Journal of Environmental Management 394 (2025) 127628

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Anthropogenic pressures drive the multidimensional homogenisation of bird diversity in a South Asian landscape

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ARTICLE INFO

Keywords:
β-diversity
Environmental filtering
Farmland
Forest
Human footprint
Landscape heterogeneity

ABSTRACT

Understanding the impact of anthropogenic pressures and their interactions with landscape heterogeneity is crucial for avian conservation and for the development of effective management strategies. Despite widespread concerns over biodiversity loss, major gaps remain in understanding how these factors influence multiple dimensions of avian diversity in highly human-dominated landscapes. We examined their effects on taxonomic, functional, and phylogenetic diversity in anthropogenic (farmland and settlement) and natural (forest and riverine) habitats within the Parsa–Koshi Complex of Nepal, a South Asian landscape undergoing rapid environmental change. Our results revealed that anthropogenic habitats consistently support lower taxonomic (α and β), functional, and phylogenetic diversity, with pronounced functional clustering in settlements, suggesting environmental filtering that favours generalist species. In contrast, natural habitats, particularly forests, exhibited stronger phylogenetic clustering, possibly due to human-mediated disturbances that promoted the persistence of the dominant clades. Increased anthropogenic pressure reduced diversity across most metrics, whereas greater landscape heterogeneity enhanced them, indicating a buffering role. These findings emphasise the importance of reducing anthropogenic pressure and maintain landscape heterogeneity as key strategies for sustaining avian diversity, while providing insights into how landscape management could support conservation amid ongoing environmental changes.

1. Introduction

Anthropogenic pressure and human-induced land-use change are major threats to global biodiversity, profoundly altering ecological communities (Jaureguiberry et al., 2022; Jones et al., 2018; Newbold et al., 2015). The conversion of natural habitats into farmlands and urban landscapes drives habitat loss, fragmentation, and degradation, which act as environmental filters by selectively favouring species with specific functional traits, ecological roles, and evolutionary histories (Geng et al., 2025; Hua et al., 2024). Consequently, synanthropic taxa

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https://doi.org/10.1016/j.jenvman.2025.127628
Received 25 July 2025; Received in revised form 18 September 2025; Accepted 9 October 2025

(wild species living in human-altered environments) increasingly dominate these modified habitats, leading to biotic homogenisation (communities across regions becoming more similar) and weakening ecological resilience (La Sorte et al., 2018; Marcacci et al., 2021). Nevertheless, greater landscape heterogeneity can buffer these effects by promoting species richness and maintaining ecological stability (do Carmo Pônzio et al., 2024; Lu et al., 2024). Therefore, understanding the interplay among bird community composition, habitat alteration, and ecological function is essential for developing targeted management and conservation strategies in human-modified environments.

While taxonomic diversity provides a fundamental measure of biodiversity metrics, contemporary conservation science increasingly emphasises the integration of functional and phylogenetic diversity to understand more nuanced community responses to anthropogenic pressures (Flynn et al., 2011; Huang et al., 2020). These dimensions provide complementary insights: functional diversity (species' trait variation) is directly related to ecosystem stability (Hallett et al., 2017), whereas phylogenetic diversity (evolutionary relationships) enhances ecosystem resilience (Cadotte et al., 2012). Although natural habitats generally sustain higher diversity across all dimensions (Carvalho et al., 2022; Newbold et al., 2015), structurally complex anthropogenic habitats, such as diversified agricultural systems with varied crop types, vegetation heights, and tree covers, can maintain comparable functional and phylogenetic diversity (García-Navas and Thuiller, 2020; Gove et al., 2013). However, land-use intensification often amplifies environmental filtering, resulting in clustered communities and reduced diversity through taxonomic homogenisation, functional trait convergence, and phylogenetic overdispersion (Marcacci et al., 2021; Penjor et al., 2022). While landscape heterogeneity may mitigate these effects, its influence depends on the spatial configuration and ecological context (do Carmo Pônzio et al., 2024; Lee and Martin, 2017; Lu et al., 2024). These contrasting processes often reflected in β-diversity patterns, where natural systems maintain turnover-driven variation, whereas human-modified landscapes increasingly exhibit nestedness-driven homogenisation (Carvalho et al., 2022; Shih et al., 2024).

Most prior studies have focused on either anthropogenic disturbances or landscape heterogeneity related to taxonomic, functional, or phylogenetic diversity. For instance, anthropogenic disturbances and urbanisation have shown to reduce taxonomic, functional, or phylogenetic diversity by favouring generalists (Marcacci et al., 2021; Matuoka et al., 2020; Palacio et al., 2018), while landscape heterogeneity either enhances (Adorno et al., 2021; Martínez-Núñez et al., 2023) or reduces (Penjor et al., 2022; Weideman et al., 2020) these diversity patterns. Although some studies have explored the combined effect of these factors (Shuai et al., 2022), comprehensive research on their ecological impacts remains limited, particularly in South Asia where population growth, urbanisation, and infrastructure development are rapidly transforming landscapes at an unprecedented rate (Bhattarai et al., 2023; Ranagalage et al., 2021). In this region, land ownership is predominately private, and diverse agricultural practices generate high spatial heterogeneity in crop types (Das et al., 2025; Katuwal et al., 2022; Sundar and Kittur, 2012). However, the consequnces of this highly heterogeneous and human-modified landscape on multiple dimensions of bird communities remain little understood. Additionally, it is uncertain whether natural habitats, such as forests, which have been heavily encroached upon for settlements, cattle grazing, hunting, and road construction, continue to support ecologically resilient and evolutionarily distinct species. Addressing these knowledge gaps is crucial for understanding the effects of human-dominated landscapes on avian biodiversity, which is essential for formulating effective conservation and management strategies.

