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ARTICLE

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Elevational pattern and seasonality of avian diversity in Kaligandaki River Basin, central Himalaya

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Abstract: This study explored bird diversity, seasonal variation, and associated factors along an elevational gradient in an important biodiversity area (IBA) of central Nepal: the Kaligandaki River basin of Annapurna Conservation Area. The field survey was carried out in 2019 over two seasons, winter (January and February) and summer (May and June) using the point count method. A total of 90 sampling plots were set up from elevations of 800m (Beni) to 3,800m (Muktinath). Data for variables including the number of fruiting trees (indicator of resource availability) and distance to the road (indicator of disturbance) were collected, and their influence on avian diversity were assessed. The results revealed a diverse assemblage of avian fauna in the study area with consistent species richness over the two seasons. A decline in species richness and diversity with increasing elevation was observed. Of the different habitat types within the study area, forest and shrubland habitats showed the strongest association with bird species distribution and richness. We emphasize the need for long-term monitoring programs with standardized sampling approaches to better understand the avifauna in the central Himalaya.

Keywords: Biodiversity pattern, birds, elevational gradient, monotonic decline, species richness.

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Author contribution: JN, LK and MKC conceptualized the project. JN carried out the field work. JN, LK and BG analyzed the data and prepared the manuscript. MKC supervised the overall research and contributed in the manuscript improvement.

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INTRODUCTION

Patterns in the diversity and composition of species along elevation gradients are key issues in ecology (Lomolino 2001) that contribute to understanding global biodiversity (McCain 2009). The spatial and temporal aspects of species variation along such gradients provide clues to understanding mechanisms of species richness and diversity, a key challenge for ecologists and conservationists (Gaston et al. 2000). Global latitudinal diversity, a well-known pattern where species richness peaks in the tropics and drops towards the poles, has been extensively explored (Rosenzweig 1992; Hillebrand 2004; Pigot et al. 2016). While elevation gradients have not been studied as expansively, they also present prominent patterns in diversity (McCain 2010).

Many studies have demonstrated elevation-related patterns in diversity and have attempted to describe underlying mechanisms, but these aspects remain under debate (Sanders & Rahbek 2012; Quintero & Jetz 2018). In general, species richness has been reported to follow one of the four main diversity patterns: decreasing with elevation, low plateau, low plateau with a midelevation peak, and mid-elevation peaks. Of these, midelevation peaks are the mostly observed patterns among vertebrates (Colwell & Lees 2000; Bertuzzo et al. 2016; Chen et al. 2017; Pandey et al. 2020). These patterns can be explained by drivers that can be both spatial (area, mid domain effect) and environmental (temperature, precipitation, productivity, and habitat heterogeneity) (Colwell et al. 2004; Wu et al. 2013; Chen et al. 2017, 2020; Pandey et al. 2020). Numerous hypotheses have been proposed to explain relationships between species richness and altitude, such as species-area relationships, mid-domain effects, climate-richness relationships, and productivity-richness relationships (Rahbek 1995; Grytnes & Vetaas 2002).

Variations in species richness of birds with elevation are among the most commonly considered aspects of bird community structure (Stevens 1992), because elevation affects the condition of the physical environment and the types and amount of resources available for breeding and foraging activities. Thus, the composition and structure of bird communities may change along these gradients (Rahbek 2005; McCain 2009). As the elevation increases, availability of resources for birds changes with differences in forest stand structure, site productivity, vegetation species composition, and available land area (Rahbek 2005). Seasons also play a significant role in determining food and cover availability, influencing reproductive success and survival of bird species

(Mengesha & Bekele 2008). The seasonal variability in the measure of precipitation and temperature and other conditions of spatial and temporal microhabitat are prime factors influencing resource accessibility for birds. Such distributions of food and cover resources determine the richness, abundance and habitat use of bird species (Waterhouse et al. 2002).

Mountains provide an extensive range of environmental factors, many of which vary with elevation (Becker et al. 2007). They often harbor a large number of species, including varied avifauna, presenting ideal situations for exploring variation in species diversity over relatively short distances (Korner 2007; Quintero & Jetz 2018). Many mountain areas are also global biodiversity hotspots for bird species (Renner 2011; Inskipp et al. 2013, 2016). Understanding the association between species richness and elevation gradients can support conservation efforts (Stevens 1992; Raman et al. 2005; Acharya et al. 2011).

The Kaligandaki River basin in the Annapurna Conservation Area (ACA) of central Nepal is a major tributary of the Ganges River basin, with a marked topographic variation originating at the border with Tibet at an elevation of 6,268m at the Nhubine Himal Glacier. The ACA is one of the Important Bird and Biodiversity Areas (IBA) of the central Himalayan region (BCN 2019). The Kaligandaki Valley is a migration corridor for birds moving south to India in winter. Around 40 species have been recorded moving along the valley, including Demoiselle Crane Grus virgo and several raptors (Inskipp & Inskipp 2003) including Steppe Eagles Aquila nipalensis, which migrate west through the ACA just south of the main Himalayan chain (de Roder 1989). The upper section of the Kaligandaki corridor, a road connecting Indian border in the south to the Chinese border in the north spanning along the Kaligandaki River axis, has heavily modified the pristine landscape of the ACA. A checklist for overall bird species of the ACA has been published (Inskipp & Inskipp 2003; Baral 2018; Neupane et al. 2020), but studies focusing on bird diversity, seasonal variation, elevation and associated factors have not been conducted. This study was carried out along Kaligandaki River basin in order to explore: i) avian diversity; ii) seasonal variation in species richness and diversity; iii) environmental factors (elevation, habitat types, number of fruiting trees and distance to the road) affecting avian species richness; and, iv) habitat association of different feeding guilds.



MATERIALS AND METHODS

Study area

This study was conducted in Kaligandaki River basin within Annapurna Conservation Area (Fig. 1). The Kaligandaki River basin is an important sub-basin of Narayani Basin in Nepal located between 27.716-29.316 °N and 82.883-84.433 °E. The area has marked topographic variation with elevation varying from 183-8,143 m. The upper ridges of the Kaligandaki River Basin are characterized by high altitude, low temperature, some glacier coverage, and dry climate with strong winds and intense sunlight receiving less than 300mm annual rainfall. Permanent snow covers about 33% of the basin, while over 50% of this snow cover occurs above 5,200m (Mishra et al. 2014). The middle region of the basin is mostly hilly with high altitude terrain; the plains in the south have a sub-tropical climate and high precipitation. The study area covered an elevation range of 800m (Beni, Myagdi District) to 3,800m (Muktinath, Mustang District) from sub-tropical to sub-alpine habitats for diverse avian fauna.

