Investigating the influence of environmental heterogeneity on plant species richness pattern of the Eastern Himalaya

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Abstract

Species richness pattern is poorly understood at local scales. Here we analyse impacts of physiography, climate, and edaphic factors on species richness pattern of the Eastern Himalaya using 376 spatial location points, collected through scientifically designed national level sampling assessment. We fitted nonlinear predictive model technique for 1470 species and selected eight least correlated predictors through multicollinearity and principal component analysis tests. Independently, physiography was poorly associated with species richness than edaphic and climatic factors. Climate explained the maximum deviance of 48 % with a dominant contribution from aridity and precipitation of the driest quarter. However, the cumulative effects of potential evaporation and temperature seasonality expressed significantly with interactions. The water stress due to dryness and low precipitation play determining role species richness pattern and long-term fluctuations in temperature increase their vulnerability to climate change. The warmer south is less likely to be affected by these changes than the north experiencing climatic extremes describing its environmental stability. The collective effect of all variables and their interactions explained the maximum deviance of 58 %; and described climate's synergy with physiography and soil in shaping species richness pattern. The study would support for conservation prioritisation of the region.

Keywords: Species richness; generalised additive model; climate; soil; physiography

1. Introduction

Species richness (SR), defined by a number of species, depends on the biophysical condition of a place, varies significantly along a broad spatial scale (Francis & Curie, 2003). However, it is poorly documented at a local scale where environmental heterogeneity plays a significant role. The physiography significantly influences species diversity at local and regional scales (Moeslund *et al*., 2013). Elevation influences climate and soil; and species' composition and phenology patterns of Eastern Himalaya (Chettri *et al*., 2001; Carpenter, 2005); and surface ruggedness causes species niche differentiation due to geographic isolation (Whittaker *et al*., 1973). Soil texture and composition influence species growth, particularly at locale scales (Ricklefs, 1987), i.e., pH in the mountains (Dubuis *et al*., 2013). Climate is a crucial factor in plant species distribution (Francis & Curie, 2003) and is primarily described by water and energy and their interactions (O`Brien, 1993). Hawkins *et al*. (2003) opined water has significant contribution in species distribution of tropics, subtropics, and warm temperate zones. How they shape SR pattern has always been an interesting topic in ecology. The Eastern Himalaya is at the convergence of the Indo-Malayan, Afro-tropic, and Indo-Chinese bio-geographical realms; and with the Himalayan and peninsular Indian features. This involved geophysical position increases plant SR of the region (Behera *et al*., 2002). Its position along subtropical latitude attributes to high solar radiation and a minimum variability in the day length (Zobel and Singh, 1997). The winter is dry and short, but warm for the latitude (Mani, 1974). The warmness of winter is due to greater light availability, and summer is less hot due to cloudiness. These tradeoffs between tropical and temperate climate influence SR pattern of the region. Its complex physiography supports rich diversity to about 5800 species in India (Myers, 1988). The microclimatic variation in the Eastern Himalaya leads to species confinement in different habitats (Hickling *et al*., 2006). Although understanding local drivers of biodiversity are significant for conservation, a little emphasis has been given at a local scale (Dufour *et al*., 2006). Most of the Himalayan studies are along elevation gradient (Grytens and Vetaas, 2002; Bhattarai *et al*., 2004, Behera and Kushwaha, 2007; Chhetri *et al*., 2010; Acharya *et al*., 2011). A comprehensive account of species-environment relationships is poorly documented especially in Indian parts of Himalaya due to lack of data. We took advantage of a large floral database, collected through scientifically designed sampling method to assess these relationships; and used a nonlinear predictive model with different predictor combinations to explore the influences of both climatic and non-climatic variables on species distribution.

