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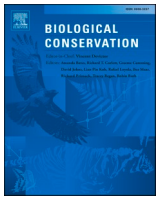

Using population monitoring programs to detect changes in mammalian communities

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ABSTRACT

The global biodiversity crisis is escalating rapidly, with nearly a million species facing extinction risk in the near future. Monitoring of Essential Biodiversity Variables (EBV; key variables measured to detect changes in biodiversity) over time is important for biodiversity conservation, which in turn necessitates baseline estimates of EBVs. Using camera-trap data for six years (2013–2018) and a Bayesian multispecies occupancy model, we estimated species richness and species-specific occupancy of a mammalian community in Pakke Tiger Reserve, India. We detected 28 species of mammals in our camera traps. The model-based estimate of species richness during the study period was 41 (95 % CRI: 39–42) species, with no evidence of any substantial temporal variation. We found that carnivore and herbivore species richness was higher in greener habitats and that omnivore species richness was higher at lower-elevation sites. Annual average species occupancy probability (at the scale of 4-km^2 sampling units) did not vary substantially between years but was lowest in 2014 (0.54, 95 % CRI: 0.20–0.84) and highest in 2013 (0.59, 95 % CRI: 0.27–0.87). Mean species-specific occupancy averaged across the years varied substantially among species, ranging from a low of 0.03 (95 % CRI: 0.00–0.08) for the masked palm civet *Paguma larvata* to a high of 0.94 (95 % CRI: 0.87–0.98) for the Asian elephant *Elephas maximus*. Mean occupancy probability was highest for herbivores followed by omnivores and carnivores. Species-specific detection probability (for a 30–60-day survey period) was not influenced by survey effort but increased with body mass for carnivores and decreased with body mass for herbivores and omnivores. We propose a framework for efficient monitoring of species and community-level EBV, utilizing data collected during the monitoring of high-profile species of conservation concern, such as tigers *Panthera tigris* in India.

1. Introduction

Long-term and consistent monitoring is critical to biodiversity conservation. It helps detect adverse changes in species distribution and abundance, and species richness, thereby enabling timely management actions that can help reverse declining trends, and it is central to assessing management efficiency and adaptively deciding on future management strategies (Yoccoz et al., 2001; Lindenmayer et al., 2012). Existing biodiversity monitoring programs such as Project Tiger in India are often specialized, focusing predominantly on single charismatic species. Single species-focused monitoring and conservation approaches have been successful in many cases. Examples include a high success rate of the Endangered Species Act in the USA in preventing the extinction of listed species (Schwartz, 2008) and the recovery of tiger *Panthera tigris* populations in India, enabled by a long-term monitoring and conservation program (Karanth et al., 2011; Karanth et al., 2004). Despite these success stories, single species monitoring programs have been critiqued for being costly and reactive to threats (Harvey et al., 2017; Laycock et al., 2011). Monitoring programs that focus on a single species can potentially lead to data that are unrepresentative of overall biodiversity; consequently, populations of understudied species might decline without notice (Jetz et al., 2019). An alternative approach shifts the

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focus from single species–centered conservation and monitoring programs to one that considers an entire biological community with an overarching goal of monitoring high-level Essential Biodiversity Variables (EBV): the key variables measured to detect changes in biodiversity such as genetic composition, species traits, species abundance, community composition, and ecosystem structure and function (Pereira et al., 2013; Jetz et al., 2019). However, it is not possible to monitor all species at all times and places, so management decisions must be made about what biodiversity metrics are most likely to be useful for conservation.

The first step towards community-level monitoring is to elucidate the composition of the biological community and understand ecological interactions therein (Parrish et al., 2003; Poiani et al., 2000). Species richness (i.e., the number of species present in a region) has long been of interest to ecologists and conservation biologists as a metric of community composition and as a unit of conservation. This is because estimating species richness is logistically pragmatic and can be easily incorporated into long-term biodiversity monitoring programs (Cheyne et al., 2016; Fleishman et al., 2006; Gaston, 2000; Yoccoz et al., 2001). However, species richness, while necessary, may not by itself be a sufficient metric to assess biological communities—even though species richness may be constant over time for a region, the underlying structure of the community need not be static as the identity of individual species might change (Farris et al., 2017; Yoccoz et al., 2001). Therefore, it is often helpful to complement data on species richness with species-specific information on distribution, abundance, space use, and ecological interactions among species (Mendenhall et al., 2014; Prat-Guitart et al., 2020; Sundqvist et al., 2013).

Conventionally, the number of species observed or detected in a given area has been used as a measure of species richness. However, detection of all species (or individuals of a particular species) present is rarely possible, and some of the species that are present may not be detected; imperfect detection of species (or individuals of a given species) inevitably results in undercounting of species and individuals (Boulinier et al., 1998; Iknayan et al., 2014; MacKenzie et al., 2018; Williams et al., 2002). Furthermore, when resources are limited, the question of which indicator species to monitor to assess overall ecosystem health becomes critical. Often charismatic species which are economically and culturally important are monitored more intensively but these monitoring efforts often also lead to the collection of large amounts of opportunistic data on several other species. Statistical methods that can utilize all focused and opportunistic data to combine species- and community-level monitoring can help managers detect changes in the community and take management actions as needed. Multi-species hierarchical occupancy models (MSOMs) provide a statistical modeling framework that allows estimation and modeling of both community- and species-specific parameters, while also accounting for imperfect detection (Dorazio and Royle, 2005; Gelfand et al., 2005; Kery and Royle, 2008). This modeling approach permits information sharing across species, which allows the inclusion of rare and undetected species in the species richness estimates and uncertainty in occupancy estimates to be propagated to community metrics (Iknayan et al., 2014; Kery et al., 2010; Kery and Royle, 2016; Steenweg et al., 2017; Zipkin et al., 2009). The hierarchical structure of MSOMs allows data from the entire sample to inform species richness estimates while explicitly accounting for the effects of the survey-, site-, and species-level drivers of detectability and occupancy (Iknayan et al., 2014; Tingley et al., 2020). Using data augmentation techniques, MSOMs can accommodate the fact that some species from the community species pool may go undetected throughout the sampling process. It does so by assuming that all species (observed and unobserved) are a random sample from the studied community which allows for estimation of mean community-level response to ecological and anthropogenic factors (Royle et al., 2007; Zipkin et al., 2009).

The wide use of increasingly cost-effective technologies, such as camera traps, has revolutionized the monitoring of terrestrial wildlife species, particularly mammals (Steenweg et al., 2016), and increased monitoring capacity while lowering associated costs. A pioneering initiative to monitor tiger populations in India nearly three decades ago (Karanth and Nichols, 1998) has over time paved the way for extensive use of camera traps in large-scale biodiversity monitoring programs across the world (Steenweg et al., 2016; Wearn and Glover-Kapfer, 2019). Even within India, the monitoring of tigers and their prey is now conducted at massive, country-wide scales, with the help of camera traps and line-transect surveys (Jhala et al., 2019). Data thus collected are used to provide information on the changes in distribution and abundance of tigers and their prey and are used to make management recommendations and funding allocation decisions for protected areas.

Despite technological and statistical advances, reliable information on non-target species distribution and abundance, and species richness and community composition, are not available from most protected areas in India, much like other regions in the Global South. This limits the capacity of scientists to address important ecological questions and hampers the ability of wildlife managers to monitor and protect ecological networks against extreme changes (Lindenmayer and Likens, 2010; Nichols and Williams, 2006). Pakke Wildlife Sanctuary and Tiger Reserve (PTR) in Northeast India (92 36′E, 26 54′N) harbors high biodiversity as it lies at the intersection of the Eastern Himalayas and Indo-Burma Biodiversity Hotspots (Myers, 2003; Myers et al., 2000). Although species such as the tiger, leopard *Panthera pardus fusca*, and dhole *Cuon alpinus* have received some attention from ecological studies, scientifically robust baseline information on most other members of the mammalian community in PTR, and ecological interactions among them, is largely missing (Selvan et al., 2014; Velho et al., 2016). The government of India collects camera-trap data at PTR every year, primarily for monitoring tiger and leopard populations; similar monitoring programs are in place at tiger reserves across India (https://ntca.gov.in/monitoring/#monitoring). These data can be leveraged to quantify community- and species-specific parameters for the mammalian community. Effective monitoring of the mammalian community in PTR is of paramount importance because Northeast India, where the park is located, is now considered to be a deforestation hotspot, making many species of mammals vulnerable to local extinction (Myers, 2003; Myers et al., 2000; Reddy et al., 2016).

Our goal was to estimate baseline community-level and species-specific metrics for mammals in PTR, which when monitored over time, can allow early detection of critical changes in the richness and composition of this mammalian community. Our second goal was to explore ecological and anthropogenic drivers of the spatial ecology of the mammalian community in PTR. Working in tandem with the wildlife managers of PTR, we applied MSOMs to six years (2013–2018) of camera trap data to quantify and understand variation in species richness and spatial ecology of the mammalian community in PTR. Our specific objectives were to 1) quantify species richness and assess the influence of ecological and anthropogenic factors affecting it; 2) explore species-specific distribution and habitat use patterns for individual species and species groups (based on body mass and diet), and 3) elucidate ecological and anthropogenic factors affecting species and group-specific occupancy. We predicted that: 1) overall species richness of PTR will not substantially vary over time—PTR is a well-managed protected area facing low anthropogenic pressure; also, our study period is not very long, so we expected the mammalian community in PTR to be stable; 2) site-specific species richness will be positively influenced by forest cover and NDVI, and negatively influenced by elevation, and distance to the park boundary and villages; 3) the influence of ecological covariates on mammalian occupancy will show species-specific and group-specific signatures while anthropogenic covariates will have a negative effect across species, especially on large herbivores and carnivores as they are more sensitive to human disturbance (Schuette et al., 2013). Our third goal was to develop a framework for utilizing data collected from long-term population monitoring programs and opportunistically from other short-term projects and MSOMs

to estimate species richness, species-specific occupancy and habitat use patterns, and factors influencing these patterns. We propose a workflow based on MSOMs to quantify baseline information for the community and species-specific EBVs; this information will be helpful for detecting any downward trends in species richness and occupancy, and for adjusting management plans when warranted.