At the lowest elevations of the study area, there are subtropical forests of broadleaved Needle-wood Tree *Schima wallichii*, Indian Chestnut *Castanopsis indica*,

with scattered Chir Pine *Pinus roxburghii* on dry slopes and Nepalese Alder *Alnus nepalensis* alongside rivers and streams. The temperate forests of mixed broadleaves and oaks *Quercus lamellosa*, *Q. lanata*, and *Q. semecarpifolia* with Rhododendrons *Rhododendron* spp. occupy the higher regions. Coniferous forests, mainly of Fir *Abies spectabilis*, Blue Pine *Pinus wallichiana* grow on the dry ridges and slopes. Above the temperate zone lie the subalpine forests of Birch *Betula utilis*, Blue Pine *Pinus wallichiana*, and junipers *Juniperus* spp.

DATA COLLECTION Bird surveys

The point count method was used to count the number of birds in the study area. This method is used mostly in avian fauna to estimate population densities, define population trends, and assess habitat preferences. It is undertaken from a fixed location for a fixed time, and can be conducted at any time of the year (Sutherland 2006). Birds were recorded from 800–3,800 m within two districts of Annapurna Conservation Area, Myagdi, and Mustang along Kaligandaki River basin. The plots were set up with every 100m-rise in elevation, which was recorded using Garmin Etrex 10 GPS. Three fixed-point count plots were set up at each elevational plot, one on

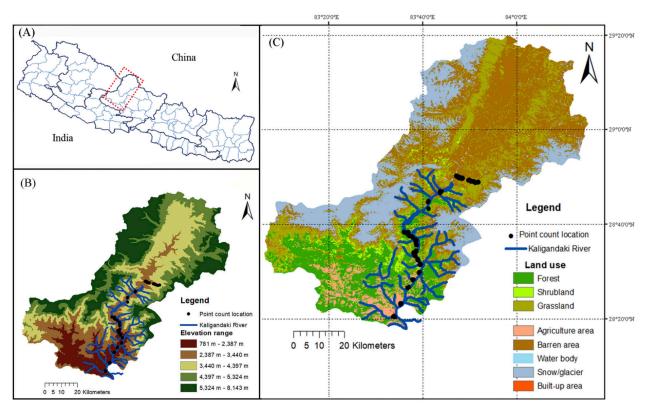


Figure 1. Study area with point count locations. A—map of Nepal showing study area | B—Annapurna Conservation Area showing elevational gradient | C—Annapurna Conservation Area showing the land-use pattern and point count locations.



the roadside and two on either side of the road about 250–350 m apart considering the site accessibility along the river basin. A total of 90 sampling plots were set up on 30 elevational points within the study area. At each plot, birds were recorded within a circle of 30m radius from the fixed point in a center, for 15min. The birds were observed directly using binoculars and photographs were taken whenever possible. For taxonomic identification, the field guide book Birds of Nepal (Grimmett et al. 2016) was used. Birds were observed in the plot from 06.00–11.00 h and 15.00–17.00 h. Data were collected in two seasons of 2019 – winter (January and February) and summer (May and June).

Call count method was also employed in the same point count locations to record all the birds seen as well as heard. This method helped for the identification of some birds that produced easily identifiable sounds that are familiar to the researchers. This approach is used for recording birds, which are difficult to see or capture in their preferred habitat. Those species which are shy and cryptic can be rarely observed even in open habitat. Similarly, in the dense habitat, it is impossible to observe the birds in the distance. Thus, the call count method is the approach of listening to the sound and noise produced by the birds and recording them.

Feeding guild classification

Observed bird species were categorized into five feeding guilds based on the field guide book Birds of Nepal (Grimmett et al. 2016) and following the literature (Katuwal et al. 2018): insectivores (feeding predominantly on insects, larva, worms, spiders, crustaceans, and mollusks), omnivores (feeding on both plants and animals), frugivores (feeding on fruits, berries, figs, drupes, and nectars), carnivores (feeding on fishes, amphibians, reptiles, birds, and mammals), and granivores (feeding on seeds, grains, and acorns).

Environmental variables

Habitats in 90 different point count sites were categorized into seven types as forest, riverbank, agricultural area, shrubland, grassland, scrubland and barren area. The GPS coordinates were overlaid in the land-cover map of ICIMOD (2010) for habitat categorization. As a proxy of resource availability for species richness and diversity, the number of fruiting trees was counted in each sampling site within the circular plot of 30m radius. Another predictor variable, distance to the road from the three-point count locations was taken as a proxy of human disturbance within the study area. These point count locations were set up in the road and

either sides away from the road about 250–350 m apart in the river basin along elevational gradient. Distance to the nearest road for each sampling point was estimated in the field and confirmed in Google Earth (https://earth.google.com/web).

DATA ANALYSIS

Diversity measures

The alpha (α) diversity of bird species of the study area during seasons and across point count stations was measured as the species diversity index (H') by using the Shannon-Wiener Function (Shannon & Weaver 1949). Species richness gives the presence of the total number of species at a particular area, and it was calculated as the total number of species recorded. The abundance of each species was calculated as the frequency of occurrence in each plot. To calculate whether the species were evenly distributed among the different point count stations and the different seasons, the evenness index (E) was used. It was calculated as

$$E = \frac{H'}{H'_{max}}$$

where,

H' = Shannon-Wiener diversity index

 H'_{max} = maximum possible value of H', if every species is equally likely and equal to ln(S)

S = species richness, the total number of species

Community similarity measurement

Sorenson's similarity index (SSI) was used for the qualitative data (presence/absence) to find the community similarity between the two study seasons. The Sorenson's Index of similarity was calculated as:

$$SSI = \frac{2C}{A + B} \times 100\%$$

where,

C = Common number of species shared by two communities (two seasons)

A = Number of species found in one community (one season)

B = Number of species found in another community (another season)

Analysis of variance

One-way ANOVA was used to test the significant variation in species richness of birds among point count stations in two seasons assuming the following null hypothesis- H_0 = there is no significant variation in species richness of birds between summer and winter seasons.



