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A pan-Himalayan test of predictions on plant species richness based on primary production and water-energy dynamics

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Abstract

Spatial variation in plant species diversity is well-documented but an overarching first-principles theory for diversity variation is lacking. Chemical energy expressed as Net Primary Production (NPP) is related to a monotonic increase in species richness at a macroscale and supports one of the leading energy-productivity hypotheses, the More individuals Hypothesis. Alternatively, water–energy dynamics (WED) hypothesizes enhanced species richness when water is freely available and energy supply is optimal. This theoretical model emphasises the amount and duration of photosynthesis across the year and therefore we include the length of the growing season and its interaction with precipitation. This seasonal-WED model assumes that biotemperature and available water represent the photosynthetically active period for the plants and hence, is directly related to NPP, especially in temperate and alpine regions. This study aims to evaluate the above-mentioned theoretical models using interpolated elevational species richness of woody and herbaceous flowering plants of the entire Himalayan range based on data compiled from databases. Generalized linear models (GLM) and generalized linear mixed models (GLMM) were used to analyse species richness (elevational gamma diversity) in the six geopolitical sectors of the Himalaya. NPP, annual precipitation, potential evapotranspiration (derived by the Holdridge formula), and length of growing season were treated as the explanatory variables and the models were evaluated using the Akaike Information Criterion (AIC) and explained deviance. Both precipitation plus potential evapotranspiration (PET), and NPP explain plant species richness in the Himalaya. The seasonal-WED model explains the species richness trends of both plant life-forms in all sectors of the Himalayan range better than the NPP-model. Despite the linear precipitation term failing to precisely capture the amount of water available to plants, the seasonal-WED model, which is based on the thermodynamical transition between water phases, is reasonably good and can forecast peaks in species richness under different climate and primary production conditions.

Highlights

- The spatial pattern of plant species richness across the Himalaya can be explained by an interaction of water, energy, and their seasonal variation (length of the growing season LGS).
- We found that a Water-energy Dynamics (WED) model, which takes into account both kinetic thermal energy and water as drivers of plant species richness, explains spatial variance in plant species richness better than the Net Primary Production (NPP) model estimated by earth observation tool (MODIS), which only considers chemical energy.
- By incorporating the seasonal temporal dimension, i.e., LGS (~ photosynthetic active period for the plants) in the WED model, especially for the high-elevation areas, it is possible to improve fits of the WED models.
- The seasonal-WED model, which considers water and energy in both the kinetic as well as chemical form as the drivers of plant species richness, provides a more flexible array of regional species richness models, with better statistical fit, than the simple NPP model.

Keywords: Elevational gradient, Gamma diversity, Growing season, Himalaya, Net primary production, Species richness, Water–energy dynamics.

Introduction

A well-supported hypothesis in ecology and biogeography is that increased thermal energy promotes higher species diversity (Wright 1983, Currie 1991, Brown et al. 2004, Clarke and Gaston 2006, Brown 2014). However, paradoxically, climate change, especially rising global and local temperatures, is expected to cause species extinction (IPCC 2018, IPBES 2019) rather than increasing species diversity. This paradox may, in part, be resolved by the synergetic effect that expanding human land-use together with climate change has on species by preventing their climate change-driven translocation, which in turn leads to species extinction. However, it may also be that the energy alone is insufficient to explain biodiversity and ought to be replaced by a better model focusing on water as well as energy. It is a basic biological fact that life on the Earth evolved in water and there is no life without liquid water. It is therefore unconvincing that many models on macroscale species diversity do not include water but focus on how energy promotes species diversity by regulating metabolism, population size, and speciation rate (Evans et al. 2005, Clarke and Gaston 2006). These energy-based models may convincingly explain why there are so many species in the warm equatorial sector and so few at the cold poles (Brown 2014), but fail to explain why the subtropics and warm-temperate sectors, which despite being relatively energy-rich, have low productivity levels and relatively few species (Vetaas et al. 2019). Such models also fail to explain species diversity variation along elevation gradients, where many organismal groups have peaks at intermediate elevations, and not in the warm tropical/subtropical lowland (Rahbek 1995). This may relate to optimal moisture conditions at mid-elevations compared to the summits (frost) and lowland (high evapotranspiration) (Peters et al. 2019, Vetaas et al. 2019, and references therein).

Globally, the spatial variation in species diversity in space is a well-documented pattern, encompassing the decline in species richness from the equatorial tropics to the Arctic and the commonly found unimodal pattern along extensive tropical mountain ranges (Rahbek 1995, Hawkins 2001, Steinbauer et al. 2016). Although several studies have shown a remarkably strong association between contemporary climate and species richness (Rohde 1992, Currie et al. 2004, Kreft and Jetz 2007, and references therein), there is still no consensus-theory on the mechanisms that determine species richness patterns on our planet. This is in fact the major unexplained pattern in natural history (cf. Jablonski et al. 2006). The empirical evidence and correlations with climate across many lifeforms and taxonomic levels have, however, generated many conjectures and hypotheses, and some constituent models and theories (Scheiner et al. 2011), such as the equilibrium theory of biodiversity dynamics (Scheiner et al. 2011, Storch and Okie 2019) and the metabolic theory of ecology (MTE) (Brown et al. 2004). The latter model, MTE, links environmental energy to the rate of metabolism (Brown et al. 2004), but unfortunately, it cannot be tested along thermal

gradients because it assumes no water limitation (Vetaas et al. 2019). Another group of theorising focus on energy- and productivity often expressed as actual evapotranspiration (Currie 1991, Rohde 1992, Currie et al. 2004). One explanation is that high energy availability increases the number of individuals that can be supported, allowing species to maintain larger populations, which then have a reduced extinction risk. The lowered probability of extinction thus elevates species richness in high-energy assemblages. This is often referred to as the More Individuals Hypothesis (MiH). MiH has a probabilistic philosophy, where NPP will generate more individuals, which, in turn, will increase the probability of more co-occurring species and survival of small populations (Wright 1983, Srivastava and Lawton 1998). The link between energy, individuals, and species richness has recently been challenged by Storch et al. (2018), while Lavers and Field (2006) argue that this link is not needed for a mechanistic species diversity theory. One possible reason for the lack of consensus is a focus on energy per se and too little focus on energy as a regulator of available liquid water. Although the importance of water for biodiversity is an established idea (cf. Hawkins et al. 2003), currently, the most detailed expression of this tenet is biological relativity of water-energy dynamics (WED), which has been articulated by O'Brien (1993) and O'Brien et al. (1998) and was elaborated to a preliminary constituent theoretical model by O'Brien (2006) (Vetaas 2006). Following this rationale, Hawkins et al. (2003) and Field et al. (2009) argue that any theoretical reasoning that overlooks water and water-energy interactions is missing a key component for explaining broad-scale patterns of species diversity. Liquid water as a limited resource is a crucial point because in the non-tropical areas water will potentially be unavailable due to water being frozen for durations ranging from a few days to almost the entire year, and the sensitivity of most plants to frost or drought may constrain their richness outside warm and humid regions (Currie et al. 2004). This will directly influence biological activity and hence the time available for metabolism and sexual reproduction, and thereby affects evolutionary speed and genetic diversity. From an evolutionary perspective, Gillman & Wright (2014) also point to water and thermal energy as drivers of evolutionary speed, and there is evidence that hotspots of species richness and high diversification rates may coincide, but it is not necessarily a general pattern (Steinbauer et al. 2016, Quintero and Jetz 2018).

