

Vulnerability of mammal communities to the combined impacts of anthropic land-use and climate change in the Himalayan conservation landscape of Bhutan

Ugyen Penjor^{a,b,*}, Sonam Wangdi^b, Tandin Tandin^b, David W. Macdonald^a

^a Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, OX13 5QL Oxfordshire, United Kingdom

^b Nature Conservation Division, Department of Forests and Park Services, Ministry of Agriculture and Forests, Thapa, Thimphu 11001, Bhutan

ARTICLE INFO

Keywords:

Camera-trapping
Climate
Conservation landscape
Land use
Multi-species occupancy model
Himalaya
Mammals

ABSTRACT

Human land-use and climate change drive biodiversity loss, precipitating the extinction crisis. The fragility of the Himalayas makes species in this landscape vulnerable to land-use and climate change. We aim to quantify the response of terrestrial mammal community to land-use and climate scenarios in the Bhutan Himalaya. Using large-scale camera-trap dataset, we examine the effects of anthropic land-use and climate variables on the terrestrial mammal assemblage using Bayesian multi-species occupancy model. Most of the terrestrial mammals in our sample displayed a strong negative relationship with anthropic land-use variables (agriculture, roads and settlement). Further, the occurrence of most species decreased with likely projections for climate variables, illustrating threats to conservation if the current trend in global warming continues. Notably, we found that biodiversity conservation in this landscape can be achieved by protecting extensive forest cover. Our findings emphasize the importance of reconciling land-use management and mammal conservation in the face of climate change and provide vital information which can be used to optimize future conservation and development plans.

1. Introduction

The impact of human activities on the current rate of global biodiversity decline will likely trigger the sixth mass extinction (Ceballos et al., 2015). The use and conversion of land have, throughout recorded history, been the pervasive, dominating force behind biodiversity loss (Maxwell et al., 2016; Johnson et al., 2017). This crisis is aggravated by invasive species (Clavero and García-Berthou, 2005), disease (Daszak et al., 2000) and livestock expansion (Morand, 2020). With the human population projected to double by the end of this century, human-induced land-use and climate change will likely interact to repeat the mass extinction of wildlife of the geological past (Barnosky et al., 2011; Williams et al., 2007). It is fundamentally important to understand the impacts of anthropogenic land-use and climate change on species communities.

The global decline of biodiversity has been attributed mainly to agricultural expansion and encroachment into nature and wilderness areas (Tilman et al., 2001; Pereira et al., 2010; Rands et al., 2010; Venter

et al., 2016). By 2070, the impact of land-use change is predicted to endanger ~1700 species of amphibians, birds and mammals globally, including species of high conservation value and functional importance, due mainly to habitat contraction (Barlow et al., 2016; Powers and Jetz, 2019). While agriculture is the backbone of socio-economic development, it often comes at the expense of biodiversity and ecosystem services (Kiffner et al., 2015; Newbold et al., 2015; Usubiaga-Liaño et al., 2019). Ironically, human well-being is at stake because biodiversity loss disrupts crucial ecosystem services which are vital to human survival and recreation (Frishkoff et al., 2014; Mendenhall et al., 2014).

On the other hand, climate change threatens one in every six species, risking ~20–30% of the species to extinction (Warren et al., 2013; Urban, 2015). At the current rate of global greenhouse gas (GHG) emission and forest loss, ~34% of species with moderate dispersal ability and ~42% of species with limited dispersal ability, respectively, would lose >50% of their range by 2080 (Warren et al., 2013). Although, some species could shift their range in response to climate change (Chen et al., 2011), most endemic species would face extinction

* Corresponding author at: Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, OX13 5QL Oxfordshire, United Kingdom.

E-mail address: upenjor@moaf.gov.bt (U. Penjor).

<https://doi.org/10.1016/j.ecolind.2020.107085>

Received 20 May 2020; Received in revised form 29 September 2020; Accepted 12 October 2020

Available online 27 October 2020

1470-160X/© 2020 The Authors. Published by Elsevier Ltd. All rights reserved.

due to disappearing local climate and habitat (Jackson and Overpeck, 2000; Beever et al., 2016). The synergy between land-use and climate change is expected to prompt a more profoundly negative impact on biodiversity than a single driver or their additive combination (Brodie, 2016; Newbold, 2018).

Eastern Himalaya is a biodiversity hotspot in south Asia (Myers et al., 2000; Dorji et al., 2018) and a critical part of Asia's water source and glacier ice repository outside the Poles (regarded as the 'Third Pole'), in the Himalayas (Sharma et al., 2019). But the biodiversity here is under siege from the threats of human land-use and climate change (Tilman et al., 2017). Bhutan is a biodiversity hotspot in the Eastern Himalaya with ~70% forest cover and >50% of the land under protection (Myers et al., 2000; DoFPS, 2011). The extreme altitudinal variation and topographical complexity influence weather pattern and create a unique microclimate which harbors a wide assemblage of plant and animal communities (Chettri et al., 2010). Yet, the fragility (erosion-prone landscape, melting glaciers and risk of flood) of the mountain ecosystem makes it vulnerable to the challenges of the Anthropocene (Chettri et al., 2010; Tse-ring et al., 2010; Kremen and Merenlender, 2018). We examined the effects of land use and climate on the occurrence of terrestrial mammal assemblages in this landscape, using a multi-species occupancy model (MSOM). The central premise of this study is that the mammal community would be adversely affected by land-use (agriculture, roads, settlement) changes, the factors which fragment and degrade habitat. Although the effect of climate might not be apparent in the overall mammalian assemblage in the shorter-term, the cumulative impact, however, could drastically compromise the species' ability to cope with the change (e.g. Bellard et al., 2012). On the other hand, we expected natural forest cover to be critical in maintaining biodiversity and perhaps mammalian community integrity in the fragile mountain ecosystem. Our study quantifies the effects of land use and climate on the mammal community of the hitherto understudied Himalayan landscape of Bhutan and proposes a generic paradigm to reconcile land management and biodiversity conservation.

2. Materials and methods

2.1. Study area and camera-trap survey

Bhutan is a small (38394 km²) country landlocked between India and China. The vegetation types vary along the altitudinal gradient and are broadly classed under agro-ecological zones namely sub-tropical, warm broadleaved, cool broadleaved, temperate, sub-alpine and alpine (DoFPS, 2011). The elevation characterizes temperature and precipitation: lower foothills with high summer temperature and heavy rainfall during monsoon while the higher mountains receive scant rainfall and experience low temperature. The elevation ranges between 100 m and 7000 m. The annual temperature ranges between 10 °C and 24 °C and annual precipitation between 300 m and 6000 m across Bhutan (NSB, 2018). Bhutan is sparsely populated with a mean density of 19 people km⁻² (NSB, 2018). The topography, in general, is steep terrain, deep gorges, and narrow river valleys.

We collected detection/non-detection data of mammals through camera trap survey between 2014 and 2015 which was part of the national tiger survey (Table S1). The national tiger survey comprised 1129 paired, unbaited, passive infra-red camera-traps (models used HCO Scoutguard, Bushnell, Cuddeback, Reconyx and U-way; see Table S2 for modelled performance on detection probability) installed across the country. Each camera station was placed within a 5 km × 5 km grid, based on the putative home range size of a female tiger (Karanth and Nichols, 2002) at an average distance of 2.9 km (1.2 km SD) ensuring there were no more than two camera stations per grid. These grids excluded areas of high-density settlement, large river network, and areas above 4500 m (DoFPS, 2015). The camera traps were randomly placed but following animal trails or frequently used sites such as mineral licks and water holes but in the context of accessibility. For logistical

convenience, the camera-traps were installed in two survey blocks: north (n = 681) and south (n = 448) (Fig. 1). The south block was surveyed between March 2014 and June 2014 and the north block between October 2014 and March 2015. Survey teams monitored the stations every 30 days to retrieve data, replace batteries and clear bushes obstructing camera lenses.

