

Environmental Covariates of Species Richness and Composition of Vascular Plants of Olangchung Gola and Ghunsa Valleys of Eastern Nepal

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ABSTRACT

Vascular plant diversity of any region is strongly affected by the environment. This study was done to understand the effects of climate, topography and land use on species richness and composition in two valleys in Eastern Nepal namely Olangchung Gola and Ghunsa. The study covered elevational gradients between 2200 and 3800 m a.s.l. along the two river valleys and included five elevation bands on both aspects of each valley. Four main land-use types, namely natural forest, exploited forest, meadow and crop land were studied in order to test the effects of human influence in a land-use gradient. In total, 515 species belonging to 104 families were recorded. Angiosperms included 477 species, followed by 30 pteridophyte species and 8 gymnosperms. Dicotyledonous plants were more species-rich (378 species) compared to monocotyledonous plants (99 species). Species composition on the plots was analyzed by Canonical Correspondence Analysis (CCA), and Generalized Linear Model (GLM) regression was carried out to test relative effects of environmental variables on the species richness of vascular plants. Species richness and composition were significantly affected by the combined effect of climatic and topographic variables. Species richness and composition also differed between land-use types. Species richness was particularly high in exploited forests where disturbance was at an intermediate level, i.e. less intensive than in the crop fields and meadows but higher than in the natural forests. The results confirm the intermediate disturbance hypothesis and indicate that the local, multifunctional forest management maintained a high species richness of vascular plants.

Keywords: Species Composition, Species Richness, Elevation Gradient, CCA, Climate, Land Use, Biodiversity, Himalaya

INTRODUCTION

Species richness and composition are widely used biodiversity metrics for understanding ecological processes, and various studies have demonstrated the impact of the environment on these biodiversity measures (Lomolino, 2001; Rahbek, 1995). At macroecological scales abiotic environmental factors have been widely studied to explain patterns of species distributions and species richness. Climatic factors have been found to act mainly at regional scales (Currie & Paquin, 1987), whereas land use, slope, aspect, or soil moisture are common factors at local scales (Sherman *et al.*, 2007). Such drivers of species diversity are particularly evident along elevational gradients (Korner, 2003; Vetaas & Grytnes, 2002).

The analyses of elevational gradients with respect to species richness and composition have often revealed strong biodiversity patterns. Besides monotonic decrease of species richness, many studies have confirmed a mid-elevation peak along the elevational gradients (Colwell *et al.*, 2004; McCain, 2004). Also in the Himalaya in Nepal species richness of various taxa showed a pronounced mid elevation peak; e.g. for vascular plants

(Bhattarai & Vetaas, 2003), ferns (Bhattarai *et al.*, 2004), lichens (Baniya *et al.*, 2010) and medicinal plants (Rokaya *et al.*, 2012). Rapoport's rule which states larger species ranges at higher latitudes has been extended to altitudinal gradients (Stevens, 1992). However, the Rapoport's rule was questioned by Colwell & Hurr (1994), and Rohde (1996) considered such effect as a local phenomenon which applies to the northern temperate zone but failed in the tropics. Instead he argued that gradients in species richness could be explained by an evolutionary approach rather than by environmental gradients. Even though the debate still remains unresolved (Lomolino, 2001), a considerable number of studies showed that species richness and composition can be explained by taking environmental gradients as predictors Sanders & Rahbek (2012) found that there are numerous factors behind that elevational gradient to explain the mechanism of the species diversity pattern. Some of the causes cited therein include climate and productivity (Rahbek, 1995), source sink dynamics (Kessler *et al.*, 2011), area (Rahbek, 1995), disturbance (Escobar *et al.*, 2007), geometric constraints (Sanders, 2002) and evolutionary history (Machac *et al.*, 2011). The effect of other factors such as land-use

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pattern and types were also assessed. Moeslund *et al.* (2013) have shown that micro-topography also explained local plant diversity as did fertilizer and moisture gradients (Hettenbergerova *et al.*, 2013). Land use types and topography also affect species composition (Paudel & Vetaas, 2014; Rodríguez-estrella, 2007). The change in species richness differs along elevation and according to the land use types in Nepal Himalaya (Rai *et al.*, 2016).

In this study, we aimed to test which environmental variable influence species richness and composition in a remote mountain area in Taplejung district, Eastern Nepal. Our main research questions were: (1) How does climate affect the distribution of vascular plants in the study area? (2) How vascular plant species are associated with different land-use types?

MATERIALS AND METHODS

The eastern Himalayan region of Nepal was selected as the study site where the plant species records were used to regress against the bioclimatic variables from the worldclim and the recorded data within the plots. Further analyses were done using R software with various packages.



