Patterns of mammal species richness in India

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This article focuses on understanding the patterns of species richness and explaining the observed patterns for Indian primates, carnivores and herbivores. Field observations of local experts and occupancy modelling permit estimation of individual species occurrence, richness within groups, and overall species richness. Average estimated richness was $\hat{\overline{SR}}_{M}$ = 7.2. Protected areas supported higher richness, but forest cover did not (exceptions were herbivores). Species richness decreased with increasing elevation and human densities, but decreased with decreasing human tolerance (exceptions were primates). Species richness patterns vary across taxonomic groups and accounting for individual species differences will be important in selection of priority conservation areas in India.

Keywords: Mammals, occupancy, protected areas, species richness.

PATTERNS in species richness and processes influencing these patterns in richness have been a key focus in macroecology[1–3]. Proposed explanations for these patterns involve spatial heterogeneity (biotic and physical), time (ecological and evolutionary), functional types, population dynamic factors (size and growth rate), constraints introduced by inter-specific interactions, molecular evolution and Rapoport's rule[2,4–9]. Other hypotheses relate to environmental stability and predictability, temperature, productivity, evapo-transpiration, solar angle and other climatic factors[10,11]. Recent explanations involve abiotic–biotic interactions, aridity, energetic equivalents and scale-hierarchy[11,12]. But few studies have incorporated anthropogenic influences on richness patterns[13].

Many studies have found that richness decreases with increasing latitude[2,8]. However, there exist exceptions to this classical pattern in species richness in several plant–animal groups, with peaks in richness occurring at varying latitudes[14–16]. Willig *et al.*[2] suggested that these exceptions result from inappropriate scaling issues, and occur primarily in aquatic flora and parasitic species. Many studies have found that spatial scale is often a confounding factor regardless of geographic zones, latitudinal bands or quadrat sizes applied[11,17–19].

In the present study, patterns in species richness were examined for a suite of 36 Indian mammals (carnivores, herbivores and primates), to see if they vary among primates, carnivores and herbivores. How protected areas, forest cover, elevation, land-cover characteristics and human factors affect richness was assessed. Using data from field observations of local experts, the occurrence of individual species, richness within groups, and overall species richness was estimated for this suite of mammals in India. I developed a priori predictions about species richness patterns, and then tested them with data on Indian mammals.

The present approach differs from previous research in several ways: (1) current field data from local experts were used and not static data sources that cover long, unspecified periods of time (e.g. typical range maps); (2) grid cell-based sampling was used; (3) both ecological and anthropogenic covariates were used to predict species occurrence, thus capturing the realities of the human-dominated landscapes in which these species presently occur, and (4) imperfect detection of species (species are sometimes present, but not detected by local experts) was incorporated to estimate and model each species occurrence.

Materials and methods

Study design, expert surveys and occupancy

A grid-based sampling approach has been used in the present study, dividing India into 1326 grid cells (average cell size 2818 sq. km). This grid cell size was chosen as it was practical to get sufficient replication of reports by local experts on the presence of multiple species[20,21]. This grid cell size allowed experts to give us their information on species presence or absence for the whole of India. It was hard to find people with sufficient expertise to cover the country for the number of species involved at finer scales. This cell size allowed collection of data on ecological and social covariates for the entire country. For each mammal species, existing information[22,23] was used to identify subsets of cells for which species occurrence was biogeographically and ecologically plausible and excluded areas where the species was historically absent[20,21]. Species presence–absence data were obtained from knowledgeable Indian wildlife experts based on their field observations rather than conduct field surveys, as this is not logistically feasible for a country the size of

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India. Wildlife experts completed survey forms between January and August 2006. Experts were selected based on their knowledge of particular regions and species[20,21,24]. Experts indicated presence of individual species only if they had personally observed either the species or its direct signs (tracks or scats) in the field within the specific grid cell(s) of interest in 2006. They were instructed to not indicate presence of a species if there was any uncertainty (e.g. in identifying scats or tracks to species) associated with an observation[20,24]. Therefore, a reported detection was indeed interpreted as reflecting presence of the species, reports of non-detection were not interpreted to mean absence of the species. This allowed the elimination of problems associated with false presences[25]. Replicate detection–non-detection data were collected by surveys of multiple experts (ranged between 2 and 37 per cell), and used to deal with imperfect detection[25]. The program PRESENCE was used to estimate occupancy for 36 Indian mammals in every cell[20,21,24].

Covariates

In most field situations, site characteristics (weather, habitat type, etc.) have the potential to influence detection probabilities and occupancy[26]. Occupancy and detection probabilities were modelled as functions of covariates using logit link functions[26]. For example, the logit of the probability of a site being occupied is expressed as:

$$\text{logit}\,(\Psi_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_u x_{iu},$$

which is a linear function of the u covariates associated with site i, with one intercept term β_0 and u regression coefficients that need to be estimated[26].

