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RESEARCH ARTICLE

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Effects of land use and climate change on functional and phylogenetic diversity of terrestrial vertebrates in a Himalayan biodiversity hotspot

Ugyen Penjor[1,2] | Samuel A. Cushman[1,3] | Żaneta M. Kaszta[1] | Sherub Sherub[4] | David W. Macdonald[1]

[1]Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Abingdon, UK

[2]Department of Forests and Park Services, Nature Conservation Division, Thimphu, Bhutan

[3]USDA, Rocky Mountain Research Station, Flagstaff, Arizona, USA

[4]Department of Forests and Park Services, Ugyen Wangchuck Institute for Conservation and Environmental Research, Bumthang, Bhutan

Correspondence
Ugyen Penjor, Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Tubney House, Abingdon Road, OX13 5QL, UK.
Email: ugyen.penjor@zoo.ox.ac.uk

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Abstract

Aim: The synergy between human land use and climate change is accelerating the global decline of biodiversity. In the fragile Himalayas, this trend has a strong ecological impact on wildlife communities, and a better understanding is needed to discern changes in the mechanisms. This study aims to understand the effects of land use and climate change on the functional (FD) and phylogenetic diversity (PD) of mammal and bird communities across the land use gradient.

Location: Eastern Himalayan biodiversity hotspot, Bhutan.

Methods: Mammal data were gathered from a camera trap survey and bird data from point counts. We used morphological and ecological traits of 45 mammal species and 336 bird species to construct functional trait space. We quantified FD and PD using standardized effect size of functional richness, functional dispersion, mean pairwise distance and mean nearest taxon distance. We used linear regression to evaluate the relationship between FD and PD and land use/climate variables.

Results: The functional space of mammals was structured by body mass (small–large) and diet (herbivore–carnivore) as one major axis, and habitat breadth (generalist-specialist) as the other, whereas bird functional space was structured by beak shape and size (large and long–small and short), body mass (small–large), foraging strata (canopy–ground) and diet (ectotherm–scavenge) along four axes. Land use (agriculture and road) negatively affected mammal FD, whereas both land use (tree cover and built-up area) and climate (temperature and precipitation) affected PD, although the effects were highly variable. Climate (temperature) had a pronounced negative effect on bird FD while land use (agriculture, built-up area and settlement) on PD.

Main conclusions: The realized functional space of the vertebrate groups can be represented by different planes on which species are clumped around a small number of functional strategies. The loss of species at the edge of functional space is non-random and could result in the loss of irreplaceable traits impacting long-term ecological and evolutionary processes. Our study demonstrates the filtering effect

of anthropogenic pressure and climate change on vertebrate FD and PD. However, the association with land use suggests the potential for ecosystem services (particularly by birds). Our findings reveal nuances of dimensions of biodiversity and provide novel insights into the structure and drivers of vertebrate assemblages in the eastern Himalayas.

KEYWORDS
anthropogenic land use, biodiversity hotspot, birds, climate, eastern Himalaya, functional diversity, mammals, phylogenetic diversity

1 | INTRODUCTION

The global expansion of agriculture and human settlement increasingly threatens natural ecosystems (Corlett, 2015; Sala et al., 2000), accelerating the risk of species extinction and corresponding loss of ecosystem services (Flynn et al., 2009). This imperilment is augmented by the rapid alteration of global climate caused largely by anthropogenic activities (Radchuk et al., 2019; Turvey & Crees, 2019). Human modification of landscapes results in altered ecological community diversity and structure (Cadotte & Tucker, 2017; Malhi et al., 2016) often leading to functional and phylogenetic homogenization (Devictor et al., 2007; Ibáñez-Álamo et al., 2017; McKinney, 2006) making an ecological community inefficient in ecosystem functioning (Clavel et al., 2011; Grab et al., 2019). The synergy between human land use and climate change increases the overall impact accelerating the global decline of biodiversity (Brodie, 2016). This is particularly amplified in a geographically dynamic and geologically unstable montane landscape such as the Himalayas and needs a better understanding to discern the changes in the mechanisms—an understanding that is a prerequisite to the effective management of ecosystems (Xu et al., 2009).

Species richness, or taxonomic diversity (TD), is a classical diversity metric that underpins the theoretical aspect of community ecology and biogeography (Colwell & Coddington, 1994). However, TD alone provides little information about the changes in phylogenetic relatedness of species and individuals within assemblages or changes in a functional trait that impacts overall ecosystem functioning (Swenson, 2013; Violle et al., 2014). For instance, several authors have reported that the overall TD remained stable despite losing functionally important species (Ernst et al., 2006; Spaak et al., 2017) indicating functional homogenization and perhaps redundancy (Aguirre-Gutiérrez et al., 2017; Petchey et al., 2007). Biodiversity is a multidimensional concept that integrates phylogenetic, functional and taxonomic diversities (de la Sancha et al., 2020; Scheiner, 2012). Phylogenetic diversity (PD) represents the evolutionary history and patterns of evolutionary relationships in a community (Faith, 1992), while functional diversity (FD) helps understand the functional uniqueness and patterns of functional trait distribution in communities (Cadotte et al., 2011; Flynn et al., 2011; Gossner et al., 2013). FD is linked with environmental conditions and biotic interactions and better predicts ecosystem functioning and services than richness (Flynn et al., 2009; Petchey et al., 2004; Swenson, 2013). PD may remain stable during community change if the newly arriving species replace the lost ones, but this does not necessarily guarantee the maintenance of ecological functions (Sobral et al., 2016). Together FD and PD provide insights into the community assembly process (Pavoine & Bonsall, 2011), ecosystem functioning (Bässler et al., 2014; Cadotte et al., 2009; Petchey et al., 2004), conservation value (Mace et al., 2003; Winter et al., 2013) and community resilience (Cadotte et al., 2012; Díaz et al., 2007; Mouillot et al., 2013). Thus, maximizing both evolutionary value and ecosystem function (Bregman et al., 2016; Ribeiro et al., 2016) is essential to maintaining community resilience to environmental perturbation (Socolar et al., 2016).