2. Methods

2.1. Study area

We carried out the study in Pakke WLS and Tiger Reserve, an 862 km^2 protected area in Arunachal Pradesh (AP) situated within the Eastern Himalayan Region (EHR) in India (Myers, 2003). The dominant vegetation type in PTR is Assam valley tropical evergreen forest, which is further divided into nine habitat types: subtropical broad-leaved primary and secondary forest (~ 40.0 %), Himalayan moist temperate forest (~ 2.0 %), tropical moist-deciduous, and semi-evergreen forest (~38.0 %), secondary bamboo forest (~4.0 %), degraded land (~4 %), wetlands and riverine (~2 %), and grassland (~1 %) (Roy et al., 2015) (Fig. 1). The terrain is undulating with an elevation ranging from 150 to 2300 m above sea level. Climate is subtropical with temperatures ranging from 12 to 36 °C. The average annual rainfall is 2500 mm, primarily received during the monsoon season (June–September). PTR is home to about 42 species of mammals, about 282 species of birds, and has high plant diversity (Kumar, 2014; Tag et al., 2012). It is protected under the Indian Wildlife Protection Act of 1972; logging and hunting are not allowed within the reserve, but regulated tourism and ranger patrols are allowed; some human habitations are located immediately outside the reserve boundary. PTR is a well-managed protected area with strong leadership that enjoys positive socio-political engagement from local tribes (Ghosh-Harihar et al., 2019). Surrounded by community-managed state forests with varying degrees of anthropogenic disturbance, PTR is a part of the Kameng Protected Area Complex, the largest (3500 km^2) contiguous forested area in the EHR (Velho et al., 2016). Other protected areas within this complex include Sonai Rupai WLS in Assam, the Eaglenest, and Sessa Orchid WLS in AP, and the reserve forests associated with them. This is an ecologically sensitive region of India because it is home to endangered species such as tiger and Asian elephant *Elephas maximus* and contains elephant migration corridors.

2.2. Camera trap surveys

Camera traps have received widespread use in wildlife research, and data generated from camera trap surveys have been used to estimate species richness, population density, and other population parameters, and to quantify occupancy, habitat use, and species interaction patterns (Rich et al., 2016; Karanth et al., 2017; Prat-Guitart et al., 2020; Sunarto et al., 2015; Tobler et al., 2008). Between 2013 and 2018, we conducted annual camera trap surveys in the winter (November – March) in Pakke Tiger Reserve (Fig. 1). We overlaid a 2 km × 2 km grid on the study area and placed 1–3 camera traps (Panthera V4, Cuddeback Attack 1149 or similar) per grid cell about 25 cm above the ground on elephant trails or human trails. Cameras were triggered by animal movement and remained active 24 h a day for 30–60 days (Table 1). No lure or bait was used. Each grid cell was considered as a replicate survey site and community and species-specific inferences were made at the grid-cell level.

Camera-trap images were managed using Camelot software version 1.5.9 (Hendry and Mann, 2018), and species were identified manually. The detection of a species within 30 min was recorded as a single detection event. We pooled detections over five full days (i.e., 5 × 24-h periods) into one camera-trap survey; thus, there were 6–12 secondary sampling periods (surveys) per year. The number of cameras per grid cell ranged from 1 to 3, and the number of surveyed grid cells in any given year ranged from 68 to 92 (Table 1). Based on the existing literature, anecdotal evidence, and our knowledge of PTR and its wildlife we created a list of 42 species of mammals that are likely to occur in PTR (Supplementary Material S1). We excluded flying, aquatic, and small burrowing mammals from this study because they would be unlikely to

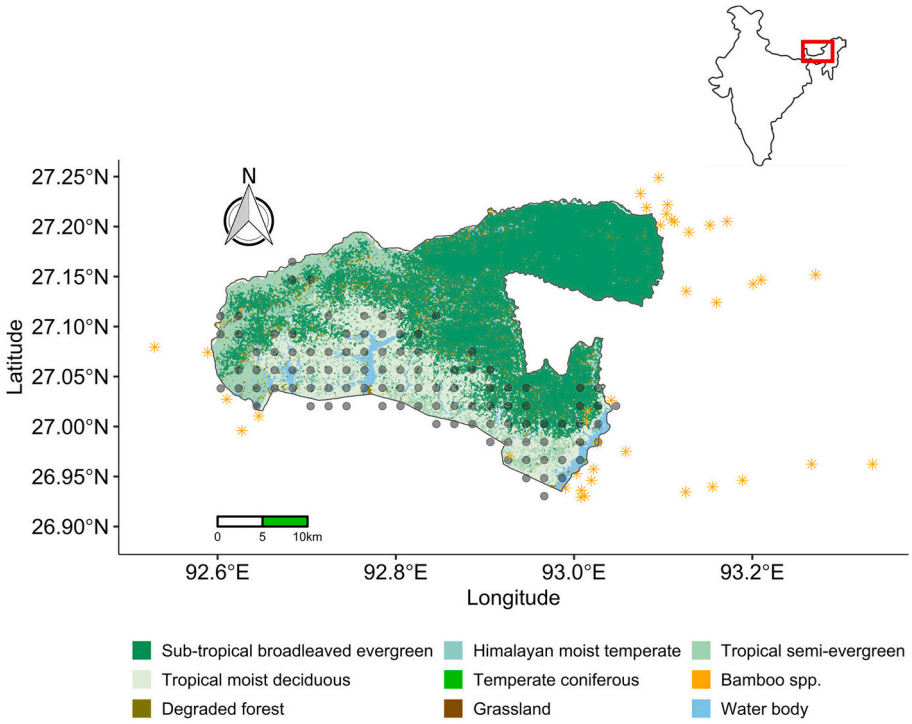

Fig. 1. Map of the study area with landcover types and camera locations marked with black circles, and human habitations (village locations) marked with orange '*' signs. Inset marks a map of India with the red square indicating the location of Pakke Tiger Reserve. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Description of camera-trap surveys conducted between 2013 and 2018 in Pakke Tiger Reserve, India. The number of 4-km^2 sampling unit grid cells, the number of surveys, the number of species of mammals detected, and the total number of carnivores, herbivores, and omnivores that were detected annually from 2013 to 2018 are presented.

Year	No. of grid cells	No. of survey periods[a]	No. of mammal species detected	No. of carnivores/ herbivores / omnivores detected
2013	70	8	24	7 / 7 / 10
2014	78	12	27	7 / 9 / 11
2015	76	12	24	7 / 8 / 9
2016	68	12	24	7 / 9 / 8
2017	80	6	25	6 / 9 / 10
2018	92	10	24	6 / 8 / 10

[a] Each survey period is composed of 5 24-h periods.

be detected by cameras under our study design.

We considered three ecological and two anthropogenic covariates that were hypothesized to influence species richness and species-specific occupancy probabilities (Table 2, Supplementary Material S2). Ecological covariates included: (*i*) the proportion of forest cover (hereafter "forest cover") in the grid cell calculated using landcover data (Roy et al., 2015); (*ii*) normalized differential vegetation index (NDVI) calculated from the United States Geological Survey (USGS) Landsat NDVI data; (*iii*) and the average elevation of the grid cell calculated from USGS digital elevation model data (hereafter "elevation"). Anthropogenic covariates included (*iv*) distance from the grid cell center to the nearest village (hereafter, "distance to the village"), and (*v*) distance from the grid cell center to the park boundary (hereafter, "distance to boundary"). The distance variables were calculated using the *distance* function from the *rgeos* package (R interface for Geometry Engine Open Source) (Bivand, 2020) implemented in the R computing environment using R 4.1 (R Core Team, 2022). All covariates were standardized to a mean of zero and a standard deviation of one. We allowed detection probability to be affected by survey effort (hereafter "effort"), defined as the product of the number of cameras in the grid cell, and the number of days cameras in the grid cell were active during a particular sampling occasion. Effort ranged from a minimum of 6 to a maximum of 36 across grid cells, with a mean of 28 ($SD = 7$). We allowed detection probability to also vary with the average body size of the species (Supplementary Material S1). Predicted effects of our chosen covariates, along with justifications, are presented in Table 2. Many of the individual species known to be part of PTR mammalian community have home range sizes larger than the survey grid cell area of 4 km^2 (Supplementary Material S1); individual home ranges can include multiple grid cells. For those species, our occupancy estimates quantify the proportion of grid cells (i.e., the study area) used by the species rather than true occupancy probability (MacKenzie et al., 2018; Mackenzie and Royle, 2005; Steenweg et al., 2018).

Table 2
Description of ecological and anthropogenic factors used to model species richness (r), probabilities of species occupancy (ψ), probabilities of species detection (p), the direction of a-priori predictions of the influence of covariates on the parameters, and data sources for the factors hypothesized to influence the occupancy probability of mammalian species of Pakke Tiger Reserve, India during 2013–18.