Based on ecological and social contextual knowledge, covariates most likely to influence the distribution of large mammals in India were selected[20,24]. These covariates represent ecological and anthropogenic influences, and recognize the importance of local ecology, habitat and anthropogenic effects on mammal distributions[10]. Presence–absence and proportion of cell covered by protected areas, presence–absence of forest cover, land cover–land use and elevation as covariates representing ecological characteristics[20]. Data on protected areas were improved and refined from the World Database on Protected Areas[27], and land cover–land use data were derived from Global Land Cover Facility 2000 (ref. 28). The land-cover and land-use categories were consolidated from 23 to 10, and the total number of pixels in each category was used for every grid cell. This allowed for a reasonable and easily interpretable model set (Table 1). The average elevation in every grid cell was calculated (using data from CGIAR–CSI[29]) and the data were rescaled. Anthropogenic influence was represented using human population density and 'human cultural tolerance' towards mammal species in India[20,21,24]. Human population density data were derived from LandScan Global Population Database 2000 (refs 30, 31). Human population density was calculated for every cell and this variable was log-transformed. A human cultural tolerance variable was developed from prior personal observations, socio-cultural knowledge and hunting patterns of local communities in the different states of India[20,32]. This covariate effectively represents both cultural tolerance of the local people and the effectiveness of official law enforcement. States were grouped from most tolerant to least tolerant (Table 1). The western states of Rajasthan and Gujarat were classified as most tolerant (category = 1), the seven northeastern hill states, Chhattisgarh and Jharkhand were classified as least tolerant (category = 3), and all other states as medium tolerant (category = 2).

Occupancy and species richness estimation

Maximum likelihood approach was used to estimate occupancy using the single-season models developed by MacKenzie *et al.*[26]. For each species, multiple models were fit, representing different hypotheses about the processes that generated the data. The models were ranked in order of parsimony, and model weights calculated using Akaike's Information Criterion (AIC)[33]. The AIC weights represent relative measures of the appropriateness of a given model relative to other models in the model set, and sum to 1 for all members in a model set. In situations where there were multiple models supported by the data[20,24], model averaging based on AIC model weights was used.

Estimates of occupancy, $\hat{\Psi}_{ij}$ for each species j, in each cell i, within the area deemed plausible for species occurrence were derived. These values reflect the probability that a cell i is occupied by the focal species, based on the covariate values associated with the cell[20,24]. Estimated mammal species richness for a particular cell ($SR_{i\text{M}}$) was computed as

$$SR_{i\text{M}} = \sum_{j \in M} \hat{\Psi}_{ij}.$$

To estimate species richness within groups of carnivores ($SR_{i\text{C}}$), herbivores ($SR_{i\text{H}}$) and primates ($SR_{i\text{P}}$), individual occupancy estimates for species belonging to that group were summed. Data on 10 carnivores, 10 herbivores and 16 primates were collected. Some species (particularly ungulates occurring in higher altitudes) were excluded, as sufficient data could not be collected for them in North and North Eastern India. Average species richness, for example, for the whole of India, was computed as

$$S\hat{\hat{M}}_{\text{M}} = \sum_{i \in S} S\hat{M}_{i\text{M}}$$

Table 1. Average species richness estimates across groups and relationship to covariates