In this study, we examined bird species composition and evaluated how taxonomic, functional, and phylogenetic diversity varies across anthropogenic (farmlands and settlements) and natural (forests and riverine areas) habitats within the Parsa-Koshi Complex (PKC) in lowland Nepal, South Asia. The PKC is among the most densely populated regions in the country, characterised by intense resource exploitation, and rapid land-use transformation (Bhattarai et al., 2023; Katuwal et al., 2022). This makes it a critical landscape for investigating how the human footprint, as a proxy for anthropogenic pressure, and landscape heterogeneity influence bird community structure and diversity metrics. We hypothesised that: (1) stronger environmental filtering in anthropogenic habitats would reduce taxonomic, functional, and phylogenetic diversity of birds; (2) taxonomic and phylogenetic diversity of birds would be positively correlated, and functional diversity may diverge due to trait redundancy or convergence, with anthropogenic habitats filtering and promoting functional and phylogenetic clustering of closely related species; and (3) anthropogenic pressure, such as increased human footprint, reduce bird diversity, whereas greater landscape heterogeneity enhances it by increasing habitat complexity and niche availability.

2. Materials and methods

2.1. Study area

This study was conducted across the Parsa–Koshi Complex, located in the Madhesh Province of Nepal (Fig. 1). This landscape stretches from the Parsa National Park (PNP) in the west to the Koshi Tappu Wildlife Reserve (KTWR) in the east, covering an area of approximately 9661 km^2. The complex spans eight districts, with a majority of the area lying outside protected areas, comprising forests, human settlements, and farmlands that provide important habitats for numerous bird species (Fig. 1). The region includes the Terai Plains and Chure (Siwalik) Hills, with elevations mostly below 1000 m above sea level. As of the 2021 census, the Madhesh Province had the highest population density in Nepal at 633 people/km2 (National Statistics Office, 2023).

Agriculture is a primary occupation in this region, supplemented by livestock rearing. Rice is predominantly cultivated during the monsoon season, whereas wheat, mustard, vegetables, and other crops are grown in the winter (Katuwal et al., 2025). Sugarcane is widely cultivated, whereas maize is typically grown during the summer and often year-round, particularly in areas with limited irrigation. The dominant vegetation includes *Shorea robusta*, *Bombax ceiba*, and *Acacia catechu*, while Eucalyptus plantations across the farmland's region are also common. The region experiences summer temperatures ranging from 38–40°C and winter temperatures from 5–10°C, with an average annual rainfall of 1000–2000 mm.

2.2. Research design

We randomly selected fifteen 5 km × 5 km grids from each of the eight districts in the PKC region of the Madhesh Province, resulting in 120 grids. Within each grid, we established three transects, with a minimum distance of 1 km between them. The transect placement was based on the availability of different habitats, such as forests, riverine areas, farmlands, and settlements. The farmland habitats consisted of both standing crops and fallow fields, while settlements were primarily composed of houses. Riverine habitats included rivers, sandbanks, and associated grassland patches. Scattered trees occured sporadically in non-forest habitats. For analysis, farmlands and settlements were classified as anthropogenic habitats (~60% of the transects), whereas forests and riverine areas were categorised as natural habitats (~40%). However, some forest patches showed sign of degradation due to human disturbances, and riverine habitats also exhibited evidence of exploitation.

Each transect was 250 m long, and birds within 50 m on either side of the transect line were recorded. The study was conducted during two seasons: winter (December 2022–January 2023) and summer (April–May 2023; few grids inside PNP were surveyed in 2024 due to access restriction caused by elephant). Surveys were conducted either in the morning (06:00–11:30) or in the afternoon (15:00–18:00) and were