2. Methods

The study area includes two Indian states of Sikkim (27°N to 28°N and 88°E to 88.8°E) and Arunachal Pradesh (25.5°N to 32°N and 91.4°E to 97°E; Figure 1) with a similar climate. They exhibit similar physiographic complexity and represent a larger extent of EH. The floral data were obtained from Biodiversity Characterization at Landscape Level, a national level project (Roy *et al*., 2012) with nested quadrat size of 20 m × 20 m for trees. Two 5 m × 5 m for shrubs at two corners and five 1 m × 1 m for herbs at all angles and the centre of the tree plot was considered for sampling (Roy *et al*., 2002). Synonymous species were verified, and standard scientific names were assigned by combining subspecies or variety names under a binomial nomenclature scheme. Thirty-three variables procured from freely available global data sources of three major types: (1) climate, (2) physiography, (3) edaphic variables were utilised for the present study. They include 21 climatic variables of which 19 were acquired from Worldclim data (Hijmans *et al*., 2005); and potential evapotranspiration and aridity index from CGIAR-CSI database (available from http:// cgiar-csi.org). The physiographic variables (aspect, elevation, and slope) were procured from the GMTED2010 database (https://lta.cr.usgs.gov). The terrain ruggedness index was derived from the elevation by subtracting adjacent cells from the central cell by using map algebra and spatial analyst tool. Eight edaphic variables were obtained from HWSD site (Fischer *et al*., 2008). To improve quality, relevance, and dependability of predictions, all environmental variables were resampled to the highest coarse resolution of 1km (0.0083333 degrees). The variables were projected to a common coordinate system of 44 °N UTM zone of World Geodesic System (WGS'84) datum. Organisation and pre-processing of environmental data layers were done using ArcGIS 10. The environmental variables were tested for multicollinearity to check model over-fitting. Using hierarchical clustering analysis of R's ‘corrplot' package (Wei and Simko, 2016), we selected one variable from each cluster. The variables with high principal component (PC) loadings of 1st two axes were nominated for modelling, subject to correlation <0.8. We applied generalised additive model (GAM; Hastie and Tibshirani, 1990) that fits nonlinear and complex relationships between species and the environment; and capable of controlling over-fitting automatically by GCV (generalised cross validation) predictive error criteria. We used cubic spline smoother and tensor product (‘te’) smoother for variables with and without interactions respectively. The ‘te’ smoother scales anisotropic variables with different units. The Akaike's information criterion (AIC) is used for optimal model selection (Akaike 1973). The % explained deviance of deviance and residual deviance on null deviance was compared. R software Version 3.2.2 was used for all statistical analyses (R Core Team).

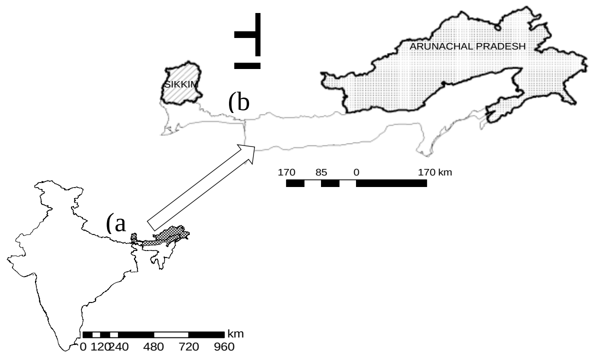

Figure 1. (a) Indian parts of Eastern Himalaya; (b) Study area

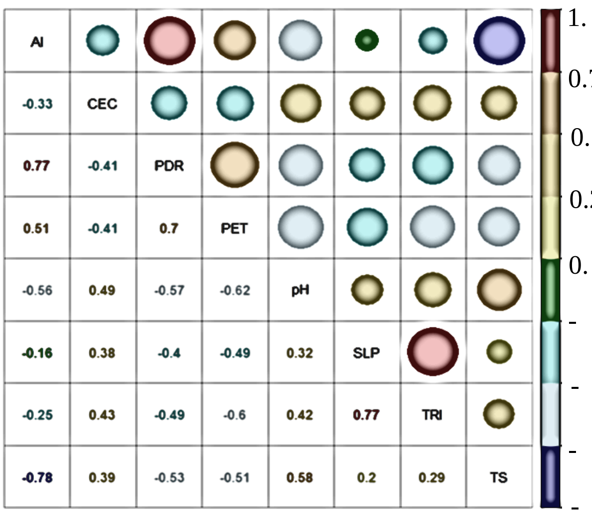

Figure 3. Correlation Plot; Bigger size of circle represents higher correlation and vice versa.