Group/ covariate	Primates (N = 16) $\hat{\hat{SR}}_{P}$	Carnivores (N = 10) $\hat{\hat{SR}}_{C}$	Herbivores (N = 10) $\hat{\hat{SR}}_{H}$	All mammals (N = 36) $\hat{\hat{SR}}_{M}$
Country-wide richness (N = 1326)	2.04 (SE = 0.03) *R*: 0.00–5.51	3.19 (SE = 0.04) *R*: 0.00–4.94	2.04 (SE = 0.03) *R*: 0.00–3.83	7.26 (SE = 0.07) *R*: 0.00–11.44
Protected area (PA)				
PA (N = 503)	2.32 (SE = 0.05) *R*: 0.00–5.48	3.43 (SE = 0.06) *R*: 0.00–4.94	1.99 (SE = 0.05) *R*: 0.00–3.83	7.73 (SE = 0.12) *R*: 0.00–11.44
No PA (N = 823)	1.87 (SE = 0.04) *R*: 0.00–5.51	3.04 (SE = 0.05) *R*: 0.00–4.94	2.07 (SE = 0.04) *R*: 0.00–3.80	6.97 (SE = 0.09) *R*: 0.00–11.12
PA type (%)				
0 (N = 823)	1.87 (SE = 0.04) *R*: 0.00–5.51	3.04 (SE = 0.05) *R*: 0.00–4.94	2.07 (SE = 0.04) *R*: 0.00–3.80	6.97 (SE = 0.09) *R*: 0.00–11.12
1–25 (N = 411)	2.39 (SE = 0.06) *R*: 0.00–5.48	3.45 (SE = 0.08) *R*: 0.00–4.91	2.00 (SE = 0.07) *R*: 0.00–3.83	7.83 (SE = 0.12) *R*: 0.00–11.14
26–50 (N = 60)	2.09 (SE = 0.16) *R*: 0.00–4.81	3.04 (SE = 0.17) *R*: 0.00–4.94	2.07 (SE = 0.14) *R*: 0.00–3.83	7.53 (SE = 0.44) *R*: 0.00–10.62
51–75 (N = 21)	1.89 (SE = 0.33) *R*: 0.00–5.15	3.12 (SE = 0.43) *R*: 0.00–4.87	1.77 (SE = 0.35) *R*: 0.00–3.83	6.78 (SE = 0.93) *R*: 0.00–11.44
>76 (N = 10)	1.65 (SE = 0.44) *R*: 0.00–4.17	3.16 (SE = 0.46) *R*: 0.00–4.87	2.15 (SE = 0.47) *R*: 0.00–3.67	6.95 (SE = 0.93) *R*: 0.00–9.94
Forest cover (FC)				
FC (N = 1107)	2.03 (SE = 0.03) *R*: 0.00–5.51	3.11 (SE = 0.04) *R*: 0.00–4.92	1.99 (SE = 0.03) *R*: 0.00–3.83	7.12 (SE = 0.08) *R*: 0.00–11.32
No FC (N = 129)	2.08 (SE = 0.09) *R*: 0.00–5.02	3.89 (SE = 0.09) *R*: 0.00–4.94	2.48 (SE = 0.08) *R*: 0.00–3.82	8.46 (SE = 0.15) *R*: 0.00–11.44
Elevation (m)				
< 1000 (N = 1124)	2.17 (SE = 0.03) *R*: 0.00–5.51	3.62 (SE = 0.03) *R*: 0.00–4.94	2.35 (SE = 0.03) *R*: 0.00–3.83	8.14 (SE = 0.07) *R*: 0.00–13.90
1001–2000 (N = 42)	3.01 (SE = 0.21) *R*: 0.00–4.90	1.74 (SE = 0.12) *R*: 0.00–4.27	0.64 (SE = 0.08) *R*: 0.00–1.78	3.01 (SE = 0.21) *R*: 0.00–10.95
2001–3000 (N=28)	1.63 (SE = 0.27) *R*: 0.00–4.16	0.86 (SE = 0.14) *R*: 0.00–1.92	0.47 (SE = 0.09) *R*: 0.00–1.00	2.98 (SE = 0.49) *R*: 0.00–7.08
3001–4000 (N = 32)	1.10 (SE = 0.22) *R*: 0.00–4.05	0.66 (SE = 0.14) *R*: 0.00–1.93	0.25 (SE = 0.07) *R*: 0.00–1.00	2.02 (SE = 0.44) *R*: 0.00–6.98
4001–5000 (N = 57)	0.56 (SE = 0.09) *R*: 0.00–3.35	0.42 (SE = 0.09) *R*: 0.00–1.90	0.05 (SE = 0.02) *R*: 0.00–0.69	1.03 (SE = 0.21) *R*: 0.00–5.94
> 5000 (N = 37)	0.31 (SE = 0.15) *R*: 0.00–3.88	0.32 (SE = 0.12) *R*: 0.00–2.79	0.09 (SE = 0.06) *R*: 0.00–1.70	0.72 (SE = 0.33) *R*: 0.00–8.37
Human population density				
< 1000 (N = 954)	1.90 (SE = 0.07) *R*: 0.00–5.48	3.17 (SE = 0.05) *R*: 0.00–4.94	2.01 (SE = 0.04) *R*: 0.00–3.83	7.07 (SE = 0.10) *R*: 0.00–11.44
1001–2000 (N = 224)	2.35 (SE = 0.06) *R*: 0.00–4.80	3.38 (SE = 0.06) *R*: 0.00–4.84	2.11 (SE = 0.06) *R*: 0.00–3.83	7.84 (SE = 0.10) *R*: 0.00–10.77
2001–3000 (N = 107)	2.42 (SE = 0.09) *R*: 0.00–5.51	2.99(SE = 0.07) *R*: 0.00–4.86	2.07 (SE = 0.06) *R*: 0.00–3.78	7.48 (SE = 0.14) *R*: 0.00–10.47
3001–4000 (N = 22)	2.41 (SE = 0.17) *R*: 0.00–4.51	3.12 (SE = 0.13) *R*: 0.00–3.12	2.27 (SE = 0.14) *R*: 0.00–2.27	7.80 (SE = 0.27) *R*: 0.00–9.55
> 4000 (N = 14)	2.90 (SE = 0.26) *R*: 0.00–4.94	3.07 (SE = 0.16) *R*: 0.00–4.26	2.16 (SE = 0.18) *R*: 0.00–3.70	8.13 (SE = 0.37) *R*: 0.00–10.40
Human cultural tolerance				
High (N = 241)	1.4 (SE = 0.05) *R*: 0.00–2.90	3.7 (SE = 0.04) *R*: 2.17–4.94	3.57 (SE = 0.02) *R*: 0.94–3.83	8.68 (SE = 0.09) *R*: 3.11–11.67
Medium (N = 880)	1.96 (SE = 0.03) *R*: 0.00–5.15	3.17 (SE = 0.05) *R*: 0.00–4.92	1.84 (SE = 0.03) *R*: 0.00–3.77	6.98 (SE = 0.10) *R*: 0.00–11.33
Low (N = 201)	3.14 (SE = 0.09) *R*: 1.20–5.51	2.63 (SE = 0.08) *R*: 1.03–4.81	1.05 (SE = 0.02) *R*: 0.27–2.52	3.14 (SE = 0.09) *R*: 0.00–8.95

R, Range.

for all mammal species in the focal group and similarly, for other groups of species, where S denotes the set of grid cells over which the average was calculated.