Many community studies have incorporated all three metrics of biodiversity, but very few have accounted for variation in detection probability while assessing them (Cannon et al., 2019; Edwards et al., 2015; Jarzyna & Jetz, 2016, 2017; Palacio et al., 2020; Si et al., 2018). It has been shown that ignoring detection probability can lead to an underestimation of these metrics (Jarzyna & Jetz, 2016; Montaño-Centellas et al., 2021; Si et al., 2018) or bias in their interpretation (Palacio et al., 2020). This happens because nuances in functional traits or phylogenetic characteristics of species lead to variation in detection (Garrard et al., 2013; Sólymos et al., 2018), which might influence predictions of functionally or phylogenetically distinct species across assemblages. This could dramatically affect FD or PD estimates if the missed species disproportionately contribute to overall FD or PD (Si et al., 2018).

Mammals and birds are well-known taxonomic groups with the easily available global trait and phylogeny data (Jetz et al., 2012; Upham et al., 2019; Wilman et al., 2014), are good indicators of wider biodiversity response to environmental change (Dirzo et al., 2014; Edwards et al., 2014) and play critical roles in ecosystem functioning (Bogoni et al., 2020; Sekercioglu, 2006). Mammals and birds are an integral part of ecological networks. When we envision a complex ecological network of interacting species and the functional and phylogenetic integrity of this intricate system, it reminds us of the "tangled bank" of Darwin (1909). This complex system, however, is under increasing stress from human modification.

Here, we studied the effects of land use and climate variables on the FD and PD of mammal and bird communities across the land use gradient in Bhutan, a global biodiversity hotspot in the eastern Himalayas (Myers et al., 2000). Specifically, we investigate the functional composition of the bird and mammal communities, the effects

of land use and climate change on FD and PD and examine whether constraints imposed by anthropogenic land use and climate result in the filtering of specific traits and lineages. The influence of biodiversity on ecosystem processes is underpinned by underlying trait distributions. A decline in FD could indicate the loss of functionally distinct species that are not readily replaced by the remaining species. We hypothesize that anthropogenic disturbances may act as filters for reducing FD and PD (Hanz et al., 2019). We also hypothesize that communities in human-dominated landscapes will be comprised of closely related species (clustering), those able to tolerate perturbations. If species sensitive to anthropogenic pressures and extreme climates were negatively impacted, this would affect the major gradient across the functional trait space and hence reduce the overall diversity (Flynn et al., 2009). This study thus enhances our understanding of the FD and PD of terrestrial vertebrates and provides new insights into the effects of anthropogenic land use and climate change in a Himalayan biodiversity hotspot.

2 | METHODS

2.1 | Data

2.1.1 | Species data

We used mammal data from the camera trapping survey conducted in 2014–15 and bird data from the point count survey in 2019–20. The camera trap survey comprised 1129 paired, unbaited, passive infrared camera traps placed across the country each within a 5 km×5 km grid at an average distance of 2.9 km (1.2 km SD, Figure S1). Trap placement followed existing animal trails, mineral licks and water holes but in the context of terrain accessibility. Details of the camera trap survey are described elsewhere (Penjor et al., 2020). The bird point count transect surveys were conducted in three geographically representative regions across Bhutan between 150 m and 1900 m elevation (Figure S2). The transects were laid along the highway between October 2019 and March 2020. Point counts were laid along the transect at 300-m interval surveying 679-point counts in total. At each sample location, a 15-min early morning (06:00–10:00 h) observation was made to record all birds (seen only) within a 50 m fixed radius of the sample location. For analysis, migrants and vagrants were excluded.

2.1.2 | Environmental data

Based on a priori hypotheses, we selected variables that have been shown to influence mammals and birds at the community level in past studies (Penjor et al., 2020, 2021): agriculture, settlement, built-up area, road, forest cover, elevation, temperature and precipitation. We rasterized vector layers of agriculture, settlement and built-up (obtained from the Department of Forests and Park Services, Bhutan). Agriculture, settlement, built-up area and forest cover were quantified as the percentage of land (%) within a fixed radius (see below), and road as the distance to the nearest road. We used global forest change (GFC) tree cover data for the year 2015 for mammals and 2019 for birds (Hansen et al., 2013). Likewise, anthropogenic variables are consistently updated by the Department of Forests and Park Services (Bhutan), and we used the data that correspond to the sampling years. Land cover changes in Bhutan are minimal (or rather insignificant to be captured by satellite, for example, tree cover changes at 30 m resolution), and therefore, the use of higher-resolution imagery (<5 m) is problematic as these tend to be expensive and inaccessible given for many time frames (Boyle et al., 2014; de la Sancha et al., 2017), as is the case for this study. We used Shuttle Radar Topography Mission's (SRTM) digital elevation model (DEM; Jarvis et al., 2008) to extract the elevation data. We used climate data from CHELSA (Karger et al., 2017) and extracted mean values of all the variables at each study site (within a 500 m radius for the camera trap and 100 m for point count location). As the bioclimatic variables were highly correlated, we used principal component analysis (PCA) to reduce the number of multicollinear predictor variables (Figures S16 and S17). We retained the first two principal components (or PCs), which accounted for more than 80% of the variance (87.8% for mammals and 92.6% for birds). PC1 of mammals captured an increase in temperature seasonality and temperature annual range ($Temp_{mammal}$), and PC2 mainly captured precipitation of the coldest quarter and driest month (hereafter precipitation). Likewise, PC1 for birds captured temperature seasonality and isothermality and PC2 captured temperature-related variables (maximum temperature of the warmest month and mean temperature of the wettest quarter; $Temp_{bird}$) (Figures S4 and S5).

