9 ± 7.13

Table 2 Summary of mammal species recorded during the nationwide camera trapping exercise in Bhutan from 2014 to 2015, and their current conservation status as per International Union for Conservation of Nature (IUCN) red list criteria (CR = Critically Endangered; EN = Endangered; VUL = Vulnerable; NT = Near Threatened and LC = Least Concerned)

Order	Family	Order\family\ scientific name	Common name	IUCN	Trophic	Size	N	Mean Relative Abundance Index			
								Overall	PA	BC	NPA
		Carnivora						31.14	**34.61**	24.95	12.46
		Ailuridae						0.44	**0.71**	0.25	0.33
Carnivora	Ailuridae	*Ailurus fulgens*[a]	Red panda	**EN**	H	M	54	0.44	**0.71**	0.25	0.33
	Canidae	Canidae						1.74	**2.36**	1.78	1.35
Carnivora	Canidae	*Cuon alpinus*	Dhole	**EN**	C	L	196	1.08	1.15	**1.35**	0.95
Carnivora	Canidae	*Vulpes ferrilata*	Tibetan fox	LC	C	M	8	0.26	**0.84**	0.00	0.00
Carnivora	Canidae	*Vulpes vulpes*	Red fox	LC	C	M	28	0.39	0.37	**0.43**	0.39
Carnivora	Canidae	*Canis aureus*	Asiatic jackal	LC	C	L	1	0.01	0.00	0.00	**0.01**
		Felidae						9.94	**14.74**	12.52	6.29
Carnivora	Felidae	*Panthera tigris*[a]	Tiger	**EN**	C	L	122	0.97	1.24	**2.01**	0.49
Carnivora	Felidae	*P. bengalensis*	Leopard cat	LC	C	M	243	2.49	**3.67**	2.56	1.77
Carnivora	Felidae	*Felis chaus*	Jungle cat	LC	C	M	7	0.01	0.00	**0.02**	0.01
Carnivora	Felidae	*Catopuma temminckii*	Asiatic golden cat	NT	C	L	261	2.56	**4.35**	2.36	1.57
Carnivora	Felidae	*Pardofelis marmorata*	Marbled cat	NT	C	M	148	1.70	**2.35**	2.32	1.12
Carnivora	Felidae	*Panthera pardus*[a]	Common leopard	VU	C	L	187	1.86	2.53	**2.75**	1.19
Carnivora	Felidae	*Neofelis nebulosi*[a]	Clouded leopard	VU	C	L	79	0.34	**0.61**	0.50	0.14
		Herpestidae						0.24	**0.52**	0.11	0.12
Carnivora	Herpestidae	*Herpestes urva*	Crab-eating mongoose	LC	C	M	39	0.23	**0.47**	0.11	0.12
Carnivora	Herpestidae	*Herpestes edwardsii*	Common mongoose	LC	C	M	2	0.01	**0.04**	0.00	0.00
Carnivora	Herpestidae	*Herpestes javanicus*	Small Indian mongoose	LC	C	S	1	0.002	0.000	0.000	**0.003**
		Mustelidae						2.60	2.42	**4.26**	2.19

Table 2 (continued)

Order	Family	Order\family\ scientific name	Common name	IUCN	Trophic	Size	N	Mean Relative Abundance Index			
								Overall	PA	BC	NPA
Carnivora	Mustelidae	*Martes flavigula*	Yellow-throated marten	LC	C	M	293	2.57	2.39	**4.20**	2.17
Carnivora	Mustelidae	*Mustela kathiah*	Yellow-bellied weasel	LC	C	S	2	0.01	**0.02**	0.00	0.01
Carnivora	Mustelidae	*Mustela sibirica*	Siberian weasel	LC	C	S	1	0.01	0.00	**0.06**	0.00
Carnivora	Mustelidae	*Melogale moschata*	Small-toothed ferret badger	LC	C	S	1	0.001	0.000	0.00	**0.002**
Carnivora	Mustelidae	*Mustela altaica*	Pale weasel	NT	C	S	2	0.005	0.004	0.00	0.007
Carnivora	Mustelidae	*Aonyx cinereus*	Asian small-clawed otter	VU	C	M	1	0.002	**0.006**	0.00	0.000
		Prionodontidae						0.06	2.42	**4.26**	2.19
Carnivora	Prionodontidae	*Prionodon pardicolor*	Spotted linsang	LC	C	S	22	0.06	0.03	**0.09**	0.07
		Ursidae						3.93	**9.48**	2.54	1.05
Carnivora	Ursidae	*Ursus thibetanus*[a]	Asiatic black bear	VU	O	L	278	3.92	**9.46**	2.54	1.05
Carnivora	Ursidae	*Arctictis binturong*	Binturong	VU	C	L	2	0.01	**0.03**	0.00	0.00
		Viverridae						2.46	**4.34**	3.40	1.06
Carnivora	Viverridae	*P. hermaphroditus*	Common palm civet	LC	C	M	37	0.64	**1.62**	0.38	0.13
Carnivora	Viverridae	*Paguma larvata*	Himalayan palm civet	LC	C	M	147	1.24	1.49	**2.24**	0.79
Carnivora	Viverridae	*Viverra zibetha*	Large Indian civet	LC	C	M	43	0.47	**0.92**	0.76	0.12
Carnivora	Viverridae	*Viverricula indica*	Small Indian civet	LC	C	M	18	0.11	**0.31**	0.01	0.02
		Cetartiodactyla						45.57	**65.60**	57.07	30.13
		Bovidae						7.72	**14.35**	8.87	3.42
Cetartiodactyla	Bovidae	*Bubalus arnee*[a]	Asiatic water buffalo	**EN**	H	L	6	0.22	**0.70**	0.00	0.00
Cetartiodactyla	Bovidae	*Capricornis thar*[a]	Himalayan serow	NT	H	L	294	3.03	**4.07**	3.70	2.21
Cetartiodactyla	Bovidae	*Naemorhaedus goral*	Himalayan goral	NT	H	L	130	1.58	2.42	**3.14**	0.60
Cetartiodactyla	Bovidae	*Bos gaurus*[a]	Gaur	VU	H	L	102	2.83	**6.98**	2.03	0.60
Cetartiodactyla	Bovidae	*Budorcas taxicolor*[a]	Takin	VU	H	L	3	0.06	**0.18**	0.00	0.01
		Cervidae						28.50	**40.38**	31.76	20.43

