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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.
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 mid-elevation peak, and mid-elevation peaks. Of these, mid-elevation 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
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 30 m radius from the fixed point in a center, for 15 min. 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 nectar), 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 30 m 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:

\[ E = \frac{H'}{H'_{\text{max}}} \]

where,

- \( H' \) = Shannon-Wiener diversity index
- \( H'_{\text{max}} \) = 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,
however, the results lacked the statistical significance (Fig. 3E & F). The beta-coefficient or slope of elevation (β_{elevation}) was -0.48 (SE = 0.05) and distance to road (β_{distance to road}) was -0.22 (SE = 0.05). The slope estimates of number fruiting tree (β_{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).

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

| Seasons | Orders | Families | Species richness | C | # of individuals | H' | E |
|---------|--------|----------|-----------------|---|------------------|----|----|
| Summer  | 6      | 29       | 95              | 56| 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 |
|-----------------|---------------------------------------------|-----------------------------------------------|
|                 | 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 |

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 Black-throated 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).

### 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.
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*
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Goldie Ratcliffe, 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 suburban habitat. Similarly, bird species such as Common Tailorbird Orthotomus sutorius, Himalayan Bulbul Pycnonotus leucogenys, Red-billed Leiothrix Leiothrix lutea, Beautiful Rosefinch Carpodacus pulcherrimus, and White-browed Fulvetta Alcippe viniceps 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 suburban 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 wallichii 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 sub-tropical to sub-alpine habitats supporting diverse avian fauna. At the lowest levels of the study area there were sub-tropical 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 pallasi, 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 sub-tropical 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.
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. There was a significant relationship between bird species assemblages and forest 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). Rompré 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 pallasi, Blue Whistling Thrush Myophonus caerulescens, 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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| 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 |
| Kali Pheasant             | Lophura leucolophus | Insectivore | Resident | Lap leu |
| **PICIFORMES**            |                 |               |                  |                                 |
| Megalaimidae              |                 |               |                  |                                 |
| Blue-throated Barbet      | Megalaima asiatica | Frugivore | Resident | Meg asi |
| Golden-throated Barbet    | Megalaima franklini | Frugivore | Resident | Meg fra |
| Great Barbet              | Megalaima virens | Frugivore | Resident | Meg vir |
| Picidae                   |                 |               |                  |                                 |
| Greater Yellow-nape       | Picus flavinucha | Insectivore | Resident | Pic fla |
| Grey-headed Woodpecker    | Picus canus     | Insectivore | Resident | Pic can |
| Fulvous-breasted Woodpecker| Dendrocolius macei | Insectivore | Resident | Den mac |
| Speckled Piculet          | Picumnus innominatus | Insectivore | Resident | Pic inn |
| **CUCULIFORMES**          |                 |               |                  |                                 |
| Cuculidae                 |                 |               |                  |                                 |
| Eurasian Cuckoo           | Cuculus canorus | Insectivore | Summer visitor | Cuc can |
| Lesser Cuckoo             | Cuculus poiocephalus | 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 ru |
| 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**         |                 |               |                  |                                 |
| Falconidae                |                 |               |                  |                                 |
| Common Kestrel            | Falco trinunculus | Carnivore | Winter visitor | Fal tin |
| **PASSERIFORMES**         |                 |               |                  |                                 |
| Prunellidae               |                 |               |                  |                                 |
| Alpine Accentor           | Prunella collaris | Omnivore | Resident | Pru col |
| Altaic Accentor           | Prunella himalayan | Omnivore | Winter visitor | Pru him |
| Brown Accentor            | Prunella fulvescens | Omnivore | Winter visitor | Pru ful |
| Corvidae                  |                 |               |                  |                                 |
| Alpine Chough             | Pyrrhocorax graculus | Omnivore | Resident | Pyr gra |
| Order, Family, Common name | Scientific name | Feeding guild | Migratory status | Species code used 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 flavivora | Frugivore | Resident         | Uro fla                       |
| **Dicruridae**            |                 |               |                  |                               |
| Ashy Drongo               | Dicrurus leucophaeus | Insectivore | Summer visitor  | Dic leu                       |
| Black Drongo              | Dicrurus macrorhynchos | Insectivore | Resident         | Dic mac                       |
| Spangled Drongo           | Dicrurus hottentottus | Insectivore | Resident         | Dic hot                       |
| **Muscicapidae**          |                 |               |                  |                               |
| Asian Paradise-flycatcher | Terpsiphone paradisi | Insectivore | Summer visitor  | Ther paradisi                 |
| Blue-capped Redstart      | Phoenicurus coereacephala | Insectivore | Winter visitor  | Pho coe                       |
| Blue-fronted Redstart     | Phoenicurus frontalis | Omnivore | Summer visitor  | Pho fra                       |
| Common Stonechat          | Saxicola torquatus | Insectivore | Resident         | Sax tor                       |
| Himalayan Bluetail        | Tarsiger rufilatus | Insectivore | Resident         | Tar ruf                       |
| Hodgson’s Redstart        | Phoenicurus hodgsoni | Insectivore | Winter visitor  | Pho hod                       |
| Little Forktail           | Enicurus sculieri | Insectivore | Resident         | Eni sco                       |