Covariate	Description	Parameter	Direction	Source
Ecological				
Elevation	Elevation of the grid-cell center from sea level	r, ψ	Varies with species	United States Geological Surveys digital elevation model
NDVI	Average Landsat normalized differential vegetation index (NDVI)	r, ψ	+	United States Geological Surveys Landsat NDVI
Forest cover	The proportion of the grid-cell categorized as 'forest'	r, ψ	+	Roy et al. (2015)
Anthropogenic				
Distance to the village	The distance of the grid-cell center to the nearest village	r, ψ	+	The geographic location of villages obtained from Pakke Tiger Reserve Forest Department
Distance to the boundary	The distance of the grid-cell center to the nearest boundary point	r, ψ	+	Geographic data files obtained from Pakke Tiger Reserve Forest Department
Detection				
Effort	Number of cameras per grid-cell x Total number of days cameras were active	p	+	Data collected during field surveys
Body mass (Not species-specific)	Average body mass of species (KG)	p	+	Supplementary Material S1

2.3. Modeling framework

The conventional approach to estimating species richness by the number of species detected at a given area typically underestimates the number of species actually present, as this approach does not account for imperfect detection, i.e., failure to detect a species that is in fact present. Occupancy modeling is a statistical framework that permits estimation and modeling of species richness and occupancy patterns while also accounting for imperfect detection (MacKenzie et al., 2002; MacKenzie et al., 2018; Tyre et al., 2003). For our study, we adopted the hierarchical formulation of community occupancy or a multi-species occupancy models (MSOM) framework with data augmentation because this approach (Dorazio and Royle, 2005; Dorazio et al., 2006; Kery and Royle, 2016): (*i*) permits estimation of species richness while accounting for imperfect detection using temporally and/or spatially replicated detection history data; (*ii*) permits community- and species-level analyses, as well as analyses based on species subsets such as guilds (Kery and Royle, 2008, 2016); and (*iii*) is efficient as it allows information sharing across species (or subsets of species), which improves the precision of parameter estimates for data-deficient species and can be used simultaneously to monitor species and communities (Devarajan et al., 2020).

We used the hierarchical MSOMs proposed by Dorazio and Royle (2005) and Kery and Royle (2008, 2016) where the model is formulated in terms of a latent binary process $z_{i,\,k,\,t}$, the true state of presence or absence of species k at a grid-cell i during year t; $z_{i,\,k,\,t} = 1$ if the species k is present in grid-cell i at time t; 0 otherwise. It was modeled as:

$$z_{i,k,t} \sim Bernoulli\left(\psi_{i,k,t}\right)$$

where $\psi_{i,\,k,\,t}$ is the grid cell and year-specific occupancy probability of species k. All $z_{i,\,k,\,t}$ are conditionally independent, given the values of covariates in the model for $\psi_{i,\,k,\,t}$.

The observed data are detection frequencies over 5 24-h periods at grid-cell i of species k during year t, denoted as $y_{i,\,k,\,t}$, and were modeled as:

$$y_{i,k,t} \sim Binomial\left(p_{i,k,t}{}^{*}z_{i,k,t}, 5\right).$$

Here, $p_{i,\,k}$ is the probability of detection of species k at grid-cell i

given the species is present in grid-cell i in a particular sampling year t and the binomial index of 5 represents the 5 secondary occasions in our design. All $y_{i,\,k,\,t}$ are conditionally independent, given $z_{i,\,k,\,t}$ and the values of covariates in the model for $p_{i,\,k}$.

We formulated the model as a hierarchical model, which included species-specific and year-specific random effects (Kery and Royle, 2008, 2016). We linked species-specific models to the community by assuming species-specific parameters were random effects drawn from a normal distribution with hyperparameters (i.e., mean and dispersion) that characterize the community, or "the average species", and the dissimilarity of the parameters among species. As different guilds (diet-groups; carnivores, herbivores, and omnivores), may have a different response to ecological and anthropogenic covariates, we divided species into their respective guilds (Supporting Material S1). Then, to assess group-level effects, we allowed for species-specific parameters to be governed by both guild- and community-level hyperparameters. Specifically, we allowed guild-specific random effects to have different means for each guild (hyper-means) but shared variance (hyper-dispersions) (see BUGS-language code of the model in the Supporting Material S10). Occupancy and detection probabilities were modeled as logit-linear functions of site-specific covariates (Table 2). We fitted a single model of occurrence probability with a limited number of covariates for which we had a priori justification (Zipkin et al., 2009; Table 2):

$$logit\left(\psi_{i,k,t}\right) = \beta_{0,k} + \beta_{1,k}X_1 + \beta_{2,k}X_2 + \ldots + \beta_{m,k}X_m + \delta_{t,k} \quad (1)$$

Here, $\beta_{0,\,k} \sim Normal\ (\mu_{\beta 0,\,\nu}, \sigma^2_{\beta 0})$, $\mu_{\beta 0,\,\nu}$ and $\sigma^2_{\beta 0}$ are the guild-(ν)-specific mean and the variance of the community prior for the occupancy intercept for species k; $\beta_{m,\,k}$ represents the slope associated with the site covariate m on species k such that

$$\beta_{m,k} \sim Normal\left(\mu_{\beta m,\nu}, \sigma^2_{\beta m}\right)$$

(note again the mean depends on guild ν and the dispersion does not), and X_m is a grid-cell specific covariate (elevation, forest cover, NDVI, distance to nearest village, and distance to the park boundary). As we linked species-specific parameters to the community-level parameter, we assumed species-specific parameters were random effects derived from normally distributed community-level hyperparameters drawn independently, with different means but the same dispersion for the three guilds. These hyperparameters specify the mean response and the variation among species of a guild and community to a covariate. We followed Broms et al. (2016) and adopted weakly informative priors so that, for each guild, the β_m coefficient was modeled as $Normal\ (\mu_{\beta m,\,\nu}, \sigma^2_{\beta m})$ where $\mu_{\beta m,\,\nu}$ is the guild-specific mean and $\sigma^2_{\beta m}$ is the community-level variance; such that $\mu_{\beta m,\,\nu} \sim Normal\ (0,\ 2.25^2 I)$, and $\sigma^2_{\beta m} \sim half - Cauchy\ (2.25^2 I)$. The half-Cauchy distribution is the same as the Student's t distribution with one degree of freedom and it is truncated below 0 (Broms et al., 2016). The parameter $\delta_{t,\,k}$ represents a random year-effect in logit(ψ) for species k such that $\delta_{i,\,k} \sim Normal\ (0,\ \sigma^2_{\delta,\,k})$. We then modeled these species-specific variances hierarchically by assuming that their log transform was a draw from another normal distribution, on the mean and SD parameters of which we placed $Uniform(0, 10)$ and $half - Cauchy\ (2.25^2 I)$ priors.

Detection probability for species k at site i was modeled as:

$$logit\ \left(p_{i,k}\right) = \alpha_{0,k,t} + \alpha_{1,k} \times effort_i + \alpha_{2,\nu(k)} \times bodymass_k + \varepsilon_{data\,i,k,t} + \varepsilon_{site\,i,k} \quad (2)$$

where $\alpha_{0,\,k,\,t}$ is the normally distributed species-specific and year-specific random effect (intercept) such that $\alpha_{0,\,k,\,t} \sim Normal\ (\mu_{\alpha 0,\,\nu}, \sigma^2_{\alpha 0})$, $\alpha_{1,\,k}$ is the normally distributed slope associated with the survey effort at site i for species k such that $\alpha_{1,\,k} \sim Normal\ (\mu_{\alpha 1,\,\nu(k)}, \sigma^2_{\alpha 1})$, and $\alpha_{2,\,\nu(k)}$ is the guild-specific slope associated with the body size for the guild ν to which species k belongs and we assumed $\alpha_{2,\,\nu(k)} \sim Normal\ (0,\ 2.25^2 I)$. Like the β parameters, we also treated α_0 and α_1 as random effects drawn from community-level normal distributions with guild-specific means, but dispersion parameters that were shared for all species (regardless of guild). $\varepsilon_{data\,i,\,k,\,t}$ and $\varepsilon_{site\,i,\,k}$ account for species-specific overdispersion at the site and at the site/year level in detection probability. We chose a more robust formulation for both by preferring a zero-centered t-distribution with 4 degrees of freedom over the more customary normal to accommodate some of the lack of fit detected in our model (see below) in exploratory runs when such Gaussian priors were chosen (the t-4 is a customary solution to lead to robust Bayesian statistical inferences relative to a normal assumption, Lunn et al., 2013). We then placed the same half-Cauchy priors as above on the dispersion parameters of both t-4 distributions.

Even though camera-trap data were collected from PTR every year, the entire reserve was not surveyed. Imperfect detection of species (or individuals) is commonplace in camera trap surveys, and it is highly likely that not all species that were present at PTR were detected by our camera traps. To account for species that were missed altogether and to make inferences about the overall species richness (or community size), we augmented the observed data (i.e., the detection histories for 28 species of mammals that we detected at least once) with 14 species that were not detected in our study, but which are known to occur in PTR. This estimate of 14 species that were potentially present at PTR but were not detected was based on our review of published or unpublished reports, field guides, and anecdotal information regarding mammalian species present in similar habitats in Northeast India. Thus, we had the augmented detection history data for a total of 42 species, including detection histories for the unobserved species composed of all zeros (indicating that these species were not detected during our study). The presence of all species k (including the augmented ones) was modeled using a latent binary variable $w(k)$, where $w(k) \sim Bernoulli\ (\Omega)$, and the probability of their presence being modeled as $\Omega \sim Uniform\ (0, 1)$; it was then linked to the site-specific occupancy as $z_{i,\,k.\,t} \sim Bernoulli\ (\psi_{i,\,k,\,t} * w_k)$ (Kery and Royle, 2008, 2016). We note that the information about undetected species arises from the null encounter history (0, 0,....,0), and so the Bayesian analysis conditions on that and obtains a posterior sample of P (p, ψ) conditional on the data. This enables estimation of a typical p and ψ for an undetected species. Furthermore, in the usual capture-recapture sense one is also able to estimate how many such species there are in the community (J.A. Royle, personal explanation). To evaluate the influences of species with low detection rate on the overall species richness, we repeated the analysis by replacing the detection histories of two least detected species (Asiatic golden cat and slow loris) by null encounter histories and comparing the results.