Table 2 (continued)

Order	Family	Order\family\ scientific name	Common name	IUCN	Trophic	Size	N	Mean Relative Abundance Index			
								Overall	PA	BC	NPA
Cetartiodactyla	Cervidae	*Muntiacus muntjak*	Barking deer	LC	H	L	528	19.53	23.80	**24.22**	15.54
Cetartiodactyla	Cervidae	*Rusa unicolor*[a]	Sambar deer	VU	H	L	363	8.97	**16.57**	7.54	4.89
		Moschidae						0.48	0.66	**0.83**	0.27
Cetartiodactyla	Moschidae	*Moschus species*[a]	Musk deer	**EN**	H	L	39	0.48	0.66	**0.83**	0.27
		Suidae						8.87	10.21	**15.61**	6.01
Cetartiodactyla	Suidae	*Sus scrofa*	Wild boar	LC	O	L	465	8.87	10.21	**15.61**	6.01
		Lagomorpha						0.14	**0.35**	0.11	0.03
		Ochotonidae						0.14	**0.35**	0.11	0.03
Lagomorpha	Ochotonidae	*Ochotona roylei*	Common pika	LC	H	S	6	0.10	**0.21**	0.11	0.03
Lagomorpha	Ochotonidae	*Lepus nigricollis*	Indian hare	LC	H	M	2	0.05	**0.15**	0.00	0.00
		Pholidota						0.01	0.00	0.00	**0.02**
		Manidae						0.01	0.00	0.00	**0.02**
Pholidota	Manidae	*Manis pentadactyla*[a]	Chinese pangolin	CR	C	M	1	0.004	0.00	0.00	**0.008**
Pholidota	Manidae	*Manis crassicaudata*[a]	Indian pangolin	**EN**	C	M	2	0.01	0.00	0.00	**0.01**
		Primates						1.39	**1.56**	1.16	1.36
		Cercopithecidae						1.39	**1.56**	1.16	1.36
Primates	Cercopithecidae	*Trachypithecus geei*[a]	Golden langur	**EN**	H	M	1	0.00	0.01	0.00	0.00
Primates	Cercopithecidae	*Semnopithecus entellus*	Grey langur	LC	H	L	9	0.04	**0.08**	0.04	0.01
Primates	Cercopithecidae	*Macaca mulatta*	Rhesus macaque	LC	O	M	11	0.24	0.01	0.28	**0.36**
Primates	Cercopithecidae	*Macaca assamensis*	Assamese macaque	NT	O	L	125	1.03	**1.42**	0.73	0.89
Primates	Cercopithecidae	*Trachypithecus pileatus*	Capped langur	VU	H	L	12	0.08	0.03	0.10	**0.11**
		Proboscidea						2.71	**7.50**	0.82	0.45
		Elephantidae						2.71	**7.50**	0.82	0.45
Proboscidea	Elephantidae	*Elephas maximus*[a]	Asian elephant	**EN**	H	L	91	2.71	**7.50**	0.82	0.45

Table 2 (continued)

Order	Family	Order\family\ scientific name	Common name	IUCN	Trophic	Size	N	Mean Relative Abundance Index			
								Overall	PA	BC	NPA
		Rodentia						2.92	3.94	3.39	2.17
		Hystricidae						2.55	**3.27**	2.94	2.00
Rodentia	Hystricidae	*Hystrix brachyura*	Himalayan crestless porcupine	LC	H	M	164	2.27	**2.99**	2.39	1.81
Rodentia	Hystricidae	*Atherurus macrourus*	Asiatic brush-tailed porcupine	LC	H	M	34	0.27	**0.28**	0.56	0.18
Rodentia	Hystricidae	*Hystrix indica*	Indian crested porcupine	LC	H	L	1	0.00	0.00	0.00	**0.01**
		Sciuridae						0.37	**0.66**	0.44	0.18
Rodentia	Sciuridae	*C. pygerythrus*	Hoary-bellied Himalayan squirrel	LC	H	S	14	0.18	**0.43**	0.10	0.05
Rodentia	Sciuridae	*Dremomys lokriah*	Orange-bellied Himalayan squirrel	LC	H	S	12	0.08	0.10	**0.20**	0.04
Rodentia	Sciuridae	*Callosciurus erythraeus*	Pallas's squirrel	LC	H	S	8	0.06	0.06	0.05	**0.07**
Rodentia	Sciuridae	*Petaurista magnificus*[a]	Hodgson's giant flying squirrel	LC	H	M	1	0.01	0.00	0.02	0.00
Rodentia	Sciuridae	*Ratufa bicolor*[a]	Malayan giant squirrel	NT	H	M	7	0.03	0.04	0.06	0.01
Rodentia	Sciuridae	*Petaurista nobilis*[a]	Bhutan giant flying squirrel	NT	H	M	7	0.01	0.02	0.02	0.01

Relative Abundance Index = the number of events divided by the sampling effort per 100 trap-nights; trophic level (*C* carnivore, *H* herbivore, *O* omnivore, *I* insectivore)

Bold indicated highest relative abundance indices of respective species compared between the protected areas, biological corridors and non-protected areas

N number of camera stations that captured the species, *PA* protected area, *BC* biological corridor, *NPA* non-protected area

[a]Totally protected species under Forests and Nature Conservation Rule (FNCR), 2017

represented by 28 species (50%). There were nine (16.1%) Rodent species, nine (16.1%) Cetartiodactyl species, five (8.9%) Primate species, two (3.57%) Pholidota species, two (3.6%) Lagomorph species, and one (1.8%) Proboscid species (Table 2). Eighteen (32.1%) of the 56 mammal species recorded were totally protected under the Forest and Nature Conservation Rule of Bhutan, 2017 (Table 2). In terms of trophic categories, there were 26 (46.4%) Carnivore, 24 (42.86%) Herbivore, two (3.6%) Insectivore, and 4 (17.1%) Omnivore species.