A priori predictions

Modelling covariates enabled the evaluation of predictions from a priori hypotheses about factors influencing probabilities of occupancy and richness. Results from previous studies conducted at many scales, involving other taxa and different biogeographic regions have led to the prediction that overall species richness (SR_M) for Indian mammal communities would decrease with latitude. Higher overall species richness has been predicted in lower latitudes[2,8,9,11]. Higher species richness might be expected in the Western Ghats and the northeastern mountainous regions[34]. Primates are expected to exhibit higher richness in these hotspots, with less distinct richness patterns expected for wider ranging carnivores and herbivores[20,21,24]. We might expect cells with protected areas to have higher species richness for species that prefer denser habitat cover[17,20,21,24,35,36], but some species can persist outside protected areas. Some land-cover types such as deciduous and evergreen forests may have higher species richness compared to barren and scrub areas. We might expect lower elevations to have higher overall species richness (except for endemics such as northeastern macaques, which might favour higher elevation areas)[8,11,19,24]. Species richness may decrease with higher human population densities (particularly for more sensitive species such as wild dog, tiger, muntjac, rhino, endemics such southern and north-eastern macaques and loris species), or we may find highest richness in medium density areas as there are some mammals that might adapt to people (such as jackal, leopard, nilgai, chinkara, wild pig, Hanuman langur, rhesus and bonnet macaque)[21,24]. With regard to cultural tolerance, higher richness may be expected in the most tolerant western states, particularly for herbivores, and lower tolerance for primates in the south and northeastern regions[21,24].

Results

Species richness

Average species richness of mammals within the focal suite for the whole of India was estimated to be $\widehat{SR}_M$ = 7.2 (range = 0.0–10.4, N = 1326). This can be viewed as an estimate of the species richness expected for a randomly selected Indian grid cell. As expected, there was a latitudinal gradient in species richness, with fewer species in the north (Figure 1 *a*). However, there emerged an east-west pattern in overall richness. For primates, average richness was $\widehat{SR}_P$ = 2.04 (range = 0.00–5.51). As predicted for primates, the richest areas were the Western Ghats and the northeastern mountain ranges (Figure 1 *b*). Among carnivores, estimated average richness was $\widehat{SR}_C$ = 3.19 (range = 0–4.79). Carnivore species richness pattern differed from that of primates, with higher richness in both southern and central India, only decreasing at the highest latitudes (Figure 1 *c*). For herbivores, estimated average richness across India was $\widehat{SR}_H$ = 2.04 (range = 0.00–3.83). Among herbivores, there was a strong east-west gradient in richness, with highest richness in the most culturally tolerant states of the west (Figure 1 *d*; Table 1). The lack of data on several ungulate species would lead us to expect higher richness even in the northern cells, particularly for herbivores.

Species richness and protected areas

The relationship between presence and type of protected area and species richness was examined. As predicted, cells with protected areas present had higher richness for all groups, except herbivores (Figure 2 *a*). Average estimated richness for unprotected cells was $\widehat{SR}_M$ = 6.97 (range = 0.00–11.12, N = 823), for protected cells was $\widehat{SR}_M$ = 7.73 (range = 0.00–11.44, N = 503) and was significantly different for protected and unprotected cells (t-test, $P < 0.0001$, df = 1064). For primates in unprotected cells, $\widehat{SR}_P$ = 1.87 (range = 0.00–5.51), in protected cells, $\widehat{SR}_P$ = 2.32 (range = 0.00–5.48) and was significantly different among them (t-test, $P < 0.0001$, df = 956). For carnivores, the average richness for unprotected cells was $\widehat{SR}_C$ = 3.04 (range = 0.00–4.90), for protected cells was $\widehat{SR}_C$ = 3.43 (range = 0.00–4.94) and was significantly different for protected and unprotected cells (t-test, $P < 0.0001$, df = 1024). Among herbivores in unprotected cells, average richness was $\widehat{SR}_H$ = 2.07 (range = 0.00–3.80), whereas richness in protected cells was $\widehat{SR}_H$ = 1.99 (range = 0.00–3.83), but not significantly different (t-test, $P > 0.10$, df = 1028).

However, when the proportion of cells covered by a protected area was examined, cells with protected areas covering 1–25% (category 2) had the highest overall richness 6.97 (Figure 2 *b*). This suggests that many species are restricted to small protected fragments present in the landscape. Richness estimates for primates mirror those of overall species richness, high diversity in smaller but protected cells. Among carnivores, cells with 1–25% and 26–50% (categories 2 and 3) of land covered by protected areas had the highest average richness estimates, whereas for herbivores, richness was highest in cells with a large proportion of land covered by protected areas >76% (category 5). (Details are given in Table 1.)

Species richness and forest cover

The relationship between presence of forest cover and mammal species richness was examined. Contrary to