Figure 1a : Nepal

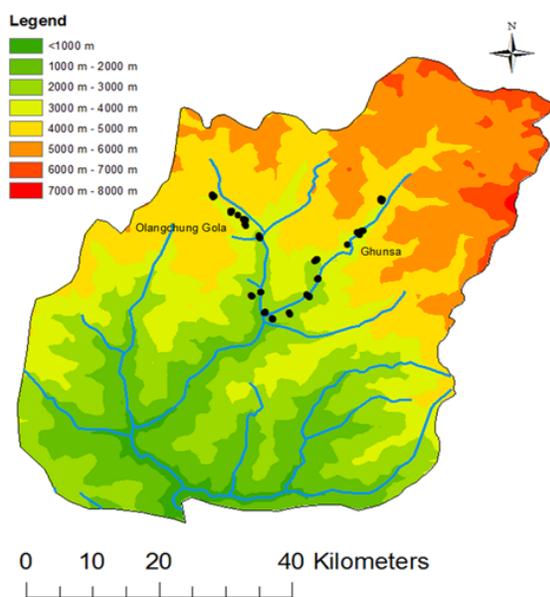


Figure 1b : Taplejung

Figure 1. Location of the study region and study sites. 1a. Map of Nepal showing the Taplejung district as shaded and 1b. Plots along the Tamor river in Olangchung Gola valley and along the Ghunsa river in Ghunsa valley.

Study area and study design

The study was conducted in the Olangchung Gola and Ghunsa river valleys of Taplejung district of Eastern Nepal from 2011 to 2013 (Fig. 1a. & 1b.).

The study covered elevational gradients between 2200 and 3800 m a.s.l. along the two river valleys and included five elevation levels on both aspects of each valley (at c. 2200, 2600, 3000, 3400, and 3800 m). Four land-use types were selected at each level, namely (a) natural forest, (b) exploited forest, (c) meadow, and (d) crop fields (Scheidegger *et al.*, 2010). The land-use types were classified on site based on visual inspections according to the methods proposed by (Gregorio & Jansen, 2000). The natural forests were far from the human settlements and trees were not used for the collection of fuelwoods and timber. The exploited forests had more than 20% of tree cover which were used by people of the nearby settlement to collect fodder, fuelwood, timber and other resources. These forests were affected by people of the nearby settlement for their daily needs. The meadows consisted of grasslands, with less than 20 % tree cover. The meadows were also affected by human activities such as livestock grazing and grass collection but not intensely managed by people. The crop fields included those sites where the vegetation cover was manipulated and created by anthropogenic activities. The vegetation cover fluctuated from nearly 100% cover during plantation season and was minimal after the harvesting season.

Crop fields were absent in the highest elevation level (3800 m) except at one site in Ghunsa valley. In each land-use type two sample plots were investigated. The plot size was 25 m x 2.5 m, which was further divided into five subplots (5 m x 2.5 m). The same numbers of plots were investigated on the other side of the river at each elevation level. Thus, 16 plots characterizing four land-use types were investigated at each elevation level. Plots were selected up to 50 meters above and below each elevation level if the land-use types were not available at the exact elevation. A total of 69 plots were investigated. All vascular plant species within each subplot were recorded. Each plot was visited twice, during different seasons, in order to record as many species as possible. Tree and shrub species remained the same however the grasses and herbaceous plants species changed in the plots with change in the seasons.

This would record plants which would grow in one season and absent in next season. To reduce the sampling bias caused by spatial autocorrelation, the replicates of each plot were established at least 50m away from the first plot (Magurran, 2004).

Species identification

Most of the flowering plant species were identified in the field by using the field identification books (Polunin & Stainton, 1984; Stainton, 1988). The specimens unidentified in the field were identified at the National Herbarium and Plant Laboratories (KATH), Godawari, Lalitpur. Voucher specimens were submitted to the KATH Herbarium.

For nomenclature of the species follows the Angiospermic Phylogenetic Group (APG III; Chase & Reveal, 2009). In the case of the unresolved names

(according to APG III), the nomenclature of Press *et al.* (2000) was applied. For pteridophytes we used the nomenclature of (Iwatsuki, 1998) and Fraser-Jenkins (2008, 2011). The individual species' presence/absence data of the merged plot were used as the response variable in the current study.

Environmental predictors

The following sets of environmental variables were used as predictors of analyses of species richness and composition (Table 1):

a. Microclimatic variables

This set of data was recorded on each plot during 2011 to 2013. HOBO data loggers U23-001 (Onset Computer Corporation, Bourne, MA 02532, USA) were used to record air humidity and air temperature two meters above the ground on each plot every 30 minutes. Soil temperatures were recorded at 10cm below the ground level using iButton (Maxim Integrated, San Jose, CA 95134, USA) on each plot. Soil temperature data were recorded at three-hours intervals. The mean, minimum and maximum values of the year-round data were derived using these data (Table 1). The non-available (NA) values of the data were interpolated from the mean of the corresponding records.