We estimated the posterior distribution of parameters using the Markov Chain Monte Carlo (MCMC) method implemented in JAGS v3.4.0 through program R version 4.1 using package jagsUI v1.5.2 (Kellner and Meredith, 2021). We generated three chains of 50,000 iterations after a burn-in of 10,000 and thinned by 40. We assessed convergence using the Gelman-Rubin statistic (Gelman et al., 2014) and by visual inspection of trace plots. To gauge the fit of our model, we conducted a Bayesian posterior predictive check (Conn et al., 2018) on a Chi squared discrepancy measure which yielded a Bayesian p-value of 0.009. That means that our data set was more variable than what we would expect under the model and the estimated parameters, and thus technically, that our model did not fit our data. However, the "lack of fit ratio", i.e., the ratio of the summed (over the data set) value of that statistic for the observed data and for the replicated (simulated) data, was only 1.17. This ratio is directly analogous to the so-called "over-dispersion factor" (c-hat) typically computed in chi-squared goodness of fit tests in the capture-recapture literature (e.g., Williams et al., 2002) or in GLMs for count data when using quasi-likelihood for a Poisson or Binomial response (McCullagh and Nelder, 1989). There, the standard way to accommodate such "overdispersion" is by multiplying standard errors of the estimates by the square-root of the value of c-hat. Informal application of such an approach in our case shows that we would then have to increase the SEs (or more precisely, posterior standard deviations) by about 8 %. We considered this as very small and therefore assumed that it was safe to ignore as we think it is inconsequential to our

inferences.

In addition, for each data point, we also computed a sort of "pseudo-residual" as the difference of the chi-squared discrepancy of the observed and of the expected (i.e., simulated) data sets. This approach lets one gauge which data points contribute particularly to a significant chi-squared Goodness of fit test result. We then plotted these pseudo-residuals against everything in our analysis (i.e., all classifications and covariates) and could not detect any striking patterns. This confirmed to us that our approach to believe that the lack of fit detected in the significant Bayesian *p*-value represented just unstructured additional noise not captured by our model, rather than a structural problem of the model.

We draw inferences on community and species-specific responses from 3000 posterior samples for each parameter and report posterior means and 95 % Bayesian credible intervals (CRI; 2.5 % and 97.5 % percentiles) unless otherwise stated. We considered the effect of a covariate to be statistically important if the 95 % CRI for the regression coefficient did not overlap with zero.

3. Results

During the study period (2013–2018), we detected a total of 28 species of mammals; these included 7 species of carnivores, 10 species of herbivores, and 11 species of omnivores. In terms of body mass, species ranged from 1.5 kg to 4000 kg; 10 were classified as large, 6 medium-sized, and 12 as small mammals (Supplementary Material S1). The slow loris was detected only once, whereas the Asian elephant (N = 3325) and sambar (N = 4390) were the most frequently detected species (Supplementary Material S3).

3.1. Species richness

The estimated overall species richness of mammals (excluding small burrowing, aquatic, and flying mammals) in PTR was 41 (95 % CRI: 39–42) species. Grid cell level estimates of species richness ranged from 19 (95 % CRI: 13–26) to 28 (95 % CRI: 24–33) (Fig. 2). There was no evidence for annual variation in species richness within the study area (Supplementary Material S4). Overall species richness and annual grid-cell level species richness remained unchanged when we replaced the data for the two least-detected species with null detection histories (Asiatic golden cat and Slow loris) (See Supplementary Material S11). Species richness decreased with elevation in the case of omnivores and increased with NDVI in the case of carnivores and increased with forest cover in case of herbivores (Table 3). Distance to the village or distance to the park boundary had no discernible effects on species richness (Table 3).

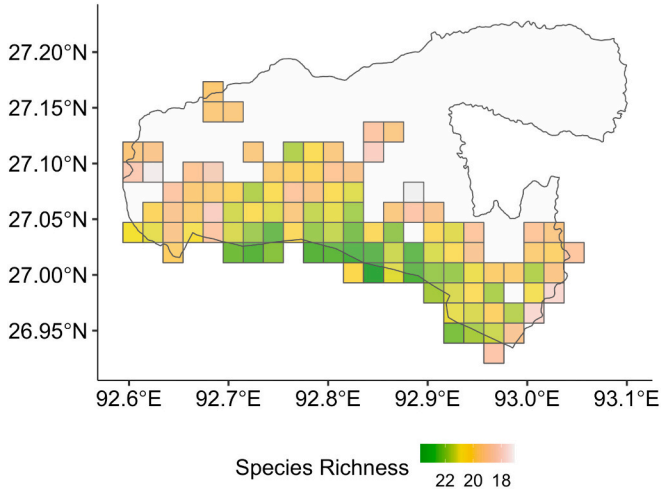

Fig. 2. Grid-cell specific species richness of mammals estimated based on data collected from camera-trap surveys conducted over six years (2013–18) in Pakke Tiger Reserve, India. Estimates presented here represent species richness estimates of 4-km^2 sampling units averaged across years (2013–2018).

3.2. Species-specific occupancy and detection probabilities

Annual occupancy probability (of 4-km^2 sampling units) averaged for all species did not vary substantially between years but was lowest in 2014 (0.54, 95 % CRI: 0.20–0.84) and highest in 2013 (0.59, 95 % CRI: 0.27–0.87). Annual variation in occupancy was stronger in the case of tiger, large Indian civet *Viverra zibetha*, small Indian civet *Vivericula indica*, serow *Capricornis thar*, sambar, and barking deer *Muntiacus muntjac* (Fig. 3, Supplementary Material S5, S6); year-to-year variation in occupancy of these species appeared random, without a directional temporal trend. Mean species-specific occupancy averaged across the years varied substantially among species, ranging from a low of 0.03 (95 % CRI: 0.00–0.08) for the masked palm civet *Paguma larvata* to a high of 0.94 (95 % CRI: 0.87–0.98) for the Asian elephant (Table 4). Occupancy was higher for herbivores compared to other dietary groups across the years (Fig. 4). Given the magnitude and direction of posterior densities, occupancy probability for most species appeared to respond negatively to elevation and positively to NDVI and forest cover; however, uncertainty was high and CRI for occupancy probability often included 0 (Supplementary Material S7). Occupancy of tiger, barking deer, sambar, leopard cat, and common civet declined with elevation, and occupancy of elephant and black bear increased with NDVI (Supplementary Material S7, S8). Similarly, most species appeared to respond positively to distance from the nearest village but CRI for occupancy probability often included 0 (Supplementary Material S7, S8). Occupancy of barking deer, wild boar, and small Indian civet declined as distance from park boundary increased (Supplementary Material S7, S8). There was no evidence that the sampling effort influenced detection probability (Table 4, Supplementary Material S9) but detection probability increased with body mass for carnivores 0.66 (95 % CRI: 0.40–0.87) and decreased with body mass for herbivores −0.70 (95 % CRI: −1.03 to −0.57). and omnivores −0.30 (95 % CRI: −0.57– -0.01).

4. Discussion

Anthropogenic land-use change is causing a significant reduction in the land and sea area available for wildlife; therefore, it is essential that protected areas like PTR are not only established and expanded but are also effectively governed based on ecologically sensible indicators that

Table 3
Posterior mean ($\bar{x}$) and 95 % credible interval (95 % CRI) estimates of the community level hyper-parameters for the factors hypothesized to influence the species richness, mean occupancy probability (covariate 1 to 5) and mean detection probability (covariate 6) of mammalian species of Pakke Tiger Reserve, India during 2013–18 (Table 2) for each guild. We report posterior means and 95 % CRI. Statistically substantial (95 % CRI do not overlap 0) community-level hyperparameters that influence species-specific occupancy and thereby species richness are in bold font.