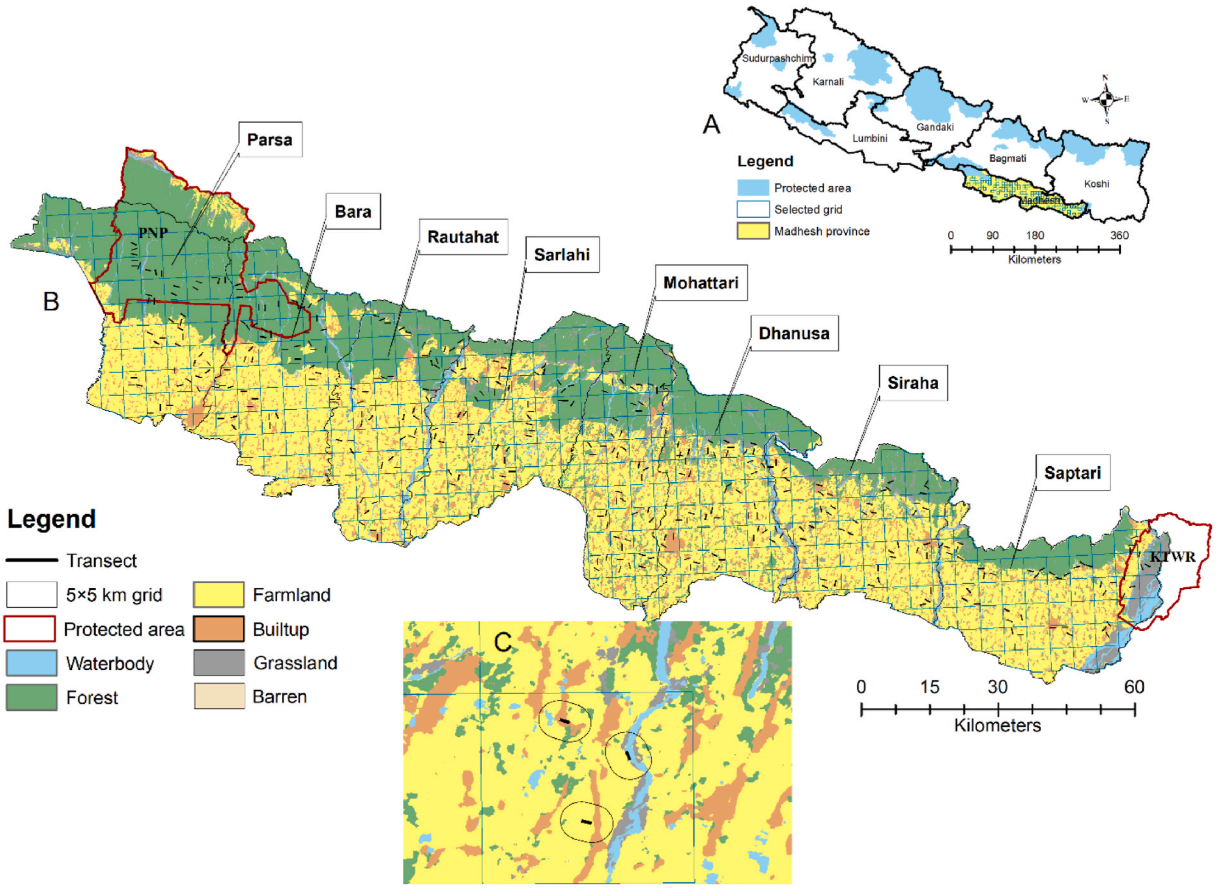

Fig. 1. Bird survey locations across the Parsa–Koshi Complex of the Madhesh Province (eight districts) of Nepal. (A) Selected sampling grids; (B) Transect lines established across the surveyed grids; (C) A zoomed-in view showing the spatial distribution of transects with 500 m buffers, overlaid on land-use patterns. Protected areas include: PNP (Parsa National Park and its buffer zone) and KTWR (Koshi Tappu Wildlife Reserve and its buffer zone).

repeated in the subsequent season. In total, 356 transects were surveyed in winter and 359 in summer (with three additional transects surveyed in summer), and most were located below 250 m. We employed a double-observer method with four survey teams, each including at least one observer who had more than 10 years of bird survey experience. All birds seen or heard calling along transects were recorded, excluding individuals flying overhead.

2.3. Data analysis

2.3.1. Bird's composition across habitats

To visualise bird community composition across habitats, we applied Non-metric Multidimensional Scaling (NMDS) based on Bray–Curtis dissimilarity using the 'vegan' package (Oksanen et al., 2025). Prior to analysis, species abundance data were Hellinger-transformed to reduce the influence of highly dominant species. The habitat variable was fitted to the NMDS ordination with 999 permutations to assess its significance, which revealed a significant influence on community composition ($p = 0.001$). The NMDS ordination results were visualised using convex hulls outlining the community structure associated with each habitat.

2.3.2. Taxonomic, functional and phylogenetic diversity of birds

Taxonomic diversity was partitioned into alpha (α) and β components. The α-diversity was measured using species richness, representing the number of species recorded per transect, and the Shannon diversity index, which incorporates both species abundance and evenness, and was calculated using the 'vegan' package in R (Oksanen et al., 2025). The β-diversity was assessed using the Sørensen index, based on species presence–absence data, which captures differences in species composition among sites. The β-diversity was further partitioned into species turnover, representing species replacement among sites, and nestedness-resultant dissimilarity, reflecting species loss or gain without replacement (Baselga, 2010). These components were calculated with the 'betapart' package in R (Baselga et al., 2023).

Functional diversity, which reflects variation in the ecological traits and roles relevant to ecosystem functioning, was measured using three indices: Functional Richness (FRic), Functional Evenness (FEve), and Functional Dispersion (FDis). FRic measures the volume of trait space occupied by a community, representing the range of functional traits and ecological strategies it contains. FEve evaluates how evenly species occupy the functional trait space, indicating how uniformly ecological roles are distributed within a community. FDis measures the mean distance of species from the centroid of all species in trait space, reflecting how functionally dispersed species are within a community. These metrics were calculated using the 'FD' package in R (Laliberté et al., 2014).

To construct the functional trait matrix, we used nine traits for each species: diet, migratory status, foraging stratum, clutch size, habitat categorisation, habitat density, dispersal ability, beak length, and body mass (Grimmett et al., 2016; Inskipp et al., 2016; Katuwal et al., 2025; Tobias et al., 2022; Supplementary Table S1). Diet was categorised based on the primary food source into four groups: herbivores (primarily consuming plant material, such as seeds, grains, fruits, and nectar, with occasional invertebrates), invertivores (mainly feeding on insects and other invertebrates, occasionally vertebrates), vertivores (primarily feeding on vertebrates with occasional invertebrates), and omnivores (feeding on a broad diet of both plant and animal matter; Inskipp et al., 2016; Tobias et al., 2022). Migratory status was categorised as resident, winter visitor, summer visitor, passage migrant, and vagrant (Grimmett et al., 2016; Katuwal et al., 2025). Foraging strata included canopy, shrub, trunk, aerial, wetland, and ground; habitat categorisation included specialist or generalist type; dispersal ability as strong, moderate, or low flier; and habitat density as dense, semi-open, or open (Tobias et al., 2022; Supplementary Table S1). Then, we calculated pairwise species dissimilarities using the 'gawdis' function, a modified Gower distance metric that assigns equal weight to each trait (de Bello et al., 2021). We performed principal coordinate analysis (PCoA) on the trait distance matrix to reduce dimensionality, retaining the first two axes for subsequent functional diversity analysis.

Phylogenetic diversity, which captures evolutionary relationships among species, was assessed using three widely applied metrics: Faith's phylogenetic diversity (PD; total evolutionary history represented by the community), Mean Pairwise Distance (MPD; average phylogenetic distance between all pairs of species), and Mean Nearest Taxon Distance (MNTD; average phylogenetic distance to the nearest relative within the community). Phylogenetic relationships were obtained from the global avian super tree available at [birdtree.org], using the Hackett backbone phylogeny (Jetz et al., 2012). We downloaded 2000 ultrametric trees and generated a single majority-rule consensus tree in Mesquite v3.70 to represent phylogeny while accounting for phylogenetic uncertainty. Using the consensus tree and the community species matrix, PD, MPD, and MNTD were calculated for each transect with the 'picante' package in R (Kembel et al., 2010).