b. Bioclimatic variables

The bioclimatic variables were taken from the Worldclim-Global climate data (Hijmans *et al.*, 2005). The data were present in 30 arc seconds ($0.93\text{km} \times 0.93\text{km} = 0.86\text{km}^2$) resolution. The values contain monthly data from 1960 to 1990 for the period of 30 years (<http://www.worldclim.org/>). The average values of the bioclimatic variables for each plot were interpolated with DIVA GIS ver. 7.5.0 (Hijmans *et al.*, 2012). The latitude and longitude of each plot were recorded with Garmin 60S GPS set. Out of the 19 bioclimatic variables as defined by the USGS Data Series 691 (O'Donnell & Ignizio, 2012), those with high Pearson correlation coefficient ($r > 0.7$) were removed and only those less than 0.7 were selected for analysis (Booth *et al.*, 1994; Dormann *et al.*, 2013) (Table 1). The Hmisc (Harrell *et al.*, 2015) package was used to check the collinearity among the variables.

c. Topographical Set

The third set of data contained the topographic plot information directly recorded in the field. Garmin GPS 60S was used to record the elevation of each plot. Brunton Compass was used to record the aspect in degree angle while a Clinometer was used to record the slope angle of the sample plots. The land-use types and the valleys were considered as the categorical variables and all the others were taken as quantitative variables (Table 1).

Data analyses

Initial data entry and management was done using MS Excel and MS Access. All subsequent analyses were performed with R ver. 3.1.2 (R Core Team, 2015). Package vegan (Oksanen *et al.*, 2015) was used for the multivariate ordination analyses. Detrended

Table 1. List of environmental predictors selected from three sets

Variables Code	Contained information
Microclimatic variables	
MeanT.H	mean air temperature
MeanT.iB	mean soil temperature
minT.iB	minimum value of soil temperature
minH.H	minimum value of air humidity
Bioclimatic variables	
BIO2	annual mean diurnal range
BIO3	isothermality
BIO4	temperature seasonality
BIO6	minimum temperature of coldest month
BIO8	mean temperature of wettest quarter
BIO14	precipitation of driest month
BIO15	precipitation seasonality
BIO16	precipitation of wettest quarter
BIO17	precipitation of driest quarter
BIO19	precipitation of coldest quarter
Topographical variables	
HABI*	land-use types (*C=crop, *M=meadow, *E= exploited forest, *F=forest)
ALTG	measured elevation
LAT	latitude
LONG	longitude
SLOP	slope angle (Sine transformed)
ASP	aspect (Cosine transformed)

Correspondence Analysis (DCA) was performed for the species data (Hill & Gauch, 1980) showing the gradient length of the first ordination axis higher than 3.5 standard units. Therefore, we used as constrained ordination method the unimodal model of the Canonical Correspondence Analysis (CCA) (Ter Braak, 1986). The best model was selected by the option "stepwise" of CCA.

Species richness was regressed against the environmental variables using generalized linear models (GLM) (McCullagh & Nelder, 1989). The models having the high deviance (D^2) were selected as the best model.

RESULTS

Species composition

The study revealed a total of 515 species of vascular plants belonging to 104 plant families. Angiosperms were represented by 477 species followed by 30 pteridophytes and 8 gymnosperms. The most dominant family was Asteraceae with 44 species followed by Poaceae (35 spp.), Rosaceae (31 spp.) and Ericaceae (25 spp.). 378 species belonged to dicots and 99 species were monocots. The herbaceous plants dominated the study area when grouped according to life forms. They included 364 species followed by 87 shrub species and 64 tree species.

The analyses of species composition by CCA were constrained using three sets of variables, namely microclimatic variables, bioclimatic variables and topographical