2.1.3 | Trait data

We compiled trait data that describe the functional morphospace and ecological strategies of mammals and birds (Cooke et al., 2019). For mammals, we used seven functional traits: body mass, litter size, habitat breadth (number of IUCN habitats listed as suitable), generation length, snout-vent length and diet (plant and animal; see below). For birds, we used 11 traits: body mass, beak length at culmen, beak depth, hand-wing index (a measure of wind shape), foraging strata (canopy, understorey and ground) and diet (ectotherm diet, invertebrates, nectar, and scavenge). We caution that the use of two different trait datasets for mammals and birds does not allow for the direct comparison of functional diversity. Instead, we infer the functional diversity for each group separately and avoid direct comparison. We gathered trait data from published sources (Cooke et al., 2019; Myhrvold et al., 2015; Sheard et al., 2020; Tobias et al., 2022; Wilman et al., 2014). To select diet, foraging strata and beak, we performed principal component analyses. PC1 of mammal PCA captured diet gradient from herbivores (plant) to carnivores, and PC2 captured general diet (Figure S6). The first four PCs explained ~60% of the total diet variance in birds. PC1 captured the invertebrate materials, PC2 captured mammal/bird materials, PC3

captured plant/seed and PC4 captured scavengers (Figure S7). For beak PCA, the first two PCs explained ~100% of the variance with beak length at culmen and beak depth emerging as important traits (Figure S9). PC1 of foraging strata PCA captured canopy and ground strata and the second captured understorey (Figure S8). Trait data were transformed: $\log_{10}$ transformation of body mass, and all other traits were scaled and centred to have 0 mean and unit variance (Cooke et al., 2019). As trait data were available for all species, no trait imputation was required.

2.1.4 | Phylogenetic data

We obtained global phylogenetic trees of mammals and birds from published sources. For birds, we averaged 100 trees based on the Hackett backbone (Hackett et al., 2008) downloaded from http://birdtree.org (Jetz et al., 2012). Similarly, for mammals, we downloaded 100 trees built based on the "backbone-and-patch" approach (Upham et al., 2019) from http://vertlife.org, averaged and pruned them to our local list for further analyses.

2.2 | Estimation of functional trait space, functional diversity and phylogenetic diversity

We built trait space from transformed and standardized traits using PCA. Across this space, the ordination of species is represented in two- (mammals) or four dimensions (birds) by integrating all final trait dimensions (Cooke et al., 2019). We estimated multivariate kernel density and calculated probability contours of trait space at different thresholds (0.50, 0.95 and 0.99) using unconstrained bandwidth selectors to smoothen the kernel (Cooke et al., 2019).

We implemented multispecies community occupancy models (MSOMs) to estimate species richness and community parameters (Dorazio & Royle, 2005). MSOMs model the latent occurrence of species while accounting for detection probability (Figure S3). The sharing of information across species strengthens the precision and accuracy of parameter estimates. This is particularly useful because sharing information allows us to retain rarely detected species for richness summaries (Iknayan et al., 2014). Full details of the modelling framework are presented elsewhere (Penjor et al., 2021).

We used the detection-corrected occurrence matrix (averaged over 2700 matrices) to estimate FD and PD. The diversity facets derived from this matrix fully account for imperfect detection (Jarzyna & Jetz, 2016). To estimate FD, we used detection-corrected site × species and species × trait matrices. We implemented Hill number correction to FD estimates by assigning relative importance to species weights through a threshold on functional distances to identify the functionally indistinct set of species (Chao et al., 2019). We estimated distance-based functional richness (FRic) and dispersion (FDis; Laliberté & Legendre, 2010; Villéger et al., 2008). FRic measures the volume of minimum convex hull enclosing all taxa and represents the maximum range of traits in a community, but this metric is sensitive to outliers (Legras et al., 2018). FDis is the average distance of each species to the centroid of trait space and describes the spread of species in functional space (Laliberté & Legendre, 2010; Villéger et al., 2008). The PD and its associated metrics were calculated using the phylogenetic tree obtained from open sources as described in the "Data" section. PD was calculated as the sum of branch lengths of the phylogenetic tree linking the species in a community at each site and represents the sum of the evolutionary history of the sampled community (Faith, 1992). FD and PD metrics are shown to correlate with species richness (Cadotte et al., 2019; Swenson, 2013). We accounted for the influence of species richness on these metrics by employing the "tip-shuffling" null model approach by comparing the observed community with 1000 null communities generated from the pool containing all species in the study. We then calculated abundance-weighted standardized effect sizes (ses) as, $\text{ses} = \frac{\mu_{\text{observed}} - \mu_{\text{expected}}}{\sigma_{\text{expected}}}$ using an independent swap algorithm (Gotelli, 2000). We computed (i) deviance of FRic and FDis as the proportionate difference between observed and null expectation (sesFRic and sesFDis), positive values suggesting overdispersion and clustering for negative, (ii) mean pairwise distance (MPD) as the average pairwise distance between species in a community (Webb et al., 2002), and mean nearest taxon distance (MNTD) as the mean distance between a species and the closest relative for PD. Positive values of sesMPD indicate functional or phylogenetic overdispersion while negative values indicate clustering relative to null communities. Positive values of sesMNTD suggest that distantly related species co-occur in the community while negative values suggest the coexistence of close relatives. Analyses were performed in R (R Core Team, 2021) using packages FD (Laliberté et al., 2014), vegan (Oksanen et al., 2007), ks (Duong, 2007), picante (Kembel et al., 2010) and mFD (Magneville et al., 2022).

We regressed the biodiversity facets (sesFRic, sesFDis, sesMPD and sesMNTD) against land use (forest cover, agriculture, built-up area and settlement) and climate (see Environmental data section for a selection of climate variables) variables using a linear mixed-effect model. We checked for spatial autocorrelation for each diversity metric using Moran's *I* test (Figures S10 and S11). For models displaying spatial autocorrelation, we treated sampling locations as random effects (e.g. for birds). We performed the regression in the Bayesian framework to derive posterior central tendency and spread (credible intervals to measure uncertainty) of the parameters using JAGS (Plummer, 2003) in R using package jagsUI (Kellner, 2019). For all measures, we assessed the significance of the regression coefficient estimates with 95% Bayesian credible intervals and model fit using Bayesian R^2 (Gelman et al., 2019).