We used Wilcoxon rank-sum test to compare bird richness and Welch's *t*-test to compare other diversity metrics between anthropogenic and natural habitats. To evaluate the relationships between the diversity dimensions, we conducted Spearman rank correlations between the taxonomic (species richness), functional, and phylogenetic diversity measures. For community assembly analysis, we calculated the Standardised Effect Sizes (SES) for FDis, MPD, and MNTD using null models, where values below zero indicated functional or phylogenetic clustering, while values above zero indicated overdispersion. We assessed the significance of all the SES metrics using one-sample t-tests against a null expectation of zero. Finally, we compared standardised metrics between habitats using Welch's *t*-test.

2.3.3. *Anthropogenic pressure, vegetation productivity and landscape heterogeneity*

We quantified the anthropogenic and environmental drivers of bird diversity by creating a 500 m (local scale) and 1000 m (landscape scale) buffer around each transect (see Fig. 1). To assess anthropogenic pressure, we used the 100 m resolution global Human Footprint (HFP) dataset for 2020, which integrates variables such as land cover change, human population density, nighttime lights, roads, and railways (Gassert et al., 2023) and calculated the HFP value within each buffered transect. Similarly, vegetation productivity was assessed using the 30 m resolution Normalized Difference Vegetation Index (NDVI) derived from the Harmonized Sentinel-2 MSI: MultiSpectral Instrument Level-2A (SR) dataset for 2023. NDVI was calculated at both scales as the annual average using the Google Earth Engine and extracted for each buffered transect. HFP and NDVI values for each area were calculated as the average of all pixel values within each scale.

To evaluate landscape heterogeneity, we used the ESRI 2023 Land Use/Land Cover dataset (Karra et al., 2021), which is based on ESA Sentinel-2 imagery at a resolution of 10 m. This dataset was selected because of its higher classification accuracy (>75%) compared to other available land-cover maps (Venter et al., 2022). The 10 m resolution also enables the detection of fine-scale features such as wetlands and urban areas that are often missed in coarser datasets. Prior to analysis, we also assessed the accuracy of this map at a local scale using a stratified random sampling approach. Specifically, we generated 100 random validation points for each focal land cover class and verified them using a combination of field-collected data and high-resolution imagery from Google Earth from 2023. The overall accuracy was 90% with a kappa hat coefficient of 0.85. Then, landscape compositional heterogeneity was quantified at both scales using Shannon's Diversity Index (SHDI), and configurational heterogeneity was assessed by calculating the weighted mean patch density (WMPD) and weighted mean edge density (WMED) using the 'landscapemetrics' package (Hesselbarth et al., 2019).

2.3.4. *Factors influencing taxonomic, functional, and phylogenetic diversity of birds*

To examine the influence of anthropogenic and landscape variables on taxonomic (α and β), functional, phylogenetic diversity of birds, we fitted generalised linear mixed models (GLMMs) using the glmmTMB package, which provides a flexible framework for mixed models with a wide range of distributions (Brooks et al., 2017). Species richness was modelled using a Poisson distribution, whereas the other diversity metrics were modelled with a Gaussian distribution. Prior to model fitting, we assessed multicollinearity among predictors and excluded variables with an absolute correlation coefficient greater than 0.7, including NDVI and WMED. Diversity metrics were log- or square-root transformed when needed, and all predictor variables (HFP, SHDI, and WMPD) were standardised (mean = 0, SD = 1). We included transects nested within the grid as random effects. We checked for overdispersion and found that none of the models were overdispersed. Significant predictors of each diversity metric were predicted using the 'ggeffects' package. All analyses were conducted using R version 4.3.2 (R Core Team, 2024).

3. Results

A total of 238 bird species were recorded during the survey (Supplementary Table S1). The NMDS ordination showed greater similarity in bird community composition between farmlands and settlements, followed by riverine habitats, whereas forests supported more distinct assemblages (Supplementary Fig. S1).

3.1. *Taxonomic, functional, and phylogenetic diversity across habitats*

We observed significant differences in the taxonomic, functional, and phylogenetic diversity of birds between habitats ($p < 0.05$ for all metrics except PD; Fig. 2). Although the mean species richness was slightly higher in winter, the seasonal variation was not significant (Wilcoxon test, $p = 0.103$).

Both mean species richness and Shannon diversity were highest in natural habitats, particularly forests, and lowest in anthropogenic habitats, especially settlements (Fig. 2; Supplementary Fig. S2). The mean species turnover was also the greatest in natural habitats, especially forests and riverine areas, and lowest in anthropogenic habitats, with settlements showing the least turnover, highlighting distinct assemblages in natural areas (Fig. 2; Supplementary Fig. S2). In contrast, nestedness was minimal in natural habitats (particularly forests) and the highest in anthropogenic habitats, peaking in settlements (Fig. 2; Supplementary Fig. S2). Consequently, overall β-diversity followed similar patterns, being greatest in forests and lowest in settlements, reflecting higher ecological variability in natural habitats (Fig. 2; Supplementary Fig. S2).

The mean functional diversity metrics (FRic, FEve, FDis), and PD were also greater in natural habitats, peaking in riverine areas, indicating broader ecological roles and deeper evolutionary history (Fig. 2; Supplementary Fig. S2). In contrast, the settlements consistently had the lowest mean values across most metrics, reflecting reduced ecological and phylogenetic complexity (Supplementary Fig. S2). Notably, both the mean MPD and MNTD were higher in anthropogenic habitats and lower in natural habitats, particularly in forests (Fig. 2; Supplementary Fig. S2).