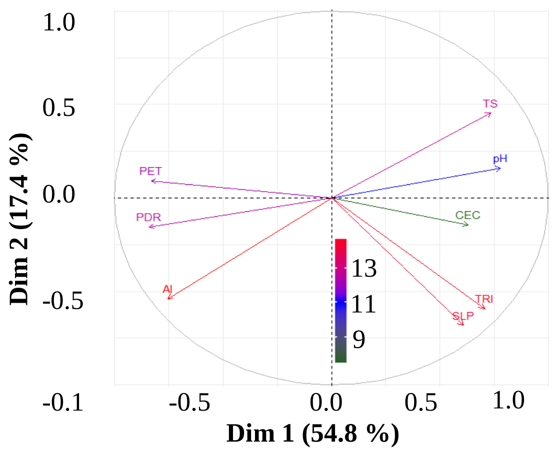

Figure 2. Contribution of variables to the principal components (PC); % Variance explained to PC axis are in parenthes.

Abbreviations: AI= Aridity index; CEC=Cation exchange capacity; PDR=Precipitation of the driest quarter; PET=Potential evapotranspiration; pH = Negative logarithm of Hydrogen ion concentration; SLP=Slope; TRI=Terrain ruggedness index; TS=Temperature seasonality

Table 1. Regression statistics using generalised additive model showing % deviance explained by each variable combination; M0 represents the intercept model.

Abbr.	Models	% Dev. Explained	AIC
M0	SR~1	—	3663.4
M1	SR~s(SLP)	8.9	3513.5
M2	SR~s(TRI)	8.4	3521.2
M3	SR~s(CEC)	18.6	3333.9
M4	SR~s(pH)	15.7	3386.1
M5	SR~s(AI)	19.3	3318.6
M6	SR~s(PDR)	17.3	3357.1
M7	SR~s(PET)	11.3	3465.4
M8	SR~s(TS)	15.3	3394.6
M9	SR~s(SLP)+s(TRI)	11.5	3474.1
M10	SR~s(SLP)+s(TRI)+te(SLP,TRI)	13.9	3460.0
M11	SR~s(CEC)+s(pH)	21.5	3286.4
M12	SR~s(AI)+s(PDR)	25.6	3216.6
M13	SR~s(AI)+s(PDR)+te(AI,PDR)	33.6	3104.2
M14	SR~s(TS)+s(PET)	19.8	3324.1
M15	SR~s(TS)+s(PET)+te(TS,PET)	34.6	3091.6
M16	SR~s(SLP)+s(TRI)+s(CEC)+s(pH)	26.8	3206.4
M17	SR~s(SLP)+s(TRI)+s(AI)+s(PDR)	32.2	3115.9
M18	SR~s(SLP)+s(TRI)+s(TS)+s(PET)	27.8	3196.6
M19	SR~s(pH)+s(CEC)+s(AI)+s(PDR)	32.3	3111.1
M20	SR~s(pH)+s(CEC)+s(TS)+s(PET)	29.8	3158.0
M21	SR~s(AI)+s(PDR)+s(TS)+s(PET)	33.4	3100.7
M22	SR~s(SLP)+s(TRI)+s(pH)+s(CEC)+s(AI)+s(PDR)	36.6	3053.0
M23	SR~s(SLP)+s(TRI)+s(pH)+s(CEC)+s(TS)+s(PET)	33.1	3115.9
M24	SR~s(SLP)+s(TRI)+s(AI)+s(PDR)+s(TS)+s(PET)	38.5	3023.5
M25	SR~s(pH)+s(CEC)+s(AI)+s(PDR)+s(TS)+s(PET)	39.4	3010.8
M26	SR~s(SLP)+s(TRI)+te(SLP,TRI)+s(AI)+s(PDR)+te(AI,PDR)	42.7	2975.4
M27	SR~s(SLP)+s(TRI)+te(SLP,TRI)+s(TS)+s(PET)+te(PET,TS)	45.1	2937.4
M28	SR~s(CEC)+s(pH)+s(AI)+s(PDR)+te(AI,PDR)	40.6	3002.2
M29	SR~s(CEC)+s(pH)+s(TS)+s(PET)+te(PET,TS)	39.6	3014.8
M30	SR~s(AI)+s(PDR)+te(AI,PDR)+s(TS)+s(PET)+te(PET,TS)	48	2887.3
M31	SR~s(SLP)+s(TRI)+te(SLP,TRI)+s(CEC)+s(pH)+s(AI)+s(PDR)+te(AI,PDR)	47.3	2914.9
M32	SR~s(SLP)+s(TRI)+te(SLP,TRI)+s(CEC)+s(pH)+s(PET)+s(TS)+te(PET,TS)	47.8	2909.1
M33	SR~s(SLP)+s(TRI)+te(SLP,TRI)+s(AI)+s(PDR)+te(AI,PDR) +s(PET)+s(TS)+te(PET,TS)	53.7	2801.5
M34	SR~s(CEC)+s(pH)+s(AI)+s(PDR)+te(AI,PDR)+s(TS)+s(PET) +te(PET,TS)	52.4	2836.1
M35	SR~s(SLP)+s(TRI)+te(SLP,TRI)+s(CEC)+s(pH)+s(AI)+s(PDR)+te(AI,PDR)+PDR)+s(TS)+s(PET)+te(PET,TS)	58	2765.1