Overall naïve occupancy of people captured on camera was 0.52 comprising 8155 photos (15.9% of the total independent photographs excluding survey team members). The naïve occupancy of people was 0.4, 0.5, and 0.5 in the PAs, BCs, and NPAs, respectively. However, mean RAI of people was higher in BCs (mean ± SE photos per period = 1310 ± 300) compared to PAs (mean ± SE photos per period = 1227 ± 298) and NPAs (mean ± SE photos per period = 910 ± 120). Livestock (cattle, horse, yak, goat, sheep, and domestic dog) was captured in 14.35% of total independent photographs from 55.7% of camera stations. The naïve occupancy of livestock was 0.6, 0.6, and 0.5 in the PAs, BCs, and NPAs, respectively. Mean RAI of livestock was higher in PAs (mean ± SE photos per period = 1363 ± 208) and BCs (mean ± SE photos per period = 1333 ± 175) compared to NPAs (mean ± SE photos per period = 1066 ± 92). Some cameras stationed along the Indian border in the south also recorded Indian poachers carrying rifles (five stations), forest fires (six stations), and a vehicle (one station).

Commonly detected mammal species were barking deer *Muntiacus muntjak*, Sambar deer *Rusa unicolor*, wild-pig *Sus scrofa*, Asiatic black bear *Ursus thibetanus*, Himalayan serow *Capricornis thar*, and gaur *Bos gaurus* (Table 2). The Asian elephant was also recorded in 91 camera stations (Table 2). Amongst the carnivores, commonly detected species were yellow-throated marten *Martes flavigula*, Asiatic golden cat *Catopuma temminckii*, leopard cat *Prionailurus bengalensis*, common leopard *Panthera pardus*, and marbled cat *Pardofelis marmorata* (Table 2).

Uncommon species, recorded at just one camera station each, were small-toothed ferret badger *Melogale moschata*, small Indian mongoose *Herpestes javanicus*, Asian small-clawed otter *Aonyx cinereus*, golden langur, and Chinese pangolin (Table 2).

Sample completeness, species richness, and species diversity

Forty-one (73.2%) species were found at all three sites, while the remaining 15 (29.82%) occurred only in one or two sites (Table 2). A total of 47, 39 and 48 species were observed in PAs, BCs, and NPAs (Table 2), respectively. Similarly, eight (14.1%) species occurred only in PAs, six (10.52%) occurred only in NPAs, and one (1.8%) species occurred only in BCs. Forty-one (73.2%) species each overlapped between PAs and BCs, PAs and NPAs, and BCs and NPAs (Table 2). Overall detection rate was higher in PAs compared to BCs and NPAs (Table 2). Detection rates of Bovidae (mean ± SE photos per period = 14.4 ± 1.2), Cervidae (mean ± SE photos per period = 40.4 ± 2.2), Ochotonidae (mean ± SE photos per period = 0.35 ± 0.07), Elephantidae (mean ± SE photos per period = 7.49 ± 0.8), Hystricidae (mean ± SE photos per period = 3.3 ± 0.2), Cercopithecidae (mean ± SE photos per period = 1.56 ± 0.115, and Sciuridae (mean ± SE photos per period = 0.7 ± 0.1) families were higher in PAs compared to BCs and NPAs (Fig. 2).

Although PAs showed higher RAIs in terms of overall mammal species diversity compared to BCs and NPAs, mean RAI for tiger and common leopard was highest in the BCs (Table 2). Similarly, mean RAI for their favored prey species such as barking deer,

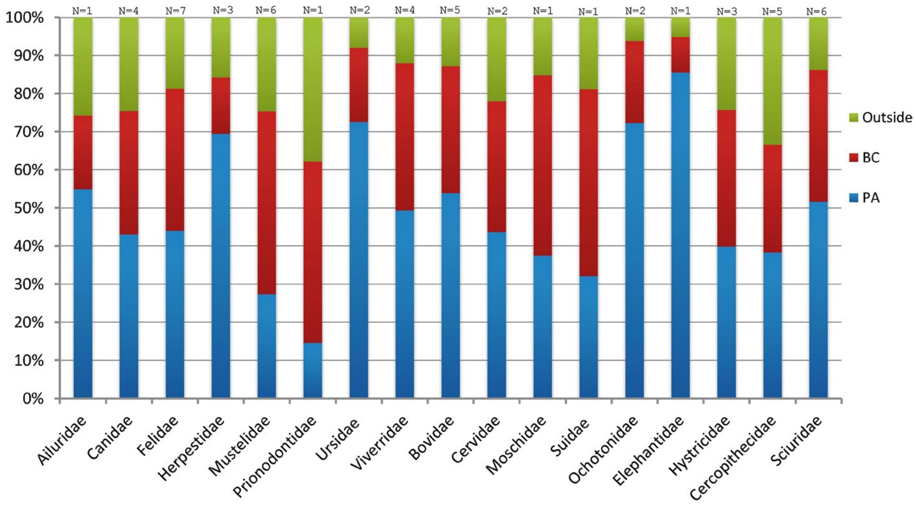


Fig. 2 Mean detection rate with standard error of terrestrial mammal family in the protected areas (PA), biological corridors (BC) and non-protected areas of Bhutan based on the nationwide camera trapping data between 2014 and 2015. N = number of species in each family

Table 3 Summary information of incidence data from a nationwide camera trapping exercise in Bhutan between 2014 and 2015 including site name (PA = protected area; BC = biological corridor; NPA = non-protected area or areas outside PA and BC)

	Site	T	S.obs	SC	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
1	NPA	12,689	48	0.99	4	2	2	3	2	1	0	1	0	1
2	BC	8280	39	1.00	0	3	0	2	0	1	0	3	0	1
3	PA	23,131	47	1.00	0	3	0	1	1	2	0	2	0	2

T number of observed sampling units in the reference sample (sample size for incidence data), *S.obs* observed species richness, *SC* sample coverage estimate

wild-pig *Sus scrofa*, and musk deer *Moschus* spp. was also higher in BCs compared to PAs and NPAs (Table 2). However, mean RAI for sambar deer was higher in PAs (Table 2). BCs also had a higher RAI for the Mustelidae family and the RAI of one species from the Prionodontidae family, the spotted lingsang *Prionodon pardicolor,* was highest in BCs (Table 2). However, both pangolin species (*Manis pentadactyla and Manis crassicaudata*) was recorded only in the NPAs. Overall RAI of mammal species was lowest in NPAs compared to PAs and BCs (Table 2).