3 | RESULTS

3.1 | Functional trait space

The first two principal components (PC) explained about 71% of the total trait variation for mammals (Figures 1a and S12). The primary axis of differentiation, PC1, integrates body mass (loading = 0.45),

snout-to-tail length (0.40) and generation length (0.40) and trade-off between herbivores (plant diet loading = 0.43), carnivores (−0.36) and litter size (−0.39). Species with high PC1 values are generally characterized by large body mass, longer body length (snout to tail length) and slow life history (long generation length) but have small litter size and are generally represented by herbivores such as elephant (*Elephas maximus*), gaur (*Bos gaurus*), water buffalo (*Bubalus arnee*), sambar deer (*Rusa unicolor*), and serow (*Capricornis thar*). On the contrary, species with low PC1 values are represented by small body mass, shorter body length and faster life history and with carnivorous diet (e.g. spotted linsang (*Prionodon pardicolor*), Chinese ferret badger (*Melogale moshata*), pangolin (*Manis* spp.), weasel (*Mustela* spp.), dhole (*Cuon alpinus*), red fox (*Vulpes vulpes*) and jackal (*Canis aureus*)). PC2 characterizes habitat generalists (habitat breadth loading = 0.57), for example tiger (*Panthera tigris*), leopard (*P. pardus*) and wild pig (*Sus scrofa*) at high PC2 values, habitat specialists at low PC2 values, for example golden langur (*Trachypithecus geei*), Asiatic brush-tailed porcupine (*Atherurus macrourus*), Indian hare (*Lepus nigricollis*) and musk deer (*Moschus* spp.).

In the case of birds, 67% of the variation in traits is captured by four PCs (Figures 1b and S13). Trait variation was centred on a dense core with species having extreme morphologies scattered at the periphery (e.g. hornbills and vultures). The first axis (PC1; 29% of trait variance) describes beak shape (length at culmen and depth; loadings = 0.47) and body mass (e.g. hornbills and herons; loadings = 0.45) primarily frugivores while PC2 (15% of trait variance) separates canopy feeders (e.g. leafbirds, flowerpeckers and orioles; loadings = 0.67) from ground feeders (e.g. pheasants, thrushes and doves; loadings = −0.55) along with trophic niche. PC3 (12% of trait variance) describes understorey (babblers and laughingthrushes; loadings = 0.56) species with a diet composed of reptiles and amphibians (ectotherms, e.g. shrikes, egrets and herons; loadings = −0.38) and the PC4 (11% of trait variance) describes scavengers (e.g. vultures; loadings = −0.43) and species with larger hand-wing index (HWI; loadings = −0.43) that are linked to migration and dispersal ability (e.g. cuckoos and swifts).

The hotspots (i.e. the smallest portion of functional space including 50% of the species (Díaz et al., 2016)) were different for mammals and birds (see also Figures S21 and S22). The mammal had a single hotspot with a bimodal distribution of species distinguishing carnivores with large litter sizes (dholes, foxes and jackals) from herbivores with small litter sizes (muntjac, goral and musk deer). In the case of birds, variation in traits is distributed such that most species occupy a dense core in the centre of trait space, with more extreme forms found towards the edges. Certain groups of species occupy distinct areas of trait space only apparent on PC axes that themselves account for low total variation, such as vultures on PC4.

3.2 | Relationship between biodiversity facets and environmental variables

Richness-corrected FRic (sesFRic) of mammals was influenced by elevation, distance to road, precipitation and temperature seasonality (R^2 = .21; Figures 2a–e, S14 and S17) and sesFDis by elevation, distance to road, precipitation and agriculture (R^2 = .012). Elevation had