No.	Covariate	Carnivores	Herbivores	Omnivores
1.		−0.32	0.06	**−0.27**
	Elevation	(−0.67–0.03)	(−0.44–0.60)	**(−0.48–0.07)**
2.	Distance to the	0.15	0.30	−0.05
	village	(−0.19–0.48)	(−0.18–0.85)	(−0.22–0.13)
3.	Distance to the	−0.33	−0.59	−0.12
	boundary	(−0.74–0.06)	(−1.50–0.08)	(−0.12–0.39)
4.	NDVI	**0.35**	−0.07	0.10
		(0.08–0.67)	(−0.62–0.37)	(−0.07–0.29)
5.	Forest cover	−0.02	**2.20**	0.49
		(−1.58–1.38)	**(0.12–4.41)**	(−0.40–1.233)
6.	Effort	−0.03	−0.01	−0.03
		(−0.07–0.0)	(−0.04–0.01)	(−0.05–0.007)

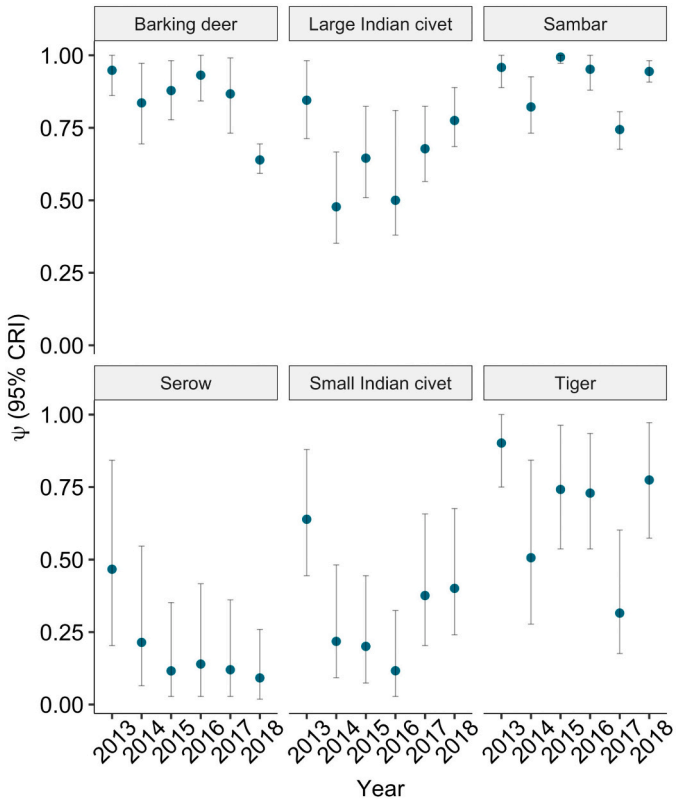

Fig. 3. Average species-specific occupancy of 4-km^2 sampling units and 95 % credible intervals for six species of mammals with substantial evidence of temporal variation in occupancy estimates for species captured during camera-trap surveys conducted over six years (2013–18) in Pakke Tiger Reserve, India.

Table 4
Species-specific naïve occupancy averaged across years and estimated occupancy (of 4-km^2 sampling units) averaged across years ($\overline{\psi}$) along with 95 % credible intervals for species $\overline{\psi}$ detected during camera-trap surveys conducted over six years (2013–2018) in Pakke Tiger Reserve, India. The sample unit to which occupancy pertains is the grid cell.

Species	Naive	$\overline{\psi}$ (95 % CRI)
Binturong (*Arctitis binturong*)	0.02	0.67 (0.07–0.97)
Gaur (*Bos gaurus*)	0.42	0.56 (0.40–0.72)
Asiatic golden cat (*Catopuma temminicki*)	0.01	0.23 (0.00–0.99)
Serow (*Capricornis thar*)	0.05	0.13 (0.04–0.32)
Dhole (*Cuon alpinus*)	0.26	0.74 (0.43–0.99)
Elephant (*Elephas maximus*)	0.84	0.94 (0.87–0.98)
Mongoose (*Herpestes* spp.)	0.11	0.58 (0.42–0.75)
Hog deer (*Axis porcinus*)	0.04	0.64 (0.07–0.99)
Porcupine (*Hystrix* spp.)	0.49	0.58 (0.42–0.75)
Otter (*Lutrogale perspicillata*)	0.03	0.04 (0.01–0.13)
Yellow-throated marten (*Martes flavigula*)	0.20	0.91 (0.62–0.99)
Macaque (*Macaca* spp.)	0.14	0.93 (0.68–0.99)
Barking deer (*Muntiacus muntjac*)	0.68	0.80 (0.65–0.94)
Himalayan goral (*Naemorhedus goral*)	0.04	0.09 (0.00–0.10)
Clouded leopard (*Neofelis nebulosa*)	0.11	0.73 (0.31–0.99)
Slow loris (*Nycticebus bengalensis*)	0.01	0.05 (0.00–0.20)
Common civet (*Paradoxurus hermaphoditis*)	0.17	0.23 (0.11–0.40)
Masked palm civet (*Paguma larvata*)	0.03	0.03 (0.00–0.08)
Marbled cat (*Pardofelis marmorata*)	0.07	0.46 (0.12–0.97)
Leopard (*Panthera pardus fusca*)	0.40	0.92 (0.72–0.99)
Tiger (*Panthera tigris*)	0.33	0.53 (0.31–0.78)
Leopard cat (*Prionailurus bengalensis*)	0.35	0.44 (0.30–0.62)
Sambar (*Rusa unicolor*)	0.85	0.89 (0.80–0.96)
Wild boar (*Sus scrofa*)	0.47	0.81 (0.57–0.99)
Capped langur (*Trachypithecus pileatus*)	0.04	0.06 (0.01–0.14)
Black bear (*Ursus thibetanus*)	0.09	0.20 (0.08–0.44)
Small Indian civet (*Vivericula indica*)	0.14	0.16 (0.05–0.30)
Large Indian civet (*Viverra zibetha*)	0.44	0.48 (0.32–0.65)

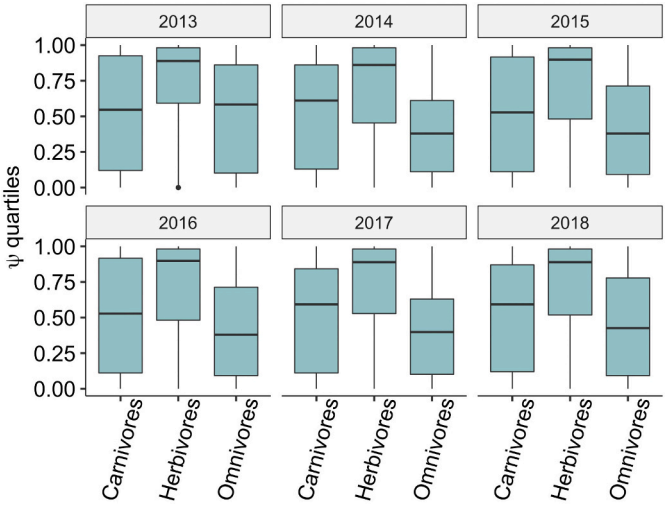

Fig. 4. Box plot showing mean, upper and lower quartile of the distribution of occupancy estimates of 4-km^2 sampling units for the three guilds (carnivores, herbivores, and omnivores) of mammals surveyed during camera-trap surveys conducted over six years (2013–18) in Pakke Tiger Reserve, India.

are monitored regularly (Watson et al., 2016). We aimed to quantify community composition (species richness) and species-specific distribution and habitat use patterns (two of the five EBVs) for mammals of PTR, a protected area situated in the ecologically diverse Eastern Himalyan Region. We applied multi-species occupancy models to six years (2013–2018) of camera trap data to provide baseline estimates of mammalian species richness and species-specific occupancy in PTR. Our results revealed that: (*i*) the mammalian community of PTR is diverse, composed of about 41 species, 28 of which were detected during our study, and is fairly stable over time; (*ii*) greener forested habitats at lower elevation supported a more diverse mammalian community compared to less green habitats at higher elevation; (*iii*) species-specific occupancy varied across species with higher occupancy for herbivores than carnivores and omnivores; and (*iv*) lower elevation greener forested habitat supported higher occupancy of most species but distance to the village and distance to the reserve boundary did not influence most species-specific or group-specific occupancy probability in a specific direction.

The mammalian community of EHR is vulnerable to anthropogenic land-use change, which is intricately linked to climate change; it also faces additional pressures such as poaching and ineffective legal enforcement of wildlife policies (Penjor et al., 2021). Long term persistence of this community depends on proactive conservation measures such as increased wildlife habitat and efficient protection efforts (Penjor et al., 2021). PTR has been under effective management, and enjoys high levels of community engagement; consequently, the reserve currently faces low (but growing) anthropogenic pressure (Ghosh-Harihar et al., 2019). Thus, we expected the mammalian community of PTR to be stable, with little or no year-to-year variation in species richness; our results were consistent with this expectation. There was minimal temporal variation in species richness with no apparent temporal trend (Supplementary Material S5). This result is consistent with the literature showing that multi-year species richness is generally stable locally or regionally, despite the general global decline in biological diversity (Batt et al., 2017). These results also emphasize the role of effective conservation strategies implemented in a well-managed protected area, such as PTR.

Consistent with our expectations, we found that greener forested habitats (driven by carnivores) and those at lower elevations (driven by omnivores) typically supported a more diverse mammalian community as compared to less green habitats and those at higher elevations. Species richness of small mammals varies with altitude, and peaks around

median elevation (Andrade and Monjeau, 2014; McCain, 2004; Rickart et al., 2011). In some tropical areas, lowlands typically support higher species richness than highlands (Drouilly et al., 2018; Gallo et al., 2009). Areas with high NDVI values tend to have higher plant species richness and primary productivity, likely supporting more species of mammals (Pau et al., 2012). For example, variation in plant species richness accounted for 75 % of the variability in species richness of the South African mammalian community (Andrews and O'Brien, 2000).

Anthropogenic pressure and species richness are usually negatively related (Farris et al., 2015; Perillo et al., 2017) which is true for some parts of EHR as well (Penjor et al., 2021). We, therefore, expected that areas closer to the reserve boundary or the local human settlements would support a less diverse community of mammals. Studies have shown land use and anthropogenic pressure to be the primary drivers of species richness and species-specific occupancy probabilities (Goswami et al., 2021; Pettorelli et al., 2010; Van der Weyde et al., 2018). Contrary to our prediction, we found no evidence that distance to the reserve boundary or to the nearest village affected mammalian species richness, likely due to the low anthropogenic pressure that PTR currently experiences. The legal protection status of PTR allows for only a limited range of human activities (i.e., ranger patrols and regulated tourism) within the park boundaries. Furthermore, with 17 people per km^2 (2011 census conducted by the Government of India) Arunachal Pradesh is one of the least populated states in India. However, anthropogenic pressure could increase in the future with greater development and expansion of the human footprint in the area. A demonstrated negative relationship between anthropogenic pressure and mammalian species richness (see Penjor et al., 2021) and space use (Goswami et al., 2021) in the EHR, suggests that maintaining PTR as an undisturbed, well-managed protected area will be key to sustaining diverse and stable mammalian community of the region.