The tenet of WED is simple: species richness will increase as thermal energy increases, but beyond a certain threshold, water deficits due to high evapotranspiration demand will reduce plant activity and ultimately richness, while water freezing at the cold end of the gradient also limits plant activity (O'Brien 1998, Hawkins et al. 2003, McCain 2007). Species richness, particularly of plants, is thus dependent on both water and energy. The linear response to precipitation and the unimodal response to potential evapotranspiration (PET) enable this model to predict

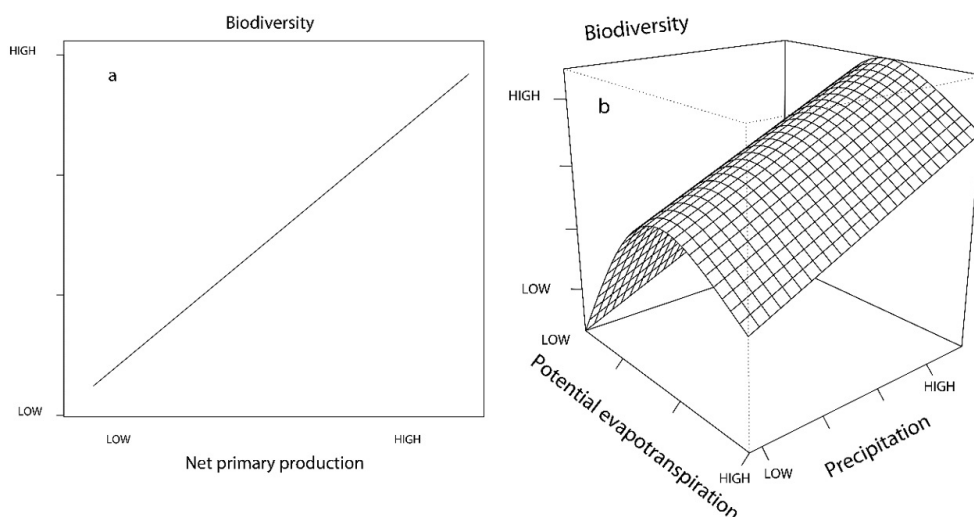


Figure 1. Graphical display of the two conceptual models on species diversity (reproduced from Vetaas et al. (2019)). (a) Net primary production (NPP) and (b) original water-energy dynamics (WED). NPP: Biodiversity is a linear function of Net Primary Production because high potential chemical energy leads to enhanced number of individuals that increase the probability of having many species. Water-Energy Dynamics: High kinetic thermal energy causes high potential evapotranspiration (PET) and high evaporation that reduce biological activity due to drought, low kinetic thermal energy causes low PET and may lead to frozen water and soil (artic-alpine) or water-logging as well as soil leaching (tropical-temperate) thereby reducing biological activity.

unique peaks for different plant life-forms, whereas models based on energy-productivity model will predict a similar optimum for most organisms. This is because most energy- and productivity-based models, independent of the expression of energy (thermal energy and environmental temperature) predict linear responses in richness along a productivity-energy gradient (Wright 1983, Evans et al. 2005, Clarke and Gaston 2006, Gillman et al. 2015, and references therein). In contrast, WED models predict a parabolic response in richness as a function of PET (Fig. 1). The Energy-productivity models, such as NPP, may also predict a linear increase, but this depends on the relationship between productivity and elevation which may be unimodal or curvilinear rather than strictly linear.

Based on this theoretical background we aim to evaluate whether the WED model or the energy-productivity model (NPP) better explains the spatial variation in species richness. This is done for interpolated elevational species richness based on data compiled from databases of woody and herbaceous flowering plants across the entire Himalayan range. In addition, on a coarse scale, we will test if there is a linear trend in richness as a function of precipitation from the drier western Himalayas to the moist eastern Himalayas, which can be deduced from the WED model. If WED explains the spatial variation in species richness better than NPP, it may indicate that WED provides a better mechanistic explanation of plant species richness than energy-productivity theories do. If NPP is superior it may indicate richness can be better explained by arguments related to the potential chemical energy of biomass than the dynamics of water and kinetic energy.

Materials and Methods

Location and physiography

The Himalaya (c. 97° 30' E – 72° 30' E longitudes and c. 27° N – 29° N (east), c. 27° N – 30° N (central) and c. 29° N – 36° N (west) latitudes) is the highest mountain system in the world, separating the Tibetan Plateau from the Indian subcontinent in South Asia (Fig. 2). The Himalaya lies in the contact zone of the Indian Plate and the Eurasian Plate and extends over a c. 2500 km southward-convex arc from east-southeast to the west-northwest (Singh and Singh 1987). It borders with the upper streams of the Brahmaputra in the east, Indus River and Naga Parbat in the west, the Tibetan Plateau in the north and the Indo-Gangetic Plains to the south. From west to east, the Himalaya spans over five geopolitical sectors (Jammu and Kashmir Himalayas, Kumaun and Garhwal Himalayas, Nepal Himalayas, Sikkim and Bhutan Himalayas and Assam Himalayas), and has a profound effect on regulating the climate and biodiversity of the region (Gansser 1964, Le Fort 1975). The complex physiography of this mountain range encompasses the largest elevational gradient on Earth (from sea level to over 8000 m above sea level) and can be broadly divided into three major east-west cis-zones: the Siwalik Range (100–1500 m a.s.l.), the Lesser Himalaya (1500–3000 m a.s.l.) and the Greater Himalaya (3000–8000 m a.s.l.)¹.

Bioclimatic zones

The vast physiography of the Himalaya has resulted in a remarkable variation in topography and climate over the region. Broadly speaking there are two seasons, a dry winter period and a wet summer period.

1. <https://www.britannica.com/place/Himalayas>, last accessed 28/02/2021.

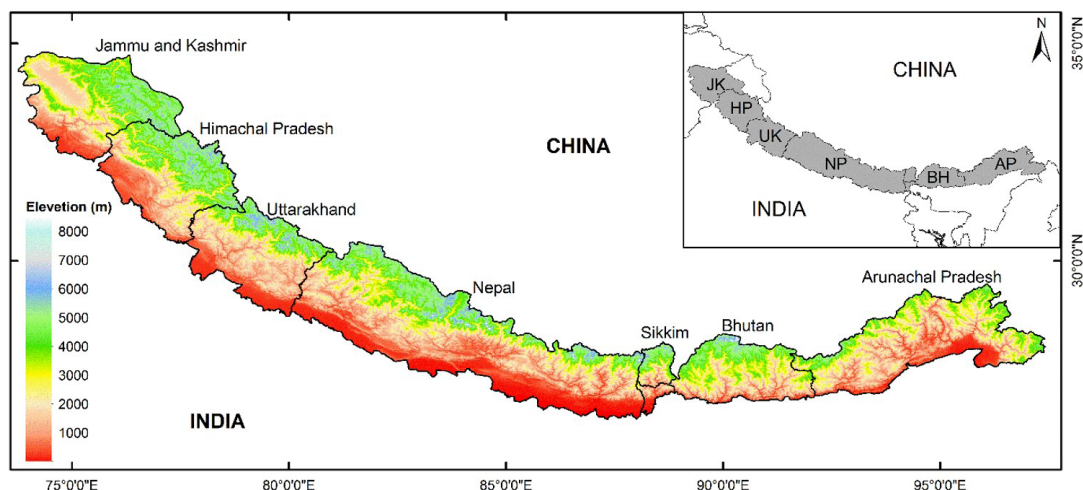


Figure 2. Location of the six geopolitical sectors along the Himalaya Mountain range. Plant species richness of each sector and that of entire mountain range was used to fit and evaluate the species diversity models. Species richness data from Sikkim and Bhutan were combined and analysed as one sector 'Bhutan (BH)'.

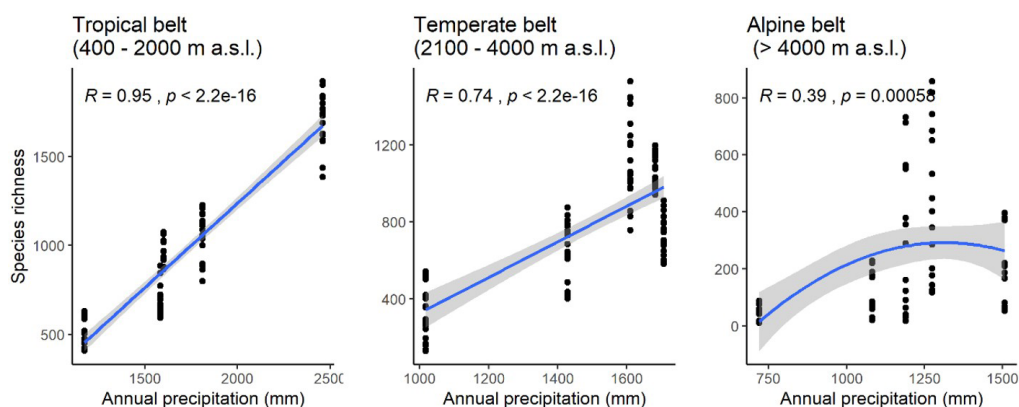


Figure 3. Variation in species richness along an east-west precipitation gradient in the Himalaya. Figures are based on linear models with first order polynomial for the tropical and temperate belts and second order polynomial for the alpine belt. Each of the models was tested up to a second order polynomial and only the statistically significant model is presented in the diagram.