Results

A floral dataset of 8768 records with 41779 individuals with 1470 species from 376 GPS locations includes 556 trees, 255 shrubs, 496 herbs, and 163 lianas were selected for the present study. We compared PC loadings of variables where the 1st two PC axes explained the variance of 54.8 % and 17.4 % respectively (Figure 1). Eight variables: aridity index, cation exchange capacity, precipitation of the driest quarter, negative logarithm of hydrogen ion concentration, potential evapotranspiration, slope, terrain ruggedness index and temperature seasonality with <0.8 correlation coefficient were modelled (Figure 2). We modelled 36 variable combinations where AIC of the null model was 3663.4.With the inclusion of variables, AIC reduced, but with high % explained deviance. Individually, the physiographic variables explained the least deviance (8.4±0.5). However, the explanatory ability of edaphic variables was significant where cation exchange capacity and pH described 18.6 % and 15.7 % respectively. The maximum deviance was described by aridity (19.3 %). Precipitation of the driest quarter explained 17.3 % deviance. Potential evapotranspiration and temperature seasonality explained 11.3 % and 15.3 % deviance respectively. Bivariate regression between slope and terrain ruggedness index increased the explanatory ability to11.5 % deviance, and further to 13.9 % with the inclusion of their interactive terms. Similarly, the collective effect of edaphic variables improved to an explained deviance of 21.5 %, significantly higher than physiography explained. Climate was highly significant with/without their interactive terms. Water (aridity and precipitation of the driest quarter) described 25.6 % deviance without interactions, improved to 33.6 % explained deviance with interactions. However, energy (potential evapotranspiration and temperature seasonality) improved their predictive ability from 19.8 % explained deviance without interactions to 34.6 % with interactions, the maximum increase with the inclusion of interaction term. The physiography and edaphic variables combined explain 26.8 % deviance, the lowest by any two groups of predictors. The predictability further improved with the inclusion of water/energy variables with/without interactions. However, the cumulative impact of physiography/edaphic with water was higher than their impacts with energy. The cumulative effect of both water and energy variables were found to have superior control on predictability with an explained deviance of 33.4 % without interactions to 48 % with interactions. The tripartite combination of variables showed some improvement in the explanatory ability of models, but climatic (water and energy) predictors influenced dominantly. The full model with a combination of all variables described the maximum up to 58 % deviance, and the same model was with the least AIC value of 2765.1.