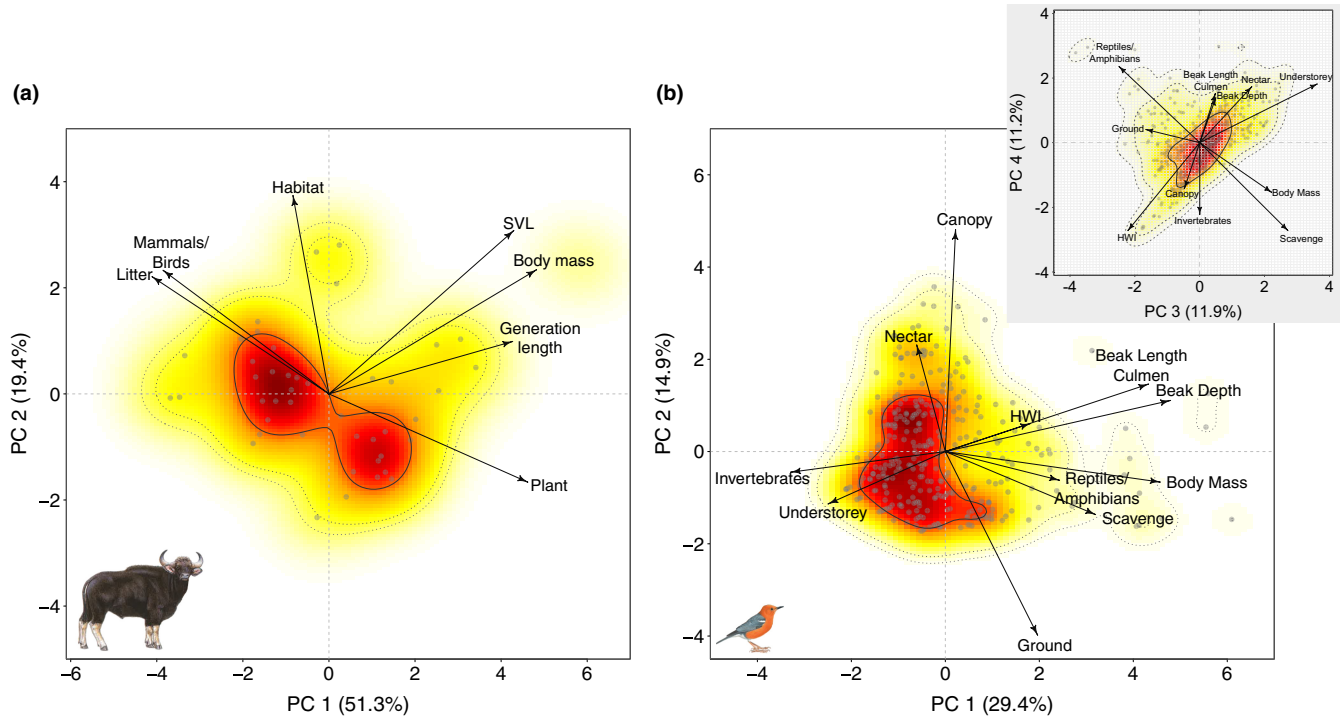

FIGURE 1 Principal component dimensions (PC) and trait loadings are based on all nine traits for mammals (a) and 11 traits for birds (b). Colours indicate the density of species (increasing from yellow to red) on each two-dimensional plane (mammal = 45 species and bird = 336 species).

an opposite effect on FD (sesFRic decreased and sesFDis increased although both showed a non-linear relationship), whereas both increased farther away from the road and with increasing precipitation (Figure 2). The sesFRic decreased with temperature seasonality while sesFDis decreased with agriculture. Similarly, for birds, sesFRic and sesFDis were influenced by three variables: settlement density, temperature and forest cover. The sesFRic increased with settlement density but decreased with temperature and sesFDis decreased with forest cover (Figure 2f–h).

Forest cover had opposing effects on mammals and birds: positive on both sesMPD and sesMNTD for mammals (Figure 3d) and negative for both sesMPD and sesMNTD for birds (Figures 3j and S18). Likewise, temperature-related variables had opposing effects: negative effect of temperature seasonality on mammals (Figure 3e) and positive effect of temperature of the warmest month on birds (Figure 3k). Mammal sesMPD was positively associated with agriculture (Figure 3a) and negatively with precipitation ($R^2 = .56$; Figures 3f and S14a). sesMNTD of mammals was negatively associated with built-up area (Figure 3b) but positively with the settlement ($R^2 = .37$, Figure 3c). On the contrary, bird sesMPD was negatively associated with agriculture (Figure 3g), built-up area (Figure 3h), settlement (Figure 3i) and precipitation ($R^2 = .31$, Figure 3l). Bird sesMNTD was negatively associated with agriculture and settlement ($R^2 = .28$; Figures 3g,l and S14b).

The overall FD and PD of both groups were lower than expected by chance indicating that communities were functionally and phylogenetically clustered (Figures 4, S19 and S20). There were, however, subtle differences between the two groups: birds had higher richness but lower dispersion than mammals. Likewise, birds were more phylogenetically clustered (lower sesMPD and sesMNTD) than mammals, but mammals highly showed variable PD (bimodal distribution). We present additional results on community occupancy and detectability in the supplementary materials (Supplementary Results).

4 | DISCUSSION

Using two groups of vertebrates, we show that realized functional trait spaces are constrained to a single plane in which species are clumped around a few strategies (Carmona et al., 2021). The diversity of mammal functional traits in the eastern Himalayas can be represented along a few axes of trait variation representing body mass, diet and habitat breadth, whereas birds can be represented along four dimensions representing beak shape and size, foraging strata, diet and HWI. The nuances of FD and PD to land use and climate variables demonstrate the complex ways in which the synergy between anthropogenic disturbance and climate change can affect different dimensions of biodiversity.

Since the Pleistocene, many large animal species have gone extinct and the rate of extinction of larger species has been higher than that of smaller species (Dirzo et al., 2014; Fordham et al., 2020). This trend is continuing, exacerbated by the burgeoning human population and consumption patterns disfavouring large-bodied species and species with longer generation lengths (Cardillo et al., 2005; Dirzo et al., 2014). However, smaller species are similarly imperilled because they tend to have low dispersal abilities making them vulnerable to extinction because of anthropogenic land use and climate change (Carmona et al., 2021). Our findings show that species with large body mass, longer generation length, and long gestation period (those occupying the boundaries of functional space, e.g. elephants, water buffalo) are much more vulnerable than smaller short-lived (shorter generation length) species with larger litter size (those occupying centre of functional space) to human disturbance (Carmona et al., 2021; Enquist et al., 2020). The loss of these vulnerable species (particularly the largest ones) could potentially create a lacuna in trait space due to the loss of unique ecological functions (Estes et al., 2011) and ecosystem services that are readily not replicated by smaller-bodied fauna (Enquist et al., 2020) and can impact ecosystem structure, function and biogeochemical cycles (Cooke et al., 2019; Rule et al., 2012).

There were two (albeit indistinct) functional trait hotspots for mammals (Figure 1); the first aligned along with species with carnivorous diet and large litter size (e.g. fox, dhole and weasel) and the second along with herbivorous diet, small litter size and habitat specialist (golden langur and musk deer). The first PC of mammal trait space, in essence, reflects trophic interactions along body mass gradient which consequently affect nutrient cycling (Ripple et al., 2017). Multiple ecological functions, for example pollination, predation, herbivory and seed dispersal, relate to body mass (Cooke et al., 2019). PC2 that explained variation in habitat breadth reflects responses of species and/or adaptability to change and/or modification of their surrounding environment (Cooke et al., 2019). A species with broad habitat breadth (generalist) has greater flexibility to environmental change and thus can shift its resource use or distribution with a greater ability to cope and persist (e.g. wild boar and common leopard) than those with narrow breadth (Cooke et al., 2019). Birds had a single hotspot that captured beak size, foraging strata, diet and hand-wing index along four axes representing trait modalities related to food acquisition, functional feeding groups, foraging techniques and dispersal ability. These hotspots captured most of the families, demonstrating a relatively high degree of convergence in ecological strategies (Cox et al., 2021). Some species, however, break the rule of conventional trait associations and therefore occupy remote corners of trait space with relatively fewer species than expected by chance (e.g. elephants and vultures). Elephants are the most distinct species upholding critical functions, such as grassland regeneration, nutrient cycling and habitat complexity. Likewise, the loss of species with a specific functional role (e.g. scavenging by vultures) could gravely impact ecosystem processes (e.g. carrion removal and control of the spread of disease).