Generalized linear model

The generalized linear model was used to assess how the bird species richness and diversity change along the elevation gradient as well as to assess the influence of resource availability (number of fruiting trees) and human disturbance (distance to the road) on species diversity and richness. Predictor variables included elevation (measured in m at the centroid of 30m circular radius), resource availability (number of the fruiting tree within 30m radius) and human disturbance (distance from the nearest road). Plausible generalized linear models (GLMs) with Poisson error distribution and log link function was run as it is a powerful tool for analyzing count data for species richness in ecology. To assess the influence of predictor variables on species diversity, multiple linear regression was used since the response variable was continuous. Six priori set of models, including the null model, were defined. The models were then ranked using the corrected Akaike Information Criterion that is adjusted for small samples (AICc) (Burnham & Anderson 2002). The beta-coefficient (slope) of covariates was examined to test the significance of their effect on the response variable (species richness and species diversity). All analyses were carried out using 'Stats Package' in R 3.1.2 (R Core Team 2013).

Canonical correspondence analysis

The relationship of bird species richness and environmental factors were explored using Canoco v.4.56. A unimodal direct gradient analysis of partial canonical correspondence analysis (CCA) was used to relate the variation of bird communities (species richness) to habitat variables. Different habitat types were put in the matrix of independent environmental factors whereas, recorded bird species were grouped in the data matrix of dependent variables. Under the reduced model of the canonical axes, Monte Carlo permutation tests (499 permutations) were used to assess the statistical significance of the association between bird species composition and habitat variables.

RESULTS

Bird diversity in Kaligandaki River basin

A total of 1,036 individuals of 120 bird species from 33 families of eight orders were recorded by point count method in the Kaligandaki River basin (Annex I). Out of the eight orders, order Passeriformes had the highest species richness (98 species) and family Muscicapidae had the highest number of bird species (17 species).

Guild structure analysis revealed that half of the total bird species were insectivores followed by omnivores, frugivores, granivores and carnivores (Fig. 2). Out of the 120 species recorded from the study area, 86 species (71.67%) were resident, 18 (15%) were summer visitors, and 16 (13.34%) were winter visitors.

Seasonal variation in species richness and diversity

A total of 459 individuals of 81 species of seven orders belonging to 27 families were recorded in the winter season and 577 individuals of 95 species of six orders belonging to 29 families were recorded from the summer season. Fifty-six species of birds were found in both summer and winter season (Table 1).

Shannon Wiener diversity index (H') for the winter season (January and February) was H' = 3.93 whereas more diverse bird assemblage was observed in the summer season (May and June) with the diversity index of H' = 4.006. The evenness index was found to be higher in winter (E = 0.6287) than in summer season (E = 0.5784) (Table 1).

Sorenson's similarity index (SSI) of species composition was observed to be 63.63% between summer and winter season. ANOVA revealed no significant variation in species richness (F = 0.487; df = 1, 175; P = 0.486] and abundance (F = 2.903; df = 1, 175; P = 0.090) of birds between two seasons among the point count locations.

Factors affecting bird diversity

The model selection results showed that elevation consistently had a negative influence on species richness and diversity; as the elevation increased the species richness decreased significantly (Estimate 2 = -0.21, P < 0.001) (Fig. 3A & B). Distance to the road as a predictor of human disturbance also had a negative influence on species richness and diversity (Fig. 3C & D). Both species richness and diversity were positively associated with the number of fruiting trees as a proxy of resource availability,

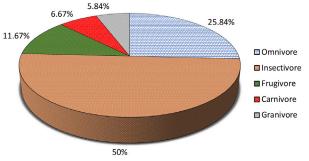


Figure 2. Species richness of birds (in percentage) among different feeding guilds.





Table 1. Seasonal variation in species richness, abundance, and diversity of birds.

Seasons	Orders	Families	Species richness	С	# of individuals	H'	E
Summer	6	29	95		577	4.006	0.5784
Winter	7	27	81	56	459	3.93	0.6287

Table 2. Regression models describing the bird species richness and diversity along the elevational gradient in the Kaligandaki River basin, ranked according to the Akaike information criterion adjusted for small sample size (AICc).

Candidate model	Poisson regression for bird species richness			Multiple linear regression for species diversity						
Candidate model	AICc	delta	Weight	logLik	Df	AICc	delta	Weight	logLik	Df
Elevation	351.58	0.00	0.46	-173.72	2	127.95	0.00	0.42	-60.84	3
Elevation + Distance to road	352.63	1.05	0.27	-173.17	3	128.85	0.89	0.27	-60.19	4
Elevation + No. of fruiting trees	353.56	1.98	0.17	-173.64	3	129.62	1.67	0.18	-60.58	4
Elevation + No. of fruiting trees + Distance to road	354.65	3.07	0.10	-173.09	4	130.50	2.55	0.12	-59.89	5
No. of fruiting trees + Distance to road	402.02	50.44	0.00	-197.87	3	167.01	39.06	0.00	-79.27	4
No. of fruiting trees	404.69	53.11	0.00	-200.28	2	168.60	40.65	0.00	-81.16	3
Distance to road	415.80	64.22	0.00	-205.83	2	179.09	51.14	0.00	-86.41	3
Intercept only	428.13	76.55	0.00	-213.04	1	187.30	59.35	0.00	-91.58	2

however, the results lacked the statistical significance (Fig. 3E & F). The beta-coefficient or slope of elevation ($\beta_{elevation}$) was -0.48 (SE = 0.05) and distance to road ($\beta_{distance to road}$) was -0.22 (SE = 0.05). The slope estimates of number fruiting tree ($\beta_{fruiting trees}$) for species richness analysis was 0.14 (SE = 0.002). The positive beta coefficient showed that for every one-unit increase in the predictor variable (no. of fruiting trees), the response variable (species richness) increased by the beta coefficient value. For negative beta coefficient, species richness decreased by beta coefficient value for every one-unit increase in elevation and distance to road. Since the 95% confidence interval of the beta-coefficients did not overlap with zero, the effects of these variables (species richness, elevation, no. of fruiting trees and distance to road) are significant (P<0.05).