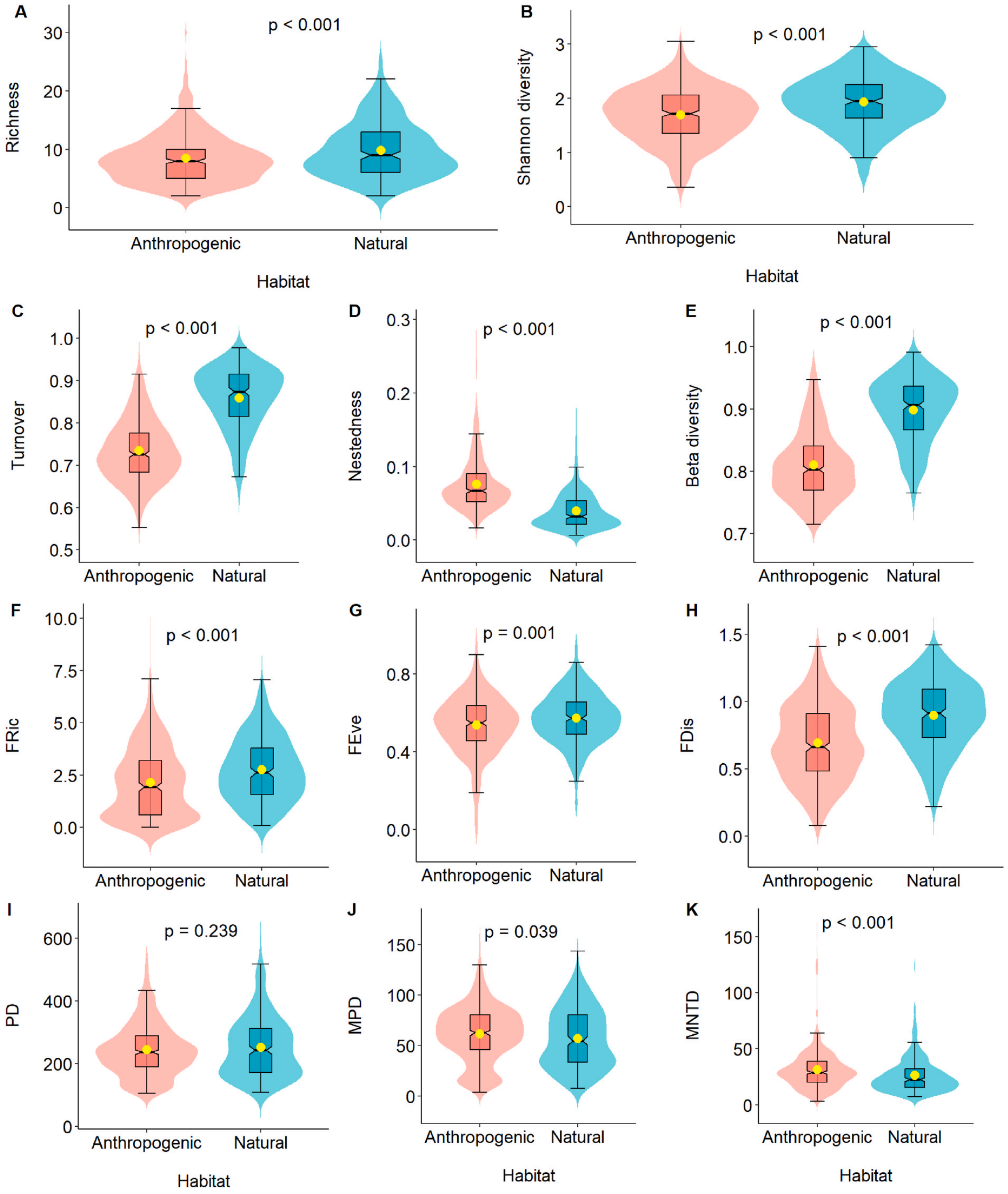

Fig. 2. Bird diversity metrics between anthropogenic and natural habitats in the Parsa–Koshi Complex, Nepal. Panels represent: taxonomic diversity (α-diversity: A – Species richness, B – Shannon diversity, and β diversity: C – Turnover, D – Nestedness, E – Overall β-diversity), functional diversity (F – Functional richness, G – Functional evenness, H – Functional dispersion), and phylogenetic diversity (I – Faith's phylogenetic diversity, J – Mean pairwise distance, K – Mean nearest taxon distance). Each violin plot displays the distribution of the data, with overlaid boxplots showing the median (central line), interquartile range (box), and whiskers. Yellow dots indicate mean values. Statistical significance between habitats was assessed using Wilcoxon rank-sum test for richness and Welch's *t*-test for others. All variables, except PD, had significant differences between habitats.

3.2. Correlations among diversity metrices and clustering patterns

There was a strong and significant positive correlation between species richness and PD ($r = 0.762$, $p < 0.001$), supporting the expected alignment between taxonomic and phylogenetic diversity. FRic also showed a strong positive correlation ($r = 0.717$, $p < 0.001$), whereas FEve exhibit no significant relationship with species richness ($r = -0.012$, $p = 0.737$), and FDis had only a weak positive correlation ($r = 0.192$, $p < 0.001$), suggesting potential trait redundancy or convergence.

We detected significant functional (SES_FDis: mean = −0.175, $t = -4.808$, $p < 0.001$) and phylogenetic clustering (SES_MPD: mean =

−0.523, t = −13.40, p < 0.001; SES_MNTD: mean = −0.516, t = −15.614, p < 0.001), indicating environmental filtering. Notably, functional clustering was higer in anthropogenic habitats, particularly in settlements, whereas phylogenetic clustering was markedly stronger in natural habitats, especially in forests, suggesting greater evolutionary relatedness among the co-occurring species in these environments (Fig. 3A–C, Supplementary Fig. S3). In contrast, riverine habitats maintained greater functional and phylogenetic dispersion than other habitats (Supplementary Fig. S3), supporting more ecologically distinct and evolutionarily diverse species assemblages.

3.3. *Impacts of the anthropogenic pressure and landscape heterogeneity on bird diversity*

At the local scale, species richness, Shannon diversity, turnover, overall β-diversity, FRic and FDis declined significantly with increasing HFP (Fig. 4; Supplementary Table S2). In contrast, nestedness, and both MPD and MNTD increased significantly with HFP (Fig. 4; Supplementary Table S2). Although turnover, overall β-diversity, and FDis were negatively associated with SHDI, nestedness, PD, MPD and MNTD increased significantly (Fig. 4; Supplementary Table S2). Similarly, Shannon diversity, overall β-diversity, FRic, FDis, PD, and MPD all increased significantly with WMPD (Fig. 4; Supplementary Table S2). In addition, the effects of anthropogenic pressure and landscape heterogeneity on diversity metrics were largely consistent at the landscape scale as well (Supplementary Table S2).