Sample size of unstandardized raw abundance data (number of individuals) combined for all mammal species was 23,131 for PAs, 8280 for BCs, and 12,689 for NPAs (Tables 3, 4). Observed species richness, Shannon diversity index, and Simpson diversity index (Hill's numbers for q = 0, 1, 2) was 47, 16, and 11 for PAs, respectively; 39, 12, and 6 for BCs, respectively; and 48, 12, and 6 for NPAs, respectively (Tables 3, 4). Estimated species richness, Shannon diversity, and Simpson diversity (Hill's numbers for q = 0, 1, 2) was 47, 16, and 11 for PAs, respectively; 39, 12, and 6 for BCs, respectively; and 52, 12, and 6 for NPAs, respectively (Tables 3, 4).

Table 4 Asymptotic diversity estimates along with related statistics for a series of rarefied and extrapolated samples for nationwide camera trapping data along with related statistics on species richness (0), Shannon Diversity Index (1), and Simpson Diversity Index (2) in PAs, BCs and NPAs of Bhutan

Site	Diversity	Observed	Estimator	SE	LCL	UCL
PA	Species richness	47	47	0.62	47.00	48.66
PA	Shannon diversity	16	16	0.11	15.73	15.95
PA	Simpson diversity	11	11	0.10	10.49	10.69
BC	Species richness	39	39	0.63	39.00	40.69
BC	Shannon diversity	12	12	0.18	11.73	12.10
BC	Simpson diversity	6	6	0.10	6.21	6.41
NPA	Species richness	48	52	5.29	48.56	76.72
NPA	Shannon diversity	12	12	0.13	11.51	11.79
NPA	Simpson diversity	6	6	0.09	5.92	6.10

F1–F10 = the first ten species incidence frequency counts in the reference sample; observed = number of species observed; estimator = estimator of the sample coverage suggested by Chao et al. (2014)

SE standard error, *LCL* lower confidence level, *UCL* upper confidence level

Although integrated sample size-based extrapolation curves at 95% confidence intervals for species richness (q = 0) showed that overall species richness was significantly higher in PAs and NPAs compared to BCs (Fig. 3a), confidence intervals for PAs and NPAs overlapped, suggesting there were no significant differences in species richness between PAs and NPAs. Sample coverage for the three sites was estimated at 100%, 100%, and 99% respectively, indicating that sampling was nearly complete for all sites (Fig. 3b). Curves reached their asymptote at a sample size of 4,500 sampling units (i.e. number of individuals) for all three sites. Both PAs and NPAs achieved their sampling asymptote well ahead of the sample reference point of 23,131 and 12,689, respectively (Fig. 3a). Similarly, both sample size and coverage-based sampling curves showed that overall species diversity was significantly higher in PAs compared to BCs and NPAs (top panel of Fig. 3a, b) for any fixed sample-size up to 23,131 and 0.99 in all orders of Hill's numbers (q = 0, 1 and 2). Diversity of species in BCs and NPAs was almost similar in all cases except that species richness was higher in NPAs between 30 and 90% coverage (left panel in Fig. 3a, b for all mammals). PERMANOVA test results on mammal abundance data also showed a strong significant difference between the three sites ($p < 0.001$; Pseudo-F = 6.40; unique perms = 9921). Further pair-wise test results also showed similar results, with strong effects between PAs and NPAs, and BCs and NPAs.

Diversity of large and medium sized mammals was significantly higher in PAs compared to BCs and NPAs (Fig. 3a). There was no significant difference in small mammal diversity between all three sites. Some differences were also observed at the general trophic level (carnivore, herbivore, and omnivore; Fig. 3b). However, species richness was significantly lower in BCs for carnivores, herbivores, large-sized, and small-sized mammal species compared to PAs and NPAs (Fig. 3a, b). There were no significant differences in species richness between PAs and NPAs at all levels. In terms of specific tropic levels, species diversity of large-sized carnivores and medium-sized carnivores was significantly higher in PAs compared to BCs and NPAs (Fig. 3c). But species richness and diversity of small carnivores, medium-sized herbivores, and small herbivores was similar in all three sites (Fig. 3c, d). Similarly, the diversity of large herbivores was significantly higher in PAs compared to BCs and NPAs, despite no significant differences in species richness among three sites (Fig. 3c, d).