2.2. Land-use and climate variables

The land-use variables at the landscape scale were selected based on our *a priori* hypotheses. We hypothesized that agriculture expansion, road density, and proximity to settlement (a proxy of human disturbance) would negatively affect mammalian species occurrence and richness while forest cover would positively influence both occurrence and richness. We considered sampling unit as an area within 1 km buffer of each camera station, roughly corresponding to less than half of the mean distance between neighboring camera stations (Sollmann et al., 2012) and extracted covariates within this buffer. This buffer was chosen to represent the average site characteristic surrounding camera traps. We accessed the land-use data from the local forest department and calculated the percentage of land area for agriculture, and distance to feature for road and settlement. Mean forest cover was obtained from the Global Forest Change data (Hansen et al., 2013). We derived annual mean precipitation and temperature from the WorldClim 1.4 database at 1 km² resolution (1960 to 1990; Hijmans et al., 2005). Responses of species to climate forecast were based on projections of Global Climate Models (GCM) for three representative concentration pathways (RCP 2.6, 4.5 and 8.5) for the year 2070. Since both the climate variables (temperature and precipitation) were highly correlated with each other (Pearson's $|r| > 0.8$; Fig. S1), we built separate models for each variable to disentangle the effects separately which otherwise would be confounded by multicollinearity (Dormann et al., 2013). All covariates were standardized to mean 0 and standard deviation 1 before analysis. We provide our model specifications in the [Supplementary Material](#).

2.3. Modelling framework

We assessed the effects of land-use and climate variables on the mammalian community using a Bayesian hierarchical MSOM (Dorazio and Royle, 2005). MSOMs provide a convenient framework which allows for composite analysis of communities or group of species while accounting for observation heterogeneity (detection probability, (Dorazio et al., 2010; Kéry and Royle, 2016). By rationalizing detections of species in a community, it improves inference even for a rare and cryptic species otherwise impossible with a single species model (Zipkin et al., 2009).

The latent ecological process underlying the true pattern of occurrence for species k at camera site i , z_{ik} is considered a Bernoulli random variable, $z_{ik} \sim \text{Bernoulli}(\psi_{ik})$ with the probability of occupancy ψ_{ik} ($z_{ik} = 1$ if species is present, 0 otherwise). The measurement of actual observation, y_{ik} is another random variable conditional on the occurrence z_{ik} such that, $y_{ik}|z_{ik} \sim \text{Bernoulli}(z_{ik} \times p_{ik})$, where species present ($z_{ik} = 1$) is detected with probability p_{ik} . At a site where the species does not occur, $z_{ik} = 0$ and $y_{ik} = 0$ and cannot be falsely detected. Thus, hierarchical occupancy models can be described as Bernoulli-Bernoulli mixture models (Kéry and Royle, 2016). The sum of Bernoulli trials yields a Binomial distribution and the observation y_{ik} can be rewritten as, $y_{ik} \sim \text{Binomial}(z_{ik} \times p_{ik}, n_i)$, where n is the total number of trials (i.e. the number of active camera-trap days at site i). We introduced the effects of covariates (cov_i) at each site i using the logistic ("logit") link function as $\text{logit}(\psi_{ik}) = \beta_{0k} + \beta_{xk} \times \text{cov}_i$, where β_{0k} is the normally distributed species-specific random effect (intercept), $\beta_{0k} \sim \text{Normal}(\mu_{\beta_{0k}}, \sigma_{\beta_{0k}}^2)$, $\sigma_{\beta_{0k}}^2$ is the variance which specifies the occupancy probability of species k at site i , and β_{xk} is the effect (slope) of site covariate on species k with a prior from a normal distribution, $\beta_{xk} \sim \text{Normal}(\mu_{\beta_{xk}}, \sigma_{\beta_{xk}}^2)$. The detection

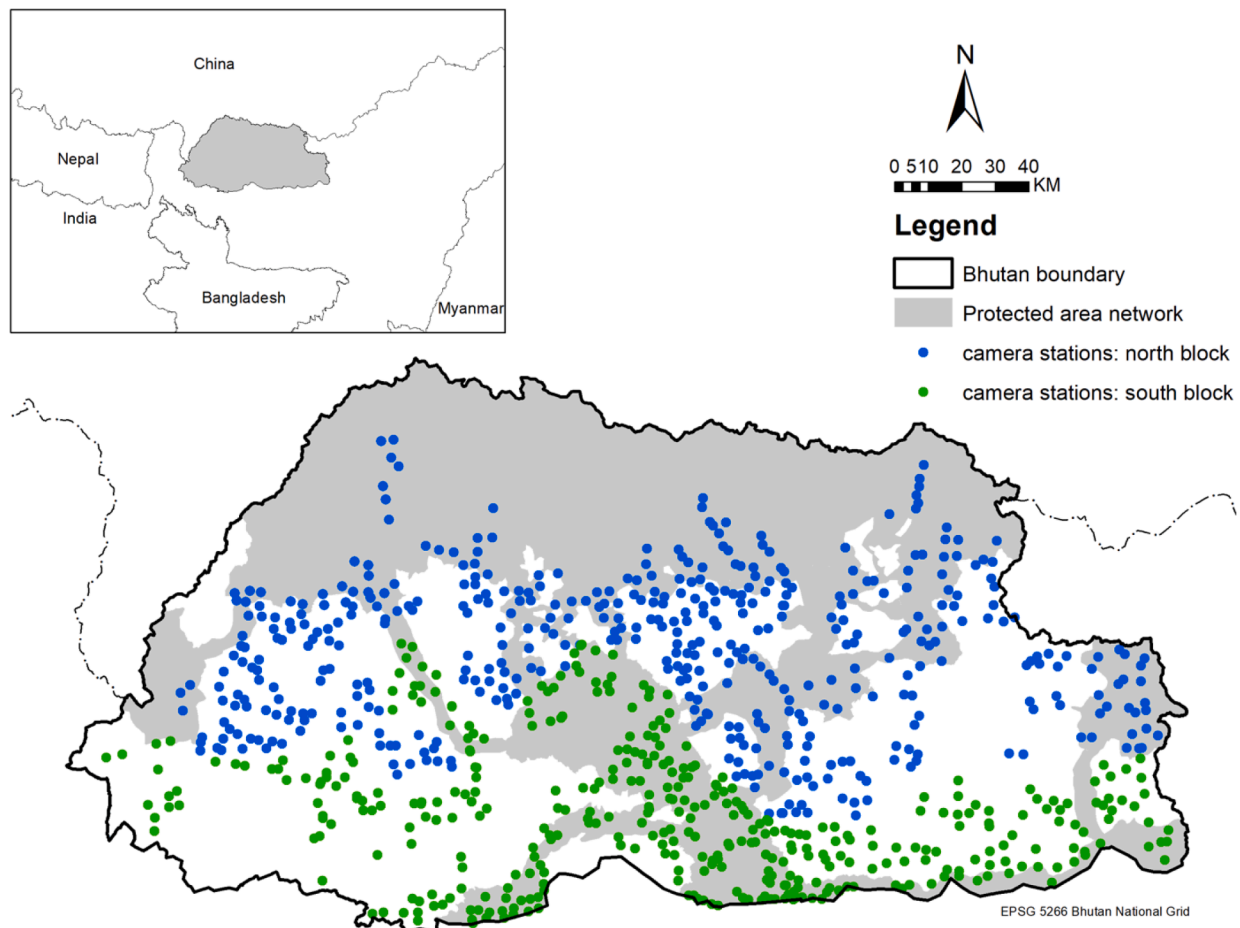


Fig. 1. The location of the study area (Bhutan) in south Asia (inset) with camera stations. Camera stations in the north are represented by blue points and in the south by green points. The grey polygons represent protected area network (national parks, wildlife sanctuaries and biological corridors) which constitute ~ 51% of the total geographical area.

probability was also modelled using the logit link function as $\text{logit}(p_{ik}) = \alpha_{0k} + \alpha_{xk} \times \text{cov}_i$, where α_{0k} is the normally distributed species-specific random effect, $\alpha_{0k} \sim \text{Normal}(\mu_{\alpha_{0k}}, \sigma_{\alpha_{0k}}^2)$, and α_{xk} is the specific-specific effect of covariates on detection probability. We modelled polynomial terms for agriculture, temperature and precipitation to allow for non-linear responses. Detection probability was modelled as a function of camera-traps placed on- or off-trail and camera models to assess the nuances in capture success due to different operative capabilities and durability of camera models. We used normal priors for means of hyperparameter, $\mu_{\beta_{0k}} \sim \text{Normal}(0, 0.001)$ for intercept and, $\mu_{\beta_{xk}} \sim \text{Normal}(0, 0.001)$ for slopes and weakly informative folded Student- t priors with four degrees of freedom ($\nu = 4$) for standard deviations of hyper-parameters, $\tau_{\beta_{0k}} \sim t(0, 2.25, \nu = 4)$ for the intercept where precision, $\tau_{\beta_{0k}} = 1/(\sigma_{\beta_{0k}} \times \sigma_{\beta_{0k}})$ and $\tau_{\beta_{xk}} \sim t(0, 2.25, \nu = 4)$, $\tau_{\beta_{xk}} = 1/(\sigma_{\beta_{xk}} \times \sigma_{\beta_{xk}})$ for the slopes which are proper but provides very weak information than any prior knowledge available (Gelman, 2006; model code in [Supplementary Material S1](#)).