4. Discussion

Our study revealed that high anthropogenic pressures in the Parsa–Koshi Complex of Nepal acts as an environmental filter, reducing taxonomic, functional, and phylogenetic diversity. Functional clustering was most pronounced in anthropogenic habitats, particularly in settlements, where communities were dominated by generalist species such as pigeons, doves, mynas and crows. In contrast, natural habitats, especially forests, had greater phylogenetic clustering, suggesting niche conservatism among forest-dependent species, with multiple representatives from clades such as flycatchers, babblers, and warblers co-occurring. Notably, landscapes with greater heterogeneity consistently supported higher biodiversity across all metrics, highlighting the critical role of habitat complexity. These findings provide new insights into how anthropogenic pressure and landscape heterogeneity interact to shape bird communities, offering a novel perspective for biodiversity conservation and management in regions undergoing rapid land-use change.

4.1. *Bird composition and diversity across habitats*

Bird community composition was similar within the anthropogenic habitats, as settlements and farmlands shared species such House crows (*Corvus splendens*), Common Mynas (*Acridotheres tristis*) and House Sparrows (*Passer domesticus*) (Inskipp et al., 2016; Katuwal et al., 2022). In contrast, natural habitats, particularly forests, supported distinct assemblages, likely due to the presence of forest specialists such as Collared scops-owls (*Otus lettia*) and Western Hooded Pitta (*Pitta sordida*). Nevertheless, several species typically associated with riverine habitats such as White Wagtail (*Motacilla alba*) and Lesser Adjutant (*Leptoptilos javanicus*), also frequently occurred in farmlands or settlements, indicating some overlap in community composition (Katuwal et al., 2022).

Our results demonstrated that anthropogenic habitats support significantly lower taxonomic bird diversity than natural habitats, consistent with the well-documented pattern of biodiversity loss in human-modified landscapes (Hua et al., 2024; Lu et al., 2024; Marcacci et al., 2021). This reduction likely driven by persistent disturbances that limit species' richness and evenness. These anthropogenic habitats are dominated by generalist species such as House Crow and Common Myna, that are shared across sites, leading to reduced β-diversity. This decline occurred not through species replacement (turnover) but through increased nestedness, whereby species-poor sites represent subsets of species-rich sites (Baselga, 2010; Carvalho et al., 2022; Sinha et al., 2022), reflecting a process of biotic homogenisation. We also found parallel declines in functional diversity, indicating trait convergence toward ecologically similar disturbance-adapted species, a phenomenon which are also consistent with previous studies (Marcacci et al., 2021; Penjor et al., 2022). While there was no variation on PD between habitats, lower MPD and MNTD in natural habitats showed

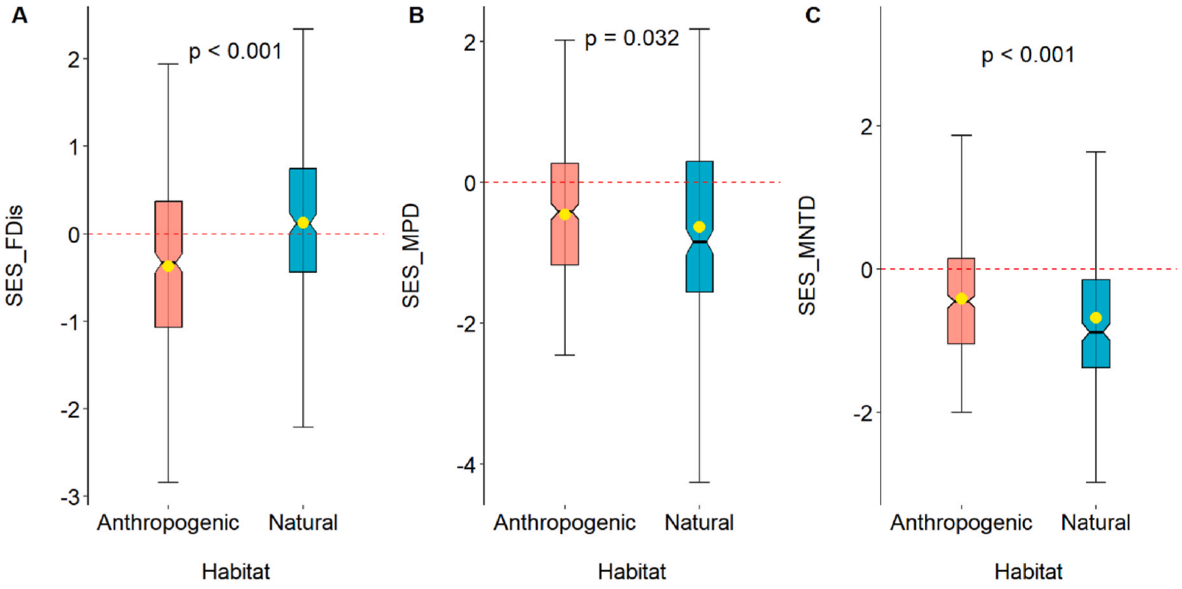

Fig. 3. Functional and phylogenetic clustering of bird communities between anthropogenic and natural habitats in the Parsa–Koshi Complex, Nepal. Boxplots indicate the median (central line), interquartile range (box), and whiskers. Yellow dots represent mean values. Horizontal lines at zero represent the null expectation of random community assembly. Standardized Effect Size (SES) values below zero indicate functional (FDis – Functional Dispersion) or phylogenetic (MPD – Mean Pairwise Distance; MNTD – Mean Nearest Taxon Distance) clustering, while values above zero indicate overdispersion. Statistical significance between habitats was assessed using *t*-test.