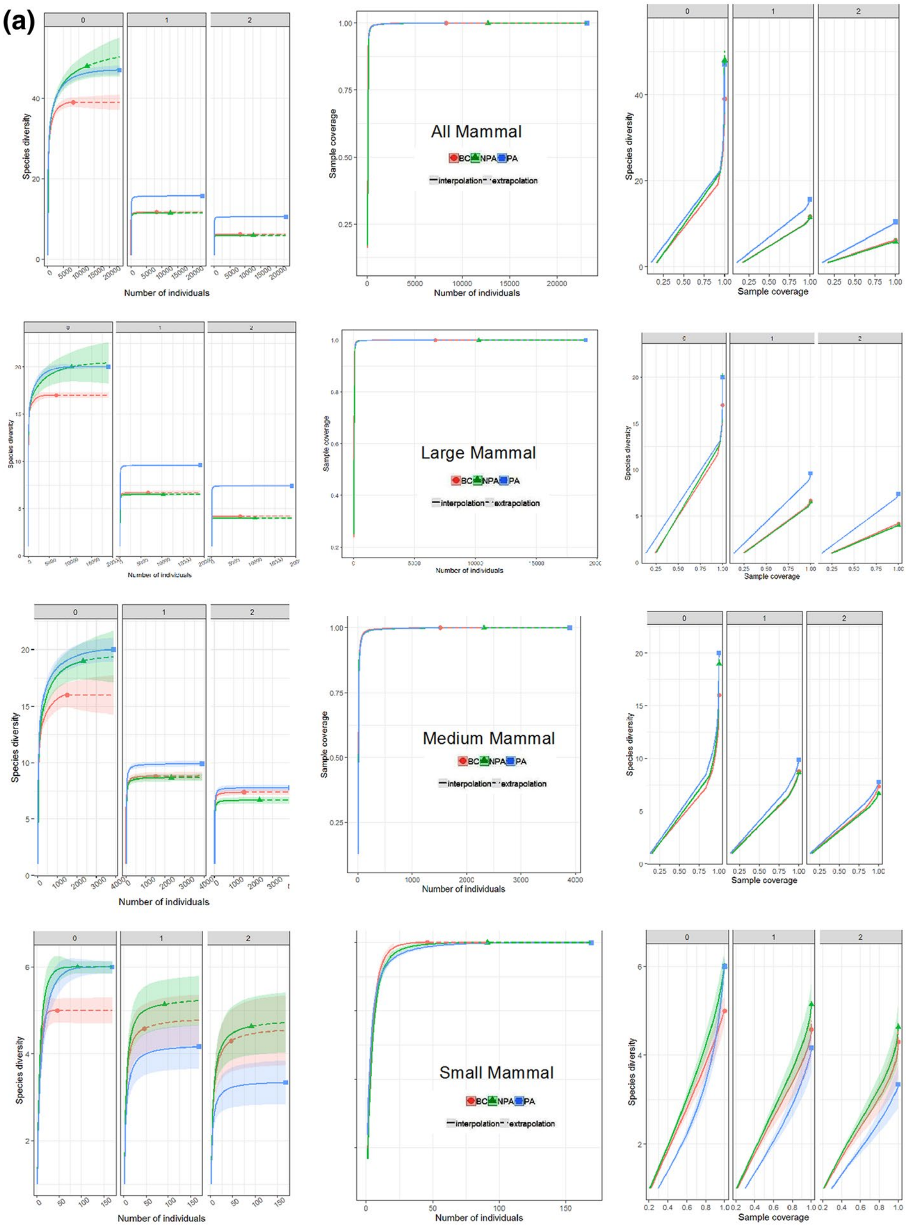


Fig. 3 Sample size and coverage-based rarefaction (solid line segment) and extrapolation (dotted line segments up to largest reference sample size) curves with 95% confidence intervals (shaded areas) using Hill numbers (q = 0, 1, 2) comparing mammal species richness and diversity from camera trapping data in the protected areas (PA), biological corridors (BC), and non-protected areas (NPA; outside the PA and BC). 95% confidence intervals were obtained by a bootstrap method based on 200 replications. Left panel = sample size-based rarefaction and extrapolation curves; middle panel = sample completeness curves; right panel = coverage-based rarefaction and extrapolation curves (all curves are based on the Hill's numbers for Q0 = Species richness; Q1 = Shannon diversity index, Q2 = Simpson diversity index). Mammals were arbitrarily categorized based on their body mass (small mammal = < 1 kgs; medium mammal = 1–10 kgs; large mammal = > 10 kgs; **a**) and trophic level (carnivores, herbivores, omnivores; **b**). **c** Denotes species richness and diversity for carnivore species. **d** Denotes species richness and diversity for herbivore species

