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Conservation status affects elevational gradient in bird diversity in the Himalaya: A new perspective

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ABSTRACT

Understanding diversity patterns along altitudinal gradients, and their underlying causes are important for conserving biodiversity. Previous studies have focused on climatic, energetic, and geographic variables (e.g., mid-domain effects), with less attention paid to human-induced habitat modifications. We used published data of bird distributions along an elevational gradient (0–4900 m) in the Nepalese Himalaya and interpolated species presence between elevational limits. The relationship between species richness and environmental variables was analyzed using generalized linear models. A low plateau relationship between bird richness and elevation was observed, with a main peak at intermediate elevations (2800 m). Across the total gradient, interpolated bird species richness had a unimodal relationship to maximum monthly precipitation and a linear response to seasonal variation in temperature, proportion of forest cover, and proportion of protected area. In lower elevations (0–2800 m), interpolated species richness had a positive and linear response to the proportion of Ramsar sites and a unimodal response to habitat heterogeneity. At higher elevations (2900–4900 m), interpolated bird richness had a positive linear response to monthly variation in temperature and a negative linear response to proportion forest cover. We conclude that factors related to human management are important drivers of elevational gradients in bird species richness.

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1. Introduction

Altitudinal gradients of species diversity have recently been a focus of biogeographical research in the Himalaya. Many such studies have reported a hump-shaped relationship between species richness and elevation, with a peak of species richness at intermediate elevations between 1500 and 3250 m (e.g. Grytnes and Vetaas, 2002; Bhattarai et al., 2004; Bhattarai and Vetaas, 2006; Vetaas and Grytnes, 2002; Grau et al., 2007; Baniya et al., 2010; Acharya et al., 2011). Various hypotheses have been proposed to explain the observed altitudinal richness patterns. One of the most common hypotheses is the mid-domain effect (MDE) (Colwell et al., 2004; McCain and Grytnes, 2010). The MDE suggests that a hump-shaped relationship between species richness and elevation is statistically inevitable when ranges of species are randomly placed within a bounded geographical domain (e.g., “hard boundaries” where mountain tops are the upper boundaries and valley bottoms are the lower boundaries) (Colwell and Lees, 2000). In contrast, environmental factors such as patch size, habitat

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heterogeneity, energy availability, and climatic variability have been proposed as explanations for observed altitudinal gradients in diversity (Rosenzweig, 1995; Körner, 2000; Hawkins et al., 2003). However, no attempt has been made to assess anthropogenic factors (e.g., protected area coverage, human population density, habitat heterogeneity, etc.) that might influence the observed distributional patterns of species richness across large gradients (see Grytnes and Vetaas, 2002; Hawkins et al., 2003; Storch et al., 2003; Bhattarai et al., 2004; Bhattarai and Vetaas, 2006; Grau et al., 2007; Baniya et al., 2010; Acharya et al., 2011; Wu et al., 2013). This is an important area of investigation because no region exists without human influences (Pimm et al., 1995) and high species richness is maintained in many areas by conservation measures such as establishing networks of protected areas (Chown et al., 2003).

Himalayan landscapes have a very high degree of heterogeneity, resulting from high elevational variation (<8848 m) over short distances (<200 km). The cumulative area of each elevational zones decreases with increasing altitude. The species–area relationship (SAR) predicts that as the area of a region increases the number of species will also increase (MacArthur and Wilson, 1967). This may result in having more species at low altitudes and therefore the effect of area must be considered in studies on elevational gradients of species richness (Rahbek, 1997; Brehm et al., 2007). Other non-biological factors such as the MDE have been suggested as important determinants of the species richness along elevational gradients (Colwell and Lees, 2000). However, little research has assessed anthropogenic factors that might relate to elevational gradients of species richness. Here we examine gradient of species richness accounting for possible environmental variables including human influences (e.g., climatic, habitat, energy, conservation practice, human disturbance—see Table 1).

Himalaya is a large mountain arc that extends for 2500 km from the Nanga Parbat mountain (8125 m) and the Indus River Gorge in the northwest to the Namche Barwa mountain (7756 m) and the Yarlungtsangpo–Brahmaputra River Gorge in the east (Ives, 2004). Nepal is situated in the central part of the Himalaya, and occupies about one-third of entire Himalayan range. Nepal has an extreme elevational gradient (67–8848 m) within a short distance (~200 km) and therefore has received thorough attention from scholars, conservation practitioners and development agency personnel to support or refute conservation theories pertaining to Himalaya (Ives, 2004).

Studies on species richness along elevational gradients of the Nepalese Himalaya have been conducted on ferns (Bhattarai et al., 2004), lichens (Baniya et al., 2010), orchids (Acharya et al., 2011), trees (Bhattarai and Vetaas, 2006) and liverworts (Grau et al., 2007). No studies to our knowledge have compared possible drivers of species richness including human footprint intensity (e.g., human population density) and conservation status (protected areas). Birds are better studied than other taxonomic groups in terms of their habitat preferences and elevational limits (Both et al., 2006). Therefore, we seek to examine diversity patterns of birds along elevational gradients and assess the hypothesis that human actions define patterns of species diversity.