| Pied Bushchat             | Saxicola caprata | Insectivore | Resident         | Sax cap                       |
| Grey Bushchat             | Saxicola ferreus | Insectivore | Resident         | Sax fer                       |
| Plumbous Water Redstart   | Rhycornis fuliginosa | Insectivore | Resident         | Rhy ful                       |
| Spotted Forktail          | Enicurus maculatus | Insectivore | Resident         | Eni mac                       |
| Venditer Flycatcher       | Eumyias tholassinus | 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     | Copyschus 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**          |                 |               |                  |                               |
| Barn Swallow              | Hirundo rustica | Insectivore | Resident         | Hir rus                       |
| **Fringillidae**          |                 |               |                  |                               |
| 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 melanoaanthos | Frugivore | Resident         | Myc mel                       |
| White-browed Roselinfch   | Carpodacus thura | Omnivore      | Summer visitor  | Car thu                       |
| White-winged Grosbeak     | Mycerobas carnipes | Frugivore | Resident         | Myc car                       |
| **Pycnonotidae**          |                 |               |                  |                               |
| Black Bulbul              | Hypsipetes leucocephalus | Omnivore | Resident         | Hyp leu                       |
| Himalayan Bulbul          | Pycnonotus leucogenys | Omnivore | Resident         | Pyc leu                       |
| Red-vented Bulbul         | Pycnonotus cafrenis | Omnivore | Resident         | Pyc caf                       |
| **Timaliidae**            |                 |               |                  |                               |
| Black-chinned Babbler     | Stachyridopsis pyrrhops | Insectivore | Resident         | Sta pyr                       |
| Order, Family, Common name | Scientific name | Feeding guild | Migratory status | Species code used in ordination |
|---------------------------|----------------|---------------|-----------------|--------------------------------|
| Paridae                   |                |               |                 |                                |
| Black-lored Tit           | Pteruthius xanthochlorus | Omnivore | Resident | Pte xan |
| Black-throated Tit        | Aegithalos cancinus | Insectivore | Resident | Aeg can |
| Coal Tit                  | Perijparus ater  | Insectivore | Resident | Per ate |
| Great Tit                 | Parus major     | Insectivore | Resident | Par maj |
| White-throated Tit        | Aegithalos niveagularis | 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 sivaraja | Frugivore | Resident | Aet siv |
| 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 albochularis | 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     | Myiophonus caeruleus | Omnivore | Resident | Myo cae |
| 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 xanthochistis | 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 viniecutus | Omnivore | Resident | Alc vin |
| Yellow-browed Warbler     | Phylloscopus inornatus | Insectivore | Winter visitor | Phy ino |
| Cinclidae                 |                |               |                 |                                |
| Brown Dipper              | Cinclus pallasi | Insectivore | Resident | Cin pal |
| Laniidae                  |                |               |                 |                                |
| Brown Shrike              | Lonius cristatus | Carnivore | Winter visitor | Lan cri |
| Grey-backed Shrike        | Lonius tephonotus | Carnivore | Summer visitor | Lan tep |
| Long-tailed Shrike        | Lonius schach   | Carnivore | Resident | Lan sch |
| Certhiidae                |                |               |                 |                                |
| Brown-throated Treecreeper| Certhia discolor | Insectivore | Resident | Cer dis |
| Sittidae                  |                |               |                 |                                |
| Chestnut-bellied Nuthatch | Sitta cinnamosventris | Omnivore | Resident | Sit cin |
| Velvet-fronted Nuthatch   | Sitta frontalis | Omnivore | Resident | Sit fro |
| Wall creeper              | Tichodroma muraria | Omnivore | Winter visitor | Tic mur |
| Order, Family, Common name | Scientific name | Feeding guild | Migratory status | Species code used in ordination |
|----------------------------|-----------------|---------------|------------------|--------------------------------|
| Common Myna                | Acridotheres tristis | Cnivore       | Resident         | Acr tri                        |
| Cisticilidae               | Orthotomus sutorius | Insectivore   | Resident         | Ort sut                        |
| Eurasian Tree Sparrow      | Passer montanus | Granivore     | Resident         | Pas mon                        |
| House Sparrow              | Passer domesticus | Granivore     | Resident         | Pas dom                        |
| Russet Sparrow             | Passer rustians | Omnivore      | Resident         | Pas rut                        |
| Passeridae                 | Orthotomus sutorius | Insectivore   | Resident         | Ort sut                        |
| Eurasian Tree Sparrow      | Passer montanus | Granivore     | Resident         | Pas mon                        |
| House Sparrow              | Passer domesticus | Granivore     | Resident         | Pas dom                        |
| Russet Sparrow             | Passer rustians | Omnivore      | Resident         | Pas rut                        |
| Motacillidae               | Motacilla cinerea | Insectivore   | Summer visitor   | Mot cin                        |
| Rosy Pipit                 | Anthus raseatus  | 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 maderspatensis | Insectivore   | Resident         | Mot mad                        |
| Yellow Wagtail             | Motacilla flavia | Insectivore   | Winter visitor   | Mot fla                        |
| Campephagidae              | Pericrocotus ethologus | Insectivore | Resident         | Per eth                        |
| Scarlet Minivet            | Pericrocotus flammeus | Insectivore | Resident         | Per fla                        |
| Zosteropidae               | Zosterops palpebrosus | Omnivore   | Resident         | Zor pal                        |
| Emberizidae                | Emberiza cia     | Granivore     | Resident         | Emb cia                        |
| Little Bunting             | Emberiza pussila | Omnivore      | Winter visitor   | Emb pus                        |
| Cisticolidae               | Prinia crinigera | Insectivore   | Resident         | Pri cri                        |
| Rhipiduridae               | Rhipidura albicollis | Insectivore | Resident         | Rhi alb                        |
| Yellow-bellied Fantail     | Chelidorhynx hypoxantha | Insectivore | Summer visitor   | Che hyp                        |
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Addendum

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