3. Discussion

About 43 % of the families were represented with either singletons or doubletons, explains the presence of a high number of rare species in the region. The findings corroborate with the earlier studies (Chatterjee, 1939; Behera *et al*., 2002; Roy and Behera, 2005) who advocated high endemism in the Eastern Himalaya. The high elevated terrain creates isolated patches of distinct habitats that might have promoted endemicity with more singleton or doubleton species. With greater terrain complexity, the northern part may have created many isolated patches and habitats that favour endemism. The positive effect of physiography on species' niche differentiation has also been reported by Whittaker *et al*. (1973). The lianas, shrubs and trees represented ca. >66 % of the species pool, demonstrates the dominance of woody species in the study site. A good number of lianas (163) may be associated with the greater tree density (526). The high annual precipitation (2196 mm) and annual temperature (16.9 °C) might have favoured liana richness. Its geophysical position along subtropical latitude attributes to high solar radiation and the minimum variation in day length (Zobel and Singh, 1997) could have played a significant role in seed germination of plants.Both edaphic variables showed better significance than physiography and approves the findings of Moser *et al*. (2005) that edaphic factors are more closely associated with SR than physiography in Austrian Alps. The moderately acidic soil (PH=4.6) was a significant factor on SR corroborate with the findings of Vetaas (1997) who reported that vascular plant richness of Himalaya has a positive correlation with pH. The spatial distribution of clay and silt in soil and its organic carbon was indicative of better nutrient availability. However, the low calcium content of soil describes water- and nutrient-holding capacity is not fair. It explains the dominance of trees because they exploit underground water efficiently. The study revealed the primacy of climate in SR pattern. Individually, aridity and precipitation of the driest quarter have the maximum control. It explains significant effect dryness on SR pattern. However, the south-eastern region of the study site receives high precipitation is less likely to get affected by dryness. Alternately, temperature seasonality showed greater influence and variability in northern parts than southern parts. It describes SR of northern part is likely to be affected by temperature fluctuations setting an overall stress condition. With greater terrain complexity, the northern part might have created many isolated patches and habitats that favour endemism. The warmer south with low physiographic complexity, but with high-temperature fluctuations could have supported more species.The explanatory power of each combination substantially increased with interactions. It indicates the contribution of variables on SR is not mutually exclusive. The interactions between physiographic variables showed insignificant improvements in explanatory ability with interactions. It explained their independent influence on SR pattern. Alternately, climatic variables with interactions showed high synergy in expression. Even though water variables shoed greater impact on SR, the interactions between energy variables were more prominent. The dependability of energy variables might explain their collective influence of energy factors on SR. The overall moist climate might have created a situation for energy predictors to facilitate seed germination in the northern part with cold climate. In general, climate defined the maximum deviance by any particular correlate type is most significant on SR pattern. Our findings corroborate with many ecologists who agree that climate is a crucial factor at regional scales (Ricklefs, 1987; Francis & Currie, 2003). However, climate controlled by water and temperature (energy) critically impact SR (Curie & Paquin, 1987); and specifically, water-energy dynamics have a major contribution to species distribution (O`Brien, 1993). Both water and energy variables were found superior predictors. Their impacts on the physiographic and edaphic variables improved performance significantly. It explains the influence of climate, physiography, and the geologic substrate on evapotranspiration, soil development, and moisture regime and thus, species distribution (Franklin, 1995). The inclusion of interactive terms shows that no single factor acts in isolation and the full model described the maximum deviance showing the synergy between predictors. The dominant woody species population set higher climatic responses on SR pattern. The subtropical position, geophysical complexity, soil with climate played a critical role. The northern part is more likely to suffer from temperature fluctuations and most probably by climate change. The present study highlights the relevance of climate, water-energy dynamics and heterogeneity hypotheses and improves our understandings of species-environment relationships that might explain the critical influence of climate change on distribution.

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