The dry period is characterised by wind blowing from the north-west, whereas the wet period is characterised by the Indian summer monsoon that enters from south-east of Himalaya and gradually drifts toward the west Himalaya. The amount and distribution of precipitation and the duration of cloud cover varies considerably in different parts of the region, but precipitation gradually decreases from east to west, which is the most likely a governing factor in the variation in species richness along the east-west Himalayan axis (Fig. 3). Along a south-north elevation gradient, precipitation generally increases from the plains to the mid-elevations and thereafter decreases linearly towards higher elevations. Most of the precipitation is received from mid-June to mid-September and the cis-Himalayan ranges (to the south of the Greater Himalaya) receive more precipitation than the trans-Himalayan ranges (north of the Greater Himalaya towards the Tibetan Plateau). Similarly, atmospheric temperatures in the Himalaya show profound variations along the elevation gradient and follow a decreasing pattern of c. 5 °C per 1 km rise in elevation. Thus, two enormous bioclimatic gradients

lie approximately orthogonal to each other along Himalayan axes. An overview of the phytogeography, vegetation and climate in the Himalayan region is presented in the Appendix S1.

Data source and selected taxa

We used the data of the flowering plants of Himalaya published by Rana et al. (2019) for estimation of species richness. The dataset consists of 8765 native angiosperm species with their life-forms and elevational distributions from six geopolitical sectors along east-west Himalayan axis namely, Arunachal Pradesh, Bhutan and Sikkim, Nepal, Uttarakhand, Himachal Pradesh and Jammu and Kashmir. Of these, Bhutan and Nepal are countries, whereas the remaining areas are states of India. The data we used, along with relevant metadata, such as the spatial coverage, and data collection and standardisation procedure are also published as an open-access database (Rana and Rawat 2017).

The life-forms and the minimum and maximum elevations of the flowering plant species in the

dataset were compiled using the published records of species in the Himalaya in the 31 local and regional Floras (see Rana and Rawat 2017, Rana et al. 2019). These Floras are based on the plants collected and/or reported from different sub-regions of the Himalaya during the period of 1903–2014. The authors of the database have resolved the taxonomic nomenclature, taxon rank as well as indigenous versus exotic status of each recorded species according to The Global Biodiversity Information Facility² and The Plant List³ databases (Rana and Rawat 2017). All the exotic species and those with unresolved taxonomic nomenclature were removed from the dataset, and the potential bias in the estimation of species' elevational limits in each Himalayan sector has also been corrected (see Rana et al. 2019). Using the elevational ranges of the species in each region, we interpolated the species presences in each 100-m elevation band between the upper and lower elevational limit of the species. Realising that different species of different life-forms reveal different responses to precipitation and temperature regimes (cf. Bhatta 2018, Bhatta et al. 2018), we estimated the total, herbaceous and woody species richness for each sector.

We extracted bioclimatic variables for each Himalayan sector from CHELSA Bioclim Version 1.2 (Karger et al. 2017). For each sector, we also estimated the total area and NPP per 100-m elevation band using the data obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor from 2000–2018 (Running et al. 2015).

Methodological framework

The response variables

In the present study, the species richness is defined as the number of species with an overlapping elevation range, i.e., the thermal energy range, because atmospheric temperature is collinear with the elevation gradient (1000 m elevational difference = 5.5 °C difference). To interpolate the species' occurrences along an elevation gradient between 400 and 5500 m a.s.l., the elevation gradient was divided into fifty-two 100-m elevation intervals (vertical elevation bands). A species was considered as being present in every 100-m band between its upper and lower elevation range limits within the considered elevation gradient (400 m – 5500 m a.s.l.). The response variable – species richness – was estimated as the total number of species found in each 100-m elevation band, which is called elevational-gamma diversity by Lomolino (2001). The general trend in elevational gamma diversity is broadly similar to the overall richness trends using small plots in Nepal Himalaya (Bhatta et al. 2018). For the analyses, we considered the elevation gradient from 400 m a.s.l. to 5500 m a.s.l. in each sector. This was done to avoid the influence of human land-use on the species richness estimations, especially towards the low-elevation (plain regions) of the Himalaya and

also to minimise the underestimation effect of species' range interpolations (Grytnes and Vetaas 2002).

Moreover, we divided the entire elevation gradient into three bioclimatic belts, namely, tropical (400 m a.s.l. – 2000 m a.s.l.), temperate (over 2000 m a.s.l. – 4000 m a.s.l.) and alpine (over 4000 m a.s.l.) and correlated the species richness in each bioclimatic belt with the east-west precipitation gradient. We did this to test if the variation in species richness along cis-Himalaya corresponds to the underlying east-west precipitation gradient. However, we excluded Arunachal Pradesh in this analysis because this sector is considered under-sampled (Rana et al. 2019) and hence, species richness of this sector cannot be compared directly with that of the remaining sectors.

The explanatory variables

(a) Bioclimate variables

For each sector, we extracted four bioclimatic variables at a resolution of 30 arc seconds (1 km) - Bio1 (Annual Mean Temperature), Bio5 (Maximum Temperature of Warmest Month), Bio 6 (Minimum Temperature of Coldest Month) and Bio12 (Annual Precipitation AP) from CHELSA Bioclim Version 1.2 (Karger et al. 2017). These variables were extracted for each 100-m elevation band for each Himalayan sector based on the Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM).

(b) Net primary production (NPP)

Remote-sensing products have been widely used to map, monitor, and model gross primary production (GPP) and NPP dynamics at the regional and global scale (Nemani et al. 2003, Zhao and Running 2010). The Moderate Resolution Imaging Spectro-radiometer (MODIS), an optical instrument installed on the Terra and Aqua satellites of the NASA Earth observation system, provides some of the most reliable, moderate spatial and high temporal resolution standard global GPP and NPP estimates. For estimating NPP we averaged the annual MODIS NPP products (MOD17A3) from 2011 to 2018 together using the Google Earth Engine and downloaded one mosaiced file for the mean NPP to be further processed in python using the ArcPy and NumPy packages (Running et al. 2015). The mean NPP was then extracted per 100-m elevation band based on the SRTM elevation model. The area of each elevation band was also extracted.

(c) Potential evapotranspiration (PET)

We estimated annual PET by using a modification of the Holdridge equation ($PET = \text{mean annual Bio-temperature, i.e., temperature} > 0 \text{ } ^\circ\text{C} \times 58.93$) (cf. Bhattarai and Vetaas 2003). It was not possible to estimate realistic Holdridge PET values for the extremely high elevation belts where the biotemperature (mean annual temperature) was below 0°C. According to CHELSA bioclimate data, 0°C in temperature is

2 . <http://www.gbif.org/>, last accessed 03/6/2017.

3 . <http://www.theplantlist.org/>, last accessed 15/04/2017.

encountered at elevations much lower (at c. 4000 m a.s.l.) than the elevations in Himalaya from which biotemperature starts to become $< 0^{\circ}\text{C}$ (at c. 5000 m a.s.l.). Therefore, for a more realistic estimation of PET, we used the maximum temperature of the warmest month in each 100-m elevation band as a proxy of the biotemperature.

(d) Length of growing season (LGS)

The estimation of the LGS (number of days in a year above 0°C biotemperature) based on the monthly averaged biotemperature data of CHELSA was too coarse as it resulted in variations in the LGS by one month (30 days) per 100-m bands along an elevation gradient, which is unrealistic. Therefore, we used Bio 5 and Bio 6 to estimate the rate of decrease of the growing days per 100-m increase in elevation. Here, we estimated the number of 100-m elevation bands (N) between the elevations from where the Bio 5 and Bio 6 start to become negative and divided the annual number of growing days (365) by N.

The models

We analysed two main models, Net primary production (NPP: M1) and Water-energy dynamics (WED: M2) (Fig. 1), as defined below with respect to species richness (S). O'Brien (1998) incorporated seasonality by using length of growing season (and $\text{PET}_{\text{max}} - \text{PET}_{\text{min}}$) in one of the WED models named interim general models (IGM1-model). We follow this line of reasoning by including an interaction term between length of growing season (LGS) and precipitation, called the seasonal-WED (M3) (cf. Vetaas et al. 2019). M3 is an attempt to express the temporal dimension (duration of precipitation) in the WED model. This is because precipitation in the form of liquid water may relatively be less available at high elevation due to a shorter growing season. LGS will also reflect productivity, which will correspond to the duration of the year the moisture will be utilised for the biological activity (Michaletz et al. 2014).