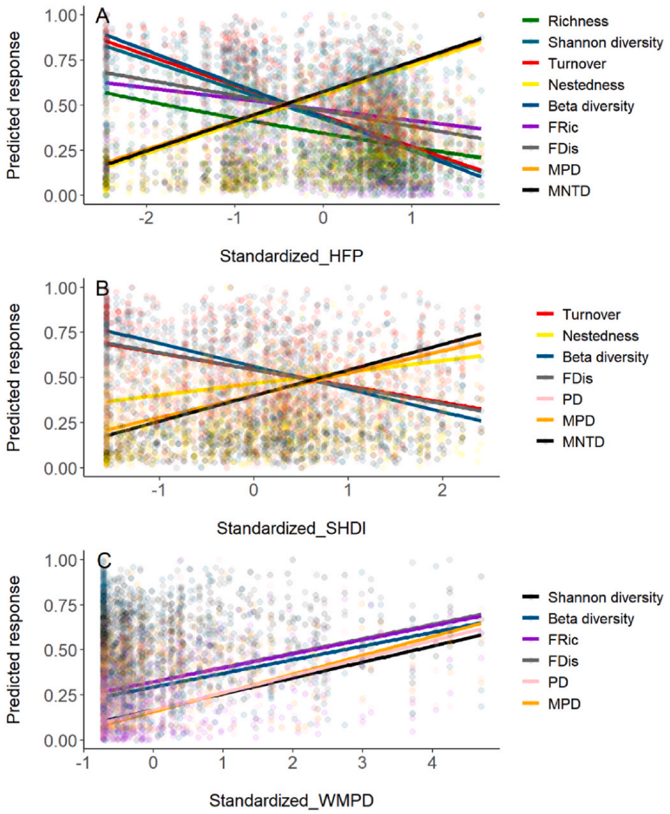

Fig. 4. Effects of anthropogenic pressure and landscape heterogeneity on bird diversity at the local scale: (A) Human Footprint Index (HFP), (B) Landscape Compositional Heterogeneity (SHDI), and (C) Landscape Configurational Heterogeneity (Weighted Mean Patch Density (WMPD). Only significant variables are shown. Predictor variables (x-axis) are scaled (mean = 0, SD = 1), while response variables (y-axis) are normalized to 0–1 for comparability. Beta diversity - Overall β-diversity, Fric – Functional Richness, FDis – Functional Distance, PD – Faith Phylogenetic diversity, MPD – Mean Pairwise Distance, MNTD – Mean Nearest Taxon Distance.

only closely related species with conserved traits that could persist under specific abiotic conditions (Tucker et al., 2017), potentially increasing community vulnerability to environmental changes or disturbances. Collectively, these findings demonstrate that landscape modification acts as an ecological filter, supporting our initial hypothesis of avian communities being progressively simplified by selectively eliminating taxonomically and functionally distinct species.

4.2. Environmental filtering drives functional and phylogenetic clustering

Our results showed a strong positive correlation between bird richness and both FRic and PD, indicating that species-rich sites tend to support broader trait diversity and deeper evolutionary histories. Similar patterns have been reported in other taxa (e.g., plants and small mammals; Li et al., 2021; Pei et al., 2022). This finding aligns with the ecological theory, which predicts that favourable environmental conditions promote the coexistence of diverse lineages and ecological strategies (Stroud and Losos, 2016). However, the lack of significant correlations between species richness and FEve and weak correlations with FDis, suggests that functional diversity is more strongly shaped by trait composition than by species numbers. This highlights that ecosystem functionality depends on which species are present, rather than on species counts alone (Carmona et al., 2021; Mouillot et al., 2013).

The significantly negative SES for FDis, MPD, and MNTD strongly supports environmental filtering as the dominant community assembly process. These clustering patterns indicate that deterministic processes shape avian communities by selecting species with similar functional traits and phylogenetic histories. Notably, functional clustering was more pronounced in anthropogenic habitats, supporting our hypothesis, likely because human disturbances favour species such as Western Spotted Doves (*Spilopelia suratensis*), Pied Bushchats (*Saxicola caprata*), and Asian Pied Starlings (*Gracupica contra*) with similar functional traits, which are well adapted to settlement and farmland environments (Marcacci et al., 2021). Within anthropogenic habitats, functional clustering was strongest in settlements, likely due to species' high adaptive capacity to intense human disturbance, reduced habitat heterogeneity and reliance on human-driven food resources, as found in Common Pigeons (*Columba livia*), House Crows and House Sparrows. However, phylogenetic clustering was markedly stronger in natural habitats, particularly forests, which contradicted our initial expectations. This pattern is likely reflected from high anthropogenic pressure and associated disturbances, including logging, settlement encroachment, road construction, and hunting, which remove sensitive species and result in ecosystem dominated by closely related species (e.g., various species of woodpeckers, bulbuls or flycatchers from the same family). Such clustering may arise from mechanisms such as niche conservatism, specialised resource use, and shared adaptations to disturbed environments (García-Llamas et al., 2019; Penjor et al., 2022). It may also be influenced by the limited survey period, which could have underrepresented migratory or forest-specialist species. Nevertheless, anthropogenic habitats also showed phylogenetic clustering, suggesting that human disturbance favour a few tolerant lineages adapted to disturbed environments.

4.3. Human pressure reduces bird diversity, while landscape heterogeneity buffers losses

Our results showed that increasing anthropogenic pressure, as quantified by HFP, consistently reduced multiple dimensions of avian biodiversity at both local and landscape scales, supporting our hypothesis. Declines in species richness, Shannon diversity, turnover, overall β-diversity, FRic, and FDis suggest that intensified human activity in our study area negatively affects these metrics and drives systematic simplification of avian communities. These patterns are indicative of environmental filtering, whereby habitat degradation and loss favour a limited subset disturbances tolerate species, leading to biotic homogenisation (Marcacci et al., 2021; Matuoka et al., 2020). Notably, nestedness and both MPD and MNTD showed positive association with HFP, potentially reflecting a non-random loss of closely related specialist species and the persistence of more phylogenetically dispersed generalists in disturbed habitats. The pattern of phylogenetic overdispersion under high anthropogenic pressure contrasts with finding from other study (Pei et al., 2022), which reported a negative association with PD, indicating the loss of species with distinct evolutionary histories. However, the decline of PD observed in our study, together with the increase in MPD and MNTD, reflects a complex response to human disturbances. This dual pattern may represent a general response of vertebrate communities to intense human modification.