2. Materials and methods

2.1. Study area

The study covers Nepal (26°22′–30°27′N, 80°4′–88°12′E), a mountainous country in the central Himalaya. Physiographic divisions of Nepal are based on the three main mountain ranges, which have average altitudes increasing from south to north (Fig. 1). In the southern part of the Nepalese Himalaya is a flat lowland strip (25–32 km wide) called the Terai (Fig. 1). The physiography of the Terai is similar to the Indo-Gangetic plain and has a tropical climate at 60–300 m elevation. To the north of this flatland, the Siwalik hills rise abruptly to an elevation of 700–1500 m and are characterized by a subtropical climate. These constitute the youngest Himalayan range and are composed of sedimentary rock of Oligocene to Pleistocene ages (Hagen, 1969). North to the Siwaliks is the Mahabharat Range, which rises from 1500 to 2700 m elevation, and is characterized by a subtropical climate in the low altitudes and a temperate climate at higher altitudes. The midlands of Nepal lie north of the Mahabharat range at an average altitude of 2000 m. The Himalayas (3000–8000 m) are north of the midlands and consist of some of the highest peaks in the world (Fig. 1). Nepal alone claims eight out of the top ten tallest mountains in the world, including Mount Everest (8848 m). The Himalayan ranges grade into the Tibetan Plateau to the north, i.e. Trans-Himalayan zone, with a climate and vegetation similar to that of the Tibetan Plateau (Hagen, 1969). Therefore, Nepal provides a unique assemblage of different habitats and a great biodiversity within a small geographical area. It covers slightly less than 0.1% of the global land area but supports a disproportionately large diversity of plants and animals. The country's 118 ecosystems harbor over 2% of the flowering plants, 3% of the pteridophytes, and 6% of the bryophytes in the world's flora. The country also harbors 3.9% of the mammals, 8.9% of the birds, and 3.7% of the world's fauna of butterflies (Paudel et al., 2012).

2.2. Data sources

We used the bird distribution data from 'Birds of Nepal' (Grimmett et al., 2000) and 'The State of Nepal's Birds' (BCN and DNPWC, 2011). These are the most reliable and up-to-date sources and are based on extensive field studies. Altogether 867 birds species are recorded in Nepal (BCN and DNPWC, 2011), some of them are rare and lack detailed information (Carol Inskipp, pers. comm.). 'Birds of Nepal' by Grimmett et al. (2000) provides elevational ranges for 760 species of birds. Most of the rare birds of Nepal are described in the 'The State of Nepal's Bird' (BCN and DNPWC, 2011). Therefore, Grimmett

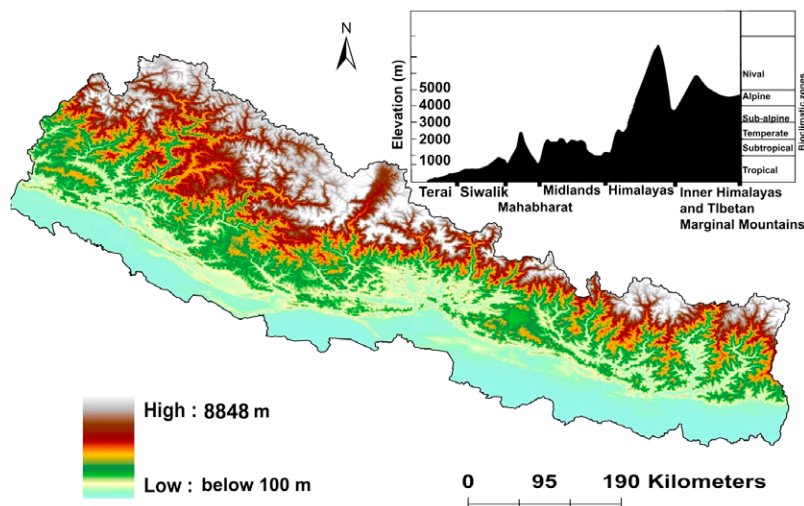


Fig. 1. Digital elevation map of Nepal (source: ASTER GDEM version 2; ASTER GDEM is a product of METI and NASA). (Inset: Bioclimatic and physiographic zones of Nepal).

Table 1

Definitions and descriptions of the environmental variables included in the analysis^a.

Environmental variables (abbreviation) [source; DDA (date of data acquisition)]	Description
1. Climatic variable^b [(Hijmans et al., 2005); DDA-1950–2000]	
1.1 Mean annual temperature (MAT)	Average of mean temperature of 12 months
1.2 Mean temperature of the coldest month (MTCM)	Average of mean temperature of January
1.3 Mean temperature of the warmest month (MTWM)	Average of mean temperature of June
1.4 Monthly variation in temperature (MVT)	Variation in mean temperature of 12 months
1.5 Seasonal variation in temperature (SVT)	Variations in average of mean temperature of four seasons
1.6 Mean annual precipitation (MAP)	Average of mean precipitation of 12 months
1.7 Maximum monthly precipitation (MxMP)	Average of mean precipitation of July
1.8 Minimum monthly precipitation (MnMP)	Average of mean precipitation of November
1.9 Seasonal variation in precipitation (SVP)	Variation in mean precipitation of four seasons
1.10 Monthly variation in precipitation (MVP)	Variation in mean precipitation of 12 months
2. Habitat variable [Roy et al., 2003; DDA-2000]	
2.1 Proportion of wetlands (ProFW)	Proportion of area covered by wetlands
2.2 Proportion of forests (ProF)	Proportion of area covered by forests
2.4 Proportion of bushes and grasslands (Probg)	Proportion of area covered by bushes and grasslands
3. Energy [(Jenkerson et al., 2010); DDA-2009]	
3.1 Normalized Difference Vegetation Index (NDVI)	Total value of Normalized Difference Vegetation Index standardized by area of respective elevation zone
4. Conservation Practice	
4.1 Proportion of protected areas (ProPAs) ^c [(MENRIS/ICIMOD, 2013); DDA-2003]	Proportion of area occupied by protected areas
4.1 Proportion of Ramsar sites (ProRSZ) [Primack et al., 2013; DDA-2003, 2007]	Proportion of area covered by Ramsar sites
4.3 Proportion of Ramsar sites by wetlands (ProRSW) [Primack et al., 2013, DDA-2003, 2007]	Proportion of wetland covered by Ramsar sites
5. Human disturbance	
5.1 Population density (PoDen) [(MENRIS/ICIMOD, 2013); DDA-2001]	Sum of kernel density value divided by area of respective elevation zone
5.2 Habitat heterogeneity (HaH) [Roy et al., 2003; DDA-2000]	Sum of habitat heterogeneity value divided by area of respective elevation zone
5.3 Proportional of settlements (ProS) [Roy et al., 2003; DDA-2000]	Proportion of area covered by settlement and agricultural land

^a All environmental variables were calculated for each of 49 elevation zones.