Species-specific occupancy did not vary strongly over time except for tigers, sambar, large and small Indian civets, serow, and barking deer. (Fig. 3). Occupancy for these species varied across years but did not appear to follow a consistent increasing or declining trend. Our results provide much-needed information on the spatial ecology of understudied species of Northeast India and Southeast Asia, including the clouded leopard *Neofelis nebulosa*, marbled cat *Pardofelis marmorata*, and Asiatic golden cat *Catopuma temminicki*. Our occupancy estimates for clouded leopard were higher than those estimated for a clouded leopard population in Nam Et-Phou Louey (NEPL) Reserve, Lao PDR (Rasphone et al., 2019), Bhutan (Penjor et al., 2018), and in Peninsular Malaysia (Tan et al., 2017). Our occupancy estimates for the marbled cat are higher than those estimated in NEPL (Johnson et al., 2009; Rasphone et al., 2019). Marbled cats are generally infrequently encountered in camera traps elsewhere in their range (Sunarto et al., 2015; Tempa et al., 2013), suggesting that they probably occur at low densities across their range. Our mean occupancy estimates for Asiatic golden cats were higher than those reported from Malaysia (Sunarto et al., 2015) and Northeastern Bangladesh (Rahman et al., 2021) and similar to those reported from NEPL (Rasphone et al., 2019). Uncertainty was high for our mean occupancy estimates for Asiatic golden cat. We note, however, that some of the differences in occupancy and detection probabilities of the above-mentioned species might be caused by differences in study design and field conditions. We found that herbivores occupied a larger proportion of surveyed grid cells as compared to carnivores and omnivores (Fig. 4). Herbivores, particularly the group-living species, typically occur at much higher densities relative to solitary large carnivores and omnivores demonstrating higher use of the surveyed grid cells.

Protected areas such as PTR are cornerstones for conservation and are essential for the maintenance of biodiversity and the persistence of threatened species (Dorji et al., 2019; Oberosler et al., 2020; Velho et al., 2016). Long-term monitoring is essential to mitigate anthropogenic and other threats to biodiversity within protected areas. However, most of the current monitoring and conservation efforts, even within protected areas are focused on a subgroup of charismatic mammalian species (Amori and Gippoliti, 2000; Ceballos and Ehrlich, 2009), and single-species focused monitoring cannot fully ensure the conservation of all co-occurring species (Bifolchi and Lode, 2005; Roberge and Angelstam, 2004). Assessing and maintaining the viability of threatened populations, such as that of declining mammalian fauna, is of conservation and management concern. In this context, estimates of community composition and species-specific distribution of such species can serve as a reliable metric for assessing the effectiveness of management efforts and quantifying the influence of increasing anthropogenic influence on biological diversity (Devarajan et al., 2020). We posit that recent advances in technology and knowledge provide a great opportunity to revisit the single-species monitoring approach and move towards a more comprehensive community-based monitoring and conservation, especially in areas where extensive monitoring efforts are already taking place for large carnivores or other charismatic species.

Like most tiger reserves in India, camera-trap surveys in our study area are conducted with a focus on tigers and other large predators; however, these surveys produce a wealth of biodiversity information by photo-capturing any species that walks in front of the camera traps (Tobler et al., 2008). We argue that these data, collected at no additional cost, could be used to conduct comprehensive biodiversity assessments to design appropriate management plans and evaluate the effectiveness of protected areas and legislation. We propose a workflow to capitalize on a large amount of existing (and future) data resulting from ongoing monitoring programs such as those targeting tigers in India (Fig. 5). Camera-trap and other data collected from legally mandated and other surveys (e.g., academic research projects) can be analyzed using the MSOMs to provide an assessment of the overall biodiversity of the region as well as species-level estimates (such as distribution and habitat-use patterns) while accounting for imperfect detection, species identity, site-specific variations (specifically ecological factors, anthropogenic threats, and protection effectiveness), and year-specific variations. Furthermore, this approach can be integrated with other research and monitoring programs to report EBVs (mainly community composition and species distribution) which can be utilized to detect anthropogenic changes and the effectiveness of conservation programs.

In this study, we provide information on two of the five EBVs (i.e., community composition and local species-specific distribution patterns) from PTR which can be used to comparatively assess the effectiveness of the management regime, and to detect changes in community composition and other community- and species-level metrics. Currently, community-level information of the type we present here is not available from much of South Asia (but see Bajaru et al., 2020; Penjor et al., 2021; Rahman et al., 2021; Syiem et al., 2018), although such information is becoming increasingly common from other parts of the world (Devarajan et al., 2020; Krebs, 2020; Rasphone et al., 2019; Zipkin et al., 2009). Our study is the first to present a robust baseline assessment of the entire mammalian community (excluding flying, aquatic, and small burrowing mammals) in PTR and from Northeast India in general. The framework we present here (Fig. 5) could be replicated in other key habitats and protected areas to reliably assess and monitor mammalian communities and other important components of biodiversity. Such monitoring efforts are critical to meet the challenges of biodiversity conservation in the Anthropocene. It allows for the incorporation of valuable but often sparse, opportunistic, and inconsistent datasets on multiple species for many of which we lack robust estimates of species-habitat association.

Our results indicated that the mammalian community in PTR was relatively stable, with no discernible change in species richness during our six-year study (2013–2018). It may be argued that, in the absence of catastrophic events, six years may not be enough time for a mammalian community to undergo detectable change, because many mammals in our study area are long-lived. We view species richness as relative in time and space, and the definition of species richness requires the specification of time and geographical range (Nichols et al., 1998). We suggest that our estimate of mammalian species richness can be used as the baseline against which to compare any future changes in richness

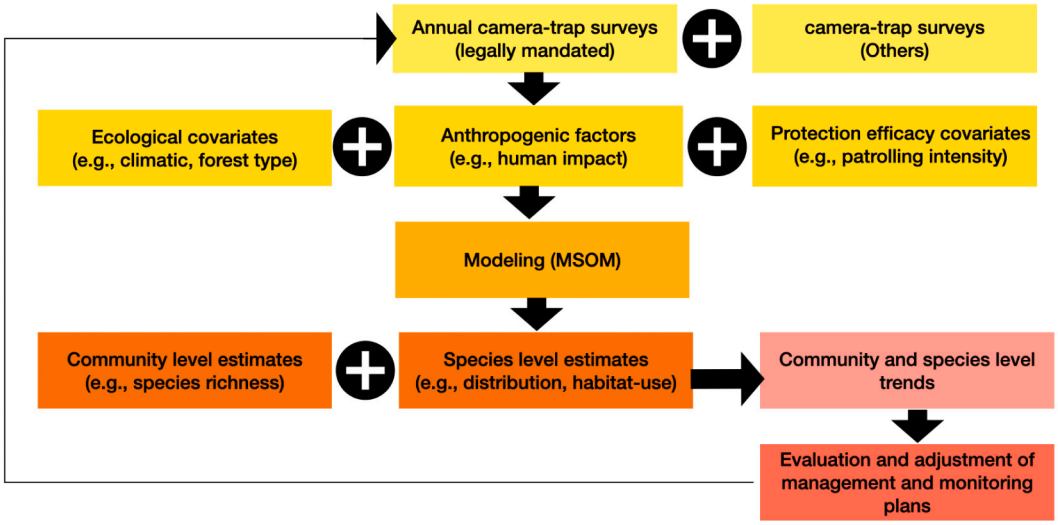

Fig. 5. A framework for capitalizing on existing datasets generated from species-focused population monitoring programs (e.g., tiger monitoring surveys in India) and other opportunistic surveys to learn about ecological communities and constituent species. These data can be analyzed using a multispecies occupancy modeling framework to estimate the baseline Essential Biodiversity Variables (EBVs), such as regional species richness and species occupancy or space use patterns as well as to understand the influence of ecological and anthropogenic (related to both disturbance and management) factors on EBVs. Monitoring these EBVs over time can potentially allow early detection of critical changes in the diversity and composition of the community and species-specific response to changes, which can be compared to baseline estimates to detect the change and implement appropriate management intervention in a timely fashion. The workflow is conceptually similar to adaptive management workflow and permits double-loop learning, and adaptation in monitoring and management (Williams and Brown, 2018).

over time to detect any downward trends so that necessary mitigation measures can be taken without delay. Hierarchical community models like MSOMs which we use here improve the precision of diversity and species-specific estimates through information sharing as data are more efficiently used relative to single species occupancy models thereby offsetting the cost of multispecies monitoring and improving individual species estimates especially for rare species (Iknayan et al., 2014; Tingley et al., 2020). These benefits arise from the Bayesian shrinkage property as each species' estimates inform the community-level mean and variance and as a result estimates of individual species are pulled towards the community mean (Iknayan et al., 2014; Tingley et al., 2020). The Bayesian MSOM modeling approach allows information sharing across species and permits simultaneous estimation of community-level and species-specific parameters even for species that are rare, elusive, and infrequently detected (Kery and Royle, 2008; Hobbs and Hooten 2015; Iknayan et al., 2014).