For both the species richness and diversity analysis, AICc based model selection predicted the elevation model having the least AICc value as the most plausible model in the candidate model set. The model with only elevation as a regressor with smallest AICc value (351.58) was the best fit as compared to other variable model sets (Table 2).

Feeding guild-wise habitat association of birds

The habitat variables that were selected to find the relationship between environmental variables and species were forest habitat, riverbank, agricultural area, shrubland, grassland, scrubland, and barren area. The Monte-Carlo permutation test of significance of all canonical axes revealed no significant relationship between the carnivorous species and habitat types (Trace=0.813, F-ratio=0.747, P=0.718) (Fig. 4A). Insectivores showed strong association (Trace= 0.843, F-ratio= 1.461, P=0.003) with shrubland and scrubland habitats, whereas grassland habitat showed less impact in their distribution. A large number of the insectivore bird species including Black-throated Tit Aegithalos concinnus, Greater Yellownape Picus flavinucha, Verditer Flycatcher Eumyias thalassinus, Black-lored Tit Parus xanthogenys, Grey-headed Woodpecker Picus canus, and Streaked Laughingthrush Garrulax lineatus were associated with forest habitat (Fig. 4B).

For frugivore species, shrubland habitat followed by the riverbank and grassland habitats had more significant impact on species distribution (Trace=0.362, F-ratio=0.125, P=0.034). Red-billed Blue Magpie *Urocissa erythrorhyncha*, Blue-throated Barbet *Megalaima asiatica*, Grey Treepie *Dendrocitta formosae*, and Blackthroated Sunbird *Aethopyga saturata* showed strong association with shrubland habitat. Barbet species like Great Barbet *Megalaima virens* and Golden-throated Barbet *Megalaima franklinii* were associated with agricultural areas. Similarly, species like White-winged Grosbeak *Mycerobas carnipes* and Crimson Sunbird *Aethopyga siparaja* were associated with forest habitat (Fig. 4C).



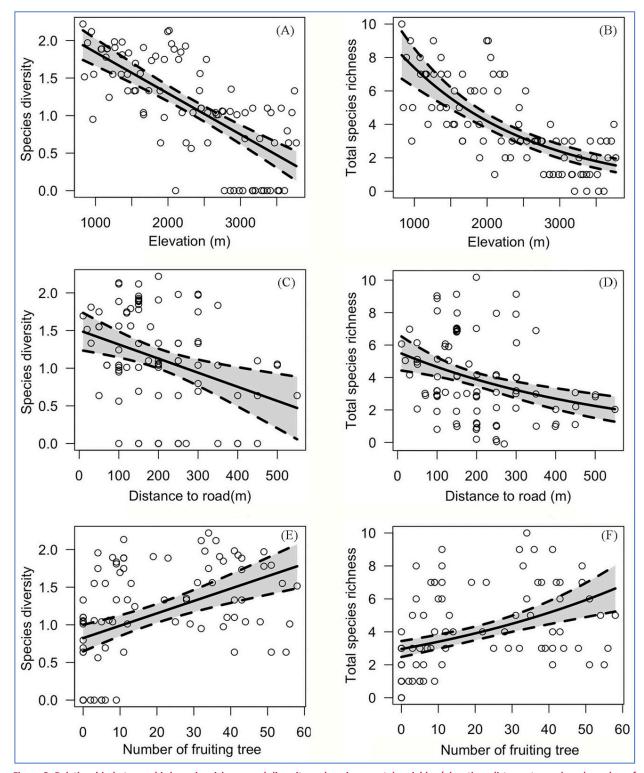


Figure 3. Relationship between bird species richness and diversity and environmental variables (elevation, distance to road, and number of fruiting trees) along an elevation gradient in the Kaligandaki River basin.

Granivore birds, represented by small number of species had no significant association (Trace= 0.459, F-ratio= 0.744, *P*= 0.828) with habitat types (Fig. 4D).

Omnivore birds depicted a significant relationship (Trace= 0.948, F-ratio= 1.351, *P*= 0.006) with habitat variables (Fig. 4E). Bird species like Oriental White-eye *Zosterops*



palpebrosos, Black Bulbul Hypsipetes leucocephalus, Asian Koel Eudynamys scolopacea, Scarlet Minivet Pericrocotus flammeus, Yellow-billed Blue Magpie Urocissa flavirostris, and Green Shrike Babbler Pteruthius xanthochlorus were associated with shrubland habitat. Similarly, bird species such as Common Tailorbird Orthotomus sutorius, Himalayan Bulbul Pycnonotus leucogenys, Red-billed Leiothrix Leothrix lutea, Beautiful Rosefinch Carpodacus pulcherrimus, and White-browed Fulvetta Alcippe vinipectus showed significant association with forest habitats. Very few species like Oriental Turtle Dove Streptopelia orientalis and Common Pigeon Columba livia showed association with other habitat variables such as scrubland, barren area and grassland habitat rather than forest and shrubland habitats. These variables appeared to have a strong impact on species distribution. Species richness in response to agricultural land as a habitat variable revealed very weak association.

DISCUSSION

Bird diversity in Kaligandaki River basin

This study recorded a highly diverse avian fauna dominated by Passeriformes in the Kaligandaki River basin. The high species richness might be attributed to habitat complexity/heterogeneity (MacArthur 1964; Pan et al. 2016; Hu et al. 2018) along an elevation gradient of the Kaligandaki River basin, comprising riverine Alnus nepalensis forest, Schima wallichi forest, mixed-forest with Tooni ciliata and Bombyx ceiba, Pinus roxburghii forest, Pinus wallichiana forest, Betula utilis forest including agricultural land, human settlement area, shrubberies, grassland and scrublands. The study area covered an elevation range of 800-3,800 m from subtropical to sub-alpine habitats supporting diverse avian fauna. At the lowest levels of the study area there were subtropical forests of broadleaved Schima wallichii, Castanopsis indica, and Pinus roxburghii on dry slopes, as well as Alder Alnus nepalensis, which mainly occurred along rivers and streams. Higher up were temperate forests of mixed broadleaves, oaks (Quercus lamellosa, Q. lanata, and Q. semecarpifolia) and rhododendrons. In the wettest places, bamboo jungles of Arundinaria species were dominant. Coniferous forests, mainly of Fir Abies spectabilis, Blue Pine Pinus wallichiana, and Hemlock Tsuga dumosa grow on the dry ridges and slopes. Above the temperate zone lie subalpine forests of Birch Betula utilis, blue pine, and junipers. Rhododendron and juniper scrub grow in the alpine zone (Inskipp & Inskipp 2003). Rivers and streams support a

good variety of birds dependent on this habitat, notably Crested Kingfisher *Megaceryle lugubris*, four forktail species, Brown Dipper *Cinclus pallasii*, White-capped Redstart *Chaimarrornis leucocephalus* and Plumbeous Water Redstart *Rhyacornis fuliginosa*. The combination of highly varied topography, climate and wide altitude range has resulted in many habitat types and associated rich bird species diversity within the study area.