^b Four seasons: winter—December, January, February; summer—March, April, May; rainy—June, July, August; Autumn—September, October, November.

^c According to National Parks and Wildlife Conservation Act of 1976, Nepal designates following categories of protected areas: national park, wildlife reserve, hunting reserve and conservation area.

et al. (2000) and BCN and DNPWC (2011) are considered adequate for the large-scale study of bird richness patterns in the Nepalese Himalaya. We excluded birds reported as extinct in Nepal and birds with undetermined elevational limits. We prepared a checklist of 850 species of bird that have a well-defined elevational range for data analysis.

The elevation gradient of the Nepalese Himalaya (0–4900 m; Fig. 1) was divided into 49 100 m elevational zones. A species was assumed to be present in each 100 m interval between its upper and lower elevation limits (e.g., Bhattarai et al., 2004; Grau et al., 2007; Beck and Kitching, 2009; Baniya et al., 2010; Acharya et al., 2011; Trigas et al., 2013; Wu et al., 2013). A species with an elevation range between 90 and 335 m, for example, was assumed to be occurred in the elevation zones 100 (0–100 m), 200 (100–200 m), 300 (200–300 m), and 400 (300–400 m). Such an approach was applied only for those species that have continuous distributions between their upper and lower elevational limits. This method is robust to sampling biases because it is not influenced by sampling intensity (i.e. presence/absence cases only were considered) and (2) gaps in recorded distribution are highly likely to be pseudo-absence cases driven by low detection probabilities (Grytnes and Vetaas, 2002; McCain and Grytnes, 2010; Beck et al., 2013).

We derived a set of environmental variables for each of the 49 elevational zones, measuring climate, habitat, conservation status, and human disturbance metrics (Table 1) to investigate their influence on interpolated bird species richness. The Normalized Difference Vegetation Index (NDVI) was used as a measure of energy availability. It is strongly and positively correlated with green leaf biomass, green-leaf area, and absorbed photosynthetically active radiation. Studies have shown that NDVI values are highly correlated with bird richness (Seto et al., 2004). The 16-day maximum value composites of 250-m MODIS (Jenkinson et al., 2010) NDVI data covering the whole of Nepal from July 2011 were obtained from the USGS MODIS data archive (<http://mrtwebdistro.cr.usgs.gov>). In Nepal, more than 80% of precipitation occurs during the monsoon from early June to October (Das, 1972). By July, the monsoon covers all of Nepal and thus this time is suitable for a good approximation of NDVI values of the country.

We obtained climate data from WorldClim (Hijmans et al., 2005, version 1.4; <http://www.worldclim.org>). WorldClim provides spatial data of mean temperature, minimum temperature, maximum temperature and precipitation for each month at 1 km × 1 km resolution. We are aware that considerable variations in temperature can occur within 1 km², especially in Himalaya. We, however, used the WorldClim data for several reasons: (1) weather stations are not uniformly distributed across the Himalayan elevational gradient; (2) WorldClim generates environmental data through interpolation of average monthly climate data from nearby weather stations (Hijmans et al., 2005) and many studies have shown that WorldClim data are correlated with the measured temperature data (Dunn et al., 2007; Machac et al., 2011); (3) we used averaged climatic data for each of 49 elevational zone from WorldClim that sufficiently depict the pattern of climatic gradient across the Himalayan elevational gradient; (4) use of WorldClim data is common to other studies of elevational diversity gradients (McCain, 2009; Machac et al., 2011), which is comparable to our study.

We extracted the value of each grid cell and calculated 10 climatic variables for each of the 49 elevational zones of Nepal (see Table 1 for details). A land cover map for Nepal was obtained from Joint Research Center of European Commission (<http://bioval.jrc.ec.europa.eu/products/glc2000/products.php>) (Roy et al., 2003). We reclassified 27 land use types into forest, grasslands and bushes and human settlements (including agriculture land) and calculated the proportion of area occupied by each category for all elevational zones.

A map of habitat heterogeneity of entire Nepal was developed using land cover map of Nepal (Roy et al., 2003). Habitat heterogeneity is defined as the total number of unique habitats present in a window size of 25 pixels (25 km²). Thus, the maximum heterogeneity value is 25, which is equivalent to 27 land use classes used in the map. We applied a 'Variety' function' in the focal statistics tool of ArcGIS to generate a layer of habitat heterogeneity of Nepal.

Aerial photograph (Department of Survey of Nepal) and a river map from ICIMOD's MENRIS website (MENRIS/ICIMOD, 2013, <http://geoportal.icimod.org/Downloads>) were used to update the wetland map of Nepal. Maps of Ramsar sites in Nepal were not available. Ramsar sites are unique wetland ecosystems of both national and global significance and listed under the Ramsar convention. Such sites are not always protected areas but are expected to meet certain conservation standards. We obtained a land-use map of certain parts of Nepal covering Ramsar sites from Department of Survey of Nepal. We updated the map of protected areas (Primack et al., 2013) of Nepal from ICIMOD's MENRIS website (<http://geoportal.icimod.org/Downloads/>).

We obtained a human settlement map from MENRIS/ICIMOD (2013). The map provides information on the human population of all municipalities as point features. We used a 'Kernel Density Function' in ArcGIS to generate a continuous-field surface showing the density of human population throughout the country. The 'Kernel' function approximates a Gaussian distribution that assigns greater importance to values near the 'kernel' center. A bandwidth of 1000 m (1 km) was used to make data resolution comparable with climatic data.