CRediT authorship contribution statement

Vratika Chaudhary: Conceptualization, Methodology- Data Curation, Data Analysis, Writing- Original draft preparation, Reviewing, and Editing.

Varun R. Goswami: Conceptualization, Supervision, Methodology- Data Curation, Writing- Reviewing and Editing.

Tana Tapi: Conceptualization, Methodology- Data Curation.

Chandan Ri: Conceptualization, Methodology- Data Curation, Writing- Reviewing.

Toh Kok Ben: Methodology- Data Analysis, Validation.

Gavin Jones: Methodology- Data Analysis, Validation, Writing- Reviewing and Editing.

Marc Kéry: Conceptualization, Data Analysis, Validation, Writing- Draft preparation, Reviewing and Editing.

Madan K. Oli: Conceptualization, Supervision, Methodology- Data Analysis, Validation, Writing- Original draft preparation, Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109778.

References

Amori, G., Gippoliti, S., 2000. What do mammalogists want to save? Ten years of mammalian conservation biology. Biodivers. Conserv. 9, 785–793.

Andrade, A., Monjeau, A., 2014. Patterns in community assemblage and species richness of small mammals across an altitudinal gradient in semi-arid Patagonia, Argentina. J. Arid Environ. 106, 18–26.

Andrews, P., O'Brien, E.M., 2000. Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. J. Zool. 251, 205–231.

Bajaru, S., Pal, S., Prabhu, M., Patel, P., Khot, R., Apte, D., 2020. A multi-species occupancy modeling approach to access the impacts of land use and land cover on terrestrial vertebrates in the Mumbai metropolitan region (MMR), Western Ghats. In: Plos One, India, p. 15.

Batt, R.D., Morley, J.W., Selden, R.L., Tingley, M.W., Pinsky, M.L., 2017. Gradual changes in range size accompany long-term trends in species richness. Ecol. Lett. 20, 1148–1157.

Bifolchi, A., Lode, T., 2005. Efficiency of conservation shortcuts: an investigation with otters as umbrella species. Biol. Conserv. 126, 523–527.

Bivand, R.R.C., 2020. rgeos: interface to geometry engine-open source (GEOS) R package.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E., Pollock, K.H., 1998. Estimating species richness: the importance of heterogeneity in species detectability. Ecology 79, 1018–1028.

Broms, K.M., Hooten, M.B., Johnson, D.S., Altwegg, R., Conquest, L.L., 2016. Dynamic occupancy models for explicit colonization processes. Ecology 97, 194–204.

Ceballos, G., Ehrlich, P.R., 2009. Discoveries of new mammal species and their implications for conservation and ecosystem services. Proceedings of the National Academy of Sciences of the United States of America 106, 3841–3846.

Cheyne, S.M., Sastramidjaja, W.J., Muhalir, Rayadin, Macdonald, D.W., 2016. Mammalian communities as indicators of disturbance across Indonesian Borneo. Global Ecology and Conservation 7, 157–173.

Conn, P.B., Johnson, D.S., Williams, P.J., Melin, S.R., Hooten, M.B., 2018. A guide to bayesian model checking for ecologists. Ecol. Monogr. 88, 526–542.

Devarajan, K., Morelli, T.L., Tenan, S., 2020. Multi-species occupancy models: review, roadmap, and recommendations. Ecography 43, 1612–1624.

Dorazio, R.M., Royle, J.A., 2005. Estimating size and composition of biological communities by modeling the occurrence of species. J. Am. Stat. Assoc. 100, 389–398.

Dorazio, R.M., Royle, J.A., Soderstrom, B., Glimskar, A., 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87, 842–854.

Dorji, S., Rajaratnam, R., Vernes, K., 2019. Mammal richness and diversity in a himalayan hotspot: the role of protected areas in conserving Bhutan's mammals. Biodivers. Conserv. 28, 3277–3297.

Drouilly, M., Clark, A., O'Riain, M.J., 2018. Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: a case for dryland systems globally. Biol. Conserv. 224, 16–25.

Farris, Z.J., Golden, C.D., Karpanty, S., Murphy, A., Stauffer, D., Ratelolahy, F., Andrianjakarivelo, V., Holmes, C.M., Kelly, M.J., 2015. Hunting, exotic carnivores, and habitat loss: Anthropogenic effects on a native carnivore community. In: Madagascar, Plos One, p. 10.

Farris, Z.J., Gerber, B.D., Valenta, K., Rafaliarison, R., Razafimahaimodison, J.C., Larney, E., Rajaonarivelo, T., Randriana, Z., Wright, P.C., Chapman, C.A., 2017a. Threats to a rainforest carnivore community: a multi-year assessment of occupancy and co-occurrence in Madagascar. Biol. Conserv. 210, 116–124.

Fleishman, E., Noss, R.F., Noon, B.R., 2006. Utility and limitations of species richness metrics for conservation planning. Ecol. Indic. 6, 543–553.

Gallo, J.A., Pasquini, L., Reyers, B., Cowling, R.M., 2009. The role of private conservation areas in biodiversity representation and target achievement within the little karoo region, south africa. Biol. Conserv. 142, 446–454.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405, 220–227.

Gelfand, A.E., Schmidt, A.E., Wu, S., Silander Jr., J.A., Latimer, A., Rebelo, A.G., 2005. Modelling species diversity through species level hierarchical modelling. Appl. Stat. 54, 1e20.

Gelman, A., Hwang, J., Vehtari, A., 2014. Understanding predictive information criteria for bayesian models. Stat. Comput. 24, 997–1016.

Ghosh-Harihar, M., An, R., Athrey, R., Borthakur, U., Chanchani, P., Chetry, D., Datta, A., Harihar, A., Karanth, K.K., Mariyam, D., Mohan, D., Onial, M., Ramakrishnan, U., Robin, V.V., Saxena, A., Shahabuddin, G., Thatte, P., Vijay, V., Wacker, K., Mathur, V.B., Pimm, S.L., Price, T.D., 2019. Protected areas and biodiversity conservation in India. Biol. Conserv. 237, 114–124.

Goswami, V.R., Vasudev, D., Joshi, B., Hait, P., Sharma, P., 2021. Coupled effects of climatic forcing and the human footprint on wildlife movement and space use in a dynamic floodplain landscape. Sci. Total Environ. 758, 144000.

Harvey, E., Gounand, I., Ward, C.L., Altermatt, F., 2017. Bridging ecology and conservation: from ecological networks to ecosystem function. J. Appl. Ecol. 54, 371–379.

Hendry, H., Mann, C., 2018. Camelot-intuitive software for camera-trap data management. Oryx 52, 15, 15.

Hobbs, N.T., Hooten, M.B., 2015. Bayesian Models. Princeton University Press.

Jetz, W., McGeoch, M.A., Guralnick, R., Ferrier, S., Beck, J., Costello, M., Fernandez, M., Geller, G.N., Keil, P., Merow, C., Meyer, C., Muller-Karger, F.E., Pereira, H.M., Regan, E.C., Schmeller, D.S., Turak, E., 2019. Essential biodiversity variables for mapping and monitoring species populations. Nature Ecology & Evolution 3, 539–551.

Jhala, Y.V., Qureshi, Q., Nayak, A.K., 2019. Status of Tigers, Co-predators and Prey in India 2018. Summary Report National Tiger Conservation Authority, Government of India, New Delhi & Wildlife Institute of India, Dehradun. https://wii.gov.in/status_of_tigers_2018.

Johnson, A., Vongkhamheng, C., Saithongdam, T., 2009. The diversity, status and conservation of small carnivores in a montane tropical forest in northern Laos. Oryx 43, 626–633.

K.J. Iknayan M.W. Tingley B.J. Furnas S.R. Beissinger Detecting diversity: emerging methods to estimate species diversity Trends Ecol. Evol. 29 2014 97 106.

Karanth, K.U., Nichols, J.D., 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79, 2852–2862.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004. Tigers and their prey: Predicting carnivore densities from prey abundance. Proc. Natl. Acad. Sci. U. S. A. 101, 4854–4858.

Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D., MacKenzie, D.I., 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. J. Appl. Ecol. 48, 1048–1056.

Karanth, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., Kumar, N.S., 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proc. R. Soc. B Biol. Sci. 284.

Kery, M., Royle, J.A., 2008. Hierarchical bayes estimation of species richness and occupancy in spatially replicated surveys. J. Appl. Ecol. 45, 589–598.

Kery, M., Royle, J.A., 2016. Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS (volume 1 – prelude and static models). Academic Press.

Kellner, K, Meredith, M, 2021. Package 'jagsUI'. https://cran.r-project.org/web/packages/jagsUI/jagsUI.pdf.

Kery, M., Gardner, B., Monnerat, C., 2010. Predicting species distributions from checklist data using site-occupancy models. J. Biogeogr. 37, 1851–1862.

Krebs, C.J., 2020. Whither mammalian ecology? J. Mammal. 101, 1224–1230.

Kumar, A., 2014. Avifauna of pakke tiger reserve and adjacent localities, Arunachal Pradesh, India. Journal Experimental Zoology India 17, 55–67.

Laycock, H.F., Moran, D., Smart, J.C.R., Raffaelli, D.G., White, P.C.L., 2011. Evaluating the effectiveness and efficiency of biodiversity conservation spending. Ecol. Econ. 70, 1789–1796.

Lindenmayer, D.B., Likens, G.E., 2010. The science and application of ecological monitoring. Biol. Conserv. 143, 1317–1328.