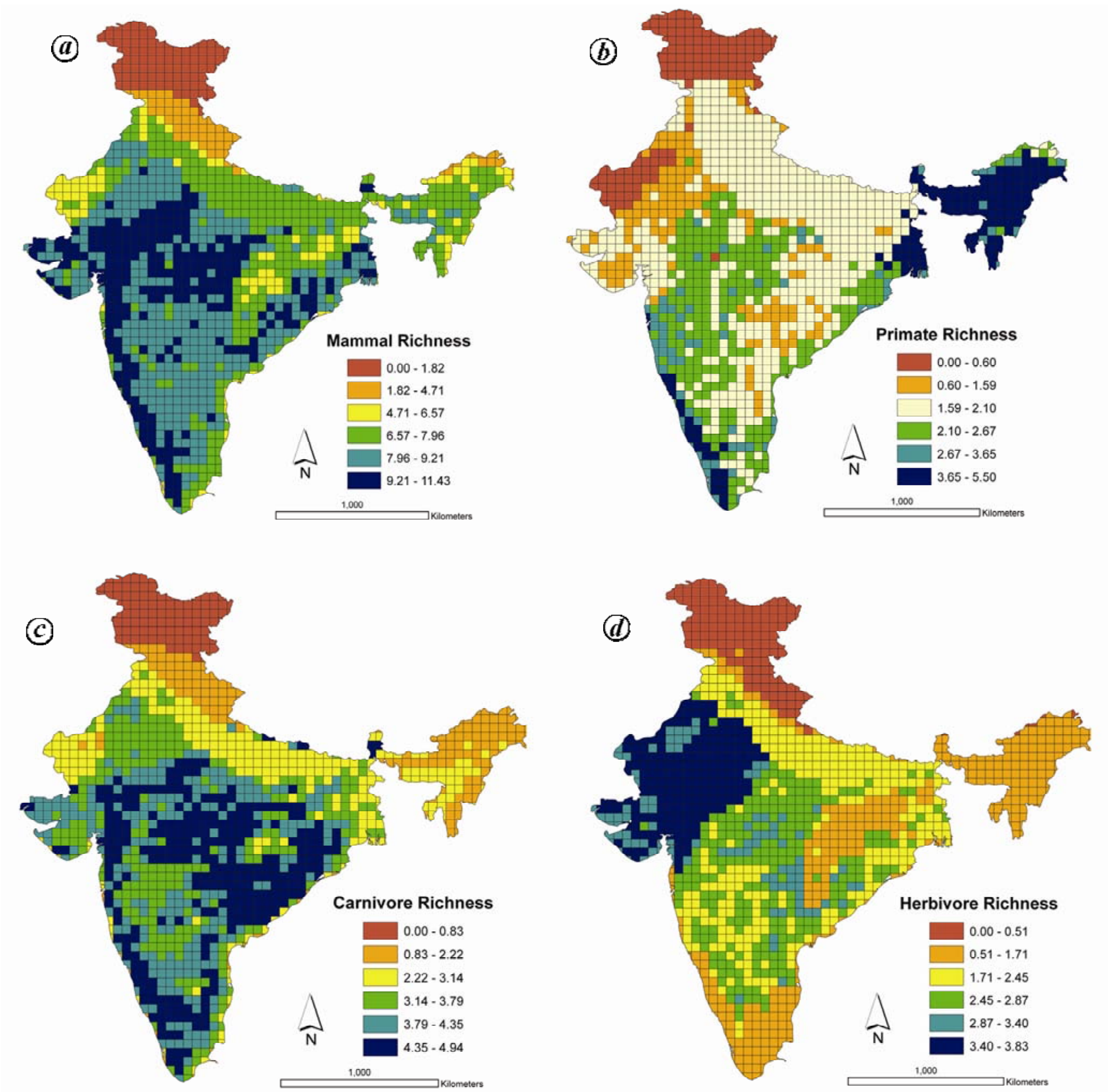

Figure 1. ***a***, Estimated overall average species richness across India for 36 species. Overall richness (SR_{M}) = $\Sigma(\hat{\Psi}_{i})$, the sum of individual species occurrence in a cell. The more blue–green a cell, the higher its richness, whereas the orange–red cells have lower richness. (For northern India, some species that live in the high-altitude regions could not be included.) ***b***, Estimated overall primate richness across India. Sum of individual occupancy of the following species: *Macaca munzala* (Arunachal macaque), *Macaca assamensis* (Assamese macaque), *Macaca thibeta* (Tibetan macaque), *Macaca radiate* (bonnet macaque), *Macaca silenus* (lion-tailed macaque), *Macaca leonine* (pig-tailed macaque), *Macaca mulatta* (Rhesus macaque), *Macaca arctoides* (stump-tailed macaque), *Semnopithecus entellus* (Hanuman langur), *Trachypithecus pileatus* (capped langur), *Trachypithecus geei* (golden langur), *Trachypithecus johnii* (Nilgiri langur), *Trachypithecus phayrei* (Phayre's leaf monkey), *Loris lyddekerianus* (slender loris), *Nyticebus bengalensis* (slow loris) and *Bunopithecus hoolock* (hoolock gibbon). ***c***, Estimated overall carnivore richness across India. Sum of individual occupancy of the following species: *Ursus thibetanus* (black bear), *Ursus arctos* (brown bear), *Melursus ursinus* (sloth bear), *Helarctos malayanus* (sun bear), *Canis aureas* (jackal), *Hyaena hyaena* (hyena), *Canis lupus* (wolf), *Cuon alpinus* (dhole), *Panthera pardus* (leopard) and *Panthera tigris* (tiger). ***d***, Estimated overall herbivore richness across India. Sum of individual occupancy of the following species: *Cervus axis* (chital), *Cervus unicolor* (sambar), *Muntiacus muntjak* (muntjac), *Antilope cervicapra* (blackbuck), *Bosephalus tragocamelus* (nilgai), *Gazella bennetti* (chinkara), *Sus scrofa* (wild pig), *Bos gaurus* (gaur), *Elephas maximus* (elephant) and *Rhinoceros unicornis* (one-horned rhinocerous).