2.3. Data analysis

We used a generalized linear model with Poisson quasi-likelihood function to regress bird richness as a response variable against area (transformed up-to third-order polynomial) as an explanatory variable. Area of elevation zones explained 13% of variability of interpolated bird species richness. Species richness tends to increase as a function of area (e.g. Gleason, 1922; Rahbek, 1997). To eliminate the effect of area in species–elevation relationship, we used Pearson's residuals from the model as a response variable. Similarly, we developed a null model from 1000 Monte Carlo simulations of empirical range size without replacements using MS Excel "add-ins" "mid-domain null" (Fig. 3) (McCain, 2004). It provides a simple

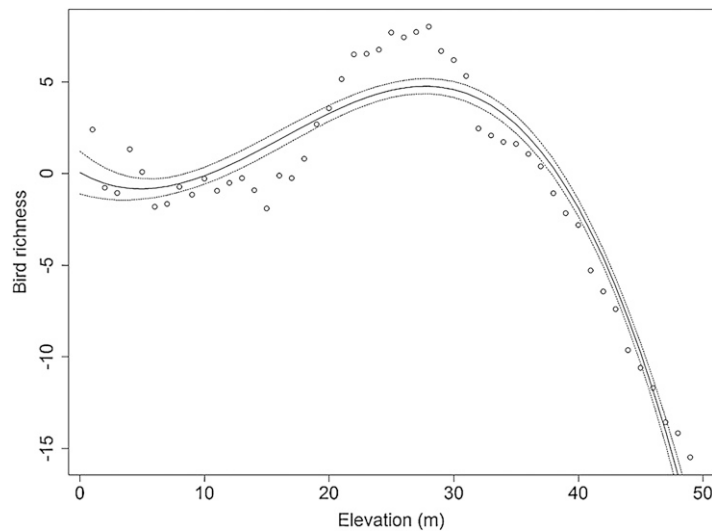


Fig. 2. Relationship between interpolated bird species richness and elevation in 100 m elevation zones along the Nepal Himalayan elevational gradient. Dependent values are Pearson's residuals from the GLM model with interpolated bird richness as a response variable and area as an explanatory variable. Therefore axis labeling is different. The fitted line represents a generalized linear model with a cubic spline, $P < 0.001$, see Table 1 for summary statistics.

non-biological explanation of mid elevation peaks of species richness without accounting influences of the environmental variation. In our data, interpolated bird richness decreased slightly up to 900 m and increased abruptly afterwards, showing a mid-elevation peak at around 2800 m (Fig. 2). We assumed that influences of environmental factors on the richness pattern are not the same in all gradients in the Himalaya (Bhattarai et al., 2004). Therefore, we divided the total elevational gradient into two sub-gradients: (1) an elevational zone from 0–2800 m (lower sub-gradient) and (2) an elevational zone from 2900–4900 m (upper sub-gradient) (Fig. 2). We used the following methods to identify uncorrelated but important combinations of variables predicting species richness for total, lower and upper elevational gradients: First, we arranged the dataset into two sub-gradients and a total gradient. For each of the three datasets, we used a GLM with Gaussian quasi-likelihood function to relate the residuals of species–area correlations as response variables with each of environmental variable. Altitude was the first variable in all models to remove its influence. We used F-test to assess significance of association and calculated partial R^2 values between interpolated species richness and environmental variables. Second, we tested multicollinearity among environmental variables using a Kendall test. Highly correlated environmental variables artificially improve the model and therefore selection of variables that are not significantly correlated is important before preparing a final statistical model (Jongman et al., 1995). A Bonferroni correction was used to account for family-wise error rate which allows measurement of a corrected significance level for each correlation by testing each individual at a significance level of α/n (where α is significance level, n is number of sample) (Dunnnett, 1955). Third, we selected those variables that had a high partial R-square value from the correlated environmental variables. We selected maximum monthly precipitation (MxMP), proportion of forest (ProF), seasonal variation in temperature (SVT), and proportion of protected areas (ProPAs) for the total gradient, proportion of Ramsar site by elevation zone (ProRSZ) and habitat heterogeneity (HaH) for the lower sub-gradient (0–2800 m), and monthly variation in temperature (MVT) and ProF for the upper sub-gradient (2900–4900 m) (see Table 1 for details of variables).

Finally, we used a GLM with Gaussian quasi-likelihood function to regress residual of the species–area correlation against selected environmental variables for the total and sub gradients. Altitude was the first variable in all models to remove variability. We used partial residual plots (Larsen and McCleary, 1972) with controlling effects of all the other variables to portray relationships between the individual predictors and interpolated species richness. Spatial autocorrelation may affect observed patterns of species richness, especially in elevational gradients (Kühn, 2007). In our data, altitudinal gradients explained 86% of variability for interpolated species richness. The Mantel test did not identify significant spatial autocorrelation in our GLM after we removed the effect of area in different altitudes. Residuals of the models were tested for outliers, and the significant extreme observation was removed from all models. We used outlier.test in R to calculate Bonferroni p -values for the largest absolute studentized residuals.

3. Results

3.1. Pattern of interpolated bird species richness

We observed a significant positive association between interpolated species richness and our mid-domain null model when the effect of area was taken into account in the model ($R^2 = 0.61$, $P < 0.001$). But this association was not significant

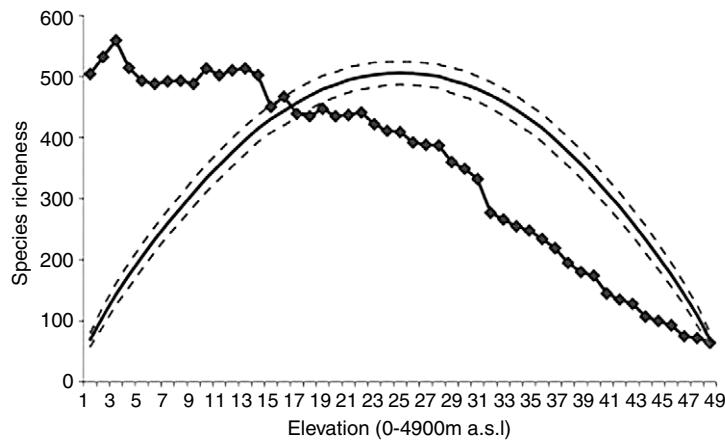


Fig. 3. A null model developed by a Monte Carlo algorithm with 5000 simulations of empirical range sizes without replacement (dark solid line) (McCain, 2004). Plotted line with dark markers depicts the empirical species richness pattern. Numbers in x-axis denote elevation band of 100 m interval ranging from 100 m to 4900 m.