We implemented the model in JAGS 4.3 (Plummer, 2003) called through R 3.6.1 (R Core Team, 2019) using the package jagsUI (Kellner, 2019). We ran three parallel chains of 200,000 Markov Chain Monte Carlo (MCMC) iterations each, discarding 100,000 during the adaptation phase and thinned by 20 for the economy of computer space. We drew inferences on species-specific and community response from 30,000 posterior samples and interpret the covariate effect based on the overlap of credible intervals (but see Ogle et al., 2019). The model convergence was assessed by visually inspecting the trace plots and by ensuring that the Gelman-Rubin statistic for all parameters was < 1.1

(Gelman et al., 2013).

3. Results

We recorded 54 mammal species in 849 camera stations (out of 1129 stations) over a total survey effort of 73 259 trap days during 2014 and 2015. We only included terrestrial mammals with bodyweight > 180 g (the smallest species in our study was mountain weasel *Mustela altaica*) and discarded rodent (squirrels and mice) and semi-aquatic species (otters; [Table S3](#)). The number of species detected per site ranged from 0 to 17. The naïve mean number of species per site was 5.49 (SD = 3.79). The mean estimated richness per site is seven (95% Bayesian credible interval (CRI) 5.65 to 9.30). We achieved convergence for all parameters in land use and climate models. The mean occupancy probability across the mammal community was 0.15 (0 – 0.70) and the mean community detection probability was 0.02 (0.004 – 0.25). The mean community detection probability was positive on trails ($\hat{\beta} = 0.32, 0.09 – 0.55$) and variable for different camera models ([Table S2](#)). The mean occupancy probability was highly variable among species, ranging from 0.004 for Bhutan takin *Budorcas taxicolor* to 0.62 for muntjac *Muntiacus muntjak* ([Fig. S2, Table S4](#)). Similarly, detection probability dramatically varied among species with lowest for binturong *Arctictis binturong* (0.004) and highest for muntjac (0.12, [Fig. S2, Table S4](#)).

3.1. Species-level response

Thirty-eight out of 45 species displayed negative response to agri-

culture, and this response was strong for nine species (CRIs exclude zero). Asian elephant, Asiatic brush-tailed porcupine *Atherurus macrourus*, common palm civet *Paradoxurus hermaphroditus*, crab-eating mongoose, gaur *Bos gaurus*, masked palm civet, large Indian civet *Viverra zibetha*, small Indian mongoose *Herpestes auro-punctatus*, and small Indian civet *Viverricula indica* displayed the strongest response (Figs. 2 and 3; Table S4). Only wild pig *Sus scrofa* displayed a significant positive association with agriculture ($\hat{\beta} = 0.16, 0.07 - 0.27$, Fig. 2). Forty-one out of 45 species displayed negative response to distance to road, of which three showed strong avoidance (CRIs exclude zero). The three species that showed strong avoidance of road were gaur ($\hat{\beta} = 0.23, 0.03 - 0.46$), red panda *Ailurus fulgens* ($\hat{\beta} = 0.23, 0.01 - 0.50$) and marbled cat *Pardofelis marmorata* ($\hat{\beta} = 0.30, 0.11 - 0.52$, Fig. 3). The response to settlement was highly variable: 21 out of 45 species showed avoidance, of which only three, that is, Asian elephant ($\hat{\beta} = 0.53, 0.24 - 0.84$), tiger ($\hat{\beta} = 0.33, 0.11 - 0.55$), and crab-eating mongoose ($\hat{\beta} = 0.63, 0.27 - 1.02$) displayed strong relationship. Thirty-five species showed a positive association with forest cover, of which 17 were strongly associated. The species strongly affiliated with forest cover were Asian elephant, Asiatic brush-tailed porcupine, Assamese macaque *Macaca assamensis*, clouded leopard *Neofelis nebulosa*, common palm civet, gaur, Asiatic black bear *Ursus thibetanus*, Malayan porcupine *Hystrix brachyura*, masked palm civet, yellow-throated marten *Martes flavigula*, large Indian civet, leopard cat *Prionailurus bengalensis*, marbled cat, muntjac, sambar deer *Rusa unicolor*, spotted linsang *Prionodon pardicolor*, and wild pig (Figs. 2 and 3). Thirty-seven species negatively responded to an increase in precipitation and temperature, respectively. Further, 15 of those species displayed a strong negative association with precipitation and temperature (CRIs exclude zero), respectively (Table S5). Masked palm civet, Himalayan serow *Capricornis thar*, yellow-throated marten, muntjac, red fox *Vulpes vulpes*, red panda, spotted linsang and wild pig showed a strong negative relationship to both temperature and precipitation (Fig. S3). Most species displayed a negative response to all three RCP scenarios indicating vulnerability to future climate extremes (Fig. 5).

3.2. Community-level response

The terrestrial mammal communities exhibited an overall negative response to agriculture (Fig. 4A, decrease in mean occupancy probability with an increase in land under agriculture cultivation, overall community response, $\hat{\beta}_{community} = -0.10, -0.16 - -0.05$) and distance to road ($\hat{\beta}_{community} = 0.10, 0.04 - 0.18$, the overall community occupancy probability tend to increase farther from roads (Fig. 4B), and to a lesser extent to distance to settlement ($\hat{\beta}_{community} = 0.04; -0.08 - 0.16$, the overall community occupancy probability tend to increase farther from settlements, Fig. 4C). The weak relationship between distance to settlement and occupancy implies that there is the variability of responses of different species to human habitation. For example, Asian elephant *Elephas maximus*, tiger *Panthera tigris* and crab-eating mongoose *Herpestes urva* strongly avoided human settlement (increasing occupancy probability away from human settlement) while masked palm civet *Paguma larvata* was present near the human settlement (higher occupancy probability closer to settlement). Community-level mean occupancy probability was strongly and positively associated with forest cover ($\hat{\beta}_{community} = 0.21, 0.04 - 0.38$, Fig. 4D). Community-level mean occupancy probabilities were strongly and negatively associated with precipitation ($\hat{\beta}_{community} = -0.25, -0.40 - -0.11$) and temperature ($\hat{\beta}_{community} = -0.25, -0.43 - -0.08$) under all RCP scenarios (Fig. 5).

4. Discussion

In a fragile mountainous landscape, human land-use pressure can

interact synergistically with climate change to further aggravate the decline in biodiversity. We found that all anthropogenically induced land-use changes like agriculture, roads and settlement were associated with decreased species richness and were avoided by a large number of species (Fig. 2). The impact of climate change may not be instantly apparent, but our findings show the inherent vulnerability of mammal communities concerning the future extremes of climate as indicated by the relationship between mean community occupancy and precipitation and temperature under all RCP scenarios (Fig. 5, Fig. S3).