predictions, cells with no forest cover had higher average species richness (Figure 3 *a*). Average estimated richness in forest-covered cells was $\hat{\overline{SR}}_{M} = 7.12$ (range = 0.00–11.33, $N = 129$), whereas richness for cells with no forest cover averaged $\hat{\overline{SR}}_{M} = 8.46$ (range = 0.00–11.44, $N = 1197$). These estimates were significantly different (*t*-test, $P < 0.00001$, d$f = 203$). For primates in forested cells, average richness was $\hat{\overline{SR}}_{P} = 2.03$ (range = 0.00–5.51),

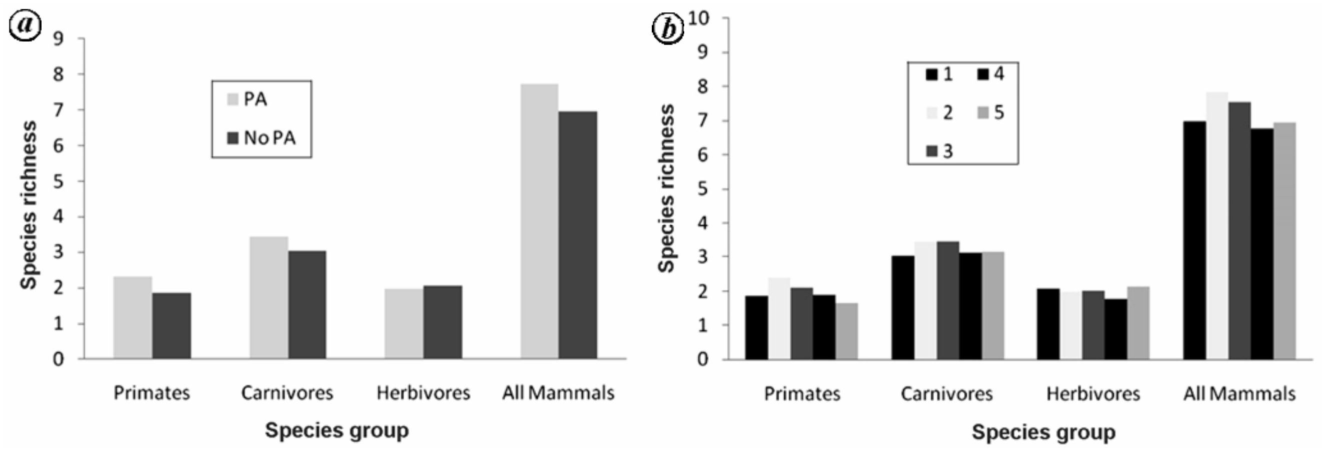

Figure 2. ***a***, Average species richness in cells with and without protected areas (PAs). ***b***, Average species richness in cells with different proportions of cell covered by PAs. Category 1, No PA; category 2 = 1–25% of cell; category 3 = 26–50%; category 4 = 51–75% and category 5 = >76%.

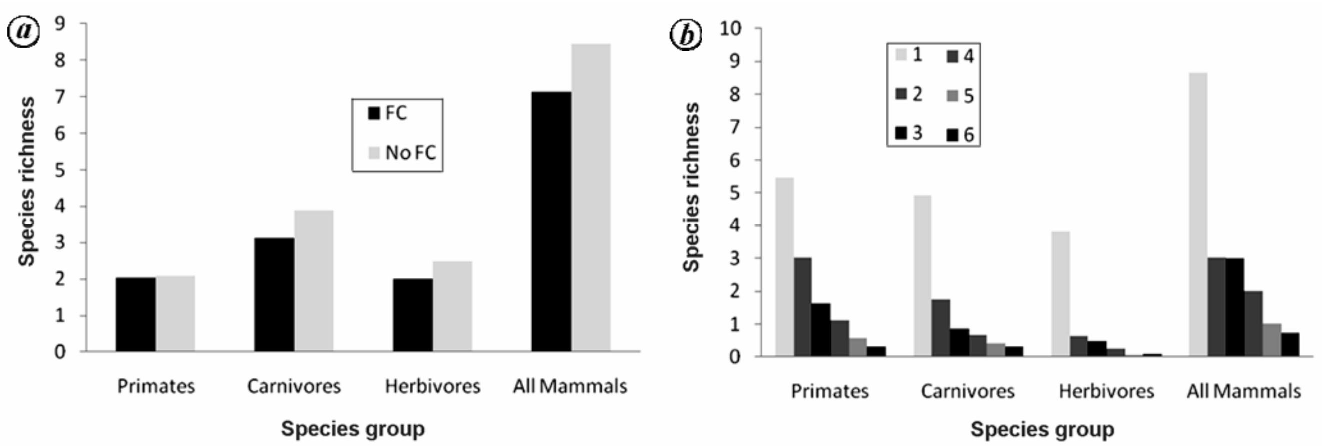

Figure 3. ***a***, Average species richness in cells with and without forest cover. ***b***, Average species richness at different average elevations across cells. Category 1, <1000 m; category 2, 1001–2000 m; category 3, 2001–3000 m; category 4, 3001–4000 m; category 5, 4001–5000 m and category 6, >5000 m.