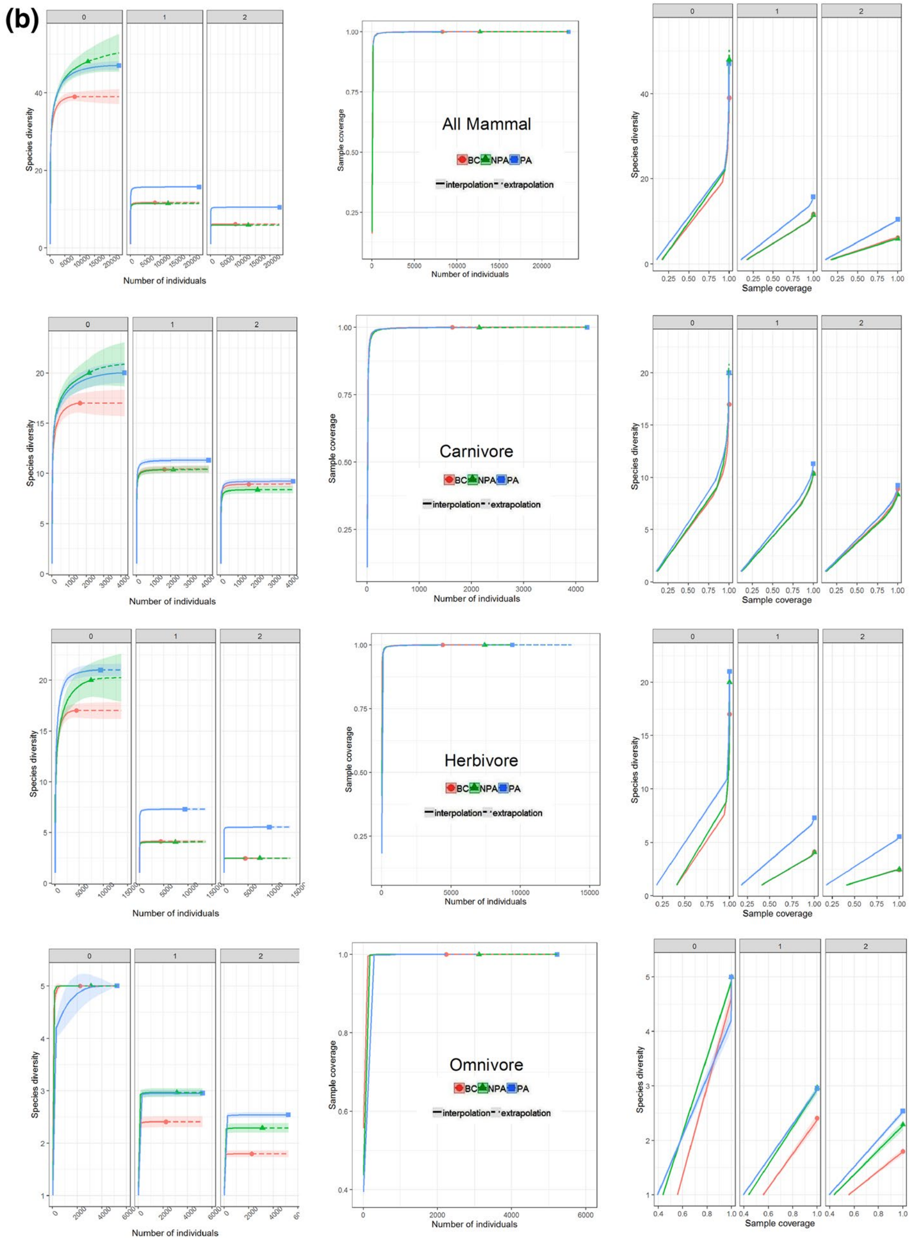
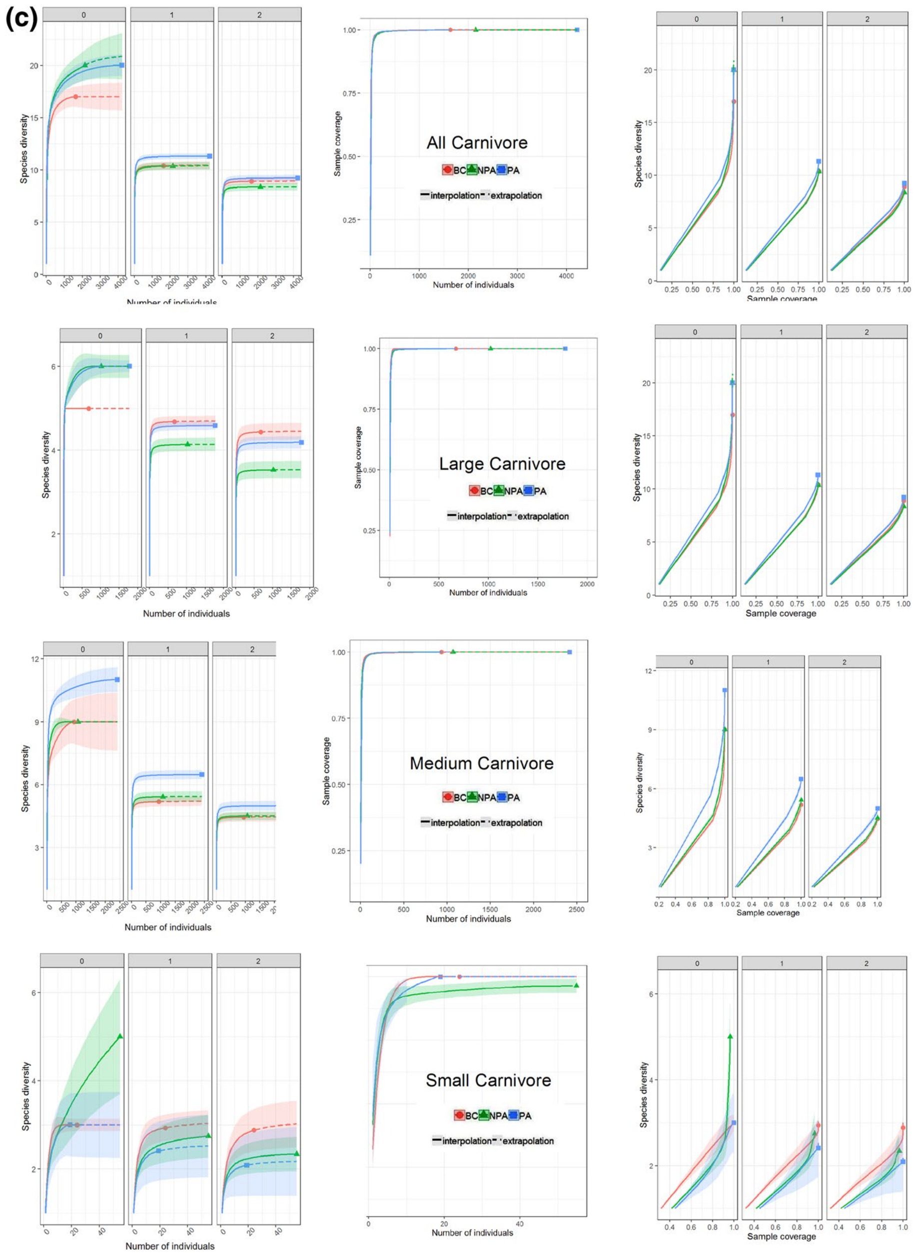


Fig. 3 (continued)