Congruent with our hypothesis that most of the terrestrial mammals would avoid agriculture land use, we found that mammals in the montane subtropical and temperate landscape are negatively associated with agricultural land. Although we found that the probabilities, across mammals, of using agricultural land are consistently low, we speculate that the mechanisms underlying this generalization may vary between species and probably include aspects of dispersal, colonization and the tolerance of stress (Flynn et al., 2009). The terrestrial mammals that we studied are forest-affiliated species and can be easily affected by habitat loss and degradation. For example, Asian elephant, Asiatic brush-tailed porcupine, common palm civet, crab-eating mongoose, gaur, large Indian civet, masked palm civet, small Indian civet and small Indian mongoose were clear losers. The only winner was the wild pig, an agriculture-adept species (Schley et al., 2008). However, wild pigs are notoriously known for crop raid (Wang et al., 2006; Schley et al., 2008) and thus, agriculture development may escalate the conflict (Liu et al., 2019).

The agricultural land-use change in the long term could lead to decreased habitat, isolated population and increased conflict with humans (Laurance, 1991). In addition to decreasing species richness, land-use intensification can, and generally does, reduce functional diversity of mammals (Flynn et al., 2009), which seems likely to be detrimental to ecosystem function and the provision of ecosystem services. While this impact may be subtle for some species, in aggregate the decrease in species richness associated with the increasing proportion of land under agriculture is a threat to biodiversity conservation. The shrinkage and fragmentation of natural habitat are also likely to increase the interface between humans and wildlife and thereby exacerbate conflict (Acharya et al., 2017). Further, edge effects at the ecotone of the forest-agriculture interface worsen conservation threats (Balme et al., 2010), including the transmission of zoonotic disease (Faust et al., 2018). Our findings tend to a pessimistic view of the hope that land-sharing can deliver the conservation of some large carnivores such as snow leopard (Johansson et al., 2016). Many of the mammalian species sampled by camera-trapping require largely forested habitat and maybe seriously ill-adapted to the agricultural matrix (Ceballos et al., 2005; Kinnaird et al., 2003). In this regard, we see merit in Green et al.'s (2005) argument for intensifying agricultural production on land already converted, while prioritizing the protection from the conversion of remaining forest (land-sparing).

The negative association of mammal community to roads illustrates a portent environmental cost associated with road development. Although only two species (marbled cat and gaur) displayed strong negative response, the majority tend to avoid roads (Fig. 2). A major loss of forest, inside and outside protected areas, in Bhutan in recent years is attributed to the rapid expansion of the road network (WMD, 2017). Such losses could be a malign indicator of wildlife habitat loss. Penetrating natural forest with new roads leads inevitably to a proliferation of secondary and tertiary road networks, opening avenues for deforestation, degradation and conduits for timber theft, poaching, encroachment and conversion (Laurance et al., 2014; Bennett, 2017) culminating in reduced mammal abundance (Vanthomme et al., 2013). Roads, in general, have been associated with cascading effects like overexploitation, habitat conversion, fire, farming and invasive species (Laurance et al., 2015; Ibisch et al., 2016). Although the effect was statistically weak, the human settlement had a generally negative association with mammalian diversity, an ominous association considering the growing human

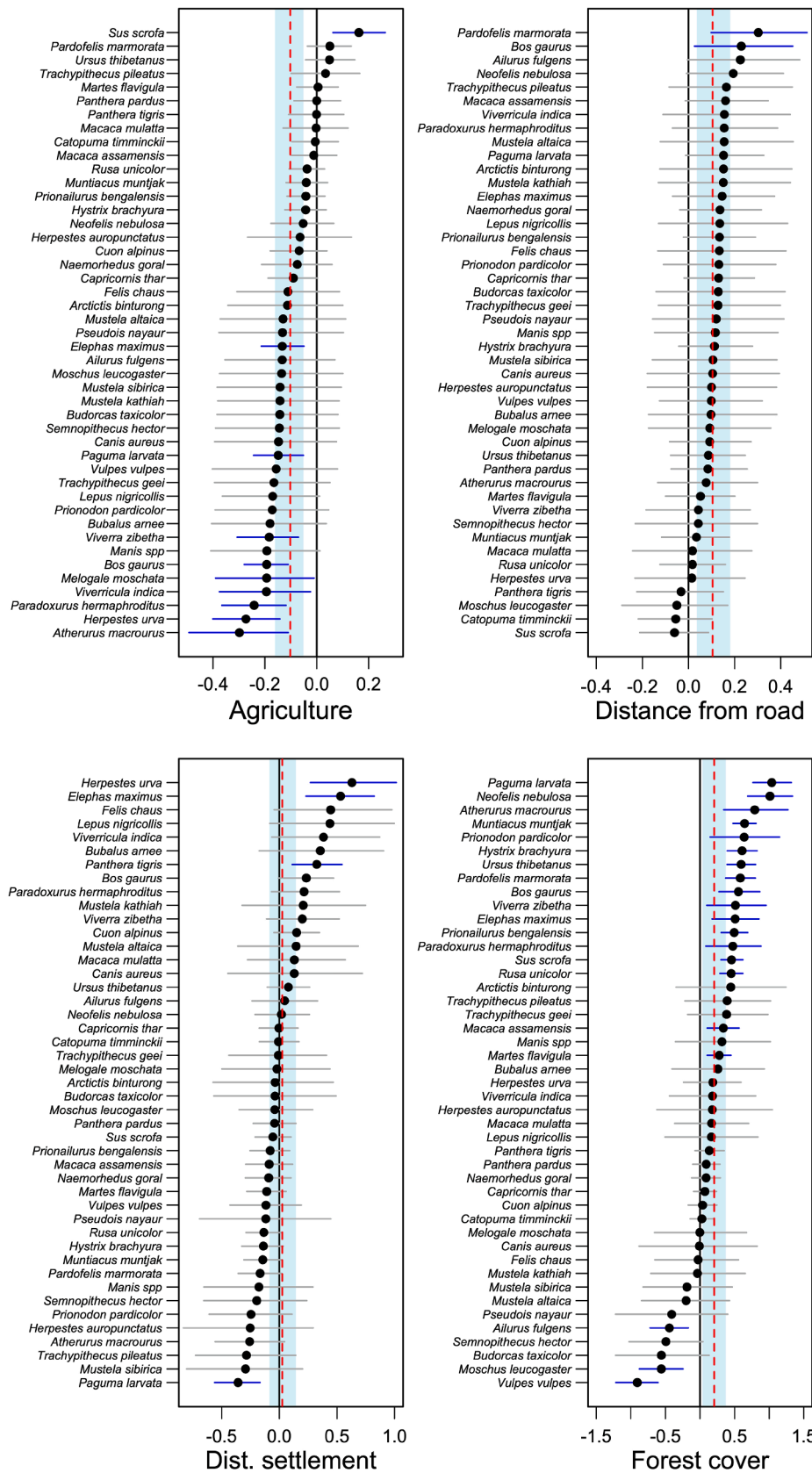


Fig. 2. The community mean and individual species' response to land-use variables (agriculture, roads, settlement and forest cover) in Bhutan. The red dashed lines indicate the posterior means and the light blue vertical bars are the 95% credible intervals. The black points are the posterior means of the individual species' response and the grey lines are 95% credible intervals. The dark blue horizontal lines represent species with a strong response (95% credible intervals non-overlapping zero).