(M1) NPP: $S = f(\text{NPP})$: $S \sim \text{NPP}$

(M2) WED: $S = f(\text{AP}, \text{PET})$: $S \sim \text{AP} + \text{poly}(\text{PET}, 2)$

(M3) seasonal-WED: $S = f(\text{AP}, \text{PET}, \text{AP} * \text{LGS})$: $S \sim \text{AP} + \text{poly}(\text{PET}, 2) + \text{LGS} * \text{AP}$

The three contrasting models (M1, M2 and M3) were fitted for the herbaceous species-, woody- and total species richness in each of the Himalayan sector and in entire Himalayan Mountain range. All explanatory variables were estimated for each of the 100-m elevation bands between 400 – 5500 m above sea level in each sector. In the first model (M1), energy translates into NPP and the number of individuals, i.e., potential chemical energy. In the second WED model (M2), kinetic energy is translated into liquid water (mm) evaporated per $^{\circ}\text{C}$ increase in temperature (Holdridge's PET (cf. Bhattarai and Vetaas 2003)). Precipitation is estimated in millimetre per year and PET is annual potential evapotranspiration expressed in mm per year.

The strict interim general model, developed for woody plant richness following the WED conceptual

framework (O'Brien 2006), incorporates annual rainfall and minimum monthly PET based on a formula by Thornthwaite (1957). This use of annual rainfall and minimum monthly PET probably originates as the model was developed in South Africa, where snowfall is very rare (and hence, rainfall = precipitation), and minimum PET was used to capture seasonality of thermal regime. However, here we evaluate a more flexible WED model that includes not only the woody plants in a region where snowfall is common and where the minimum mean monthly PET will be insufficiently discriminating (Moser et al. 2005). Therefore, we use precipitation and annual PET, as suggested by the Holdridge equation (cf. Bhattarai and Vetaas 2003). We evaluate a WED model including precipitation and annual PET, versus an NPP model including estimated NPP with respect to elevational interpolated species richness of angiosperms across the Himalaya. For each Himalayan sector, elevational patterns of the explanatory variables in the M1, M2 and M3 are presented in Fig. 4.

Model assessment

We fitted all the species richness models described above using generalised linear models (GLM) and generalised linear mixed models (GLMM) within the maximum likelihood framework, assuming a Poisson distribution of error. We compared the performance of the area-unaccounted as well as the area-accounted models using Akaike's Information Criterion (AIC) and deviance explained in the model. The variables included are theoretically justified from the two potential general theories of species biodiversity described above. Primarily, we aim to compare NPP and our WED model, and the latter model is then elaborated with an interaction term (M3, seasonal-WED). The AIC measures the relative likelihood of the model's performance and is proportional to the likelihood of the model and the number of parameters used to generate it. The best model is the one with the lowest AIC (less Kullback-Leibler information is lost), and other models are usually considered less plausible if the difference in AIC between them is larger than two AIC values. Hence, a difference value of $\text{AIC} < 2$ indicates that a model is equally good (Burnham and Anderson 2002). In addition, we used deviance explained to evaluate the models (NPP vs. WED vs. seasonal-WED).

If the AIC indicated that a second-order energy term needs to be included, we performed a chi-test on the precipitation term to elucidate whether it has any explanatory power in addition to the PET terms. Precipitation is a difficult variable to model because it is a resource gradient that an organism may consume (in contrast to energy, which is a regulator gradient) and can move away from where it was deposited. We therefore performed a post-hoc elaboration of our original WED model, i.e., included an interaction term of precipitation and length of growing season (LGS) (M3).

Finally, we tested the influence of the potential co-variate area on the observed patterns. For this,

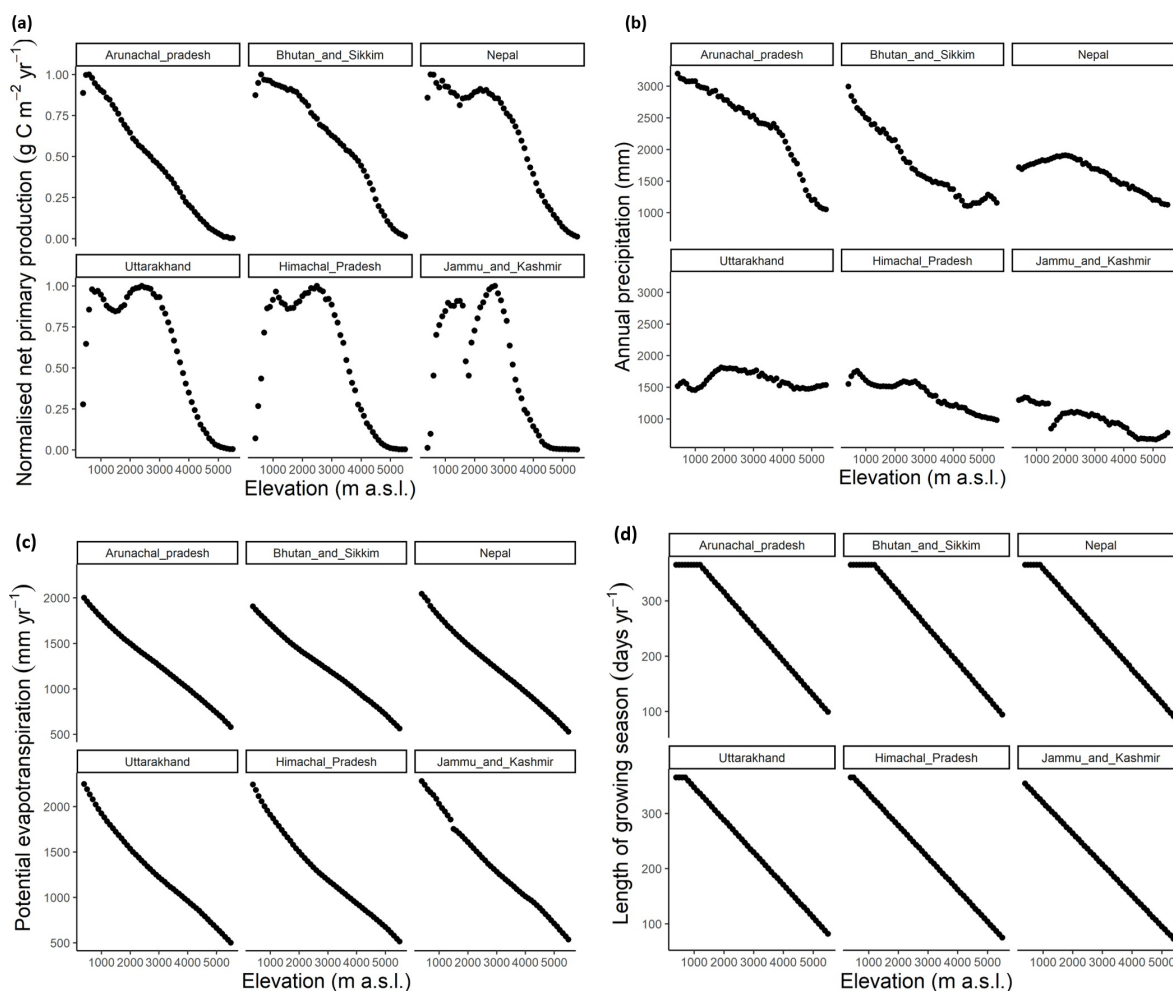


Figure 4. Elevational patterns of the explanatory factors in the species diversity models. (a) net primary production (average annual MODIS NPP products 2011–2018), (b) annual precipitation (CHELSA Bioclim Bio12), (c) potential evapotranspiration (derived by applying Holdridge formula on maximum temperature of warmest month CHELSA Bioclim Bio5), and (d) length of the growing season (number of days in a year above 0 °C biotemperature).

we applied three well-established approaches: First, following the procedure of Galmán et al. (2018), we extracted the residuals of each model and performed regression against area as a predictor variable to see if there is significant influence of area on the observed patterns after accounting for the main explanatory factors. Secondly, for each Himalayan sector, we added the area of each 100-m elevation band as a first term variable in the NPP, WED and seasonal-WED model and then compared the AIC values of the models. Thirdly, we performed a Generalised Linear Mixed Model (GLMM) analysis for each of the contrasting species richness models using “lme4” package in R (Bates et al. 2015). Here, we fitted four different mixed models for each of the competing model, considering “area” and “Himalayan sector” in different combinations as random effect variables as well as by adding “area” to the main explanatory variables as the fixed effect variable. Then we compared the four mixed models using Analysis of Variance (ANOVA), which summarizes the differences in fit between the models (Bates et al. 2015). By using “car” package in R (Fox and Weisberg 2019), we detected the collinearity

among the predictor variables by estimating the Gross Variance Inflation Factor (GVIF) of the best fitted model of the GLMM. A predictor variable with GVIF > 10 was considered as a collinear variable. All the analyses were performed in R3.6.3 (R Core Team 2020).