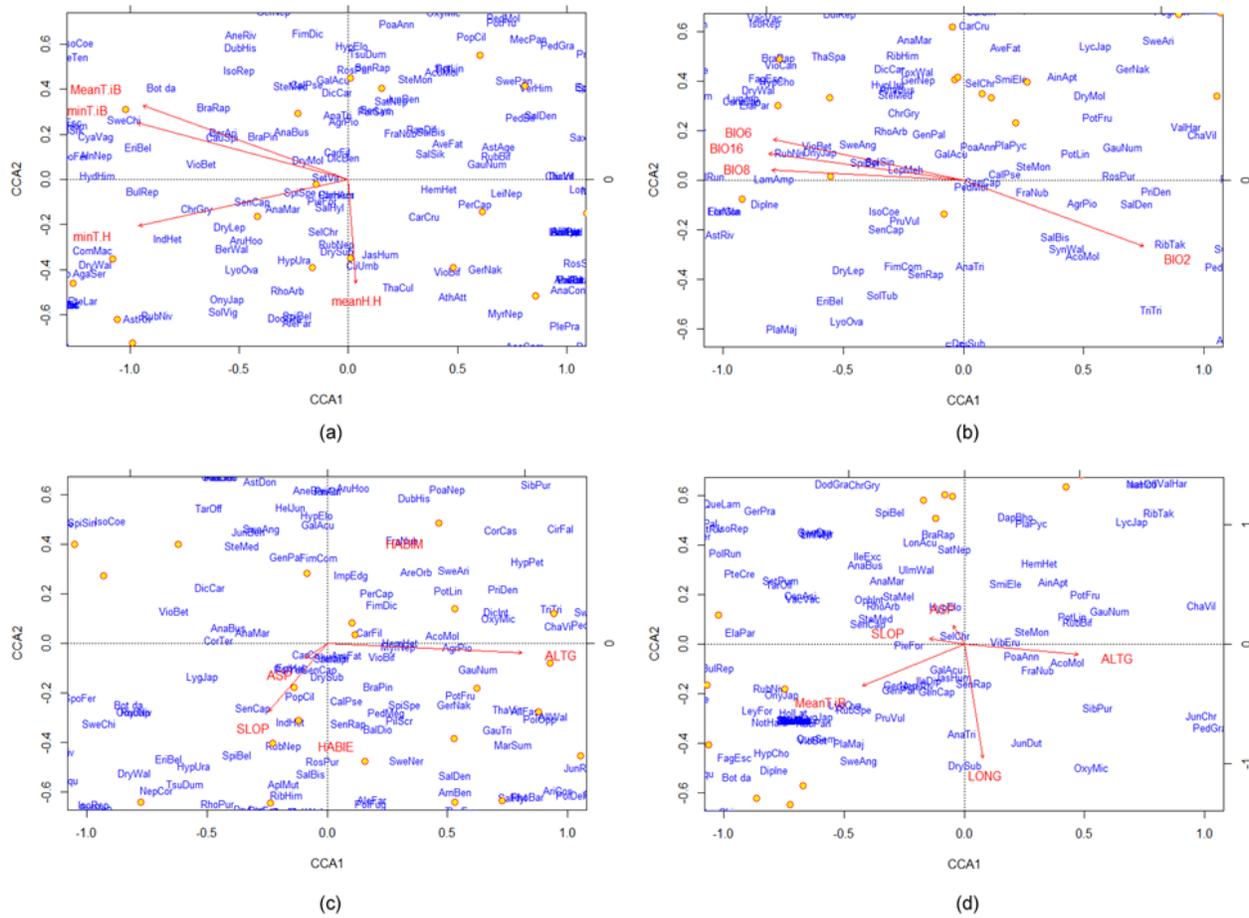


Figure 2. CCA biplots showing the effects of environmental variables on species composition. 2a. constrained by microclimate, 2b. by bioclimatic predictors, 2c. by topographical predictors, and 2d. by the combined set of all predictors (for abbreviation of predictors see Table 1)

Table 2. ANOVA testing for CCA the “marginal effect” of predictors on species composition, i.e. testing the effect of a single predictor in a model with all other predictors.

Variable Set	Code	Df	Chi Square	F	Pr(>F)	Significance Code
Loggers	minT.H	1	0.1851	1.3943	0.009	**
	meanH.H	1	0.1617	1.2185	0.156	
	MeanT.iB	1	0.1535	1.1561	0.144	
	minT.iB	1	0.1445	1.0888	0.248	
	Residual	64	8.4948			
Bioclim	BIO8	1	0.2753	2.1107	0.001	***
	BIO6	1	0.2629	2.0155	0.001	***
	BIO16	1	0.2493	1.9116	0.001	***
	BIO2	1	0.2486	1.9061	0.001	***
	Residual	64	8.3465			
Spatial	ALTG	1	0.4093	3.1705	0.001	***
	HABI	3	0.6474	1.6718	0.001	***
	ASP	1	0.157	1.2163	0.043	*
	SLOP	1	0.1526	1.182	0.082	.
	Residual	62	8.0031			
AllVar	LONG	1	0.2751	2.1436	0.001	***
	ALTG	1	0.2459	1.9159	0.001	***
	MeanT.iB	1	0.2297	1.7901	0.001	***
	SLOP	1	0.1894	1.4763	0.001	***
	ASP	1	0.1672	1.3033	0.014	*
	Residual	63	8.0843			

Table 3. The percentage of constrained variation in species composition explained by Canonical Correspondence Analysis.

Data Set	Total Inertia	Constrained Inertia	Axes	Eigenvalues	Percentage constrained variation explained	Cumulative Variation %
Microclimatic	9.499	1.004	CCA1	0.4735	47.16	
			CCA2	0.2418	24.08	71
			CCA3	0.1568	15.62	87
			CCA4	0.1323	13.18	100
Bioclimatic		1.153	CCA1	0.4854	42.10	
			CCA2	0.2962	25.69	68
			CCA3	0.2212	19.18	87
			CCA4	0.1498	12.99	100
Topographical		1.893	CCA1	0.5011	26.47	
			CCA2	0.362	19.12	46
			CCA3	0.3453	18.24	64
			CCA4	0.2138	11.29	75
			CCA5	0.2048	10.82	86
			CCA6	0.1597	8.44	94
			CCA7	0.1064	5.62	100
Combined		1.415	CCA1	0.4936	34.88	
			CCA2	0.3462	24.47	59
			CCA3	0.2395	16.93	76
			CCA4	0.1883	13.31	90
			CCA5	0.1471	10.40	100

Table 4. Summary statistics of generalized linear models with Poisson distribution of species richness regressed against predictors.