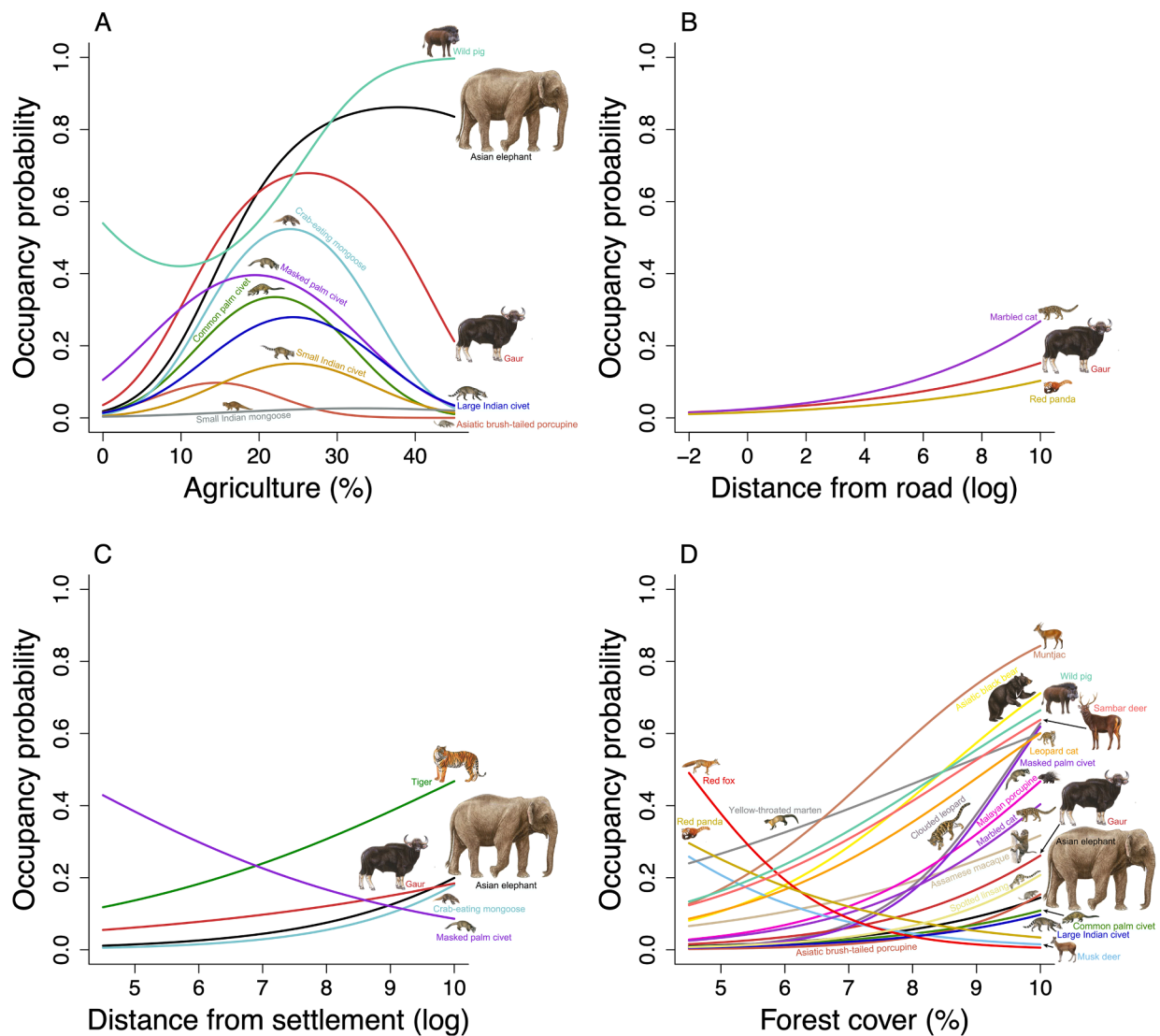


Fig. 3. Posterior occupancy probabilities of species displaying strong (95% credible intervals non-overlapping zero) association (positive/winner or negative/loser) with agriculture, distance to road, distance to settlement and forest cover in Bhutan. Image courtesy: (Francis, 2019).

footprint (Torres et al., 2016; Gaynor et al., 2018). Asian elephant, tiger and crab-eating mongoose selected sites farther from human settlement. This corroborated the findings of previous studies, in Bhutan and elsewhere, that tiger and elephant avoided dense human settlement (Rood et al., 2010; Bishnu Prasad and Pavel, 2018; Penjor et al., 2019). Most of the conflicts associated with tiger and elephant occur proximate to human settlement. Our finding suggests that proximity to human habitation could aggravate the human-wildlife conflict. One species (i.e. masked palm civet) displayed a peculiar response to human settlement-high occupancy probability near human settlement. It is unclear why masked palm civet shows affinity to human habitation, but we surmise probable high density of rodents and fruit trees may provide easy pickings for this omnivorous species (Zhou et al., 2008).

The effects of land-use change can be limited only by setting aside protected forest. Our model shows that mammal community occupancy increases with an increase in forest cover. The strongest effects on Asian elephant, Asiatic brush-tailed porcupine, tiger, clouded leopard, common palm civet, gaur, Asiatic black bear, Malayan porcupine, masked palm civet, yellow-throated marten, large Indian civet, leopard cat, marbled cat, muntjac, sambar deer, spotted linsang and wild pig highlight the importance of forest in maintaining functional assemblage and/or diversity, and ecological integrity besides provision of the basic need

such as food, shelter and cover (Cassano et al., 2014). Further, such protection delivers reduced carbon emissions (Daily and Matson, 2008; Mendenhall et al., 2014; Frishkoff et al., 2014).

A strong negative response displayed by mammal communities to temperature and precipitation for the current (Fig. S3), as well as future predictions (Fig. 5), resonates with global apprehension regarding likely impacts of climate change for biodiversity and, in this case, terrestrial mammals. Novel climates result in habitat shifts mostly toward upper latitude and elevation (Chen et al., 2011). Species with limited ability to track this change may be imperiled. For instance, the Asian elephant is a tropical species and migration to upper latitudes may not be possible due to steep topography of Bhutan. This situation is aggravated by growing human settlement and agriculture expansion across the border further constricting their range. Although habitat generalists like common leopard *Panthera pardus*, dhole *Cuon alpinus*, goral *Naemorhedus goral*, Himalayan serow and primates may adapt to habitat shifts induced by climate change, the synergistic effect of climate and land use can be far-reaching (Brodie, 2016) and needs evaluation. It underscores the need to conserve large connected landscapes, facilitating species movement (McGuire et al., 2016). No less concerning is the threat to the livelihoods of people living in these landscapes, resulting from compromised ecosystem services, decreased agriculture production through decreased