The avian assemblage in any area or habitat type often changes seasonally (Avery & Riper 1989; Moning & Müller 2008; Collins & Edward 2014), under the influence of microclimatic and environmental factors like temperature, humidity, rainfall, and food availability. Birds typically migrate from north to south in the winter, and most arrive for breeding in Nepal in the summer. We observed no significant difference in species richness between summer (95 species) and winter (81 species).

Factors affecting bird diversity

We observed a decline in species richness with increasing elevation in the Kaligandaki River basin. Similar observations have been reported for other taxa and regions (Rahbek 1995, 2005; Basnet et al. 2016; Santillan et al. 2018), but the few studies in the Himalaya have reported high species richness at middle elevations compared to higher and lower elevations (Bhattarai & Vetaas 2006; Acharya et al. 2011; Joshi & Bhat 2015; Hu et al. 2018; Ding et al. 2019; Xingcheng et al. 2019; Pandey et al. 2020). Our result is in line with previous studies showing a decline of species richness along elevational gradients (McCain 2009; Santhakumar et al. 2018), which has been attributed to limiting abiotic and biotic factors, such as harsh climatic conditions or reduced resource availability at high elevations. As elevation increases, the vegetation types and land topography gradually change from lower sub-tropical to sub-alpine, with decreasing forest cover and increased low-productivity scrub and meadows. Observed species richness was highest at 850m and 2,000m within the study area. At 850m the dense well-structured subtropical forest of Schima wallichii, Alnus nepalensis, Bombyx ceiba, and Tooni ciliata harbored a higher number of species. Additionally, the riverine area and cultivated land with human settlement at this elevation supported more avian fauna than in the higher altitudes. In general, richness peaks at intermediate elevations appear to correspond closely to transition zones between different vegetation types (Lomolino 2001). At 2,000m around the Ghasa forest, the transition zone between the two forest types, the sub-tropical forest and temperate forest predominately with Pinus wallichiana



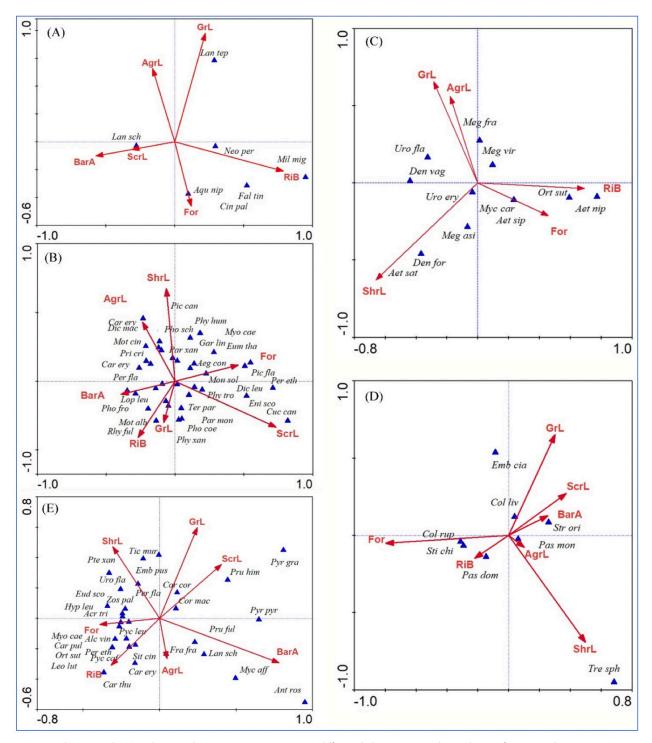


Figure 4. The CCA ordination diagram showing species response to different habitat types in the study area (Monte Carlo permutation test of significance with 499 permutations): A—carnivores | B—insectivores | C—frugivores | D—granivores | E—omnivores. Abbreviations: For—Forest habitat | RiB—River Bank | ShrL—Shrubland | GrL—Grassland | AgrL—Agricultural area | BarA—Barren area | ScrL—Scrubland. Triangle represents the particular species and the arrow indicates each of the habitat variables plotted to in the direction of maximum change in the explanatory variables. Species codes are given in Annex I.

might have contributed to the richness peak seen in this region. The gradual decline of species richness above 2,000 m might suggest an abrupt change in factors that

limit avian richness, including poor vegetation and harsh climatic conditions. At higher elevations the stature of the forest decreased dramatically, and the climatic



conditions became increasingly severe with heavy winds during summer and snowfall in winter. Such harsh and unproductive environment at higher altitudes cause a decline in abundance and distribution of invertebrate resources and scarcity of food items for birds, and favors a very small number of species (Blake & Loiselle 2000; Hu et al. 2018). Besides this, trees were replaced by bushes, shrubs and rocky-mountains, which negatively affected the avian fauna in this region.