Results

The interpolated richness of 7764 species of flowering plants recorded between 400 m a.s.l. and 5500 m a.s.l. in the Himalaya was used for analysing the variation in species richness along the precipitation gradient of cis-Himalaya and for fitting the species richness models.

The coarse analysis across the six Himalayan sectors (Fig. 3) from the dry west towards the moist east revealed strong responses in plant species richness as a function of precipitation in all three elevation zones, i.e., subtropical, temperate, and the alpine zones. Variations in species richness within the tropical and temperate zones had a linear response as predicted by WED, whereas the same analyses for the alpine belt revealed a curvilinear response in species richness (Fig. 3).

The main model assessment of NPP vs WED is based on 63 GLM regression models of species richness in the Himalayan Mountain range (9 models for each Himalayan sector as well as the whole Himalaya, for each of which models M1, M2 and M3 was fitted for the herbaceous-, woody- and total species richness) (Table 1, Table S1).

The net primary production model (M1) had much higher AIC values and lower percentage deviance explained than the WED model (M2), which holds true for total-, herbaceous- as well as woody-species richness of all Himalayan sectors and of the entire mountain range (Table 1). This indicates that the WED model captured more of the variation in species richness than the NPP model (Table 1, Figs. 5, 6, 7). Although herbaceous and woody species richness peak at different points along the energy-elevation gradient in the six sectors of Himalaya, variations in richness of the two plant life-forms tend to show similar responses to the water and energy gradients (WED model) within each sector, although also strongly

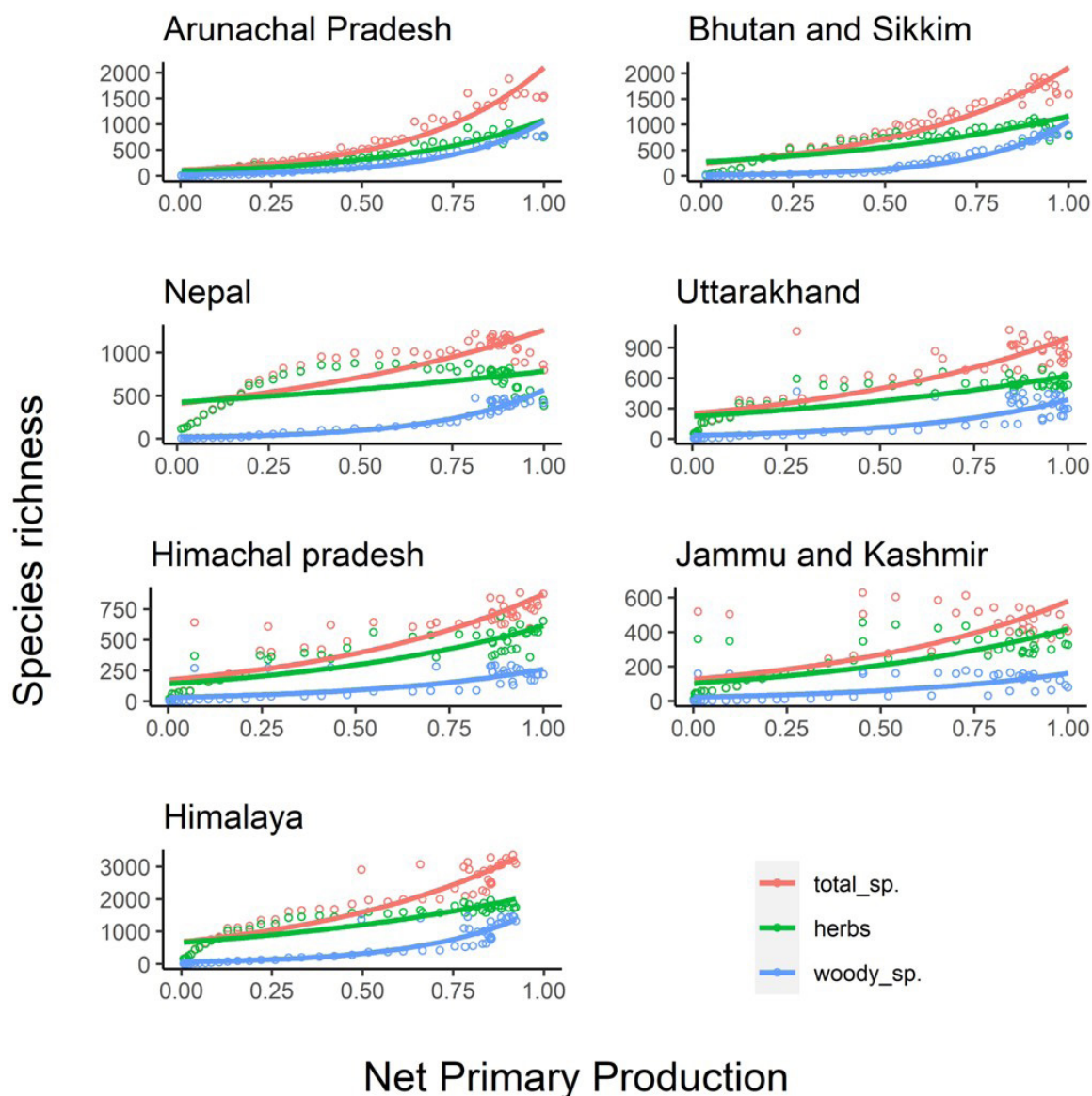
contrasting responses are noticeable between sectors (Fig. 6, 7, Table S2).

The WED models were superior to the NPP model in terms of AIC and percentage deviance explained by the model. However, the correlation between annual precipitation term and species richness in the WED models varied across the plant life-forms and across the Himalayan sectors (Fig. 7). The seasonal-WED model (M3), with an interaction term between length of growing season (LGS) and precipitation (MAP), further improved the variation explained, particularly for herb richness (Table 1). However, the seasonal-WED models for the woody species richness are inconsistent with respect to individual terms and their statistical significance.

We evaluated each model by checking how much of the residual deviance could be correlated with area in each of the elevation-bands. Area was statistically significant in most of the NPP models for different plant life-forms, whereas area was statistically insignificant in all WED and seasonal-WED models (Table 2, Table S3a). However, area appeared as a statistically significant co-

Table 1. Evaluation of three species diversity models based on Generalised Linear Models (GLM) analysis of the flowering plant species richness in six geopolitical sectors along Himalayan mountain range. The models are net primary production (M1: NPP), a general water-energy dynamics model (M2: WED) including annual precipitation (precip) and potential evapotranspiration (PET), and a seasonal water-energy dynamics model (M3: seasonal-WED) incorporating an interaction of precip and length of growing season (LGS) into the WED model. The best model has the lowest AIC (**bold**) and the highest deviance explained (% Expl. dev). All M1 and M2 GLM-models are significant ($p < 0.001$). M3 models in which at least one of the explanatory factors was insignificant are marked with “*”. Three forms of species richness, i.e., total species richness (total sp.), herb species richness (herbs) and woody species richness (woody sp.) were used to fit the models. Degrees of freedom for M1, M2 and M3 are 50, 48 and 46, respectively. Statistical details are presented in Table S1.