Lindenmayer, D.B., et al., 2012. Improving biodiversity monitoring. Austral Ecology 37, 285–294.

Lunn, D., Jackson, C., Best, N., Thomas, A., Spiegelhalter, D., 2013. The BUGS book: a practical introduction to bayesian analysis. Chapman & Hall/CRC.

Mackenzie, D.I., Royle, J.A., 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. 42, 1105–1114.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2018. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier, London, U.K.

McCain, C.M., 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. J. Biogeogr. 31, 19–31.

McCullagh, P., Nelder, J.A., 1989. Generalized linear models. Chapman & Hall, London.

Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A., Daily, G.C., 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509, 213-+.

Myers, N., 2003. Biodiversity hotspots revisited. Bioscience 53, 916–917.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H., Sauer, J.R., 1998. Inference methods for spatial variation in species richness and community composition when not all species are detected. Conserv. Biol. 12 (6), 1390–1398. https://doi.org/10.1111/j.1523-1739.1998.97331.x. Dec;1.

Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. Trends Ecol. Evol. 21, 668–673.

Oberosler, V., Tenan, S., Zipkin, E.F., Rovero, F., 2020. When parks work: effect of anthropogenic disturbance on occupancy of tropical forest mammals. Ecology and Evolution 10, 3881–3894.

Parrish, J.D., Braun, D.P., Unnasch, R.S., 2003. Are we conserving what we say we are? Measuring ecological integrity within protected areas. Bioscience 53, 851–860.

Pau, S., Gillespie, T.W., Wolkovich, E.M., 2012. Dissecting NDVI-species richness relationships in hawaiian dry forests. J. Biogeogr. 39, 1678–1686.

Penjor, U., Macdonald, D.W., Wangchuk, S., Tandin, T., Tan, C.K.W., 2018. Identifying important conservation areas for the clouded leopard Neofelis nebulosa in a mountainous landscape: inference from spatial modeling techniques. Ecology and Evolution 8, 4278–4291.

Penjor, U., Wangdi, S., Tandin, T., Macdonald, D.W., 2021. Vulnerability of mammal communities to the combined impacts of anthropic land-use and climate change in the himalayan conservation landscape of bhutan. Ecol. Indic. 121.

Pereira, H.M., Walters, M., Geller, G.N., Jongman, R.H., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S.H., Cardoso, A.C., Coops, N.C., 2013. 2013. Science 339 (6117), 277–278. https://doi.org/10.1126/science.1229931. Jan 18.

Perillo, A., Mazzoni, L.G., Passos, L.F., Goulart, V., Duca, C., Young, R.J., 2017. Anthropogenic noise reduces bird species richness and diversity in urban parks. Ibis 159, 638–646.

Pettorelli, N., Lobora, A.L., Msuha, M.J., Foley, C., Durant, S.M., 2010. Carnivore biodiversity in tanzania: revealing the distribution patterns of secretive mammals using camera traps. Anim. Conserv. 13, 131–139.
Poiani, K.A., Richter, B.D., Anderson, M.G., Richter, H.E., 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. Bioscience 50, 133–146.
Prat-Guitart, M., Onorato, D.P., Hines, J.E., Oli, M.K., 2020. Spatiotemporal pattern of interactions between an apex predator and sympatric species. J. Mammal. 101, 1279–1288.
R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/.
Rahman, H.A., McCarthy, K.P., McCarthy, J.L., Faisal, M.M., 2021. Application of multi-species occupancy modeling to assess mammal diversity in Northeast Bangladesh. Global Ecology and Conservation 25.
Rasphone, A., Kery, M., Kamler, J.F., Macdonald, D.W., 2019. Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR's most prized protected area: Nam Et - Phou Louey. Global Ecology and Conservation 20.
Reddy, C.S., Jha, C.S., Dadhwal, V.K., Krishna, P.H., Pasha, S.V., Satish, K.V., Dutta, K., Saranya, K.R.L., Rakesh, F., Rajashekar, G., Diwakar, P.G., 2016. Quantification and monitoring of deforestation in India over eight decades (1930–2013). Biodivers. Conserv. 25, 93–116.
Rich, L.N., Miller, D.A.W., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an african mammal community. J. Appl. Ecol. 53, 1225–1235.
Rickart, E.A., Heaney, L.R., Balete, D.S., Tabaranza, B.R., 2011. Small mammal diversity along an elevational gradient in northern Luzon, Philippines. Mamm. Biol. 76, 12–21.
Roberge, J.M., Angelstam, P., 2004. Usefulness of the umbrella species concept as a conservation tool. Conserv. Biol. 18, 76–85.
Roy, P.S., et al., 2015. New vegetation type map of India prepared using satellite remote sensing: comparison with global vegetation maps and utilities. Int. J. Appl. Earth Obs. Geoinf. 39, 142–159.
Royle, J.A., Kéry, M., Gautier, R., Schmid, H., 2007. Hierarchical spatial models of abundance and occurrence from imperfect survey data. Ecol. Monogr. 77 (3), 465–481. https://doi.org/10.1890/06-0912.1. Aug.
Schuette, P., Wagner, A.P., Wagner, M.E., Creel, S., 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biol. Conserv. 158, 301–312.
Schwartz, M.W., 2008. The performance of the endangered species act. Annu. Rev. Ecol. Evol. Syst. 39, 279–299.
Selvan, K.M., Lyngdoh, S., Habib, B., Gopi, G.V., 2014. Population density and abundance of sympatric large carnivores in the lowland tropical evergreen forest of indian eastern Himalayas. Mamm. Biol. 79, 254–258.
Steenweg, R., Whittington, J., Hebblewhite, M., Forshner, A., Johnston, B., Petersen, D., Shepherd, B., Lukacs, P.M., 2016. Camera-based occupancy monitoring at large scales: power to detect trends in grizzly bears across the Canadian rockies. Biol. Conserv. 201, 192–200.
Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J.T., Burton, C., Townsend, S.E., Carbone, C., Rowcliffe, J.M., Whittington, J., Brodie, J., Royle, J.A., Switalski, A., Clevenger, A.P., Heim, N., Rich, L.N., 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. Front. Ecol. Environ. 15, 26–34.
Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., McKelvey, K., 2018. Sampling scales define occupancy and underlying occupancy-abundance relationships in animals. Ecology 99, 172–183.
Sunarto, S., Kelly, M.J., Parakkasi, K., Hutajulu, M.B., 2015. Cat coexistence in Central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. J. Zool. 296, 104–115.
Sundqvist, M.K., Sanders, N.J., Wardle, D.A., 2013. In: Futuyma, D.J. (Ed.), Community and Ecosystem Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global Change, In Annual Review of Ecology, Evolution, and Systematics, 44, pp. 261–280.
Syiem, B.L., Goswami, V.R., Vasudevz, D., 2018. "In a tree by the brook, there's a songbird who sings": woodlands in an agricultural matrix maintain functionality of a wintering bird community. Plos One 13.
Tag, H., Jeri, L., Mingki, T., Das, J.T.A.K., 2012. In: Higher Plant Diversity in Pakke Wildlife Sanctuary and Tiger Reserve in East Kameng District of Arunachal Pradesh: Checklist - I. Pleione, 6, pp. 149–162.
Tan, K., Rocha, D.G., Clements, G.R., Brenes-Mora, E., Hedges, L., Kawanishi, K., Mohamad, S.W., Rayan, D.M., Bolongon, G., Moore, J., Wadey, J., Campos-Arceiz, A., Macdonald, D.W., 2017. Habitat use and predicted range for the mainland clouded leopard Neofelis nebulosa in peninsular Malaysia. Biol. Conserv. 206, 65–74.
Tempa, T., Hebblewhite, M., Mills, L.S., Wangchuk, T.R., Norbu, N., Wangchuk, T., Nidup, T., Dendup, P., Wangchuk, D., Wangdi, Y., Dorji, T., 2013. Royal manas national park, Bhutan: a hot spot for wild felids. Oryx 47, 207–210.
Tingley, M.W., Nadeau, C.P., Sandor, M.E., 2020. Multi-species occupancy models as robust estimators of community richness. Methods Ecol. Evol. 11, 633–642.
Tobler, M.W., Carrillo-Percastegui, S.E., Pitman, R.L., Mares, R., Powell, G., 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim. Conserv. 11, 169–178.
Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K., Possingham, H.P., 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecol. Appl. 13, 1790–1801.
Van der Weyde, L.K., Mbisana, C., Klein, R., 2018. Multi-species occupancy modelling of a carnivore guild in wildlife management areas in the kalahari. Biol. Conserv. 220, 21–28.
Velho, N., Sreekar, R., Laurance, W.F., 2016. Terrestrial species in protected areas and community-managed lands in Arunachal Pradesh. In: Northeast India, Land, p. 5.
Watson, J.E.M., Darling, E.S., Venter, O., Maron, M., Walston, J., Possingham, H.P., Dudley, N., Hockings, M., Barnes, M., Brooks, T.M., 2016. Bolder science needed now for protected areas. Conserv. Biol. 30, 243–248.
Wearn, O.R., Glover-Kapfer, P., 2019. Snap happy: camera traps are an effective sampling tool when compared with alternative methods. royal society open. Science 6.
Williams, B.K., Brown, E.D., 2018. Double-loop learning in adaptive management: the need, the challenge, and the opportunity. Environ. Manag. 62, 995–1006.
Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and management of animal populations. Academic Press, San Diego.
Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. Trends Ecol. Evol. 16, 446–453.
Zipkin, E.F., Dewan, A., Royle, J.A., 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. J. Appl. Ecol. 46, 815–822.