Name of variables	AIC	Residual deviance	D ²	Percentage change in D ²
Microclimate Model				
MeanT.H	710.04	298.09	0.07	
MeanT.H+MeanT.iB	695.16	281.22	0.12	79.88
MeanT.H+MeanT.iB+minH.H	691.73	275.78	0.14	14.32
Backward Elimination	691.73	275.78	0.14	0.00
Full model (all variables)	643.39	215.44	0.33	
Bioclimatic model				
BIO3	685.28	273.33	0.14	
BIO3+BIO4	673.07	259.12	0.19	30.97
BIO3+BIO4+BIO14	675.07	259.12	0.19	0.00
BIO3+BIO4+BIO14+BIO15	662.4	244.46	0.23	24.40
BIO3+BIO4+BIO14+BIO15+BIO17	651.35	231.41	0.28	17.46
BIO3+BIO4+BIO14+BIO15+BIO17+BIO19	638.15	216.21	0.32	17.31
Backward Elimination	638.15	216.21	0.32	
Stepwise regression (backward elimination & forward selection)	598.12	166.18	0.48	48.57
Full model (all variables)	606.54	164.6	0.48	
Topographic model				
ALTG	706.54	294.6	0.08	
ALTG+LAT	708.09	294.15	0.08	1.83
ALTG+LAT+LONG	694.83	278.89	0.13	60.89
ALTG+LAT+LONG+ASP	694.28	276.34	0.13	6.32
ALTG+LAT+LONG+ASP+SLOP	692.52	272.57	0.15	8.79
LAT+LONG+ASP+SLOP	690.59	272.65	0.15	
Backward Elimination	702.65	286.71	0.10	-30.20
Stepwise regression (backward & forward)	650.94	231	0.28	171.42
Full model (all variables)	661.57	227.63	0.29	
Combined model				
ALTG	706.54	294.6	0.08	
ALTG+BIO1	698.1	284.15	0.11	42.46
ALTG+BIO1+BIO12	674.19	258.25	0.19	73.87
MeanT.H+MeanT.iB+BIO3+BIO14+BIO17+BIO19+LONG+ASP	615.88	189.94	0.40	112.06
Stepwise regression (backward & forward)	609.43	179.49	0.44	8.08
Full model (all variables)	539.12	55.176	0.83	

variables. In case of microclimate set, minimum air temperature (minT.H) was the only significant predictor ($F=1.39$, $p<0.01$) in ANOVA. The mean soil temperature (MeanT.iB), minimum soil temperature (minT.iB) and minimum air temperature (minT.H) are oriented along the first CCA axis and mean air humidity (meanH.H) is placed along the second axis (Fig. 2a). In case of bioclimatic variables (Fig. 2b), annual mean diurnal range (BIO2), minimum temperature of the coldest month (BIO6), mean temperature of the wettest quarter (BIO8) and precipitation of the wettest quarter (BIO16) were found to be significant ($F_{all}>1.9$ at $p<0.001$). The topographical variables, land-use types ($F=1.67$, $p<0.001$), elevation ($F=3.17$, $p<0.01$), slope ($F=1.182$, $p>0.001$), aspect ($F=1.22$, $p<0.001$) affected the species composition significantly (Table 2 and Fig. 2c). The combined constrained effects of all variable remaining after controlling for collinearity. Among them, soil temperature and topographical variables showed significant effects on composition (Table 2 and Fig. 2d). The variation explained by the first CCA axis was 47.16% for the model using microclimate variables alone and 42.1%, 26.47% and 34.88 % for the bioclimatic, topographical and combined variable set respectively (Table 3).

Species Richness Models

Different GLM models with species richness as response and Poisson distribution for count variables were built using the same three sets of predictor variables and the combined set (Table 4). For the microclimatic model, the linear combination of mean air temperature (MeanT.H) and mean soil temperature (MeanT.iB) along with the minimum air humidity (minH.H) showed the lowest values of AIC (691.73) based on forward selection with an explained deviance $D^2 = 0.14$. Backward elimination starting with all variables did not improve the model (Table 4). The model with the bioclimatic predictors and built by forward selection consisted of six variables, i.e. isothermality (BIO3), temperature seasonality (BIO4), precipitation of driest month (BIO14), precipitation seasonality (BIO15), precipitation of driest quarter (BIO17) and precipitation of coldest quarter (BIO19). It performed better than the previous model (AIC=638.15, $D^2=0.32$). Backward elimination of all predictor variables did not improve the model, however, stepwise backward elimination and forward selection improved the model further (AIC=598.12 & $D^2=0.48$). In the topography set, linear combination of latitude (LAT), longitude (LONG), aspect (ASP) and slope angle (SLOP) of the plots had more effect than other models while doing the forward selection (AIC=690.59 & $D^2=0.15$). Backward elimination did not improve the model, however, stepwise backward elimination and forward selection method produced better results (AIC=650.94, $D^2=0.28$). Inclusion of all variables and elevation was not effective for the topographic model (Table 4).