Himalayan sector	Response group	M1: NPP		M2: WED		M3: seasonal-WED	
		AIC	% Expl. dev.	AIC	% Expl. dev.	AIC	% Expl. dev.
Arunachal Pradesh	total sp.	2898.30	90.95	1117.30	97.40	892.19	98.23
Bhutan and Sikkim	herbs	2237.50	85.61	940.48	95.67	754.34	97.13
	woody sp.	1377.60	93.39	515.54	98.78	*491.59	98.96
	total sp.	3175.00	86.95	1439.90	95.26	727.75	98.68
Nepal	herbs	3903.80	64.59	1565.60	88.45	692.45	97.37
	woody sp.	1030.70	95.93	409.43	99.71	*401.84	99.78
	total sp.	3306.00	64.88	800.07	95.69	692.83	97.05
Uttarakhand	herbs	4129.50	25.52	751.13	93.61	680.75	95.10
	woody sp.	901.54	93.32	482.07	98.46	*395.96	99.55
	total sp.	3393.60	70.13	1370.00	90.53	686.74	97.44
Himachal Pradesh	herbs	2372.40	59.27	1427.10	78.96	637.44	95.41
	woody sp.	3267.40	63.92	497.12	98.11	*412.38	99.19
	total sp.	3622.70	70.60	1728.30	87.94	*916.35	95.39
Jammu and Kashmir	herbs	2838.60	66.15	1651.70	82.62	831.08	94.01
	woody sp.	2870.90	54.99	504.83	96.66	*408.92	98.41
	total sp.	4574.50	52.15	889.07	94.17	*738.64	95.92
Whole Himalaya	herbs	2956.90	53.41	829.51	91.69	*713.79	93.83
	woody sp.	2670.20	41.26	440.50	95.58	*348.63	97.91
	total sp.	6390.30	80.82	1783.20	95.79	*853.44	98.82
	herbs	4808.60	68.50	1957.90	89.22	*789.25	97.72
	woody sp.	5566.70	80.14	575.45	99.32	*473.74	99.73



Net Primary Production

Figure 5. Species richness along normalised net primary production gradients across the Himalaya. Figures are based on generalised linear models with first order polynomial (as assumed by NPP model) and assuming a Poisson distribution of errors. Each of the models are statistically significant ($p < 0.001$) (Table S1), however, most of the models are also area-inflated (S3a, S3b, S3c).

variate when we included it as a first term variable in each model, and also when treated it as a random as well as fixed effect variable in the generalised linear mixed models. Even so, including the area of each 100 m elevation belt did not influence the relative performance of the competing species richness models. Among the area-included models, the seasonal-WED model always performed slightly better than the WED model and the WED revealed significantly better-fit than the NPP model (Table S3b, S3c).

Estimations of the Generalized Variance Inflation Factor (GVIF) in the best-fitted mixed models revealed that length of the growing season (LGS) (GVIF = 12.38) and potential evapotranspiration at a second order polynomial (GVIF = 4.74) are highly correlated in the seasonal-WED model. However, LGS in an interaction

with precipitation has lowest GVIF value (GVIF = 1.82) in the model (Table S3c).

Discussion

The comparison of the three species richness models based on GLM regression parameters revealed significant differences between the models, where the seasonal-WED model explains best the species richness patterns, followed successively by the standard WED model and the NPP model. Although the NPP model explains a significantly high proportion of the variation in richness (Fig. 5; Table 1), the seasonal-WED model has much lower (0.1 to 0.4 times) AIC values than the NPP model. This illustrates that the WED model in general, and the seasonal version in particular; capture the variation in richness much better than NPP alone.

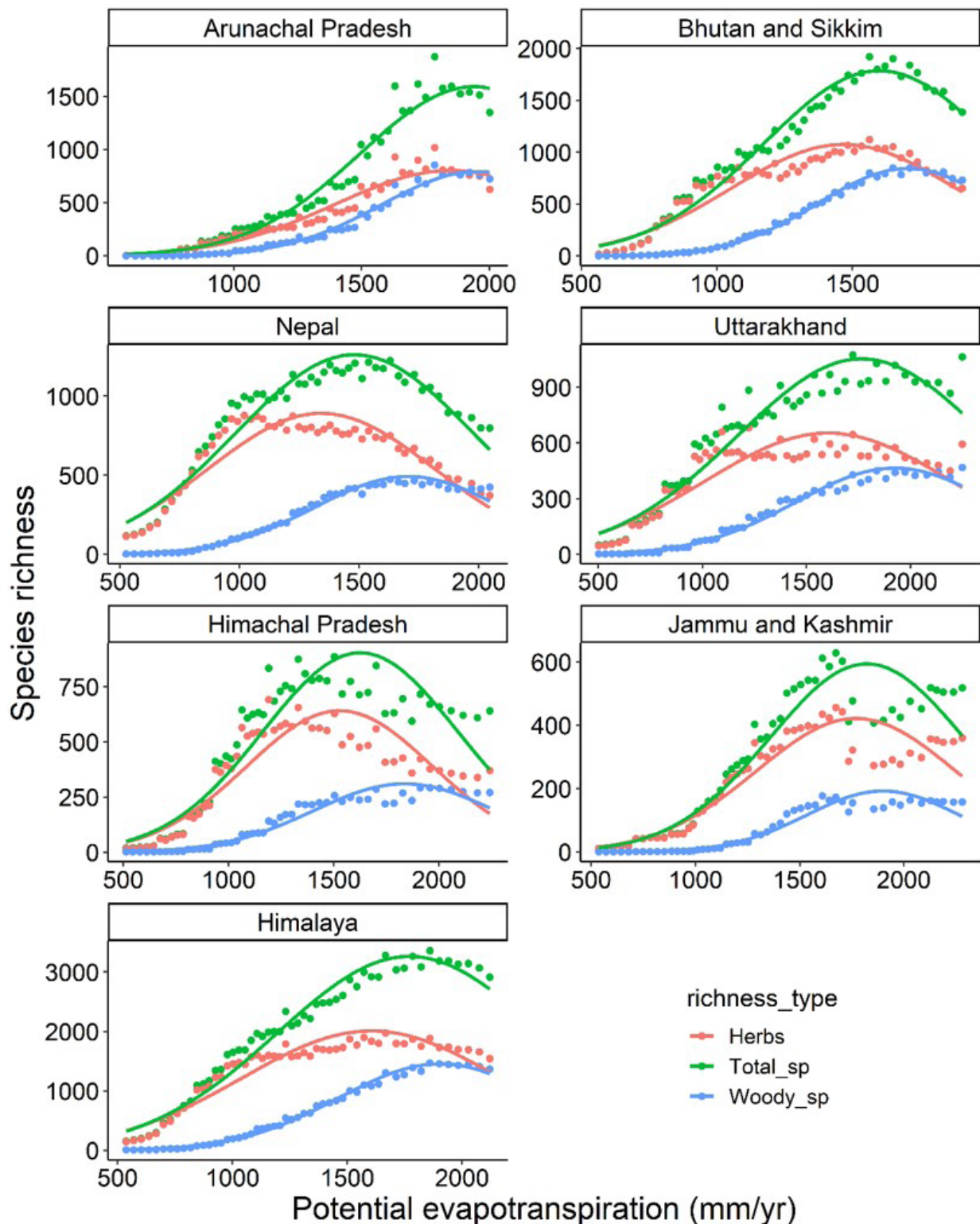


Figure 6. Species richness of two plant life-forms and total richness along a thermal energy gradient expressed as potential evapotranspiration (PET = maximum temperature of the warmest month \times 58.93), in six Himalayan sectors and the whole Himalaya. Figures are based on generalised linear models with second order polynomial (as assumed by the original WED model) and assuming Poisson distribution of errors. Each of the models are statistically significant ($p < 0.001$) (Table S2).