Bird species richness and diversity suggested a positive association with the number of fruiting trees taken as proxy of resource availability within the study area. Food availability is considered one of the most important factors limiting bird richness and abundance (Strong & Sherry 2000; Wu et al. 2013; Douglas et al. 2014; Pan et al. 2016). As the number of fruiting trees increased, species richness was also higher, illustrating the positive impact of forest resources on avian diversity. This might be particularly a case for insectivorous species as the insectivore species constitute substantial pool of overall species richness. These results are consistent with previous studies which have supported the energy (resource)-diversity hypothesis (Hurlbert & Haskell 2003; Price et al. 2014; Pan et al. 2016), explaining that the sites with greater available energy can support more individuals and, hence, more species. Further, increase in number of trees provides food resources, roosting and nesting sites to most of the forest birds. Additionally, the fruiting trees with flowers, fruits, and seeds attract a number of insects and hence support the insectivores resulting in overall species richness increase. was a significant relationship between bird species assemblages and tree species assemblages in the eastern forests of North America (Lee & Rotenberry 2005). This is consistent with the findings that the species richness of insectivorous feeding guilds was associated to vegetation structure and invertebrate biomass, while the richness of frugivores was linked with fruit abundance, both supported by the forest stand and cover (Ferger 2014). The distribution and abundance of many bird species are determined by the configuration and composition of the vegetation (trees species and number) that comprises a major element of their habitat (Morrison 1992; Block & Brennan 1993). As number of trees stands changes along geographical and environmental gradients, any particular bird species may appear, increase in abundance, decrease, and fade as habitat becomes more or less suitable for its existence (Pidgeon et al. 2007).

The impacts of roads on wildlife populations are extensive and well documented around the globe (Fahrig & Rytwinski 2009). Distance to road as a representation

of disturbance variable with species richness and diversity was tested and strong negative correlation was observed, revealing increase in species richness near road and vice versa. Many studies on birds have shown negative association to the roads such that abundance, occurrence and species richness of birds are reduced near roads, with larger reductions near high-traffic roads than near lower traffic roads (Reijnen et al. 1995; Brotons & Herrando 2001; Fuller et al. 2001; Burton et al. 2002; Rheindt 2003; Peris & Pescador 2004; Pocock & Lawrence 2005; Palomino & Carrascal 2007; Griffith et al. 2010). Similar findings with road distance and species richness was discussed where empirical findings showed that there was a negative impact of roads and settlements on threatened birds of Chitwan National Park, Nepal (Adhikari et al. 2019). The main cause of the higher bird richness near roads in the Kaligandaki River basin may due to low traffic in newly constructed roads and sparse human settlements and movements. High species richness near the road may be due to higher detectability by the observers and possible preference of open habitats by the birds.

Habitat association of the birds

Canonical correspondence analysis showed that most of the feeding guilds including insectivores, omnivores and frugivores were associated with forest, shrubland, and agricultural area. The observed bird species preferred forest habitat in comparison to other habitat types within the study area. The main reason for such preference could be available resources supplement by forest area in comparison to other land use types. Forests provide the indispensable resources required for the accomplishment of life cycles of birds, including food for adults and nestlings and nesting sites. Avian fauna occurs on several trophic heights in forests from primary consumers to vertebrate predators, as well as omnivores and scavengers. Birds get nutrients from nectar, fruits, seeds, and vegetative tissues including roots, shoots, and leaves. Birds that consume the vegetative parts of plants may also supplement their diet with other sources of protein such as invertebrates found in different strata in forest habitat, supporting insectivore species (Stratford & Sekercioglu 2015). These findings are supported by many studies that explained increased structural complexity of vegetation is associated with increased avian species richness (MacArthur & MacArthur 1961; MacArthur et al. 1962; MacArthur et al. 1966; Orians & Wittenberger 1991).

One characteristic of forest structure is foliage height diversity and is defined by the variation in the layers



of a forest which positively supports species richness. Increasing foliage height diversity is associated with increasing avian diversity, particularly insectivores (MacArthur & MacArthur 1961; MacArthur et al. 1962), with increasing foraging sites and increased niches available to exploit (MacArthur et al. 1966). Another study of avian communities in urban parks across Beijing showed that the vegetation structure and foliage height diversity was the most important factor influencing avian species diversity than park area (Xie et al. 2016). Rompre et al. (2007) found that plant species richness, precipitation, forest age, and topography strongly affected avian diversity in lowland, Panama rain forests. In the present study, lower number of species in scrubland and barren area in higher altitudes (above 2,600m) could be attributed to scarce vegetation and low productivity due to climatic constraints. The presence of forest stands, forest edges and shrubs, therefore, supports more bird species are important factors in driving species composition (Basnet et al. 2016). Similar results were described in farmland in central Uganda, where richness of forest-dependent bird species showed a positive relationship with the number of native tree species (Douglas et al. 2014). Significant association of species with river bank area can be explained by the presence of aquatic avian fauna such as Brown Dipper Cinclus pallasii, Blue Whistling Thrush Myophonus caeruleus, Plumbeous Water Redstart Rhyacornis fuliginosa, White-capped Redstart Chaimarrornis leucocephalus, forktails, and wagtails dwelling near and around streams and rivers depending mostly on aquatic invertebrates in or under the water, river banks, and riverine vegetation. Study on Tibetan region of the Himalaya indicated that the species richness of overall birds is positively correlated with forest habitat, productivity, and habitat heterogeneity (Pan et al. 2016). Higher species richness in forest habitats especially in lower elevations and strong association of birds with fruiting trees for resource utilization along the Kaligandaki River basin indicate that the existing primary forest in the basin is important for avian conservation.

Our survey of birds during summer and winter showed highly diverse avian fauna, but it did not cover all seasons, nor all of the Annapurna Conservation Area. A more extensive study is recommended to more comprehensively explore avian species within this area. Apart from developing checklists of birds, studies of patterns and processes affecting species, and diversity of avian fauna in other parts of the conservation area are recommended to assist conservation efforts.

CONCLUSIONS

The Kaligandaki Valley river basin, an important part of the Annapurna Conservation Area, one of the IBAs in central Himalaya has highly diverse avian fauna dominated by Passeriformes. High abundance of resident insectivores does not bring much variation in species richness between summer and winter. Restrictive abiotic and biotic factors, such as harsh climatic conditions or reduced resource availability at high elevations, cause a decline in bird species richness with elevation. The number of fruiting trees has a positive influence on avian species richness and diversity.