whereas primate richness for cells with no forest cover was $\widehat{SR}_{\mathrm{P}} = 2.08$ (range = 0.00–5.02). These estimates were not significantly different (*t*-test, $P > 0.10$, df = 166). For carnivores, average richness in forest-covered cells was $\widehat{SR}_{\mathrm{C}} = 3.11$ (range = 0.00–4.92), and carnivore richness for cells with no forest cover was $\widehat{SR}_{\mathrm{C}} = 3.89$ (range = 0.00–4.94). These estimates were significantly different (*t*-test, $P < 0.00001$, df = 186). Among herbivores, estimated richness in forested cells was $\widehat{SR}_{\mathrm{H}} = 1.99$ (range = 0.00–3.83) and estimated richness in non-forested cells was $\widehat{SR}_{\mathrm{H}} = 2.48$ (range = 0.00–3.82). These estimates were significantly different (*t*-test, $P < 0.00001$, df = 164). These findings suggest that forest cover alone is insufficient to maintain mammal richness and diversity (Table 1).

Species richness and elevation

The relationship between richness and six elevation categories (category 1, <1000 up to category 6, >5000 m) was examined. Some species found at higher altitudes were excluded due to insufficient data. Some support was found for the predictions. Overall, species richness decreased with elevation, with the exception of primates. Average estimate of species richness was $\widehat{SR}_{\mathrm{M}} = 8.14$ (range = 0.00–14.28) and was highest for cells with average elevation < 1000 m, with richness declining with increase in elevation (Figure 3 *b*). These estimates differed significantly above and below 1000 m (*t*-test, $P < 0.00001$, df = 220). For primates, $\widehat{SR}_{\mathrm{P}} = 3.01$ (range = 0.00–4.91), and highest richness was in mid elevations of 2000–3000 m. These differences were significant comparing estimates above and below 1000 m (*t*-test, $P < 0.00001$, df = 229). Among carnivores, highest richness was $\widehat{SR}_{\mathrm{C}} = 3.62$ (range = 0.00–4.94) and these differences were significant comparing estimates above and below 1000 m (*t*-test, $P < 0.00001$, df = 277). For herbivores, highest richness was $\widehat{SR}_{\mathrm{H}} = 2.35$ (range = 0.00–3.83) in cells with average elevation < 1000 m (Figure 3 *b*), and these differences were significant comparing

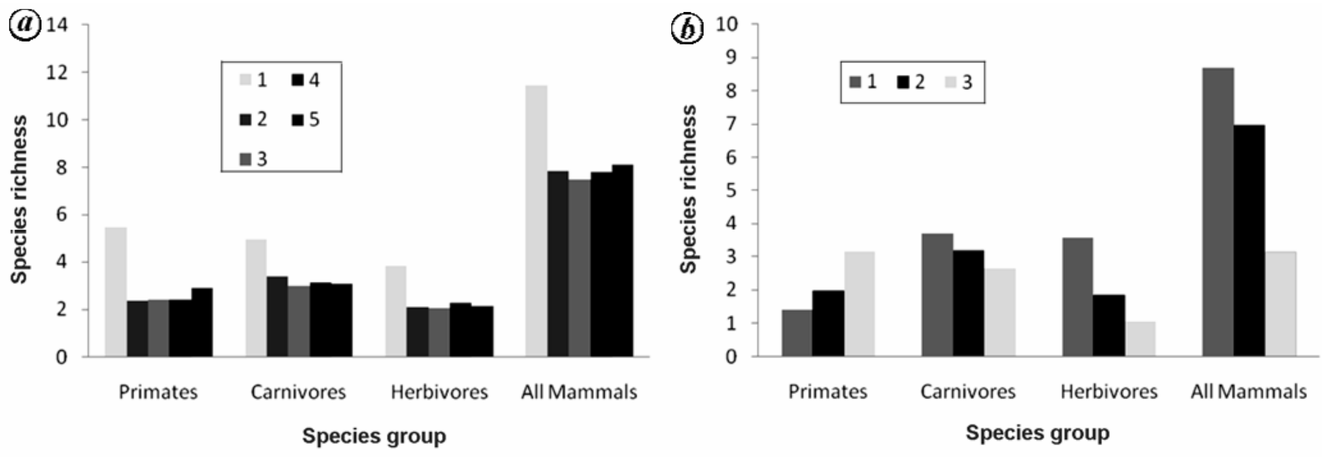

Figure 4. ***a***, Average species richness at different human densities. The number represents the total number of people in every pixel in each grid cell divided by 1000. Category 1, <1000; category 2, 1001–2000; category 3, 2001–3000; category 4, 3001–4000 and category 5, >4000. ***b***, Average species richness in different cultural tolerance levels. Category 1, High tolerance; category 2, Medium tolerance and category 3, Low tolerance.

estimates above and below 1000 m (t-test, $P < 0.00001$, $df = 549$) (Table 1).