The NPP estimates by 'MODIS NPP products' are of course also a function of energy, nutrients, and water in the soil (Zhao and Running 2010, Running et al. 2015), which illustrates why WED and energy-productivity

models belong to the same research programme (Gillman et al. 2015). However, the models differ in addressing how energy influences species richness. The energy-NPP model assumes the influence of net

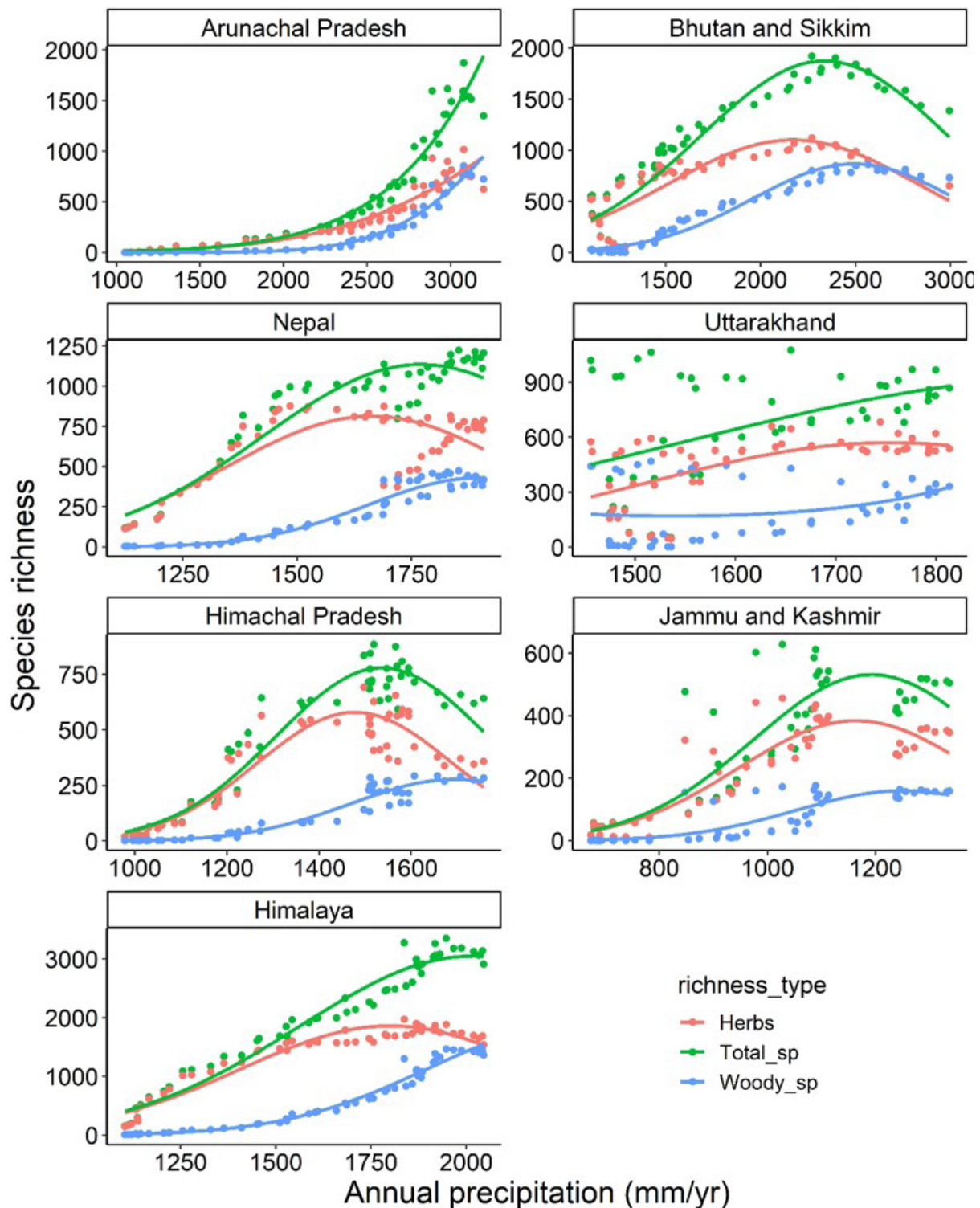


Figure 7. Species richness of two plant life-forms and total richness along a precipitation gradient in six Himalayan sectors and the whole Himalaya. Figures are based on generalised linear models with second order polynomial and assuming Poisson distribution of errors. Each of the models are statistically significant at first as well as second order polynomial ($p < 0.001$) (Table S2).

primary production, i.e., potential (chemical) energy synthesised by the vegetation on species richness, whereas we argue that the WED hypothesis proposes regulation of biodiversity by kinetic form of thermal energy by influencing the availability of liquid water

(and hence primary production and subsequent biological activity) in the biological system. These results lead to the question: why do the WED models perform much better than the Energy-productivity model expressed as NPP?

Table 2. Generalised Linear Model (GLM) regression with residuals of three species diversity models for each Himalayan sector as response and area of sector as a predictor variable. The models are Net Primary Production (M1: NPP), water-energy dynamics model (M2: WED) and a seasonal water-energy dynamics model (M3: seasonal-WED). Regression model with area as a significant explanatory variable are marked **bold**. Three forms of species richness, i.e., total species richness (total sp.), herb species richness (herbs) and woody species richness (woody sp.) were used to fit the models. Degrees of freedom for M1, M2 and M3 are 51, 51 and 50, respectively. Statistical details are presented in Table S3a.

Himalayan sector	Response group	M1: NPP		M2: WED		M3: seasonal-WED	
		AIC	Pr(> z)	AIC	Pr(> z)	AIC	Pr(> z)
Arunachal Pradesh	total sp.	301.94	0.02	294.09	0.52	269.15	0.40
	herbs	273.28	< 0.001	280.61	0.41	254.51	0.37
	woody sp.	277.66	0.43	224.27	0.24	212.91	0.34
Bhutan and Sikkim	total sp.	299.20	< 0.001	309.97	0.10	240.20	0.88
	herbs	318.07	< 0.001	318.09	0.17	236.64	0.95
	woody sp.	252.64	< 0.001	167.39	0.14	134.46	0.72
Nepal	total sp.	368.56	0.25	278.65	0.58	233.01	0.89
	herbs	369.52	< 0.001	267.91	0.43	233.61	0.75
	woody sp.	308.40	< 0.001	226.43	0.97	135.50	0.67
Uttarakhand	total sp.	359.75	< 0.001	314.44	0.89	236.00	0.82
	herbs	349.58	0.05	319.16	0.84	228.78	0.94
	woody sp.	326.61	< 0.001	219.71	0.55	164.94	0.67
Himachal Pradesh	total sp.	378.60	0.77	337.95	0.25	271.04	0.42
	herbs	359.22	0.02	329.42	0.20	263.50	0.63
	woody sp.	350.73	< 0.002	253.12	0.73	181.33	0.46
Jammu and Kashmir	total sp.	377.02	< 0.001	314.27	0.86	568.34	0.52
	herbs	353.02	< 0.001	300.52	0.94	543.25	0.48
	woody sp.	345.75	< 0.001	252.54	0.75	444.93	0.75

Role of energy

Both herbs and woody plant richness have peaks in the lower half of the entire spatial energy elevation gradient in all sectors (Fig. S1). These peaks in herbaceous and woody species richness may differ within a sector (cf. Vetaas and Grytnes 2002, Bhatta et al. 2018, Rana et al. 2019). However, overall variations in richness of both the life-forms in response to the thermal energy elevation gradient was approximately similar across the Himalayan sectors. This implies thermal energy is a core regulator of plant species richness regardless of the plant life-forms. This corroborates with the underpinning mechanism that generate the richness patterns, i.e., all plants have an upper and lower thermal energy limit (Whittaker 1967), and more species may potentially overlap in the middle of the extensive elevation-energy gradient because this is far away from areas that may at a long time scale experience glaciation or desertification (cf. McCain 2007, Sun et al. 2020).

The second order polynomial PET-term in the WED model captures this pattern in richness much better than NPP, although the NPP has peaks at lower to mid-elevations in several of the Himalayan sectors, where the richness peaks (Fig. 4). There is, however, considerable confusion related to causal links between species richness and energy-productivity (Whittaker 2010, Craven et al. 2020). Many authors point to the issue of scale; in general, the relationship strengthens

at coarser scales (Wright 1983, Currie et al. 2004, Craven et al. 2020, and references therein). The spatial scale of this current study has a huge environmental extent (subtropical to alpine), but the spatial resolution is coarser than the landscape scale and much finer than the macro-scale studies with grain size of 50 x 50 km or 100 x 100 km. The scale of this study is in a range that the single term model of NPP should have a fair chance to explain a large proportion of the variation in plant species richness (cf. Craven et al. 2020). Although NPP provides a fairly good model, the seasonal-WED model with four terms is much better according to the AIC-values (0.1-0.4 times smaller AIC values). This was unexpected if one takes into consideration that AIC is designed to penalize the models with several terms compared to those with few or one, as the NPP model. This indicates that mechanisms related to the WED model are plausible, and it is likely that PET and growing season are regulating the amount of liquid soil water and hence, influencing the biological activity in the system (Hawkins et al. 2003, O'Brien 2006, Whittaker et al. 2007, Cassemiro and Diniz-Filho 2010, McCain and Grytnes 2010). This finding corroborates the patterns revealed by a similar study from Nepal based on richness patterns of 12 taxa in response to energy gradient (Vetaas et al. 2019) and many other studies of different scale on species richness patterns along extensive energy-elevation gradients across the globe (e.g., Hawkins et al. 2003, Rahbek 2005,

McCain and Grytnes 2010, and references therein, Sun et al. 2020).