Table 2

Results from GLM (depicted in Fig. 4)—interpolated bird species richness along total gradient in relation to elevation (SN), maximum monthly precipitation (MxMP), seasonal variation in temperature (SVT), proportion of forest (ProF) and proportion of protected areas (ProPAs). Relationship between environmental variables and interpolated bird richness was best explained by higher order polynomial functions. Degree of smoothness was estimated using the generalized cross-validation criterion. “bs” represents “B-Spline”.

Parameters	d.f.	Deviance	Residual d.f.	Residual deviance	F	P
NULL			46	1355.94		
bs (SN)	3	911.3	43	444.24	752.74	<0.001
bs (MxMP)	3	173.64	40	270.6	143.36	<0.001
bs (proF)	3	173.68	37	96.92	143.39	<0.001
bs (SVT)	3	77.49	34	19.43	63.98	<0.001
bs (ProPAs)	3	6.91	31	12.52	5.70	0.003

when the effect of area was not considered ($R^2 = 0.22$, $P = 0.115$). Interpolated bird species richness showed a low plateau pattern with a broad peak at 2800 m ($F_{3,43} = 103.64$, $P < 0.001$) (Fig. 2). Thus, there were two clear trends: (1) high diversity between 0 and 2800 m, where interpolated species richness showed monotonic decrease with increasing elevation up to 900 m and then increased attaining the highest peak at an elevation of ca. 2800 m. This trend was significant along the elevation gradient ($F_{3,24} = 14.15$, $P = 0.001$) (Fig. 2). (2) In the upper sub-gradient (2900–4900 m), there was a significant and monotonically decreasing trend of the interpolated species richness along the elevational gradient ($F_{3,15} = 17.60$, $P < 0.001$) (Fig. 2). The maximum modeled and observed bird richness occurred approximately at the same altitude (2800–2900 m) (Fig. 2).

3.2. Effect of environmental variables on the interpolated species richness pattern

The most parsimonious combination of environmental variables to explain variability of interpolated bird richness along Himalayan elevation gradient is given in Table 2. For the total gradient, interpolated bird richness had a unimodal relationship to maximum monthly precipitation (MxMP) (Fig. 4b). There was a positive relationship with proportion of protected areas (ProPAs) (Fig. 4e) and seasonal variation in temperature (SVT) (Fig. 4d), but the association between interpolated bird richness and proportion of forest (ProF) was negative (Fig. 4c). In the lower sub-gradient, interpolated bird species richness was significantly positively related with proportion of Ramsar sites (ProRSZ) (Fig. 5a) whereas the association between interpolated bird richness and habitat heterogeneity was unimodal (Fig. 5b) (Table 3). In the upper sub-gradient, interpolated bird richness showed a negative linear relation with proportion of forest (ProF) and altitude and a positive linear relation with MVT (Table 4, Fig. 6).

4. Discussion

Total interpolated bird species richness along an elevational gradient showed slightly a low plateau pattern with a prominent mid-elevational peak at 2800, providing no support for the mid-domain effect. This is similar to one of four bird diversity patterns on montane gradient described by McCain (2009): (1) decreasing, (2) low plateau, (3) low plateau with a mid-elevational peak and (4) mid-elevational peaks. Such low plateau pattern is more frequently documented on humid