The decrease in mammal FRic with elevation indicates that the functional trait space decreases at higher elevations perhaps also decreasing the range of traits represented in a community (Legras et al., 2018) probably due to the filtering effect of cold temperature allowing only closely related species that can tolerate extremes

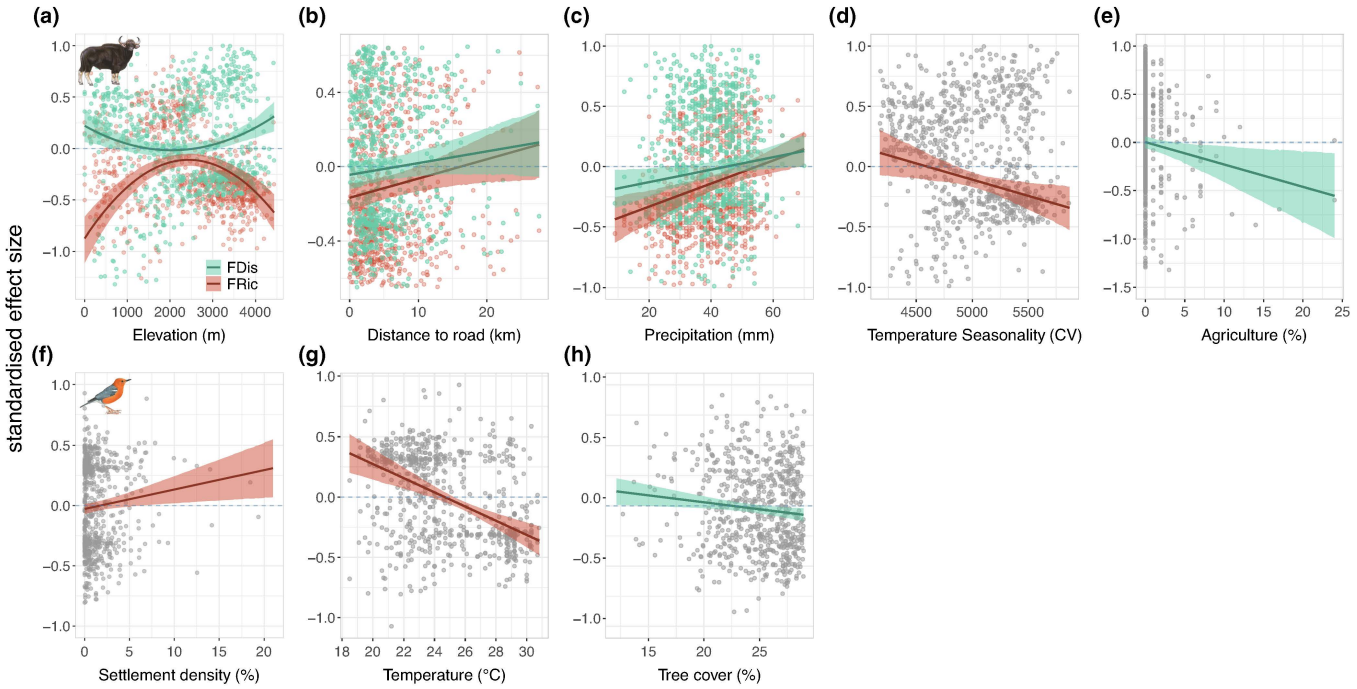

FIGURE 2 Relationship between FD (represented by FRic and FDis) and land use and climate variables for mammals (a–e) and birds (f–h). Predictions were made from the top model. Solid lines indicate the mean, and polygons represent 95% credible intervals.