Conversely, both compositional (SHDI) and configurational (WMPD) landscape heterogeneity, showed positive effects on most biodiversity metrices and emerged as critical buffers against biodiversity loss at both spatial scales (do Carmo Pônzio et al., 2024; Lu et al., 2024). A higher SHDI was associated with greater nestedness and phylogenetic components, indicating that diverse land-cover types maintain a broader evolutionary representation (Adorno et al., 2021), but the negetive association with turnover, overall β-diversity and FDis suggests that more diverse landscape may exhibit lower species turnover, less community differentiation and reduced functional disperson, possibly due to the dominance of a few widespread species or the prevalence of certain functional traits acorss the landscape. Similarly, WMPD enhanced multiple biodiversity dimensions, indicating that landscapes with greater structural complexity support richer avian assemblages (Lu et al., 2024). These positive relationships likely arise because heterogeneous patch distributions create more ecological niches that allow species with diverse traits to coexist, thereby maintaining evolutionary lineages through complementary resources and complex spatial arrangements that buffer against environmental filters. Collectively, these results support our hypothesis that maintaining landscape heterogeneity is crucial strategy for mitigating anthropogenic impacts and conserving avian biodiversity across multiple dimensions (Martínez-Núñez et al., 2023).

4.4. Possible limitations of the study

Our study provides important insights but has some limitations. First, sampling was uneven across habitats, with a slightly greater representation of anthropogenic areas, particularly farmland than riverine habitats. Although we classified riverine and forest areas as 'natural' habitats, many sites experienced human disturbances, as most were located outside protected areas. This, together with the potential differences in species detectability across habitats (particularly in forests), and the use of broad habitat classifications, may have obscured finer-scale ecological variation. Secondly, our functional diversity estimates were constrained by availability of traits, including a broader range of ecological traits that could offer a more comprehensive understanding. Finally, the study was conducted over the course of a single year and within a limited seasonal window, which may not fully reflect temporal dynamics such as migratory patterns or interannual variability. These factors should be considered when interpreting our results and design of future studies.

5. Conclusions and management implications

Our study shows that anthropogenic habitats, which are expanding in Nepal's Parsa–Koshi Complex, support significantly lower avian biodiversity across taxonomic, functional, and phylogenetic dimensions, primarily due to strong environmental filtering. Functional clustering was more pronounced in human-modified habitats, favouring generalist species with similar traits, whereas phylogenetic clustering was stronger in natural habitats, reflecting the dominance of ecologically similar clades with shared evolutionary histories. Importantly, increasing anthropogenic pressure negatively affected nearly all diversity metrics, whereas landscape heterogeneity generally supported avian diversity.

These findings highlight the urgent need to mitigate anthropogenic disturbances and maintain landscape heterogeneity in biodiversity-rich regions like the Parsa-Koshi Complex in South Asia, which are facing rapid population growth, urbanisation, habitat fragmentation, use of agrochemicals, wetland loss, hunting and climate change impacts. Effective management strategies should focus on protecting natural habitats, such as forests and riverine areas, by reducing disturbances like logging, hunting and sand or gravel extraction. In farmlands, promoting bird-friendly farming practices, such as protecting mature trees, reducing agrochemical use, and cultivating mixed crops, and enhancing green cover through tree planting in settlements, are essential. Additional measures include restoring degraded habitats, improving connectivity between fragmented patches, strengthening enforcement against hunting, ensuring sustainable irrigation practices, and implementing land-zoning policies. Implementing these strategies requires collaborative efforts among conservationists, practitioners, local communities, farmers, and policymakers to balance human needs and biodiversity protection in Nepal's threatened lowland ecosystems and similar regions across South Asia.

CRediT authorship contribution statement

Hem Bahadur Katuwal: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Bishnu Prasad Bhattarai:** Writing – review & editing, Visualization, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Sandeep Regmi:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Amrit Nepali:** Writing – review & editing, Investigation, Data curation. **Sabin KC:** Writing – review & editing, Investigation, Data curation. **Ramji Gautam:** Writing – review & editing, Investigation, Data curation. **Prashant Rokka:** Writing – review & editing, Investigation, Data curation. **Nikeet Pradhan:** Writing – review & editing, Investigation, Data curation. **Sabina Koirala:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Dev Narayan Mandal:** Writing – review & editing, Resources, Project administration, Methodology. **Hari Prasad Sharma:** Writing – review & editing, Visualization, Validation, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Rui-Chang Quan:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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

This study was supported by the Tribhuvan University National Priority Area Research Grant (TU-NPAR-2078/79-ERG-04) of Tribhuvan University, Nepal and CAS-SEABRI (Y4ZK111B01). We thank the Department of Forest and Soil Conservation, the Department of National Parks and Wildlife Conservation, the Parsa National Park, the Koshi Tappu Wildlife Reserve, and the Division Forest Offices of the Madhesh Province for providing research permission. We thank Jaya Nath Bhandari, Yubin Shrestha, Tek Gharti Magar, and Tek Bahadur Gurung for helping data collection. We would also like to thank the biodiversity conservation initiatives from Southeast Asia Biodiversity Research Institute (SEABRI) and Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (CAS), advancing the implementation of the Kunming-Montreal Global Biodiversity Framework (GBF). We also thank two anonymous reviewers for their constructive feedback on this article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.127628.

Data availability

The bird dataset will be available from https://doi.org/10.6084/m9.figshare.29815670.

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