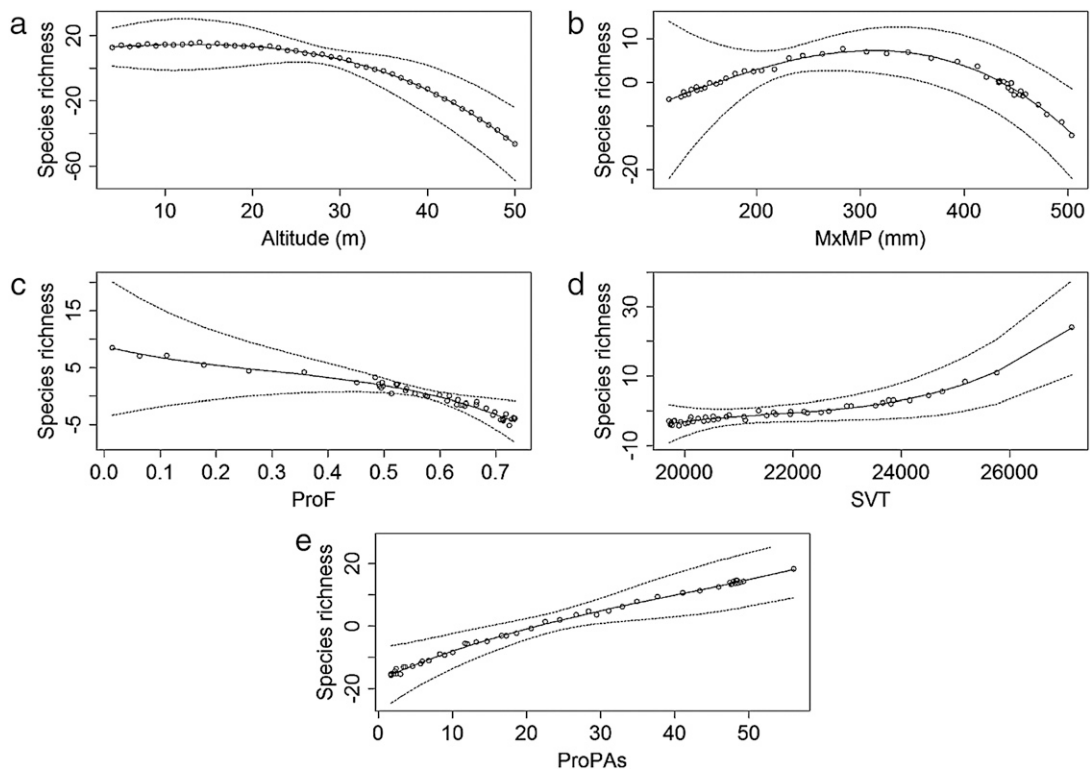


Fig. 4. Pattern of interpolated bird species richness in relation to (a) altitude, (b) maximum monthly precipitation (MxMP), (c) proportion of forest (ProF), (d) seasonal variation in temperature (SVT), and (E) proportion of protected areas (ProPAs) in the total altitudinal gradient (0–4900 m). Statistical results presented in Table 2.

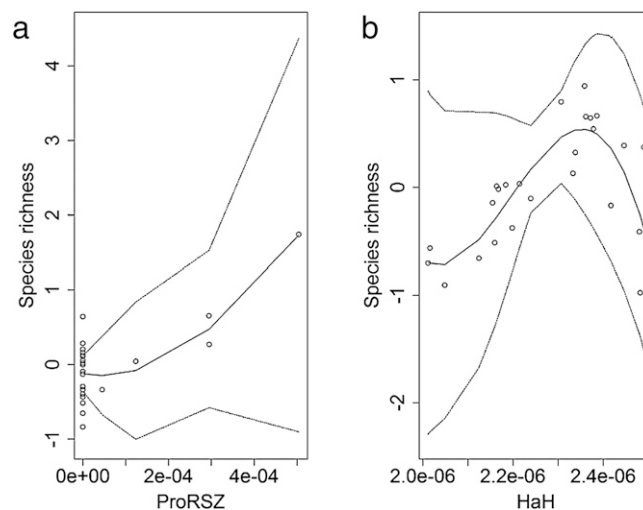


Fig. 5. Interpolated bird richness in relation to (a) habitat heterogeneity and (b) proportion of Ramsar site in the lower sub-gradient (0–2800 m) of Nepalese Himalaya. Statistical results are presented in Table 3.

mountains of Asia and North America than mountains of continental Africa and Europe (McCain, 2009). However, most studies in the Nepalese Himalaya have documented unimodal patterns with peaks at intermediate elevations (1000–3500 m) (e.g., tree (Bhattarai and Vetaas, 2006), fern (Bhattarai et al., 2004), lichens (Baniya et al., 2010), orchids (Acharya et al., 2011) and liverworts (Grau et al., 2007)). There is no information about diversity gradients of fauna, including birds in the Nepalese Himalaya. Similar studies on bird in the Sikkim Himalaya and elsewhere reported mid-elevational peaks (e.g. Acharya et al., 2011; Wu et al., 2013). In the Sikkim Himalaya, Acharya et al. (2011) reported a peak approximately 800 m lower than our

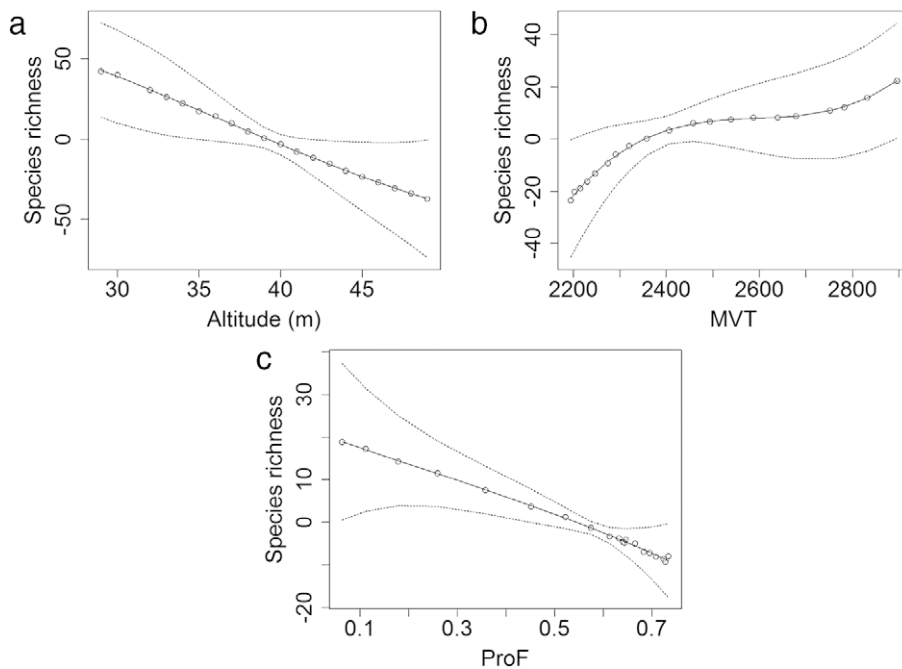


Fig. 6. Relationships between interpolated bird richness and environmental variables in the upper elevation sub-gradient (2900–4900 m) of Nepal Himalaya: (a) altitude, (b) monthly variation in temperature (MVT) and (c) proportion of forest (ProF). Statistical results are presented in Table 4.

Table 3

Interpolated bird species richness along lower sub-gradient (0–2800 m). Among four variables (proportion of Ramsar sites (ProRSZ), habitat heterogeneity (HaH), protected areas (ProPAs) and proportion of human settlements (ProS)), only two environmental variables (HaH and ProRSZ) significantly explained the pattern of interpolated species richness (depicted in Fig. 5). Analysis was carried out by using GLM. Degree of smoothness was estimated using the generalized cross-validation criterion. “bs” represents “B-Spline”. “SN” represents “elevation”.