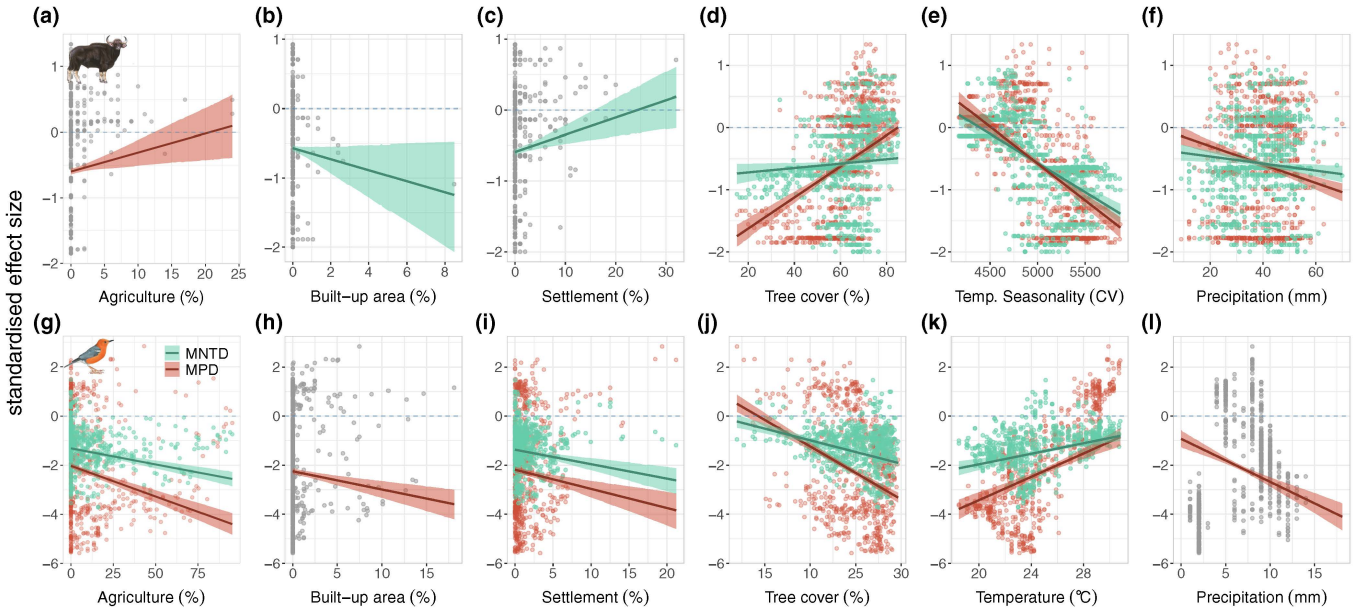

FIGURE 3 Relationship between PD (represented by MPD and MNTD) and land use and climate variables for mammals (a–f) and birds (g–l). Predictions were made from the top model. Solid lines indicate the mean, and polygons represent 95% credible intervals.

to cluster in trait space (Hughes et al., 2021; Voskamp et al., 2017). Large-bodied ungulates are rare at high elevation habitats (e.g. elephant, Asiatic water buffalo and gaur), and hence, the services provided by them are absent or reduced. The negative relationship between FRic and temperature seasonality suggests that temperature significantly influences seasonal variation in FD and thus may be a limiting factor for forage or habitat availability for mammals (via an effect on primary production) and/or that seasonal temperature may be a direct or an indirect limiting variable for reproduction (i.e. via energetic constraints on thermoregulation) (McLean & Guralnick, 2021). On the contrary, precipitation of the coldest quarter positively influenced FRic and FDis. Given that precipitation drives primary productivity (and influences habitat complexity) in most plant ecosystems, food availability is critical in maintaining a

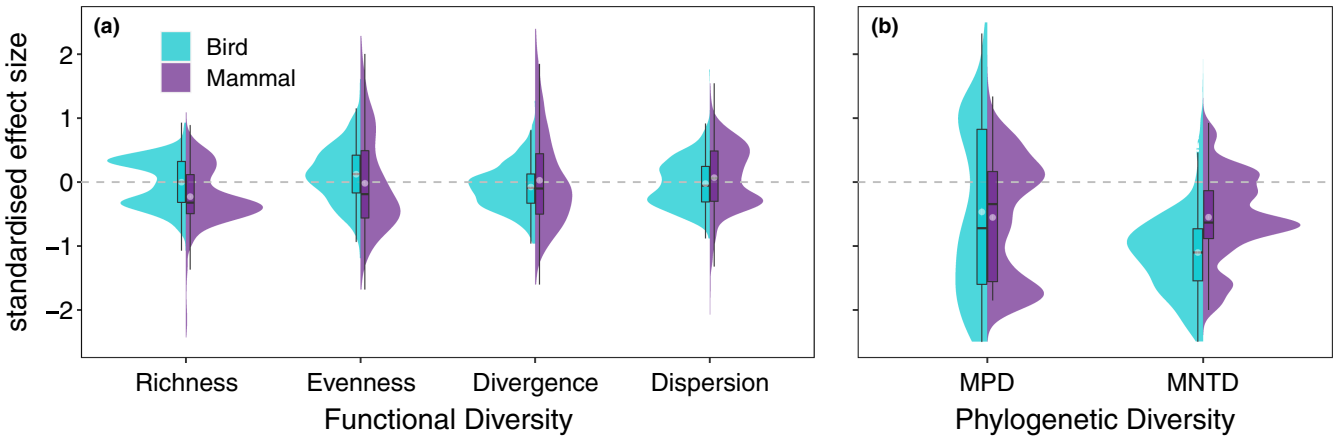

FIGURE 4 Overall FD and PD (corrected for species richness) of mammals and birds. Boxplots complement density plots with means indicated by white dots and medians by horizontal bars.

positive energy balance to support mammal reproduction (Bronson & Perrigo, 1987), suggesting areas with higher precipitation support higher functional trait diversity. During the cold and dry season, it is likely that species in the Himalayas face greater stress due to water deficiency because the preponderance of rainfall occurs mainly during the monsoon (between July and September). In general, our findings concur with previous studies that energy and water (i.e. temperature seasonality and precipitation) play key roles in explaining the richness of species and functional traits (Panda et al., 2017; Ruggiero & Hawkins, 2008). Although the effects of precipitation and temperature on FD were nuanced, their synergy underpins the mechanism by which the contemporary climate affects the overall FD.

Similarly, the decrease in sesFRic with increasing maximum temperature of the warmest month suggests that during the warm season, temperature rise might impose additional stress on the energetics in endotherms. The increasing temperature and heatwaves likely affect the basal metabolic rates of birds reducing their overall efficiency in foraging, reproduction, and dispersal (Sekercioglu, 2012).

Interestingly, sesFDis decreased with forest cover suggesting potential trait homogeneity in bird assemblages due to change in forest cover (Cisneros et al., 2015). Forest interiors may harbour foraging and habitat specialists thus increasing functional redundancy due to similarity in traits (e.g. trait conservatism). On the contrary, forest edges may offer higher accessibility and visibility and favour assemblages (but mostly generalists) with divergent foraging traits thus increasing trait diversity (Penjor et al., 2021). Furthermore, a change in canopy structure could affect canopy specialists that occupy the boundary of functional trait space.