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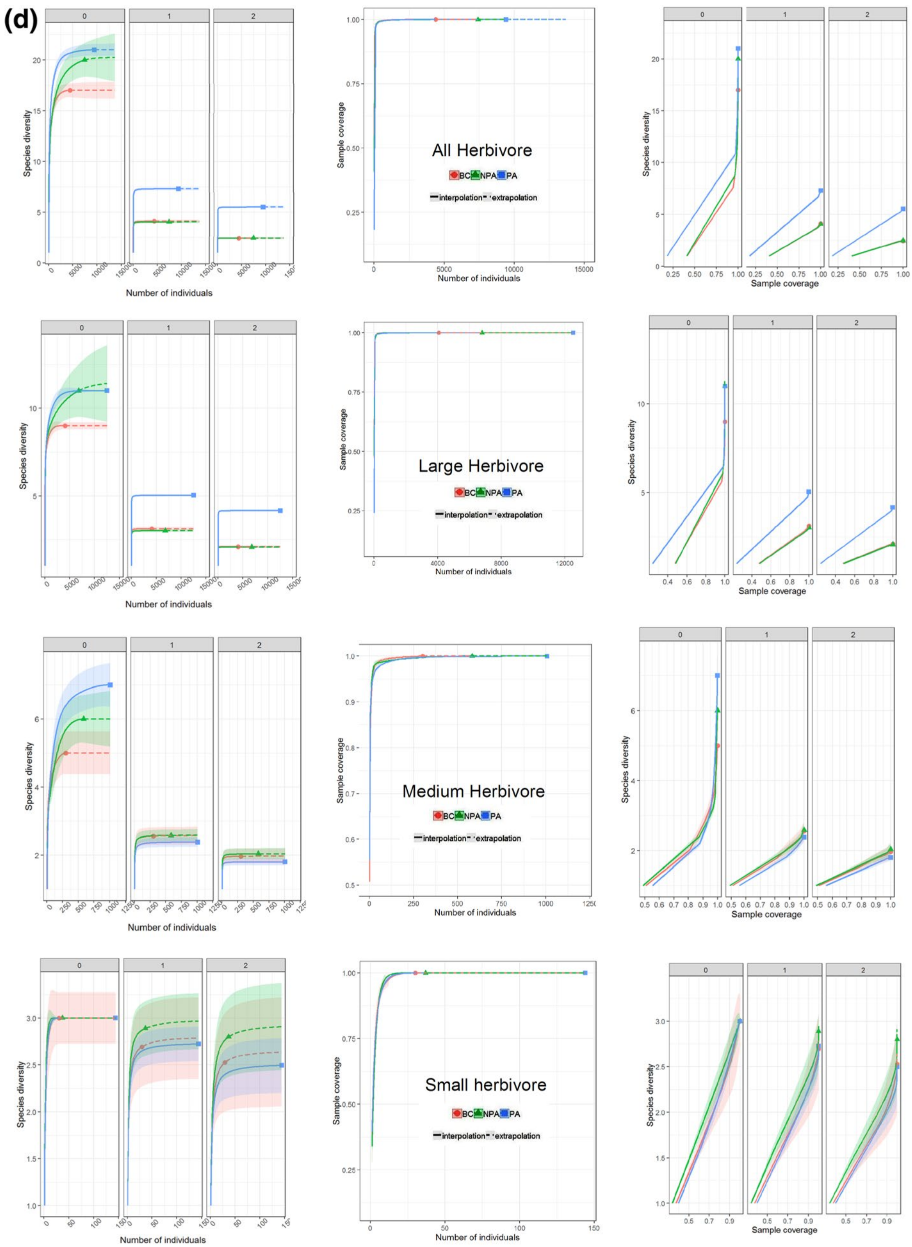

Fig. 3 (continued)

Discussion

Efficacy of Bhutan's protected area network

Over 21% of global mammal species including those in the Eastern Himalayas are currently threatened with extinction (Dorji et al. 2018; IUCN 2018) from habitat alteration (Crooks et al. 2017; Schipper et al. 2008). Protected areas are integral for biodiversity conservation and play a vital role in preventing species extinction, preserving habitat integrity, and conserving species diversity especially across the Eastern Himalayas (Chettri et al. 2008; Dorji et al. 2018). However, Eastern Himalayan protected areas are becoming isolated pockets amidst unrelenting habitat conversion that is causing irreversible damage to the landscape and the region's biodiversity (Chettri et al. 2008; Sharma et al. 2008; Dorji et al. 2018). Bhutan is one of the few global countries which has achieved the novel idea of securing at least half of the earth, as suggested by Wilson (2016) to address the species-extinction crisis, conserve biodiversity, and prevent collapse of vital services provided by ecosystems, such as carbon sequestration and climate regulation (Dinerstein et al. 2017). Our study further shows that Bhutan's PAs are effectively conserving medium and large mammal species, as demonstrated through the significant difference in mammal diversity between PAs, BCs, and NPAs with the strongest difference between PAs and NPAs (Fig. 3; Table 3). Furthermore, results from our sample size and coverage-based sampling curves established a greater diversity of mammals in PAs relative to BCs and NPAs, while BCs and NPAs shared an almost similar pattern of mammal diversity. PAs in Bhutan afford better habitat protection because consumptive uses (firewood, non-timber forest products and timber for rural house construction) are heavily regulated, and no commercial activities (such as mining, hydropower damming and commercial logging) are allowed (Wangchuk 2007). PAs also effectively prevented up to 63% of net forest cover loss, with early established protected areas and the less fire-sensitive broadleaf forests showing higher effectiveness (e.g. Royal Manas and Jigme Dorji National Parks) (Bruggeman et al. 2018). However, confidence intervals in species diversity curves for BCs and NPAs eventually converge, indicating that these two landscape types share similar mammal species diversity. This can be possibly attributed to a land management perspective, as both BCs and NPAs are managed by Bhutan's various Territorial Divisions for multiple land-use purposes (Bruggeman et al. 2018; Katel and Schmidt-Vogt 2015; Lham et al. 2018). Moreover, only three of the eight BCs are currently operational and have conservation management plans in place (Dorji and Wangdi 2018). However, resource use and accessibility in operationalized BCs are more regulated with tighter rules, than NPAs.