Parameters	d.f.	Deviance	Residual d.f.	Residual deviance	F	P
NULL			24	10.92		
bs (SN)	3	1.94	21	8.97	3.37	0.0501
bs (ProRSZ)	3	3.61	18	5.36	6.26	0.0073
bs (HaH)	3	2.51	15	2.85	4.35	0.0248
bs (ProPAs)	1	0.02	14	2.83	0.11	0.7349
bs (ProS)	1	0.33	13	2.49	1.72	0.2118

Table 4

Results of GLM—interpolated bird species richness along upper sub-gradient (2900–4900 m). Only two variables (monthly variation in temperature (MVT) and proportion of forest (ProF)) significantly explained the pattern of interpolated bird species richness (depicted in Fig. 6). Species–environment relationship was evaluated using a GLM procedure. Degree of smoothness was estimated using the generalized cross-validation criterion. “bs” represents “B-Spline”. “SN” represents “elevation”.

Parameters	d.f.	Deviance	Residual d.f.	Residual deviance	F	P
NULL			19	505.44		
bs (SN)	3	438.77	16	66.68	487.11	<0.001
bs (MVT)	3	56.71	13	9.97	62.95	<0.001
bs (ProF)	3	6.97	10	3.00	7.73	0.005

result suggests. This might be due to climatic and other historical factors. To date, comparative studies between different Himalayan elevational gradients have not been carried out but are urgently needed.

Understanding the ecological processes governing patterns of species richness along elevational gradients is crucial for conservation biology. The Himalaya is an excellent place to perform such studies due to its high climatic variability within a short distance. Various drivers (e.g., sampling, spatial, climatic, and evolutionary) have been proposed to explain elevational gradients of species richness but there is no specific mechanism that consistently gives a satisfactory explanation (McCain and Grytnes, 2010). Grytnes and Vetaas (2002) argue that the interpolation method underestimates species richness at gradient extremes and thus produces a hump shaped interpolated species richness pattern. We acknowledge that there might be sampling imperfection as ornithological surveys in Nepal's high mountains have not been carried out as high intensity as in the lower elevations. However, this will not affect our results. Interpolation is a reasonable approach when data from regional surveys are used (Lees et al., 1999). Grimmer et al. (2000) takes account of all reliable references

available up to 1999, including author's extensive field study in Nepal (pers. comm. Carol Inskipp). Such approach of interpolating presence and absence of birds within their elevational range throughout country eliminates effect of sampling biases (McCain and Grytnes, 2010; Beck et al., 2013, but also see Grytnes and Vetaas, 2002 for a detailed discussion). The asymmetric and low plateau pattern of interpolated species richness in our study suggests influence of other environmental factors. Mid-elevational peaks, in particular, are argued to be generated artificially, when large ranges are placed randomly within the hard boundaries present at both ends of the elevational gradient. (e.g., Colwell et al., 2004). Poor fit of the interpolated bird richness pattern with the null-model suggests no support for MDE ($R^2 = 0.22$, $P = 0.115$), implying that biological mechanisms define the ranges of species (Hawkins and Diniz-Filho, 2002; Colwell et al., 2004). However, we found strong support for the mid-domain effect when effect of area was controlled for ($R^2 = 0.61$, $P < 0.001$). We think that such a pattern might be due to climatic variables (e.g., rainfall) that exhibit mid-elevation peaks along Himalayan elevational gradient (Shrestha et al., 2012). This is also consistent with the detailed analysis of bird elevational diversity at the global scale that indicated no strong support for MDE (McCain, 2009). Since our results indicated a low plateau pattern of interpolated species richness, it can be argued that low elevation peak might be generated by small to medium ranged species which are mostly habitat specialist and endemic to region (Colwell et al., 2004; Aliabadina et al., 2008).

The classic species–area relationship is another spatial hypothesis that can influence pattern in interpolated species richness. It hypothesizes that as area increases the number of species also increases because large areas provide structurally complex habitats and thus diverse opportunities for exploiting environmental resources (MacArthur and Wilson, 1967; Rosenzweig, 1995). On mountains, elevational area at lower altitudes (e.g. mountain base) is larger than those of high altitudes (e.g., mountain top) and therefore more species are expected at low elevational zones. In this study, area of elevational zones explained some of the variability in the gradient of interpolated species richness, implying that area of island (or elevational band in our case) is one of the crucial factors affecting species richness (Rosenzweig, 1995). After adjusting effect of area, a rapid decrease of interpolated species richness from its maxima (2800 m) could be multiplicative result of effects eco-physiological constraints (e.g., reduced growing season, low temperatures and low energy—Colwell and Hurr, 1994; Körner, 2000; Brown, 2001), which warrant a detailed analysis in relation to environmental factors (see below).

4.1. Environmental factors and interpolated species richness

4.1.1. Total gradient

Interpolated bird richness in Himalayan elevational gradient was best explained by maximum monthly precipitation (MxMP), seasonal variation in temperature (SVT), proportion of forest (ProF) and proportion of protected areas (ProPAs). The association between MxMP and interpolated bird richness was unimodal whereas the association between SVT and bird richness was positive and linear. Therefore, interpolated bird richness may be linked to the interplay between temperature and precipitation. In the Central Himalaya, the highest rainfall belt occurs both at low elevations [(average altitudes of (~500–700) and at intermediate elevations (average altitudes of ~2000–2200 m)] (Shrestha et al., 2012), similar to peaks of bird richness in our results. Our data suggest a monotonically decreasing trend of temperature with increasing elevation. But SVT is U-shaped along the elevational gradient. This implies that both ends of the gradient have a high variability of temperature. Thus, it seems that our results accord the “climatic variability” or “the seasonal variability hypothesis”, proposed by Stevens (1992). The rule states that the greater seasonal temperature fluctuations at high altitudes make species tolerant to greater climatic variations and therefore species have higher altitudinal ranges. Thus, the rule argues that there would be higher species diversity at lower elevations. However, peaks of bird richness at lower and intermediate elevations in our results do not corroborate the rule and therefore provide support for water–energy dynamics (O'Brien, 2006).