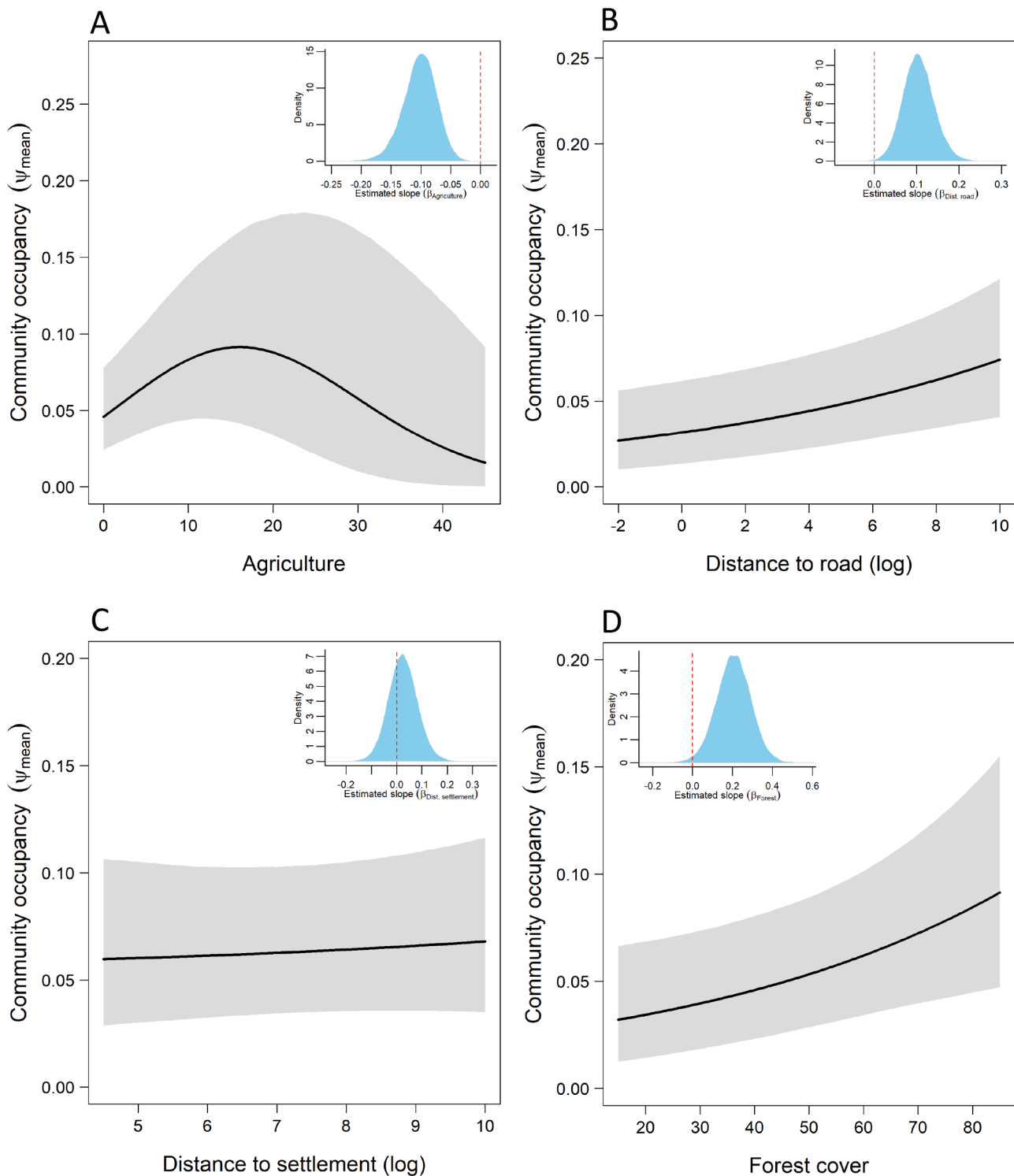


Fig. 4. The response of the mammal community to land-use variables (A, B, C, D) and their posterior probability densities of beta coefficients (insets) in Bhutan. The overall mammal assemblage shows decreasing mean occupancy probability with the increase in agriculture land (A), increases further away from the road (B), settlement (C) and in areas with a high percentage of forest cover (D). The solid black lines indicate the mean probability and grey polygons represent the 95% credible intervals.

rainfall (Newbold et al., 2016; Roxy et al., 2017). Economic development is entwined with ecosystem services, and economies dependent on natural capital such as hydropower and tourism, are particularly at risk (Williams et al., 2007).

4.1. Management implications

The most effective approach to conserving biodiversity is to minimize the impacts of extrinsic factors such as human impacts on unfragmented natural wildlands (Barlow et al., 2016). A judicious approach to land management, with changing patterns of consumption

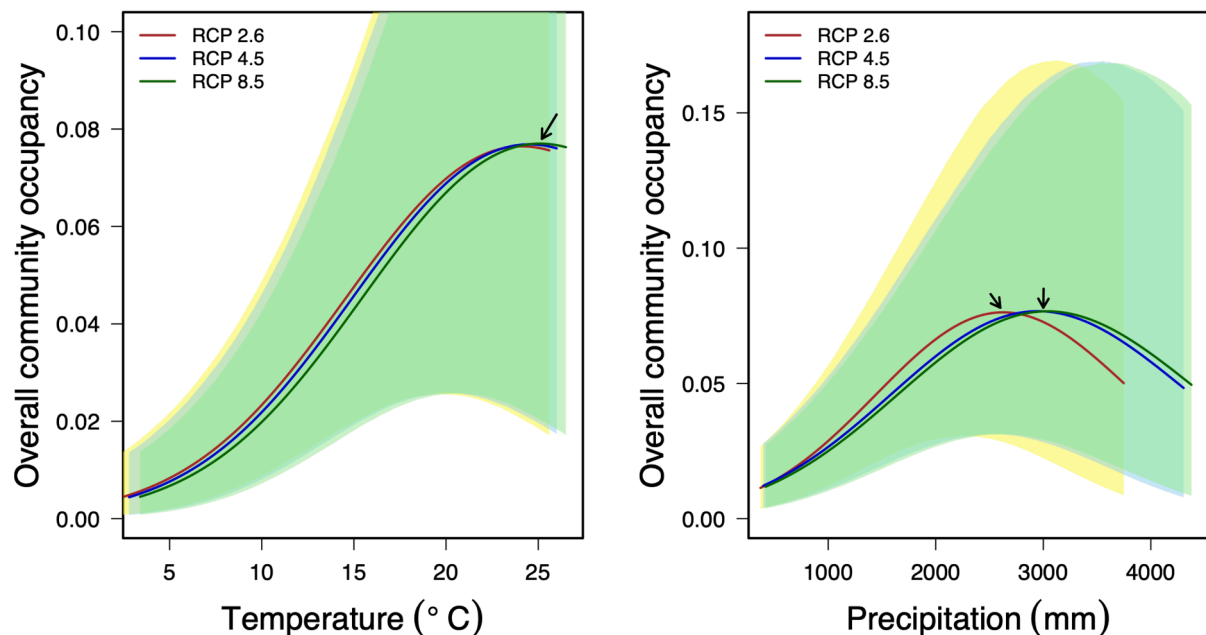


Fig. 5. Estimated effects of temperature and precipitation on terrestrial mammal community under RCP scenarios (RCP 2.6, 4.5 and 8.5) in the year 2070. The arrows indicate the threshold beyond which the overall community occupancy begins to dip. The coloured curves indicate different scenarios and the corresponding 95% credible intervals by the shaded polygon.

and increasing agriculture productivity and concomitant reduction of land conversion to agriculture, is necessary (Stehfest et al., 2019). To cope with climate change, species will require contiguous habitat and linking corridor, together with providing refuges and facilitating movement (Chen et al., 2011; Tilman et al., 2017). Further, the synergy between land use and climate is not only interactive but also correlative (Tilman et al., 2017). For example, climate change is not only caused by greenhouse gas (GHG) emission but also significantly worsened by agricultural imperatives to clear land, deploy chemical fertilizer and methane gas associated with livestock production (Balmford et al., 2009; Tilman et al., 2017). While, where it is feasible, conservation has much to gain from land-sharing (Feber et al., 2015), in many of the areas we have studied in this paper, land-sparing is more appropriate to deliver the conservation of the terrestrial vertebrates. In a landscape where the human footprint is growing, long-term species persistence requires minimizing and mitigating anthropogenically-induced land-use change (e.g. Petracca et al., 2019). Besides land-use change, inadequately regulated hunting and ineffective enforcement regarding wildlife trade are amongst burgeoning issues that threaten local, regional and global biodiversity conservation and require a scrupulous examination (Ripple et al., 2016; Benítez-López et al., 2017).

4.2. Conclusions

We provide sufficient evidence for the need of preemptive and proactive conservation measures such as increased land protection and preservation of natural habitat which can further be coupled with scaled-up anti-poaching patrols and community engagement to achieve maximum conservation benefits. Considering the likelihood that global forest cover will decline due to climate change, in Bhutan, as elsewhere, both the protection of ecologically rich areas and the restoration of damaged ecosystems are crucially important (Bastin et al., 2019; Dorji et al., 2019).

Conservation is shifting its focus from single- to multi-species considerations. Our analyses demonstrate that communities of terrestrial mammals, sampled by camera-trapping, in a fragile mountain landscape are susceptible to land-use and future climate change. We further show how individual species respond to these changes when considered under

a multi-species framework. A clear conclusion is that conservation of this component of biodiversity necessitates minimizing conversion of natural wildlands and protecting inviolate forest cover. A co-benefit of these recommendations will be safeguarding human wellbeing, insofar as this is inextricably linked to the natural ecosystem. The need to reconcile land-use management and conservation is heightened in the face of the stochasticity of climate change. Our results on mammal assemblages, and the factors affecting their diversity and abundance in Bhutan, provide insight into the drivers of community dynamics and provide policy-relevant evidence germane to the impacts of land-use and climate change on biodiversity.

CRediT authorship contribution statement

Ugyen Penjor: Conceptualization, Data curation, Methodology, Formal analysis, Validation, Writing - original draft, Writing - review & editing. **Sonam Wangdi:** Project administration, Resources. **Tandin Tandin:** Data curation. **David W. Macdonald:** Conceptualization, Funding acquisition, Resources, Supervision, Validation, Writing - review & 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.