Previous studies from the region show that human disturbance adversely affects the abundance and conservation of small and large mammals (Dorji et al. 2012; Mishra et al. 2006; Panthi et al. 2017; Velho et al. 2016). Although forest cover in Bhutan increased between 1990 and 2010 with an annual net-gain of 0.22% (average annual growth rate of 59-km^2/year) (Gilani et al. 2015), habitat quality did degrade in some areas because of infrastructure development such as hydropower dams, road-network expansion, industrial development, urbanization, selective logging, and mining (Bruggeman et al. 2016; Watershed Management Division 2017). Greater forest cover loss was also observed along the periphery of PA boundaries compared to areas inside and further away (Bruggeman et al. 2018). Most developments were initiated in the last three decades and mainly occurred in the NPAs and BCs, before BCs were operationalized. For example, all nine of Bhutan's major hydropower dams, forest management units for logging, and district urban towns (except Gasa which has < 500 residents) are in NPAs. Based on studies by Tshering (2003) and Wangchuk (2002), livestock grazing was once thought to be the main threat to biodiversity conservation in Bhutan's PAs. It has, however, subsequently decreased due to change in livestock grazing patterns and the promotion of intensive livestock management practices (Samdup et al. 2010; Wangchuk et al. 2014). In particular, local free ranging breeds of cows were progressively replaced by improved dairy crossbred cattle, which are mainly stall-fed (Samdup et al. 2010). PAs and BCs also have a higher proportion of shrub lands and grasslands relative to NPAs (Gilani et al. 2015). Such habitats are important for herbivores (Gibson 2009; Sankaran 2009). Similarly, only 4% of agricultural and human inhabited areas in the country fall inside PAs including BCs (Dorji and Wangdi 2018). Furthermore, habitat degradation from agricultural activities has decreased in the last two decades due to agricultural intensification, a ban on shifting cultivation, and increased agricultural imports (Bruggeman et al. 2016; Phuntsho et al. 2015; Roder et al. 1992). Therefore, despite human presence in Bhutan's protected area network (Dorji et al. 2012), anthropogenic impacts are relatively low compared to NPAs, thus delivering better efficacy in maintaining and conserving mammal diversity.

Mammal species diversity and conservation

By virtue of adequate landscape protection, higher mammal diversity in PAs relative to BCs and NPAs is attributed to the presence of large and medium-sized carnivore species such as the tiger, dhole *Cuon alpinus,* Binturong, clouded leopard and Tibetan fox *Vulpes ferrilata*, along with large herbivore species such as Asiatic water buffalo *Bubalus arnee,* golden langur, musk deer, and Asian elephant (Table 2 and Fig. 3a, b). However, the presence of the critically endangered Chinese pangolin and endangered Indian Pangolin which are priority species for the Eastern Himalayas (Dorji et al. 2018), was only confirmed in NPAs (Table 2). NPAs also recorded higher diversity of omnivore species such as Asiatic black bear, wild pig *Sus scrofa*, Assamese macaque *Macaca assamensis*, Rhesus macaque *Macaca mulatta*, and yellow-throated marten *Martes flavigula*. A realignment of PA and BC boundaries to capture areas of NPAs known to support these species is, therefore, warranted and feasible in Bhutan where the vast majority of the landscape still remains forested regardless of tenure. This will be especially crucial for the survival of the endangered Chinese and Indian pangolins. Furthermore, all omnivorous species occurred at all three sites and are categorised as problematic species in the national human-wildlife conflict management strategy of Bhutan (Nature Conservation Division 2008), and thus, require immediate conservation and management intervention.

Bhutan has high carnivore diversity (39 species; Wangchuk et al. 2014) within large tracts of undisturbed habitat. Of the 56 terrestrial mammal species we detected, more than 50% were carnivores and about 16% were ungulates which are important prey (Wang and Macdonald 2009a, Table 1). This high carnivore diversity and associated prey can be largely attributed to the diverse array of habitats ranging from subtropical forests in the lowlands, to temperate broadleaf and mixed conifer forests at higher elevations across two biogeographical realms (Dinerstein et al. 2017). We detected nine (81.8%) of Bhutan's 11 resident felid species across this landscape, and consistent with results from previous studies (Tempa et al. 2013; Wang and Macdonald 2009b), our study also showcases the effectiveness of Bhutan's PAs in conserving large carnivores and their prey. BCs, in particular, have a higher diversity of large carnivores like tigers, clouded leopard, dhole and, common leopards, and prey species such as barking deer, sambar, wild-pig, and musk deer. This clearly indicates that Bhutan's BCs are currently functional and facilitating movement, breeding or range expansion of these big cats (Wangchuk 2007). Because our study area stopped at the tree line (4500 m asl), we did not record high elevation felids like the snow leopard and Pallas's cat *Otocolobus manul*. However, > 95% of areas above 4500 m asl are in the protected area network, with guaranteed protection (Dorji and Wangdi 2018).

Our comprehensive landscape survey recorded the presence of some rare mammals previously only known from sporadic records. This included the Chinese pangolin, Indian pangolin, mountain weasel *Mustela altaica,* small-toothed ferret badger, Binturong, Asian small clawed otter, and Bhutan giant flying squirrel *Petaurista nobilis*. However, we did not record the critically endangered pygmy hog *Porcula salnania* and vulnerable Indian rhinoceros *Rhinoceros unicornis*, previously recorded in the Royal Manas National Park (Wikramanayake and Wangchuk 1993) and only confirmed through anecdotal information in the last decade (Dorji 2014a, b). This may be because of their relative low density due to a reduction of grassland, shrubland, and associated barren areas (Gilani et al. 2015) which are key habitat requirements (Dinerstein and Price 1991; Mary et al. 2013). Grassland cover reduction in Bhutan is due to poor or non-existent habitat management, and invasion by exotics such as *Lantana camara* and *Eupatorium odoratum* (Dorji 2014a, b; Wangdi 2015).

Thirty-three percent (n = 19) of our detected mammal species are totally protected under the Forest and Nature Conservation Rules of Bhutan, and 31% (n = 18) are threatened under the IUCN category of threatened species. Despite stringent legislation, high mammal species diversity in PAs, and a strong political will for nature conservation, our detection of local people, domestic livestock, foreign poachers, and forest fires reveal inherent threats to resident mammals. This finding reinforces local and regional threats to mammals from agricultural activities, livestock grazing, timber collection, poaching and illegal trading of wildlife parts, forest fire, and human-wildlife conflict (Dendup and Lham 2018; Dorji et al. 2018; Velho et al. 2012). Despite these anthropogenic threats, Bhutan's network of PAs and BCs still harbor a rich mammal community through the government's ability to reconcile biodiversity conservation goals with social and economic issues. The importance of local communities within PAs and BCs is further recognized and integrated into PA conservation goals, and stewardship promoted through incentive-based conservation programs (Lham et al. 2018; Tshering 2003). This integration of landscape protection (PAs) and connectivity (BCs) along with harmonious coexistence with local communities, will ensure the conservation of Bhutan's mammal diversity well into the future.

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