In case of combined model, significant variables from each set were selected to initially reduce the number of predictors (similar to, Wohlgemuth *et al.*, 2008). Among them, mean air temperature and mean soil temperature of the plot, isothermality, precipitation of driest month, precipitation of driest quarter, precipitation of

coldest quarter along with longitude and aspect have shown a stronger effect on the species richness (AIC=615.88 & $D^2=0.40$) than other models. Stepwise regression with backward elimination and forward selection further improved the model (AIC=609.43 & $D^2=0.44$).

The significance of each variable on the model performance was also calculated (Table 5). Mean air temperature was the most significant variable ($p<0.001$) followed by soil temperature and minimum humidity of the plots in microclimate set. In case of the bioclimatic set, all variables were significant ($p<0.001$) except precipitation seasonality. In the topography set, the latitude had a higher significance ($p<0.001$) followed by longitude ($p<0.01$). Slope and aspect were also significant at $p<0.05$. While combining all variables in the synthetic model, their effect was also changed. Slope and aspect were no longer significant in that model.

The relative effect of those predictor variables on the species richness in different land-use types are also fitted with the generalized linear models (Figure 3a-d).

DISCUSSION

Species composition

From the bioclimatic set the most informative variables for species composition were minimum temperature of the coldest month, mean temperature of the wettest quarter and precipitation of the wettest quarter. The wettest quarter in the study area is during summer months when the monsoon cloud from the Bay of Bengal reaches its peak in July (Kansakar *et al.*, 2004). The higher precipitation delivers water for the growing vegetation and the ambient temperature is also favorable during the summer monsoon. Similar results were found for annual plants in Mongolia (Yan *et al.*, 2015) and primates (Wang *et al.*, 2013) in South East Asia.

For the topographical variables, elevation, aspect, slope and land use types show significant effect on the plant composition and richness. Moeslund *et al.* (2013) had similar results where local plant diversity patterns were controlled by soil moisture and local hydrology which were in turn affected by topography. The slope and aspect are also responsible for heterogeneity of habitats where the solar radiation also varies. The radiation has direct effects on light availability, soil and air temperature and soil moisture. In our study, species composition was significantly affected by minimum and mean soil and air temperatures (Figure 2a, Table 2).

In the Figure 2c meadows (HABIM) and exploited forest (HABIE) have been displayed. While increasing the scale of the figure, the crop fields are placed far away from the meadow and the natural forest is placed near to the exploited forest. The species composition of the crop fields changes according to the season and during crop plantation, harvest and ploughing. The highly different species composition of crop fields was expected because of its intensive management by the people. Moura *et al.* (2016) also asserted that species richness and thus compositions are affected synergistically by various variables, even though, the climate itself was also a good explanatory variable. The competition regimes are

Table 5. The test statistics of the predictor variables obtained after performing the ANOVA of the chosen GLMs of species richness.

Variable Set	Variables	Estimate	S.E	p	
Microclimate	(Intercept)	3.71E+00	1.55E-01	2.00E-16	***
	MeanT.H	5.09E-02	1.04E-02	8.94E-07	***
	MeanT.iB	-3.54E-02	1.08E-02	1.06E-03	**
	minH.H	4.34E-03	1.87E-03	2.04E-02	*
Bioclimatic	(Intercept)	1.73E+01	2.41E+00	7.21E-13	***
	BIO3	-1.62E-01	2.30E-02	2.03E-12	***
	BIO4	-1.11E-03	3.28E-04	6.73E-04	***
	BIO14	-1.63E-01	3.18E-02	2.65E-07	***
	BIO15	2.20E-03	1.44E-02	8.78E-01	n.s.
	BIO17	-1.06E-01	2.46E-02	1.82E-05	***
	BIO19	1.04E-01	1.79E-02	6.38E-09	***
Topographic	(Intercept)	9.71E+01	2.23E+01	1.41E-05	***
	LAT	-9.64E-01	2.57E-01	1.74E-04	***
	LONG	-7.56E-01	2.34E-01	1.27E-03	**
	ASP	5.62E-02	2.54E-02	2.69E-02	*
	SLOP	2.03E-01	9.63E-02	3.51E-02	*
Combined	(Intercept)	1.17E+02	2.50E+01	3.08E-06	***
	MeanT.H	5.52E-02	1.33E-02	3.21E-05	***
	MeanT.iB	-3.22E-02	1.08E-02	2.78E-03	**
	BIO3	-1.36E-01	2.23E-02	1.15E-09	***
	BIO14	-1.04E-01	3.28E-02	1.46E-03	**
	BIO17	-6.82E-02	1.64E-02	3.32E-05	***
	BIO19	8.16E-02	1.42E-02	8.76E-09	***
	LONG	-1.22E+00	2.85E-01	2.03E-05	***
ASP	4.70E-02	2.59E-02	6.93E-02	.	