Water and energy are both resources and simultaneous regulators of each other. They are positively correlated with the primary productivity (Seto et al., 2004). Peak at low elevations might be the result of high energy availability as predicted by Rosenzweig (1995). At higher elevations, rainfall peaks along the Lesser Himalayas at altitude between 2000–2200 m (Shrestha et al., 2012) whereas seasonal variation in temperature starts increasing from 2200 m. Therefore, peaks of bird richness at about 2800 m might be caused by influence of precipitation and temperature. This zone, characterized by high humidity (e.g., precipitation) and oscillation of temperature (e.g., seasonal variation of temperature), offers favorable conditions for evolving different life forms (e.g., plants, insects) which many species can exploit (Vetaas, 2006). We thus find support for the water to energy proposed by Hawkins et al. (2003) and O'Brien (2006). Such assumption on underlying mechanism of elevational gradient of species diversity is also documented in other taxa in Nepal Himalaya (e.g. Bhattarai et al., 2004; Acharya et al., 2011). We suggest this zone should be cloud forests in the greater Himalayas at altitude between 2500 and 3200 m (Dobremez, 1976).

A statistically significant positive linear relationship between interpolated bird richness and protected area reported in our study was expected, but this positive association does not mean that as protected areas increases, species richness also increases. In Nepal, protected areas are disproportionately placed at higher elevations, unproductive lands and steeper slopes. Consequently, biodiversity rich regions at lower and intermediate elevations are poorly preserved in the protected area network (Supplementary data Fig. A1 in Appendix A). These regions also harbor highest human population in the country (Supplementary data Fig. A2 in Appendix A). Generally, species richness and human settlement are strongly associated with increasing levels of primary productivity. Therefore, protected areas in the densely settled regions are the last refugia of bird diversity. Chown et al. (2003) reports a positive relationship between bird richness and human density in

productive region of South Africa where high species richness is maintained in densely settled region due to reserves. This is also true for Nepal. This indicates that diversity gradient of species is constrained by human modifications and without their consideration, climatic and other factors are not enough to assess elevational gradient of species diversity.

4.1.2. Upper and lower sub-gradients

Proportion of Ramsar site (ProRSZ) and habitat heterogeneity (HaH) were the most significant variables for elevation gradient of interpolated bird diversity in the lower sub-gradient. The significant positive relationship between interpolated bird richness and ProRSZ is expected as wetlands are essential for many resident and migratory bird species. More than 80% of the Ramsar sites (wetlands of international importance) of Nepal are located in the lower sub-gradient. Therefore, Ramsar sites act as bird diversity hotspots because nearly 25% of Nepal's birds partially or fully depend on the wetlands (IUCN, 2004).

Our findings provide interesting evidence that interpolated species richness does not increase linearly with increasing levels of habitat heterogeneity. At lower elevations, relationship between interpolated bird richness and HaH was unimodal, in line with previous findings (e.g. Allouche et al., 2012). However, Hortal et al. (2013) argued that such a unimodal relationship was just a well known pattern of species and altitude relationship. Our results agree with the predictions of Allouche et al. (2012) that species richness increases with increasing levels of heterogeneity when area is not limiting factor, that is, increasing heterogeneity at the expense of patch size may result in decreasing species diversity (Roxburgh et al., 2004).

Climatic factors are some of the important descriptors of altitudinal gradients in species richness but choices of primary constraint depend on where the study is focused (Hawkins et al., 2003; McCain, 2007). In our case, the strongest factors describing interpolated species richness at high elevations were monthly variation in temperature (MVT) and proportion of forests (ProF). A negative relationship between interpolated bird diversity and ProF is consistent with a decreasing trend of forest coverage at the higher altitudes. At the same time, high altitude zones increasingly support grasslands, bushes and meadows. A positive and linear association between MVT and interpolated bird richness is consistent with our findings for total gradient, where seasonal variation in temperature (SVT) was a limiting factor. Although SVT and MVT are closely related, high variation in temperature within a short period (e.g. month) may be more important at high altitude ecosystems as it controls diversity, abundance and distribution of herbaceous plants and scrub vegetation that characterizes high altitude ecosystems (Ram et al., 1989).

5. Implications for conservation

The most challenging task for conservation biologists is to identify factors affecting diversity patterns of species. Previous studies on various taxonomic groups in Himalayan elevational gradients showed that climatic factors are some of the important drivers determining gradient of species richness (see Grytnes and Vetaas, 2002; Hawkins et al., 2003; Bhattarai et al., 2004; Bhattarai and Vetaas, 2006; Grau et al., 2007; Baniya et al., 2010; Acharya et al., 2011; Wu et al., 2013). Thus, the basic assumption of underlying drivers of richness pattern in Nepal Himalaya centers on 'water–energy–dynamics' (O'Brien, 2006). However, our results showed that human activities were no less important than climatic factors. We showed that apart from climate, proportions of protected areas in the total gradient and protected wetlands (Ramsar sites) in lower sub-gradient were among the most important determinants of interpolated bird richness pattern in Himalayan altitudinal gradient. Both protected areas and Ramsar sites are cornerstones of species conservation. The Himalayas are one of the biological treasures of the world and are under immediate threat of species extinctions and habitat destruction (Mittermeier et al., 2005). In order to conserve birds in the Nepalese Himalaya, we recommend the extension of protected areas in intermediate elevations, which despite being rich in bird richness are poorly protected. In order to implement a site specific conservation plan, we recommend more research enabling comparisons among several gradients at local levels using repeated field surveys.

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Authors contributions PKP designed the research. PKP collected data. PKP and JS designed models, analyzed results and wrote the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2014.10.012>.

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