Acknowledgements

UP thank Wildlife Conservation Research Unit (WildCRU), Robertson Foundation, WWF-EFN Russell E. Train, LMH College, Oxford and the Rhodes Trust for the funding support. DWM thank the Robertson Foundation. UP, SW and T thank the Royal Government of Bhutan (RGoB), IDA-World Bank, WWF-Bhutan and Bhutan Foundation for funding and equipment support during the survey. The authors thank the RGoB and Department of Forests and Park Services for the necessary approvals. UP deeply acknowledges Dechen Dorji, Country Representative (2013-19), WWF-Bhutan and, Mike Meredith and Ngumbang

Juat, BCSS-Malaysia for their advice and guidance. The authors thank field crew members for data collection. We thank all anonymous reviewers for providing useful comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.107085>.

References

- Acharya, K.P., Paudel, P.K., Jnawali, S.R., Neupane, P.R., Köhl, M., 2017. Can forest fragmentation and configuration work as indicators of human-wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal. *Ecol. Ind.* 80, 74–83.
- Balme, G.A., Slotow, R., Hunter, L.T.B., 2010. Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuzi Complex, South Africa. *Anim. Conserv.* 13, 315–323.
- Balmford, A., Carey, P., Kapos, V., Manica, A., Rodrigues, A.S.L., Scharlemann, J.P.W., Green, R., Capturing the Many Dimensions of Threat: Comment on Salafsky, E., et al., 2009. *Conserv. Biol.* 23, 482–487.
- Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R.M., Thomson, J. R., Ferraz, S.F.D.B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro De Castro Solar, R., Vieira, L.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., de Oliveira, R.C., Souza, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-De-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535, 144–147.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.
- Bastin, J.-F., Finegold, Y., García, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C. M., Crowther, T.W., 2019. The global tree restoration potential. *Science* 365, 76.
- Beever, E.A., O'Leary, J., Mengelt, C., West, J.M., Julius, S., Green, N., Magness, D., Petes, L., Stein, B., Nicotra, A.B., Hellmann, J.J., Robertson, A.L., Staudinger, M.D., Rosenberg, A.A., Babji, E., Brennan, J., Schuurman, G.W., Hofmann, G.E., 2016. Improving Conservation Outcomes with a New Paradigm for Understanding Species' Fundamental and Realized Adaptive Capacity. *Conservation Letters* 9, 131–137.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377.
- Benítez-López, A., Alkemade, R., Schipper, A.M., Ingram, D.J., Verweij, P.A., Eikelboom, J.A.J., Huijbregts, M.A.J., 2017. The impact of hunting on tropical mammal and bird populations. *Science* 356, 180.
- Bennett, V.J., 2017. Effects of Road Density and Pattern on the Conservation of Species and Biodiversity. *Current Landscape Ecology Reports* 2, 1–11.
- Bishnu Prasad, B., Pavel, K., 2018. Human Disturbance is the Major Determinant of the Habitat and Prey Preference of the Bengal Tiger (*Panthera tigris tigris*) in the Chitwan National Park, Nepal. *European Journal of Ecology* 4, 13–21.
- Brodie, J.F., 2016. Synergistic effects of climate change and agricultural land use on mammals. *Front. Ecol. Environ.* 14, 20–26.
- Cassano, C.R., Barlow, J., Pardini, R., 2014. Forest loss or management intensification? Identifying causes of mammal decline in cacao agroforests. *Biol. Conserv.* 169, 14–22.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* 1, e1400253.
- Ceballos, G., Ehrlich, P.R., Soberón, J., Salazar, I., Fay, J.P., 2005. Global Mammal Conservation: What Must We Manage? *Science* 309, 603.
- Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* 333, 1024.
- Chettri, N., Sharma, E., Shaky, B., Thapa, R., Bajracharya, B., Uddin, K., Choudhury, D., Oli, K.P., 2010. Biodiversity in the Eastern Himalayas: Status, trends and vulnerability to climate change. *International Centre for Integrated Mountain Development (ICIMOD)*.
- Clavero, M., García-Berthou, E., 2005. Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* 20, 110.
- Daily, G.C., Matson, P.A., 2008. Ecosystem services: From theory to implementation. *Proc. Natl. Acad. Sci.* 105, 9455.
- Daszak, P., Cunningham, A.A., Hyatt, A.D., 2000. Emerging Infectious Diseases of Wildlife—Threats to Biodiversity and Human Health. *Science* 287, 443.
- DOFPS 2011. *Forestry Development in Bhutan: Policies, Programmes and Institutions*. Department of Forests and Park Services, Ministry of Agriculture and Forest, Thimphu, Bhutan.
- DOFPS, 2015. *Counting Tigers in Bhutan: Report on the National Tiger Survey of Bhutan 2014–2015*. Department of Forests and Park Services, Ministry of Agriculture and Forest, Thimphu, Bhutan.
- Dorazio, R.M., Kéry, M., Royle, J.A., Plattner, M., 2010. Models for inference in dynamic metacommunity systems. *Ecology* 91, 2466–2475.
- 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.
- Dorji, S., Rajaratnam, R., Falconi, L., Williams, S.E., Sinha, P., Vernes, K., 2018. Identifying conservation priorities for threatened Eastern Himalayan mammals. *Conserv. Biol.* 32, 1162–1173.
- 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.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46.
- Faust, C.L., McCallum, H.L., Bloomfield, L.S.P., Gottdenker, N.L., Gillespie, T.R., Torney, C.J., Dobson, A.P., Plowright, R.K., 2018. Pathogen spillover during land conversion. *Ecol. Lett.* 21, 471–483.
- Feber, R., Johnson, P., Chamberlain, D., Firkbank, L., Fuller, R., Hart, B. & Manley, W., 2015. Does organic farming affect biodiversity?
- Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., Declerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* 12, 22–33.
- Francis, C., 2019. *Field guide to the mammals of South-east Asia*. Bloomsbury Publishing.
- Frishkoff, L.O., Karp, D.S., M'Gonigle, L.K., Mendenhall, C.D., Zook, J., Kremen, C., Hadly, E.A., Daily, G.C., 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. *Science* 345, 1343.
- Gaynor, K.M., Hohnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232.
- Gelman, A., 2006. Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Anal.* 1, 515–534.
- Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B., 2013. *Bayesian data analysis*. Chapman and Hall/CRC.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the Fate of Wild Nature. *Science* 307, 550.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* 342, 850.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Ibisch, P.L., Hoffmann, M.T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L., Dellasala, D.A., Vale, M.M., Hobson, P.R., Selva, N., 2016. A global map of roadless areas and their conservation status. *Science* 354, 1423.
- Jackson, S.T., Overpeck, J.T., 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26, 194–220.
- Johansson, Ö., Rauset, G.R., Samelius, G., McCarthy, T., Andrén, H., Tumursukh, L., Mishra, C., 2016. Land sharing is essential for snow leopard conservation. *Biol. Conserv.* 203, 1–7.
- Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. *Science* 356, 270.
- Karanth, K.U., Nichols, J.D., 2002. *Monitoring tigers and their prey: A manual for wildlife researchers, managers and conservationists in tropical Asia*. Bangalore, India, Centre for Wildlife Studies.
- Kellner, K., 2019. JagsUI: A wrapper around "rjags" to streamline "JAGS" analyses. v.1.4.9.
- Kéry, M., Royle, J., 2016. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS*, 1st Edition Academic Press & Elsevier, London, United Kingdom.
- Kiffner, C., Wenner, C., Lavoie, A., Yeh, K., Kioko, J., 2015. From savannah to farmland: effects of land-use on mammal communities in the Tarangire-Manara ecosystem, Tanzania. *Afr. J. Ecol.* 53, 156–166.
- Kinnaird, M.F., Sanderson, E.W., O'Brien, T.G., Wibisono, H.T., Woolmer, G., 2003. Deforestation Trends in a Tropical Landscape and Implications for Endangered Large Mammals. *Conserv. Biol.* 17, 245–257.
- Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. *Science* 362, eaau6020.
- Laurance, W.F., 1991. Edge effects in tropical forest fragments: Application of a model for the design of nature reserves. *Biol. Conserv.* 57, 205–219.
- Laurance, W.F., Clements, G.R., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., Balmford, A., van der Ree, R., Arrea, I.B., 2014. A global strategy for road building. *Nature* 513, 229–232.
- Laurance, W.F., Peletier-Jellema, A., Geenen, B., Koster, H., Verweij, P., van Dijk, P., Lovejoy, T.E., Schleicher, J., van Kuijk, M., 2015. Reducing the global environmental impacts of rapid infrastructure expansion. *Curr. Biol.* 25, R259–R262.
- Liu, Q., Yan, K., Lu, Y.-F., Li, M., Yan, Y.-Y., 2019. Conflict between wild boars (*Sus scrofa*) and farmers: distribution, impacts, and suggestions for management of wild boars in the Three Gorges Reservoir Area. *J. Mountain Sci.* 16, 2404–2416.
- Maxwell, S.L., Fuller, R.A., Brooks, T.M., Watson, J.E., 2016. Biodiversity: The ravages of guns, nets and bulldozers. *Nature News* 536, 143.
- McGuire, J.L., Lawler, J.J., McRae, B.H., Nuñez, T.A., Theobald, D.M., 2016. Achieving climate connectivity in a fragmented landscape. *Proc. Natl. Acad. Sci.* 113, 7195.
- 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, 213–217.
- Morand, S., 2020. Emerging diseases, livestock expansion and biodiversity loss are positively related at global scale. *Biol. Conserv.* 248, 108707.