The Himalayas, in general, face greater pressure from anthropogenic disturbance. Mammal FRic and FDis increased further away from the road, whereas FDis decreased with agriculture suggesting possible niche packing with redundant traits in agricultural landscapes (Hughes et al., 2021). On the contrary, bird FRic increased at a higher settlement density. It suggests that mammals are intolerant of human disturbance, whereas some level of human disturbance may be tolerated by birds supporting the intermediate disturbance hypothesis. Besides habitat loss and fragmentation, a decline in primary food sources (plants, insects and smaller organisms' abundance) as a result of land use intensification and climate change may contribute to the decline of the bird and mammal populations (Raven & Wagner, 2021). The risk of global climate change is more likely to be pronounced in local communities because functional redundancy is low in local communities with fewer species and extinction of a species (particularly those at the boundary of trait space) is likely to alter functioning with effects amplified across the trophic (Donohue et al., 2017).

The effect of agriculture, settlement, forest cover and temperature was nuanced for mammal and bird PD. Although the anthropogenic variables (e.g. agriculture, built-up area and settlement) had negative effects on the PD of birds resulting in clustering and suggesting that species assemblages are non-random relative to land use, and an altered landscape could potentially compromise the evolutionary uniqueness. Homogenization of the physical environment across the Himalayan landscape may be creating filters allowing only some lineages to persist thus increasing phylogenetic homogenization (decreasing MPD and MNTD in birds) (McKinney, 2006; Sol et al., 2017). This has implications for the health of community structure because closely related lineages are vulnerable to pathogens and diseases which, in turn, increases the risk of disease emergence in human populations (Dharmarajan et al., 2021).

The positive relationship between mammal PD and human land use suggests that species attracted to agriculture and human settlement are distantly related (e.g. muntjac *Muntiacus muntjak* and wild boar) but not necessarily indicative of phylogenetic overdispersion. One possible explanation for higher PD may be due to the spillover of species from the nearby forest abutting settlement (i.e. edge effect). Another possibility is that the so-called "winners" in anthropogenic environments may be disproportionately represented in a few distantly related clades (e.g. wild boar, the only member of the Suidae family in this study) often lacking close relatives in the same community thus partially explaining phylogenetic overdispersion. Some species perceive human environments as ecological

opportunities (Cox & Gaston, 2018), often dominating communities close to the settlement despite being rare in the surrounding natural environments (Møller et al., 2015) but still contributing to the regional PD. In our study, Assamese macaque (*Macaca assammensis*), Malayan porcupine (*Hystrix brachyura*) and muntjac, all distantly related, were positively associated with agriculture and settlement although infrequently detected at sites in deeper forests concurring with our field observations.

The increase in the phylogenetic distance between an individual and its neighbour (sesMNTD) of mammals indicates that habitats in forests are different from those in the human settlement in species composition and abundance (Matos et al., 2017), making communities more likely to have evolved from lineages at more terminal parts of the phylogenetic tree. On the contrary, decreasing sesMNTD for bird communities indicates the existence of close relatives between sampled communities and those forest habitat specialists are clustered within the phylogeny (Sol et al., 2017). Overall, our findings provide evidence of the emergence of novel communities with different phylogenetic and functional properties due to ongoing land modification (Lurgi et al., 2012).

Mammals showed phylogenetic clustering with temperature and precipitation suggesting that extreme heat and precipitation may act as abiotic filters (Cunningham et al., 2021; Harrison et al., 2020). The increasing sesMPD and sesMNTD with temperature in birds indicates that only closely related species, probably those tolerant of a warmer climate, occur together. However, this contrasts with the FRic that showed a decreasing trend with temperature suggesting that a higher PD does not correlate with FD and that a warmer climate may not necessarily harbour diverse functional traits.

The cross-taxon comparison is highly susceptible to differences in trait resolution (Kohli & Jarzyna, 2021). For example, a recent study shows that coarse categorical traits (e.g. trophic foraging niche and foraging strata) produce unreliable non-random functional structures (Kohli & Jarzyna, 2021). Our analyses were based on both coarse (categorical and fuzzy) and fine resolution (continuous) traits, and we acknowledge that coarse traits may diminish the ability to predict changes in biodiversity (Kohli & Jarzyna, 2021). Furthermore, to quantify the FD patterns, we used different functional characters and the number of traits for the two groups. This resulted in PCAs producing a different number of PCs (for example, the variation in birds was explained by four PCs compared with two in mammals). Consequently, this makes the functional trait space between the two groups incomparable. Future studies should consider trait resolution biases and where possible use standard traits when comparing two different organism groups.

5 | CONCLUSIONS

Our findings have broad implications for biodiversity conservation across human land use gradients. We show that the projected loss of species on the edge of functional space due to anthropogenic pressures is non-random and could lead to the loss of irreplaceable functional traits and perhaps services associated with them. And could impact the long-term sustainability of ecological and evolutionary processes (Dirzo et al., 2014). Our study demonstrates that anthropogenic pressures act as habitat filters resulting in low levels of FD and PD (particularly mammal communities) suggesting possible loss of unique traits and distinct evolutionary lineages. Such losses are malign indicators of the decline of ecosystem services (Flynn et al., 2009). On the contrary, a higher diversity of birds close to human settlement suggests the opportunity for ecosystem services but with caveats (e.g. human–wildlife conflict). Our work reveals novel insights into the structure and drivers of vertebrate assemblages in the eastern Himalayas.

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CONFLICT OF INTEREST

The authors have no conflicts of interests to declare.

DATA AVAILABILITY STATEMENT

Data and R scripts are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.hqbzkh1gt (Penjor et al., 2022).

PEER REVIEW

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ORCID

Ugyen Penjor https://orcid.org/0000-0002-9270-7446

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BIOSKETCH

The authors share a common interest in understanding the impacts of anthropogenic land use and climate change on biodiversity and developing practical conservation measures. Individual research interests and current activities can be found at https://www.wildcru.org/members/ and https://www.uwice.gov.bt/about_us.php#tab30.

Author contributions: U.P. conceptualized and designed analyses, S.S. designed bird survey and collected data, U.P. and S.S. curated data, U.P. analysed the data and interpreted the results, U.P. wrote the first draft. All authors contributed to revisions and gave final approval for submission.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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