The causal link between high PET and lower richness in the warm subtropical lowlands (O'Brien 2006), is not as clear as the aforementioned temperate to alpine parts of the thermal gradient. Although it is probable that extreme high potential evapotranspiration limits the amount of liquid soil-water to be used by species and consequently, resulting in low species richness in the lowland, there is also a substantial influence of human land-use, particularly related to forestry and agriculture within these regions (Vetaas and Grytnes 2002, Nogués-Bravo et al. 2008). The drop in richness in warm tropical and subtropical lowland in the foothills of large mountain ranges (Rahbek 2005, and references therein) was for instance not reported from a multi-organism study in Kilimanjaro based on field sampling in landscapes with low human footprints (Peters et al. 2016).

Role of water-energy interaction

In addition to parabolic response in richness as function of PET (cf. above), one may deduce a linear response in richness as a function of precipitation, which was tested across the Himalayan sectors as depicted in Figure 3. We found a significant correspondence between west-east variation in species richness and the underlying precipitation gradient (Fig. 3), which supports the proposition that precipitation is an important driver of plant species richness. This finding corroborates partly the inferences of many regional studies (e.g., Rana et al. 2019, Chen and Su 2020, Sun et al. 2020) and global studies on climatic drivers of species richness (Francis and Currie 2003, Kreft and Jetz 2007). However, a closer examination of the WED-models reveals some variation in the richness-precipitation relationship across the Himalaya, where species richness in general starts to decline from c. 1500–2000 mm precipitation, resulting in a curvilinear response of species richness along the precipitation gradient (Fig. 7, Table S2). The most likely cause of this discrepancy is that the WED models' annual precipitation term is derived from the CHELSA bioclim Bio12, which is a composite variable that involves not only annual rainfall but also snow, which is not necessarily used for photosynthesis in the location where it is deposited. This, along with several other factors such as slope inclination, sun and wind exposure, soil temperature, soil texture, wind direction and speed, and atmospheric humidity, all affect the liquid water supply to plants in mountainous areas. As a result, annual precipitation does not accurately represent the amount of liquid soil water available to plants. The other potential reason for this variation is that the correlation between the east-west precipitation gradient and species richness weakens with increasing elevation and becomes strongly linear to curvilinear (Fig. 3) where seasonality becomes an important factor. The high elevation areas in the mountains are dominated by the herbs, for which seasonality is

as important as annual precipitation. Therefore, we have included an interaction of the LGS and annual precipitation in the seasonal-WED model.

The rationale of the WED model relies on the crucial role of available liquid water, which is unevenly distributed not only in space but also in time. Hence the seasonal-WED model included the interaction of LGS and MAP (M3), which improved the explanatory power of the model, as indicated by lower AIC and higher explained deviance of the model as compared to those in the M1 and M2. LGS can be used as simple and straightforward proxy for primary production (Michaletz et al. 2014, Vetaas et al. 2019). If so, a higher explanatory power of the seasonal-WED (M3) is absolutely reasonable because incorporating the LGS (photosynthetically active time period \sim NPP) in the WED model means the variation explained by M1 and M2 is integrated into a broader model (M3). However, none of the competing energy-productivity theories has included a seasonal component, but this was done by O'Brien (1998) for prediction of richness globally by her interim general model. Based on this line of reasoning, the seasonal-WED model (M3) including PET, precipitation, and its interaction with LGS can be regarded as a unification of the NPP (M1) and WED (M2) models (Vetaas et al. 2019). Although AIC is lower and the explained deviance is higher in M3 than those in M1 and M2, the explanatory variables (PET, MAP and LGS in different combinations) are not statistically significant, especially for the woody species richness (Table S1). This indicates that seasonality (such as LGS) may have a more pronounced influence on persistence and growth of short-living (annual and biennial) herbs than on that of the perennial woody plants. A counterargument for the inclusion of LGS in the seasonal-WED model is the correlation between PET and LGS, which may be the case in most potential study sites. A correlation between PET and MAP is less problematic because this is an established model (O'Brien 2006, and references therein), and collinearity may vary from site to site, and the crucial variable is (PET – PET²) and not PET as such⁴. Regression models including polynomial variables in first and second-order (as PET) and interaction term like (MAP*LGS) will inevitably cause collinearity between the single term (e.g. LGS: VIF = 12.5) and the product (LGS*MAP = 1.8) do not represent a statistical problem⁴.

The difference between the two models is also revealed concerning the covariate area, which is a crucial factor in all species diversity studies (Whittaker et al. 2001). As a part of the model diagnostics, we found a correlation with area and the residuals of the NPP model, whereas the residual of the seasonal-WED model did not have a significant correlation with area. However, if we analyse all the sectors simultaneously in a mixed model approach (GLMM) with the area as a random factor, it is clear that area is an underpinning variable for all the models, though least significant in WED model, and notably, it does not alter the fact that the WED models provide superior fits to the NPP model.

4 . <https://statisticalhorizons.com/multicollinearity>, last accessed 10/02/2021.

Conclusions

WED and seasonal-WED models address the roles of water and energy in both kinetic (PET) (O'Brien 2006) and potential form (LGS/productivity) (Vetaas et al. 2019), and hence, explain better the variation in species richness in a biological system than a simple NPP model. The latter model focuses solely on metabolic (potential) energy, and hence, fails to adequately explain variations in species richness. The seasonal-WED model includes the key climatic factors that represent different forms of energy and water, and therefore, allows the model to be more flexible and with better statistical fit. However, the linear precipitation term does not always reflect the available liquid water in these mountainous environments. This model is almost the only theoretical framework of biodiversity that is based on the first principles of thermodynamics where energy controls the dynamic relationship of the physical state and availability of water (O'Brien et al. 1998, O'Brien 2006) and thus its availability in time and space for biological life. It also captures the long-term perspective because it is always safe from an evolutionary perspective to be far away from areas that may be overheated (desertification) or covered by glaciers, which is implicit in the theoretical framework of WED. However, distinguishing the role of different operational forms of energy in this model would be vital for a proper elucidation of the mechanisms of species richness patterns. Our findings illustrate that plant species richness is inevitably related to energy, but the causal link between energy, productivity, and species richness is weak in this study; in contrast, energy as a regulator of liquid water resources provides a more mechanistic explanation of species richness based on the first principles of thermodynamics.

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Author Contributions

KPB: Conceived the ideas, analysed data, and led writing; BAR: Provided data, manuscript editing; MKS: Provided data, manuscript editing; ORV: Conceived the ideas, contributed to writing, manuscript editing.

Data Availability

Species richness data used in the study are available in Rana et al. (2019) and in Rana and Rawat (2017).

Supplementary Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Appendix S1. An overview of the phytogeography, vegetation, and climate in the Himalayan region.

Table S1. Summary statistics of three species diversity models based on Generalised Linear Models (GLM) analysis of the flowering plant species richness in six geopolitical sectors along Himalayan mountain range.

Table S2. Generalised Linear Models (GLM) regression of the flowering plant richness in six geopolitical sectors along the Himalayan mountain range, where species richness is the response variable and potential evapotranspiration (PET) and annual precipitation (precipitation) are the predictor variables.

Table S3a. Generalised Linear Model (GLM) regression with residuals of three plant species diversity models for each Himalayan sector as the response variable and area of sector as a predictor variable.

Table S3b. Summary statistics of the three species diversity models based on Generalised Linear Models (GLM) regression of the flowering plant species richness in the six Himalayan sectors, where each model is first fitted as such and then by including area per 100-m elevation band (Area) as a first term in the model.

Table S3c. Outputs of Generalised Linear Mixed Model (GLMM) regression of the three species diversity models, where “area” per 100-m elevation belt (area) and “Himalayan sector” (6 level factor = sector) are the random effect variables.

Figure S1. Flowering plant species richness along elevation gradient in the six Himalayan sectors.

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