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Annex I. Checklist of bird species from Kaligandaki River basin, Annapurna Conservation Area, Nepal

Order, Family, Common name	Scientific name	Feeding guild	Migratory status	Species code used in ordination
GALLIFORMES				
Phasianidae				
Black Francolin	Francolinus francolinus	Omnivore	Resident	Fra fra
Kalij Pheasant	Lophura leucomelanos	Insectivore	Resident	Lop leu
PICIFORMES				
Megalaimidae				
Blue-throated Barbet	Megalaima asiatica	Frugivore	Resident	Meg asi
Golden-throated Barbet	Megalaima franklinii	Frugivore	Resident	Meg fra
Great Barbet	Megalaima virens	Frugivore	Resident	Meg vir
Picidae				
Greater Yellownape	Picus flavinucha	Insectivore	Resident	Pic fla
Grey-headed Woodpecker	Picus canus	Insectivore	Resident	Pic can
Fulvous-breasted Woodpecker	Dendrocopos macei	Insectivore	Resident	Den mac
Speckled Piculet	Picumnus innominatus	Insectivore	Resident	Pic inn
CUCULIFORMES		ı	1	
Cuculidae				1
Eurasian Cuckoo	Cuculus canorus	Insectivore	Summer visitor	Cuc can
Lesser Cuckoo	Cuculus poliocephalus	Insectivore	Summer visitor	Cuc pol
Asian Koel	Eudynamys scolopaceus	Omnivore	Resident	Eud sco
COLUMBIFORMES				
Columbidae				
Common Pigeon	Columba livia	Granivore	Resident	Col liv
Hill Pigeon	Columba rupestris	Granivore	Resident	Col rup
Oriental Turtle Dove	Streptopelia orientalis	Granivore	Summer visitor	Str ori
Spotted Dove	Stigmatopelia chinensis	Granivore	Resident	Sti chi
Wedge-tailed green Pigeon	Treron sphenurus	Granivore	Resident	Tre sph
CICONIFORMES				
Scolopacidae				
Green Sandpiper	Tringa ochropus	Insectivore	Winter visitor	Tri och
ACCIPITRIFORMES				
Accipitridae				-
Black Kite	Milvus migrans	Carnivore	Winter visitor	Mil mig
Steppe Eagle	Aquila nipalensis	Carnivore	Winter visitor	Aqu nip
Egyptian Vulture	Neophron percnopterus	Carnivore	Resident	Neo per
FALCONIFORMES	1			
Falconidae				1
Common Kestrel	Falco tinnunculus	Carnivore	Winter visitor	Fal tin
PASSERIFORMES				
Prunellidae	1			1
Alpine Accentor	Prunella collaris	Omnivore	Resident	Pru col
Altai Accentor	Prunella himalayana	Omnivore	Winter visitor	Pru him
Brown Accentor	Prunella fulvescens	Omnivore	Winter visitor	Pru ful
Corvidae	ý -	1	1	. ,
Alpine Chough	Pyrrhocorax graculus	Omnivore	Resident	+



Order, Family, Common name	Scientific name	Feeding guild	Migratory status	Species code use in ordination
House Crow	Corvus splendens	Omnivore	Resident	Cor spl
Large-billed Crow	Corvus macrorhynchos	Omnivore	Resident	Cor mac
Northern Raven	Corvus corax	Omnivore	Resident	Cor cor
Red-billed Blue Magpie	Urocissa erythrorhyncha	Frugivore	Resident	Uro ery
Red-billed Chough	Pyrrhocorax pyrrhocorax	Omnivores	Resident	Pyr pyr
Rufous Treepie	Dendrocitta vagabunda	Frugivore	Resident	Den vag
Grey Treepie	Dendrocitta formosae	Frugivore	Resident	Den for
Yellow-billed Blue Magpie	Urocissa flavirostris	Frugivore	Resident	Uro fla
Dicruridae				
Ashy Drongo	Dicrurus leucophaeus	Insectivore	Summer visitor	Dic leu
Black Drongo	Dicrurus macrocercus	Insectivore	Resident	Dic mac
Spangled Drongo	Dicrurus hottentottus	Insectivore	Resident	Dic hot
Muscicapidae				
Asian Paradise-flycatcher	Terpsiphone paradisi	Insectivore	Summer visitor	Ter par
Blue-capped Redstart	Phoenicurus coeruleocephala	Insectivore	Winter visitor	Pho coe
Blue-fronted Redstart	Phoenicurus frontalis	Omnivore	Summer visitor	Pho fro
Common Stonechat	Saxicola torquatus	Insectivore	Resident	Sax tor
Himalayan Bluetail	Tarsiger rufilatus	Insectivore	Resident	Tar ruf
Hogdson's Redstart	Phoenicurus hodgsoni	Insectivore	Winter visitor	Pho hod
Little Forktail	Enicurus scouleri	Insectivore	Resident	Eni sco
Pied Bushchat	Saxicola caprata	Insectivore	Resident	Ѕах сар
Grey Bushchat	Saxicola ferreus	Insectivore	Resident	Sax fer
Plumbous Water Redstart	Rhyacornis fuliginosa	Insectivore	Resident	Rhy ful
Spotted Forktail	Enicurus maculatus	Insectivore	Resident	Eni mac
Verditer Flycatcher	Eumyias thalassinus	Insectivore	Summer visitor	Eum tha
White-capped Redstart	Chaimarrornis leucocephalus	Insectivore	Resident	Cha leu
White-browed Bush Robin	Tarsiger indicus	Insectivore	Resident	Tar ind
Oriental Magpie Robin	Copsychus saularis	Insectivore	Resident	Cop sau
White-tailed Rubythroat	Luscinia pectoralis	Insectivore	Resident	Lus pec
White-throated Redstart	Phoenicurus schisticeps	Insectivore	Winter visitor	Pho sch
Hirundinidae			ı	
Barn Swallow	Hirundo rustica	Insectivore	Resident	Hir rus
Fringillidae			l	
Beautiful Rosefinch	Carpodacus pulcherrimus	Omnivore	Summer visitor	Car pul
Collared Grosbeak	Mycerobas affinis	Omnivore	Resident	Myc aff
Common Rosefinch	Carpodacus erythrinus	Omnivore	Summer visitor	Car ery
Spot-winged Grosbeak	Mycerobas melanozanthos	Frugivore	Resident	Myc mel
White-browed Rosefinch	Carpodacus thura	Omnivore	Summer visitor	Car thu
White-winged Grosbeak	Mycerobas carnipes	Frugivore	Resident	Myc car
Pycnonotidae	<u>, </u>	1 -	1	1 '
Black Bulbul	Hypsipetes leucocephalus	Omnivore	Resident	Hyp leu
Himalayan Bulbul	Pycnonotus leucogenys	Omnivore	Resident	Pyc leu
Red-vented Bulbul	Pycnonotus cafer	Omnivore	Resident	Pyc caf
Timallidae	,,	1	1	. 70 000
Black-chinned Babbler	Stachyridopsis pyrrhops	Insectivore	Resident	Sta pyr