different for species occurring at crop fields and those at forests. Kouba *et al.* (2015) assessed the species composition in different landscape with different land use history in the Mediterranean basin and found that the composition pattern differed significantly according to successional stage. Baniya *et al.* (2009) have also assessed the species diversity in different land use types taking temporal gradient as an explanatory variable in trans-Himalayan region of Nepal. They found the hump shape of species diversity along the gradient which agrees with the intermediate species richness hypothesis (Connell, 1978). The forest and exploited forest share common species and crop fields share very less species with the forests in this study. Some species of the meadow also occur in the exploited forest. The partial clearing of the forest will create the suitable space and environment for the species occurring in the meadows. Current study does not match the results of Sharma & Vetaas (2015) who have revealed difference in the species composition of forest land and farmland, even if they shared some common species of trees in the mid-hills of Nepal. In our study, the tree species which are commonly planted on the corners of the fields were not recorded.

Species richness

Species richness was low in crop fields and higher in the exploited followed by that in meadows and natural forest. The low species richness of crop field was expected because of intensive management by the farmers that included yearly ploughing the fields in spring. Species richness is high in the crop field during plantation and most of the weeds are uprooted in the next cropping season. The high species richness in the exploited forest agrees with the intermediate disturbance hypothesis (Connell, 1978). Sharma *et al.* (2013) have found the high species richness at the grassland center and less at the forest interior. They have attributed that observation as the asymmetric mass effect due to habitat heterogeneity.

The models of different predictor variable sets performed differently in explaining species richness and composition. The microclimatic model and topographical model have less deviance than the bioclimatic model. The microclimate data and topographical data were recorded from the plots. The predictive power of those variables might be limited for plant species richness at local scale instead of their high spatial resolution. The microclimate data was recorded only for two years. This short period