- 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.
- Newbold, T., 2018. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B: Biological Sciences* 285, 20180792.
- Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., de Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J.P.W., Purvis, A., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* 353, 288.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., de Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhousseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G. M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50.
- NSB, 2018. Statistical Yearbook of Bhutan 2017. National Statistics Bureau, Thimphu, Bhutan.
- Ogle, K., Peltier, D., Fell, M., Guo, J., Kropp, H., Barber, J., 2019. Should we be concerned about multiple comparisons in hierarchical Bayesian models? *Methods Ecol. Evol.* 10, 553–564.
- Penjor, U., Tan, C.K.W., Wangdi, S., Macdonald, D.W., 2019. Understanding the environmental and anthropogenic correlates of tiger presence in a montane conservation landscape. *Biol. Conserv.* 238, 108196 <https://doi.org/10.1016/j.biocon.2019.108196>.
- Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for Global Biodiversity in the 21st Century. *Science* 330, 1496.
- Petracca, L.S., Funston, P.J., Henschel, P., Cohen, J.B., MacIennan, S., Frair, J.L., 2019. Modeling community occupancy from line transect data: a case study with large mammals in post-war Angola. *Anim. Conserv.* 23 (4), 420–433. <https://doi.org/10.1111/acv.12555>.
- Plummer, M., JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd international workshop on distributed statistical computing*, 2003. Vienna, Austria, 1–10.
- Powers, R.P., Jetz, W., 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Change* 9, 323–329.
- R CORE TEAM 2019. R: A Language and Environment for Statistical Computing (Version 3.6.1, R Foundation for Statistical Computing, Vienna, Austria, 2019).
- Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J., Vira, B., 2010. Biodiversity Conservation: Challenges Beyond 2010. *Science* 329, 1298.
- Ripple, W.J., Chapron, G., López-Bao, J.V., Durant, S.M., Macdonald, D.W., Lindsey, P. A., Bennett, E.L., Beschta, R.L., Bruskotter, J.T., Campos-Arceiz, A., Corlett, R.T., Darimont, C.T., Dickman, A.J., Dirzo, R., Dublin, H.T., Estes, J.A., Everatt, K.T., Galetti, M., Goswami, V.R., Hayward, M.W., Hedges, S., Hoffmann, M., Hunter, L.T. B., Kerley, G.I.H., Letnic, M., Levi, T., Maisels, F., Morrison, J.C., Nelson, M.P., Newsome, T.M., Painter, L., Pringle, R.M., Sandom, C.J., Terborgh, J., Treves, A., van Valkenburgh, B., Vucetich, J.A., Wirsing, A.J., Wallach, A.D., Wolf, C., Woodroffe, R., Young, H., Zhang, L., 2016. Saving the World's Terrestrial Megafauna. *Bioscience* 66, 807–812.
- Rood, E., Ganie, A.A., Nijman, V., 2010. Using presence-only modelling to predict Asian elephant habitat use in a tropical forest landscape: implications for conservation. *Divers. Distrib.* 16, 975–984.
- Roxy, M.K., Ghosh, S., Pathak, A., Athulya, R., Mujumdar, M., Murtugudde, R., Terray, P., Rajeevan, M., 2017. A threefold rise in widespread extreme rain events over central India. *Nat. Commun.* 8, 708.
- Schley, L., Dufrene, M., Krier, A., Frantz, A.C., 2008. Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. *Eur. J. Wildl. Res.* 54, 589.
- Sharma, E., Molden, D., Rahman, A., Khatiwada, Y. R., Zhang, L., Singh, S. P., Yao, T. & Wester, P. 2019. Introduction to the Hindu Kush Himalaya Assessment. In: WESTER, P., MISHRA, A., MUKHERJI, A. & SHRESTHA, A. B. (eds.) *The Hindu Kush Himalaya Assessment: Mountains, Climate Change, Sustainability and People*. Cham: Springer International Publishing.
- Sollmann, R., Furtado, M.M., Hofer, H., Jácomo, A.T.A., Torres, N.M., Silveira, L., 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mamm. Biol.* 77, 41–46.
- Stehfest, E., van Zeist, W.-J., Valin, H., Havlik, P., Popp, A., Kyle, P., Tabeau, A., Mason-D'Croz, D., Hasegawa, T., Bodirsky, B.L., Calvin, K., Doelman, J.C., Fujimori, S., Humpenöder, F., Lotze-Campen, H., van Meijl, H., Wiebe, K., 2019. Key determinants of global land-use projections. *Nat. Commun.* 10, 2166.
- Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. *Nature* 546, 73–81.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and Productivity in a Long-Term Grassland Experiment. *Science* 294, 843.
- Torres, A., Jaeger, J.A.G., Alonso, J.C., 2016. Assessing large-scale wildlife responses to human infrastructure development. *Proc. Natl. Acad. Sci.* 113, 8472.
- TSE-RING, K., SHARMA, E., CHETTRI, N. & SHRESTHA, A. B. 2010. Climate change vulnerability of mountain ecosystems in the Eastern Himalayas. International centre for integrated mountain development (ICIMOD).
- Urban, M.C., 2015. Accelerating extinction risk from climate change. *Science* 348, 571.
- Usubiaga-Liano, A., Mace, G.M., Ekins, P., 2019. Limits to agricultural land for retaining acceptable levels of local biodiversity. *Nat. Sustainability* 2, 491–498.
- Vanthomme, H., Kolowski, J., Korte, L., Alonso, A., 2013. Distribution of a Community of Mammals in Relation to Roads and Other Human Disturbances in Gabon, Central Africa. *Conserv. Biol.* 27, 281–291.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E. M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* 7, 12558.
- Wang, S.W., Curtis, P.D., Lassoie, J.P., 2006. Farmer Perceptions of Crop Damage by Wildlife in Jigme Singye Wangchuck National Park, Bhutan. *Wildl. Soc. Bull.* 34, 359–365.
- Warren, R., Vanderwal, J., Price, J., Welbergen, J.A., Atkinson, I., Ramirez-Villegas, J., Osborn, T.J., Jarvis, A., Shoo, L.P., Williams, S.E., Lowe, J., 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nat. Clim. Change* 3, 678–682.
- Williams, J.W., Jackson, S.T., Kutzbach, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci.* 104, 5738.
- WMD, 2017. Direct drivers of deforestation and forest degradation. Drivers of deforestation and forest degradation in Bhutan. Department of Forests and Park Services, Ministry of Agriculture and Forests, Thimphu, Bhutan.
- Zhou, Y., Zhang, J., Slade, E., Zhang, L., Palomares, F., Chen, J., Wang, X., Zhang, S., 2008. Dietary Shifts in Relation to Fruit Availability among Masked Palm Civets (*Paguma larvata*) in Central China. *J. Mammal.* 89, 435–447.
- 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.