Order, Family, Common name	Scientific name	Feeding guild	Migratory status	Species code use in ordination
Green Shrike Babbler	Pteruthius xanthochlorus	Omnivore	Resident	Pte xan
Paridae				
Black-lored Tit	Parus xanthogenys	Insectivore	Resident	Par xan
Black-throated Tit	Aegithalos concinnus	Insectivore	Resident	Aeg con
Coal Tit	Periparus ater	Insectivore	Resident	Per ate
Great Tit	Parus major	Insectivore	Resident	Par maj
White-throated Tit	Aegithalos niveogularis	Insectivore	Resident	Aeg niv
Green-backed Tit	Parus monticolus	Insectivore	Resident	Par mon
Nectarinidae				
Black-throated Sunbird	Aethopyga saturata	Frugivore	Resident	Aet sat
Crimson Sunbird	Aethopyga siparaja	Frugivore	Resident	Aet sip
Fire-breasted Flowerpecker	Dicaeum ignipectus	Frugivore	Resident	Dic ign
Green-tailed Sunbird	Aethopyga nipalensis	Frugivore	Resident	Aet nip
Purple Sunbird	Nectarinia asiatica	Frugivore	Resident	Nec asi
Turdidae				
White-throated Laughingthrush	Garrulax albogularis	Insectivore	Resident	Gar alb
Blue-capped Rock Thrush	Monticola cinclorhynchus	Insectivore	Summer visitor	Mon cin
Blue Rock Thrush	Monticola solitarius	Insectivore	Summer visitor	Mon sol
Blue Whistling Thrush	Myophonus caeruleus	Omnivore	Resident	Муо сае
Streaked Laughing Thrush	Garrulax lineatus	Insectivore	Resident	Gar lin
Variegated Laughing Thrush	Garrulax variegatus	Insectivore	Resident	Gar var
Sylviidae		'		
Blyth's Leaf Warbler	Phylloscopus reguloides	Insectivore	Resident	Phy reg
Grey-hooded Warbler	Phylloscopus xanthoschistos	Insectivore	Resident	Phy xan
Greenish Warbler	Phylloscopus trochiloides	Insectivore	Resident	Phy tro
Hume's Leaf Warbler	Phylloscopus humei	Insectivore	Summer visitor	Phy hum
Lemon-rumped Warbler	Phylloscopus chloronotus	Insectivore	Winter visitor	Phy chl
Red-billed Leiothrix	Leiothrix lutea	Omnivore	Resident	Leo lut
Rufous Sibia	Malacias capistratus	Omnivore	Resident	Mal cap
Stripe-throated Yuhina	Yuhina gularis	Omnivore	Resident	Yuh gul
White-browed Fulvetta	Alcippe vinipectus	Omnivore	Resident	Alc vin
Yellow-browed Warbler	Phylloscoppus inornatus	Insectivore	Winter visitor	Phy ino
Cinclidae				
Brown Dipper	Cinclus pallasii	Insectivore	Resident	Cin pal
Laniidae				
Brown Shrike	Lanius cristatus	Carnivore	Winter visitor	Lan cri
Grey-backed Shrike	Lanius tephronotus	Carnivore	Summer visitor	Lan tep
Long-tailed Shrike	Lanius schach	Carnivore	Resident	Lan sch
Certhiidae	,	,		
Brown-throated Treecreeper	Certhia discolor	Insectivore	Resident	Cer dis
Sittidae				
Chestnut-bellied Nuthatch	Sitta cinnamoventris	Omnivore	Resident	Sit cin
Velvet-fronted Nuthatch	Sitta frontalis	Omnivore	Resident	Sit fro
Wall creeper	Tichodroma muraria	Omnivore	Winter visitor	Tic mur
Sturnidae	1			1



Order, Family, Common name	Scientific name	Feeding guild	Migratory status	Species code used in ordination			
Common Myna	Acridotheres tristis	Cmnivore	Resident	Acr tri			
Cisticilidae							
Common Tailorbird	Orthotomus sutorius	Insectivore	Resident	Ort sut			
Passeridae							
Eurasian Tree Sparrow	Passer montanus	Granivore	Resident	Pas mon			
House Sparrow	Passer domesticus	Granivore	Resident	Pas dom			
Russet Sparrow	Passer rutilans	Omnivore	Resident	Pas rut			
Motacillidae		,					
Grey Wagtail	Motacilla cinerea	Insectivore	Summer visitor	Mot cin			
Rosy Pipit	Anthus roseatus	Omnivore	Summer Visitor	Ant ros			
Olive-backed Pipit	Anthus hodgsoni	Insectivore	Winter visitor	Ant hod			
White Wagtail	Motacilla alba	Insectivore	Summer visitor	Mot alb			
White-browed Wagtail	Motacilla maderaspatensis	Insectivore	Resident	Mot mad			
Yellow Wagtail	Motacilla flava	Insectivore	Winter visitor	Mot fla			
Campephagidae							
Long-tailed Minivet	Pericrocotus ethologus	Insectivore	Resident	Per eth			
Scarlet Minivet	Pericrocotus flammeus	Insectivore	Resident	Per fla			
Zosteropidae							
Oriental White-eye	Zosterops palpebrosus	Omnivore	Resident	Zor pal			
Emberizidae							
Rock Bunting	Emberiza cia	Granivore	Resident	Emb cia			
Little Bunting	Emberiza pussila	Omnivore	Winter visitor	Emb pus			
Cisticolidae							
Striated Prinia	Prinia crinigera	Insectivore	Resident	Pri cri			
Rhipiduridae							
White-throated Fantail	Rhipidura albicollis	Insectivore	Resident	Rhi alb			
Yellow-bellied Fantail	Chelidorhynx hypoxantha	Insectivore	Summer visitor	Che hyp			



Image 1. Blue-throated Barbet Megalaima asiatica



Image 2. Egyptian Vulture Neophron percnopterus







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Addendum

Erratum and addenda to the article 'A history of primatology in India'

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