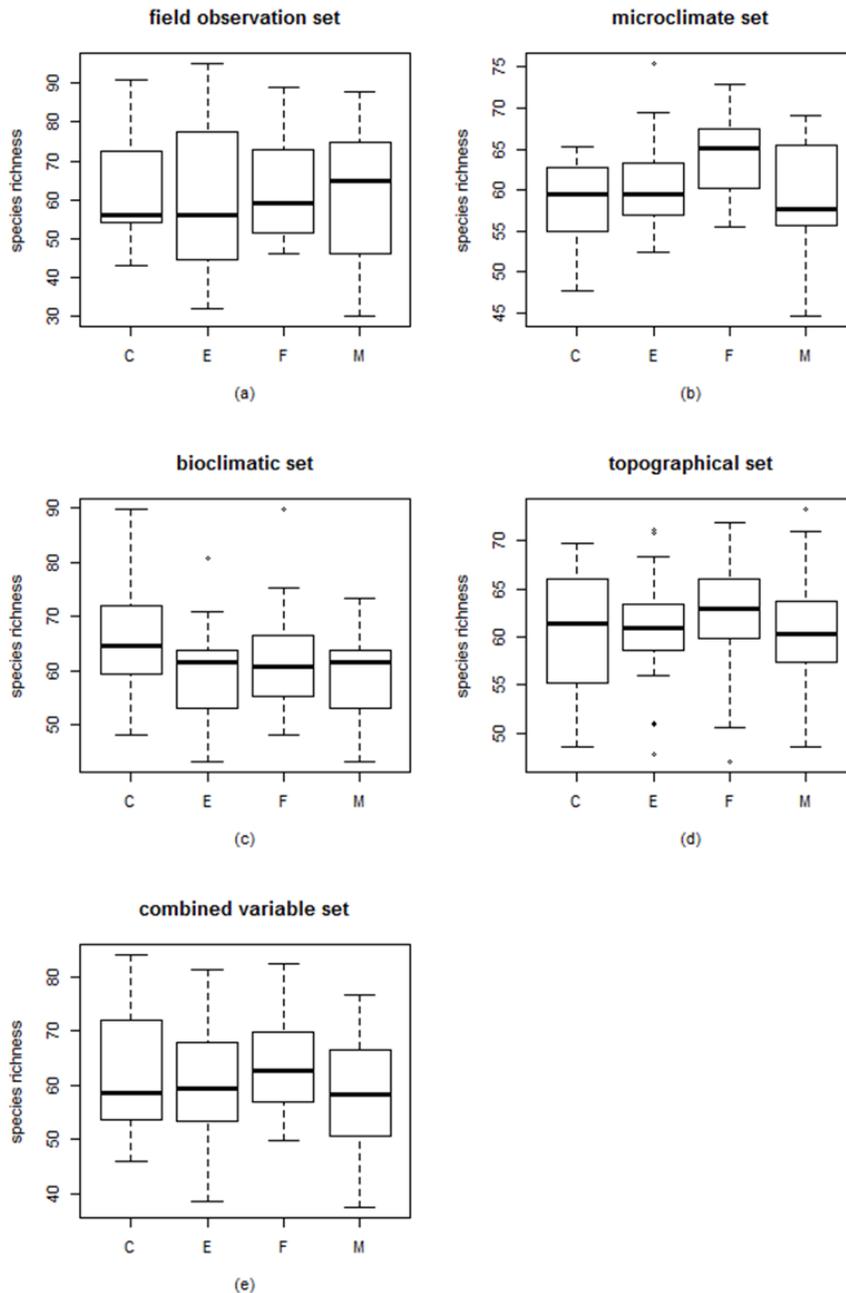


Figure 3. Observed (a) and predicted (b-d) species richness of the different land-use types. Predictions are based on the microclimate model (a), bioclimate model (b) topography model (d) and combined model (e).

may limit the performance of these data as a predictor of species richness and composition. The bioclimatic data were interpolated from the 30 arc second resolution which is $(0.93 \times 0.93) = 0.86$ sq. km at the equator. The bioclimatic data and the synthetic model were more robust than the previous two models. The importance of climatic factors in other taxa have also been established for example the synergistic association between climate and vegetation has a significant effect on vertebrates (Moura *et al.*, 2016).

Predicted species richness changed for the different richness models (Fig. 3). In the microclimate model, the minimum humidity was also found to be significantly affecting the species richness. Hettenbergerova *et al.*

(2013) have also similar results in bryophytes where the richness decreased from high moisture index to the dry plots. The dryness of the plots enhances the transpiration rate and soil moisture is depleted in faster rate. The species richness in the crop field is seen higher than the natural and exploited forest in the fitted GLMs. Since, the local conditions of crop field including vegetation cover can be changed by humans the effect of variables seem justified. Land use types are also considered as biotic factor influencing the species diversity (Moura *et al.*, 2016). Moeslund *et al.* (2013) showed that local plant diversity is controlled by the topographical factors which in turn affect the soil moisture and microclimate hydrology. The soil moisture is essential for the growth of

plants. Aranda *et al.* (2014) found that the geographical factors had limited influence on the species diversity of bryophytes whereas climate and habitat showed strong effect on it. In our study, the topographical *set alone* was not good enough to explain the species richness however when combined with bioclimatic and microclimatic variables, the synergistic effect produced a good model. Similar phenomena were obtained by Stein *et al.* (2014) when doing the meta-analysis of 1148 points of 192 studies worldwide. They found that species richness was explained by land cover, vegetation, climate, soil and topography.

CONCLUSION

The microclimatic variables did not show significant effect on species composition except minimum air temperature. The percentage of variation of plant species composition explained by the first and second axis are high, but total constrained inertia is low (1.004) out of total inertia (9.499). The topographical variables elevation, aspect and slope showed significant effect on the species composition. Species compositions also differ with different land-use types. In case of bioclimatic variables, the seasonal and diurnal fluctuations such as mean diurnal range, minimum temperature of the coldest month, mean temperature and precipitation of the wettest quarter were significantly affecting species composition. The mean annual temperature and mean annual precipitation did not show significant effects. We conclude that the seasonal effect of climatic variables is more pronounced than the annual mean of such variables. This phenomenon of seasonal effect agrees with the limiting factor hypothesis. The variability of such temperature and precipitation are crucial not during the optimal growth condition but when there are extreme high or low condition reaching to physiological tolerance level (Zimmermann *et al.*, 2009).

Species richness is higher in the exploited forests and meadows than intensively managed crop fields and relatively less disturbed natural forests. The results of our study support the intermediate disturbance hypothesis. The species richness decreases as the elevation increases. The previous studies have shown the mid elevational peaks, but our study area does not fall within that range. Instead, we have observed the effects of microclimate, bioclimate, topography and land use types on the species richness within the elevational range from 2200 m to 3800 m. Different generalized linear models were compared for their strength to shape the species richness after regressed with three sets of predictors and one synthetic set incorporating all predictors at one place. Mean soil and air temperature and minimum humidity of the plots significantly affected the species richness in microclimate set. In case of bioclimatic set, the isothermality, temperature seasonality, precipitation of driest month, precipitation seasonality, that of driest and coldest quarter affected the species richness significantly. The elevation, aspect and slope of the plots also showed significant effects. The species richness and composition according to different land use types.

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