Species richness and people

The relationship between richness and five human population density categories (category 1, < 1000 up to category 5, > 4000; the number of people per pixel in every grid cell divided by a 1000) was examined. Mixed support was found for the predictions. Overall, species richness decreased with increasing human density (category 1, Figure 4 *a*), lending support to the prediction that areas with low human density richness have higher richness. Estimates in lowest human density areas (category 1 cells) were $\hat{SR}_M = 7.07$ (range = 0.00–11.44, $N = 955$) and these were significantly different for the lowest density cells (t-test, $P < 0.00001$, $df = 1223$). In these cells, for primates $\hat{SR}_P = 1.90$ (range = 0.00–5.48) and estimates were significantly different for the lowest density cells (t-test, $P < 0.00001$, $df = 790$). For carnivores, $\hat{SR}_C = 3.17$ (range = 0.00–4.94) and estimates were not significantly different for the lowest density cells (t-test, $P > 0.10$, $df = 1130$). For herbivores, $\hat{SR}_H = 2.01$ (range = 0.00–3.83) and estimates were significantly different for the lowest density cells (t-test, $P < 0.05$, $df = 1051$). For primates and overall species richness, category 5 with high human density was also found to support moderate richness (Figure 4 *a*). But for carnivores and herbivores, richness decreased with increasing human density (Table 1).

It was examined whether higher cultural tolerance supported increased species richness. In most tolerant states (category 1), with the exception of primates, for all other richness groupings, richness decreased with tolerance. Overall, species richness decreased with decreasing tolerance (category 1, Figure 4 *b*), lending support to the predictions in the present study. Comparing high and medium tolerance cells to low tolerance cells, estimates in high tolerance areas (category 1 cells) were $\hat{SR}_M = 8.68$ (range = 3.11–11.67) and high and medium tolerance cells differed significantly from low tolerance cells (t-test, $P < 0.00001$, $df = 669$). For primates, highest richness was in lowest tolerance areas $\hat{SR}_P = 3.14$ (range = 1.20–5.11) and this was significantly different among high and medium compared to low tolerance cells (t-test, $P < 0.00001$, $df = 245$). For carnivores, $\hat{SR}_C = 3.7$ (range = 2.17–4.14), and this was significantly different among high and medium compared to low tolerance cells (t-test, $P < 0.00001$, $df = 315$). For herbivores, $\hat{SR}_H = 3.57$ (range = 0.94–3.83); highest richness was in the most tolerant states and this was significantly different among high and medium compared to low tolerance cells (t-test, $P < 0.00001$, $df = 1277$) (Table 1).

Discussion

Patterns of mammal species richness in India were examined using ecological and anthropogenic covariates. Recent advances in occupancy modelling permit accounting for imperfect species detection to derive estimates of individual species occurrence and overall species richness. The relationships between different species groups and the effects of ecological and anthropogenic covariates were also assessed. Methodologically, this approach differs from previous macroecological analyses. First, predictions were based on average annual species richness using current field data from >100 wildlife experts in India. This differs from cumulative richness indices derived from static sources which are often outdated and may cover long periods of time (museum records, range maps, etc.). Second, macroecological studies often apply a pattern recognition approach to gain insights. I prefer deducing a priori predictions and then conducting analyses to test them. Third, since most species are seldom detected with certainty in any sampling situations, the approach used here accounts for detection probabilities <1 to derive occupancy estimates.

The results conform well with predictions for some patterns, and there are other unexpected relationships. Evidence from other studies conducted at different scales, on many taxa and in different biogeographic regions[14–16] led us to expect that overall species richness ($SR_{i\mathrm{M}}$) would decrease with increasing latitude. Overall species richness decreased with increasing latitude, but differences between primates, carnivores and herbivores emerged (Figure 1 *a–d*). These findings concur with those of other studies[36] which suggest that relying on groups of species or particular taxa to conserve biodiversity may not be sufficient, particularly for range-restricted and endemic species.

As predicted, overall estimated richness was higher for cells with protected areas (Figures 1 *a* and 2 *a*). However, the proportion of a cell covered by a protected area has a different effect across species groups. Primates are found in smaller geographic areas, whereas carnivores and herbivores require larger and more contiguous space. Variation in distribution of different taxonomic groups has been found by other studies[35–37]. Contrary to expectations, forest cover alone did not support higher species richness. Although India's forest cover is between 15% and 20% of total land area, it appears that protection has a stronger influence on species persistence, and some species are found outside forested areas[20,24]. Overall, as predicted, species richness decreased with elevation with the exception of primates in low elevation (< 1000 m) areas. There was difference in richness patterns with respect to human density, with richness decreasing with increasing human density for carnivores and herbivores, but not for primates. As expected, species richness declined with decreasing human tolerance (Figure 4 *b*) for most groups, except primates. This aspect is unique to places in India and South Asia, and represents an important factor that needs consideration when attempting to improve species persistence prospects.

Species richness is an important and widely used indicator of where conservation initiatives and funding need to be directed[17]. This requires determining where species occur and identifying factors that support species persistence[20,24]. Rather than relying on static or outdated range maps, using local expertise and field data to develop monitoring efforts for species at local, regional and national scales will be essential for successful conservation. Occupancy modelling combined with simple presence–absence surveys are invaluable to such efforts[26]. Differential responses among species groups suggest that conservation efforts which focus on a single species or taxonomic group may be futile. In human-dominated landscapes such as India, linking fragmented areas and improving protection efforts will be important to species conservation, rather than depending solely on forest cover to ensure species survival. Factoring human interests and fostering local support for wildlife will be critical to ensuring long-term species diversity and persistence.

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